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SUCCESSION PATTERNS AFTER PIG DIGGING IN GRASSLAND COMMUNITIES ON MAUNA LOA, HAWAII

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ABSTRACT

The influence of feral pigs on the composition of grassland communities on the east flank of Mauna Loa, Hawaii, was studied for the one year period from July, 1971, to August, 1972. Actual pig-disturbed areas as well as artificially scalped plots were included in the study. The succession on those plots was measured by both frequency and cover measurements.

It was found that pig digging greatly enlarges the component of introduced species in communities with a former high percentage of native species.

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INTRODUCTION

The pig (Sus scrofa L.) is a relatively early addition to the biota of the Hawaiian Islands. Pigs of Asian ancestry were probably brought to Hawaii by the first Polynesian settlers, about 1-2,000 years ago. These animals are presumed to have been rather small in size, and to have remained readily in domestication. Captain Cook in 1778 brought English pigs on his first voyage to Hawaii, and many importations have followed (Tomich, 1969). The old Polynesian type of Sus scrofa has been absorbed or replaced by stocks of European origin. Today the island of Hawaii supports the largest and densest population of pigs in the Hawaiian Archipelago.

Although the land that includes the study area became a part of the Hawaii Volcanoes National Park in 1916, the last cattle were not removed until 1948. With the absence of cattle, the former pasture land has shown a considerable change in vegetation towards a more natural condition (Mueller-Dombois 1967).

Baldwin and Fagerland in 1943 considered the influence of herbivores other than cattle to be negligible, but since the removal of cattle, goats (Spatz and Mueller-Dombois 1972) and pigs can be seen to be major agents disturbing a natural succession towards a more native and well balanced ecosystem. High pig activity especially is evident throughout the study area. Mueller-Dombois (1967) drew attention to the role of pigs in converting the native Deschampsia australis grassland into one dominated by the introduced temperate grass Holcus lanatus.

This study provides some insight into the effects of pigs on the composition of the analysed grassland communities.

MATERIALS AND METHODS

The study area and sites

The study area lies on Mauna Loa's east flank within Hawaii Volcanoes

National Park between 2027 m (6650 ft) and 1219 m (4000 ft) elevation (FIG. 1).

The area was described in some detail by Mueller-Dombois (1967). Two of the study sites are located in the mountain parkland, an open landscape with a pattern of Acacia koa colonies, native scrub and grassland. The grassland is composed in parts of the endemic grasses Deschampsia australis and Panicum tenuifolium, but the introduced temperate grass Holcus lanatus grows scattered throughout and is locally abundant.

A third study site is located in the savanna grassland which is a grassland with scattered trees of Acacia koa and Sapindus saponaria. Due to the deep ash soil, a very vigorous grass growth has formed a dense cover. Paspalum dilatatum, Holcus lanatus, and Cynodon dactylon, all introduced, are the most common species. The indigenous fern Pteridium aquilinium var. decompositum is usually found among them.

The climate throughout the area is tropical-montane with a short dry season in the summer (June-July). Clouds occur frequently near the ground. TABLE 1 shows the more important environmental variations among the three study sites.

Plots and treatments

A number of plots were established at each site, 5 plots at site 1, 7 plots at site 2 and 5 plots at site 3. Six of these plots were established where pigs had dug recently in the grassland. The other plots were artificially disturbed. TABLE 2 shows the plot numbers by treatment, site location and type of sample unit. Natural pig digging consists of irregular disturbances. Certain patches of grass sod (several square meters in size) may be uprooted and cleared in such a way that a portion of the soil is more or less completely exposed. In this process, the uprooted plants may be piled up in a layer in another part of the disturbed place. Occasionally, pigs may return and dig at the same place.

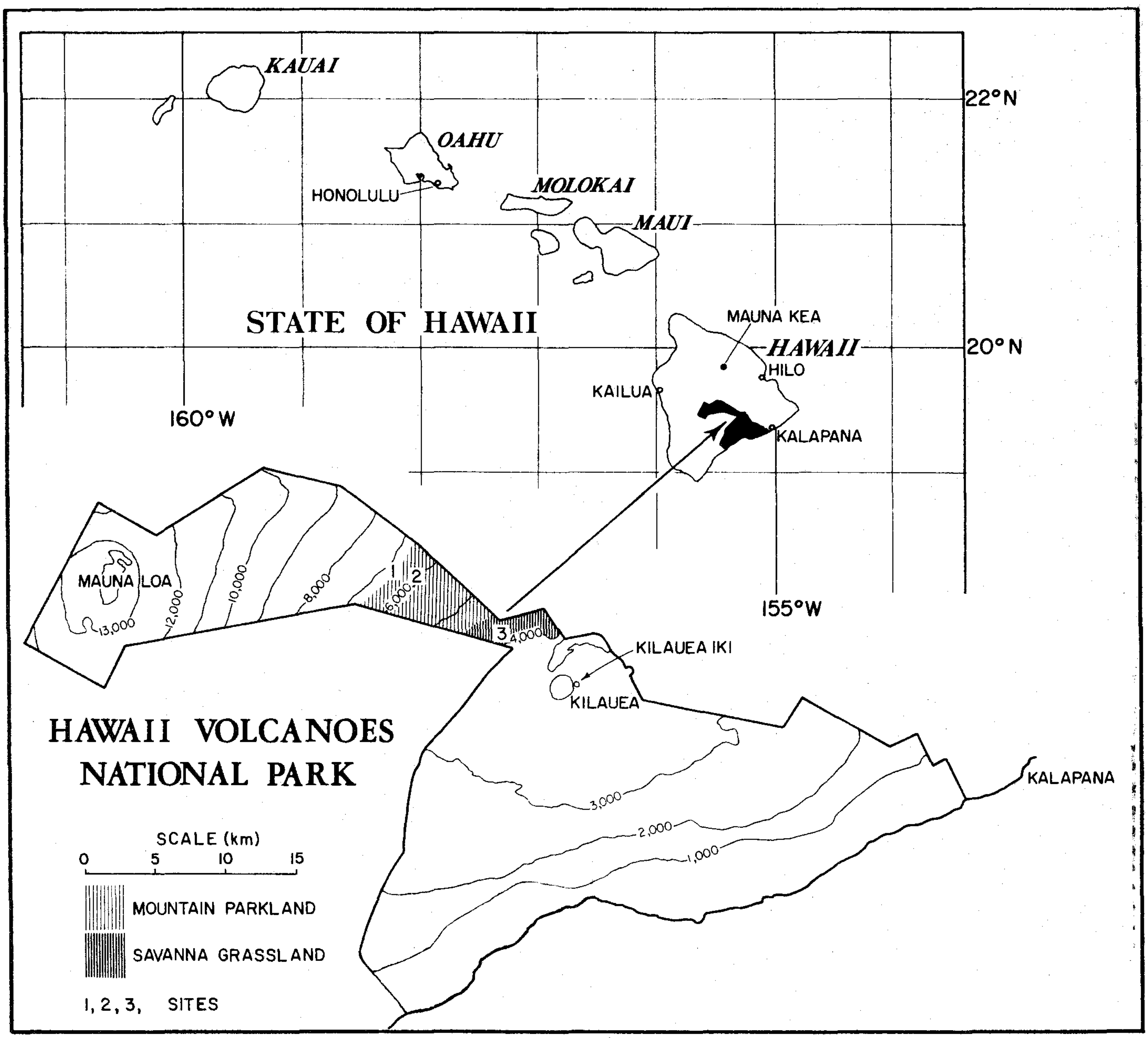

FIG. 1. Map of Hawaii Volcanoes National Park showing the study area and location of the three study sites on Mauna Loa.

TABLE 1. Envircnmental variations among study sites.

	Site 1	Site 2	Site 3
Ecosystem	Mt. Parkland	Mt. Parkland	Savanna
Elevation	2030 m (6650 ft)	1890 m (6200 ft)	1220 m (4000 ft)
Mean annual rainfall	1100 mm	1200 mm	1500 mm
Mean annual air temperature	$12^{o}C$	$12^{o}C$	$16^{o}C$
Soil	10-50 cm deep continuous ash-soil	10-50 cm continuous ash-soil	deep ($<$ 1 m) melanized ash-soil

TABLE 2. Plot locations and kind of sampling units by treatment.

Naturally disturbed by pigs			Artificially disturbed once at start of experiment			Artificially disturbed cleared monthly		
Plot no.	Location	Sample unit	Plot no.	Location	Sample unit	Plot no.	Location	Sample unit
1	Site 2	(3 x 5 m)f	4	Site 1	(1 x 10 m)f	12a	Site 1	(1 x 2 m)
2	Site 2	(line intercept)	5	Site 2	(1 x 10 m)f	12b	Site 1	(1 x 2 m)
3	Site 2	(line intercept)	9	Site 3	(1 x 10 m)f	12c	Site 1	(1 x 2 m)
6	Site 2	(line intercept)	10	Site 3	(1 x 10 m)f	13a	Site 3	(1 x 2 m)
7	Site 2	(line intercept)	11	Site 1	(1 x 10 m)f	13b	Site 3	(1 x 2 m)
8	Site 2	(line intercept)				13c	Site 3	(1 x 2 m)

f = plots in which local frequency was measured

These variations were simulated by the artificial disturbance treatments. These consisted of:

a) scalping or clearing, which involved complete removal of the shoot material and of all the root and rhizome parts to a depth of 5 cm.

b) digging, which involved a similar disturbance by cutting off all plants with a spade, but by leaving the plant parts on the disturbed place.

c) repeated clearing, which involved removal of all plants that appeared as seedlings or vegetative shoots at the monthly reanalysis.

d) clipping. This was an additional treatment consisting of monthly clipping of shoot growth. The purpose was to test shoot regrowth under a less harsh disturbance, which simulated grazing.

FIG. 2 shows diagrams of the four kinds of sampling units used. Two of these were used for the artificial disturbance treatments, transectal 1 x 10 m plots and 1 x 2 m plots. In the 1 x 10 m plots each, a 5 m section was scalped and the other 5 m section was dug. In the 1 x 2 m plots each, one half (1 m^2) was scalped or cleared, and the other half (1 m^2) was clipped. The naturally pig-disturbed units consisted of a large 3 x 5 m plot (site 2, plot no. 1) and of five 10 m long line-intercept transects (also all at site 2). The large 3 x 5 m plot was established at site 2 in a place that was dug by pigs shortly before the start of the study. The five line-intercept plots were established to evaluate a cross-section of natural pig-disturbance variations.

Measurements

Frequency. - A one square meter frame, subdivided into 100 equal subsquares (each 1 dm^2), was used to measure local frequency as described by Mueller-Dombois and Cooray (1968). Measurement consisted of enumerating a species when rooted in a subsquare. The frame was used for frequency determinations in the scalped

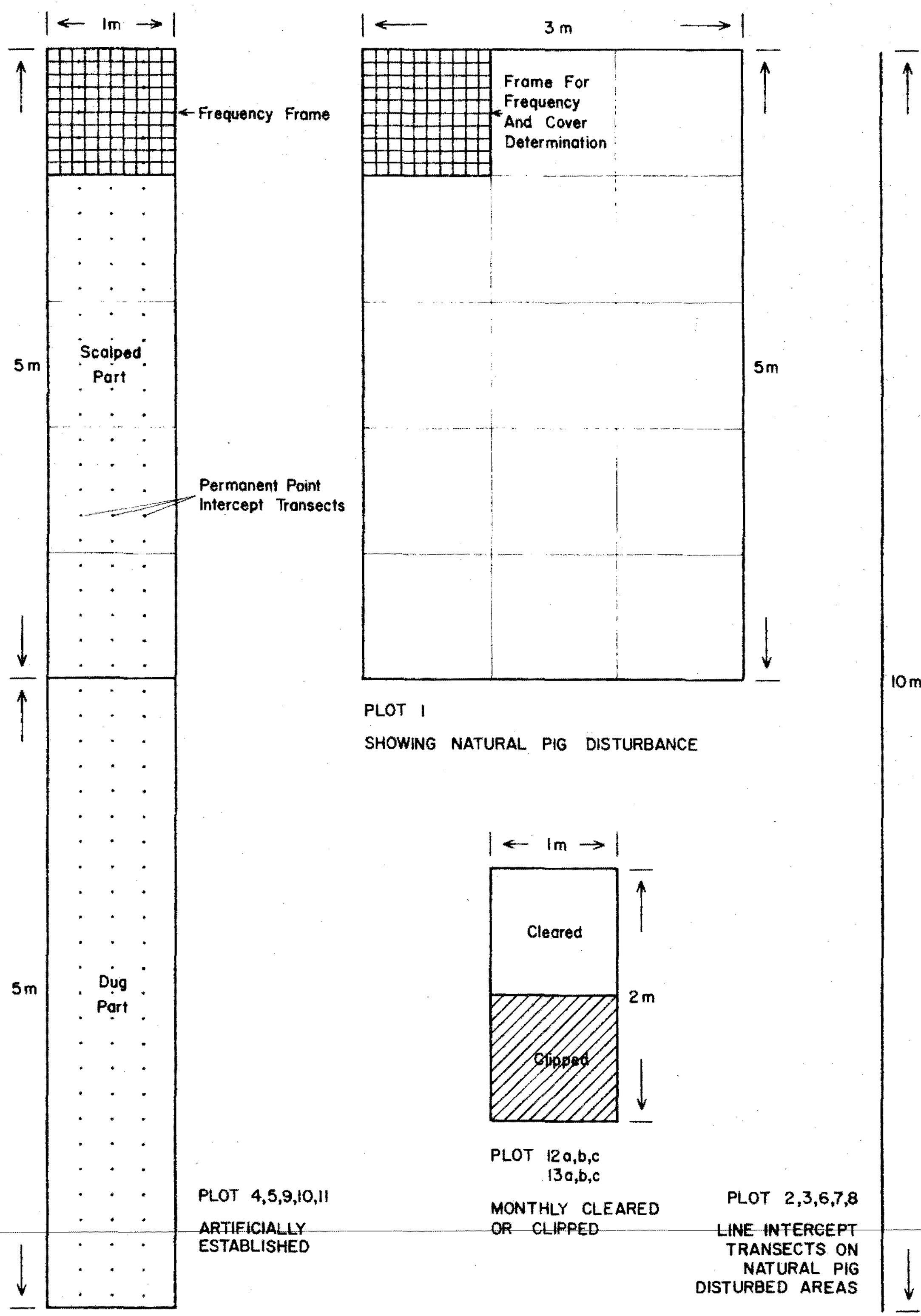

FIG. 2. Scale-diagrams of the four kinds of sampling units used in this study. The 1 x 10 m and 1 x 2 m units were used for artificial disturbance experiments, the 3 x 5 unit and the line-intercept transects were used to evaluate natural pig-disturbance at site 2.

(5 m) section of each 1 x 10 m experimental plot (nos. 4, 5, 9, 10 and 11) at all three sites and in the larger, naturally disturbed plot (no. 5) at site 2. The plots in which frequency was measured are identified by an "f" on TABLE 2. Measurements were repeated every one or two months for a full year, from summer 1971 to summer 1972.

Cover. - This was measured by using the quadrat-charting method for the large 3 x 5 m plot (no. 1), the point-intercept method for the 1 x 10 m plots (no's. 4, 5, 9, 10, 11) (Levy and Madden 1933) and the line-intercept method for line-plots (no's. 2, 3, 6, 7, 8, TABLE 2) (Canfield 1941). The end-points of the line plots were permanently marked. In the 1 x 10 m plots separate records were kept for the scalped and dug plot-halves and point intercepts were run in three parallel transects along the 10 m lengths as shown on FIG. 2. Point-sampling was done with sharpened steel rods mounted in a wooden, one-meter long frame. Five points were sampled per meter resulting in 150 points for each 1 x 10 m plot.

Species listing. - On plots 12 a, b, c and 13 a, b, c (TABLE 2, FIG. 2), the species invading the cleared halves were listed each month. Similarly, the species present or appearing on the clipped halves were listed monthly.

RESULTS

Succession at site 1

At this high elevation site (2030 m) near the upper border in the mountain parkland, we had two (1 x 10 m) artificially disturbed plots (no. 4 and 11, TABLE 2). The three monthly cleared plots (12 a, b, c) at this site will be discussed in a separate section below.

Frequency on scalped plots: a) Changes in a *Deschampsia*-dominated stand. - FIG. 3 shows the frequency curves for plot 4 (scalped 1 x 5 m section) in three

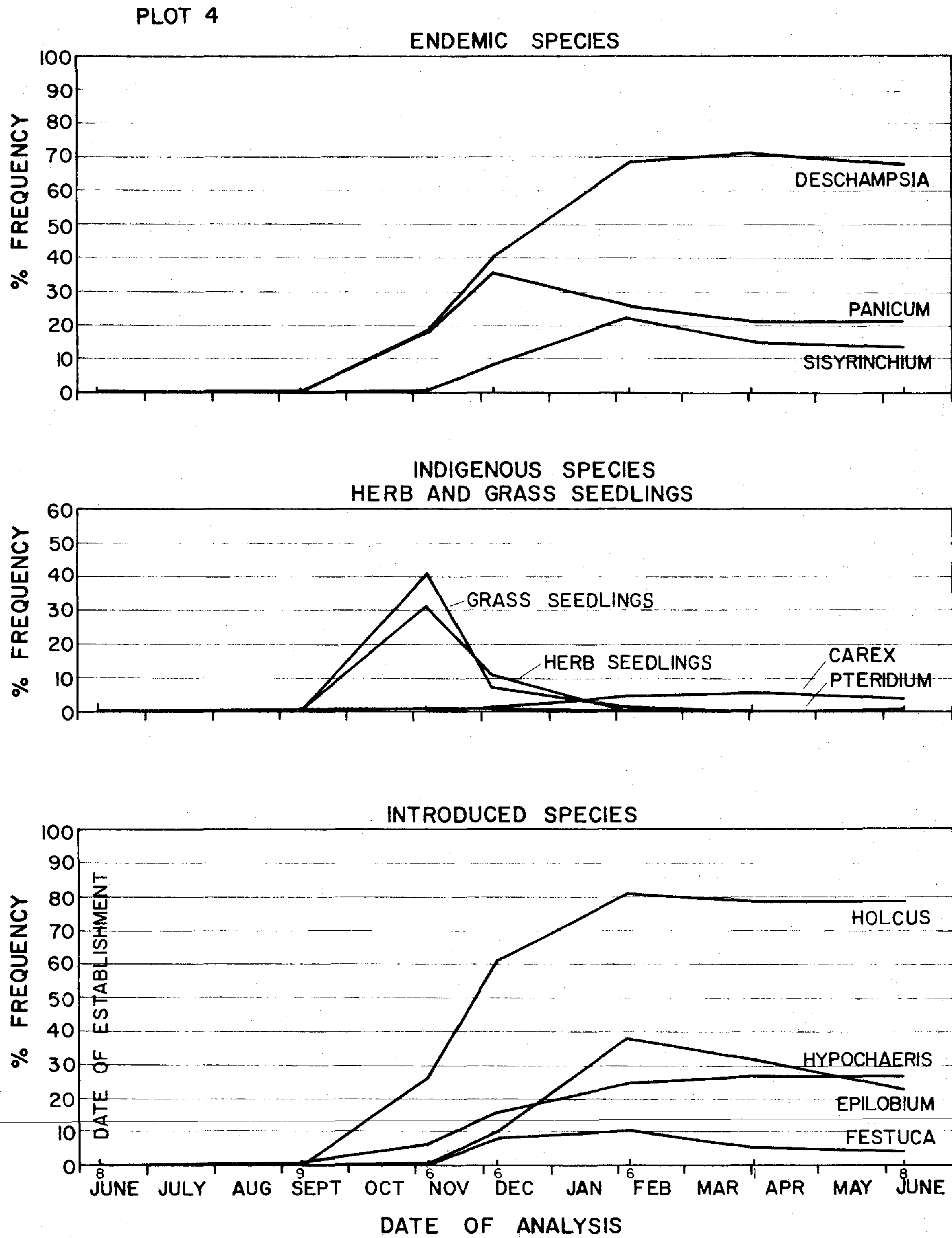

FIG. 3. Site frequency curves for endemic, indigenous and introduced species and for seedlings in scalped plot no. 4 surrounded mostly by native grasses.

graphs separately for the endemic species (those that evolved in Hawaii), the indigenous species (those that arrived without man's assistance in Hawaii but occur also in other regions of the world) and the man-introduced (exotic) species. The seedlings that could initially be identified only as either grass or herb (i.e. forb) seedlings, but not by species are shown in the indigenous species graph. The frequency curve of the endemic bunchgrass Deschampsia australis increases steeply, starting September 1971 to a peak in February, from when on it levels off. This indicates a rapid numerical invasion of Deschampsia seedlings. The slight indentation of the Deschampsia curve in November is merely an artifact that resulted from an inability to identify the young monocot seedlings in November as either Deschampsia, Panicum tenuifolium, Holcus lanatus, Festuca megalura, Carex macloviana or Sisyrinchium acre seedlings. The November frequency peak on the seedling graph undoubtedly contained a high proportion of Deschampsia grass seedlings. If these had been identified at that time, the Deschampsia curve would have probably shown a smooth trend and not an identation. The same explanation applies to the frequency curve of the introduced temperate-zone grass Holcus lanatus (FIG. 3). When comparing the Deschampsia and Holcus curves it becomes clear that these two species are almost equally aggressive invaders in this plot. Both attained a high frequency during the first rainy season (November through April) after complete removal from scalping. The other species were less dominant in frequency. The second endemic bunchgrass Panicum tenuifolium invaded the scalped plot as rapidly as Deschampsia,but from November on Panicum declined (seedling mortality) and then it remained relatively stable. Other important early invaders were the endemic forb Sisyrinchium acre and the exotic forbs Hypochaeris radicata and Epilobium oligodontum. Of low quantitative importance were the second exotic grass Festuca magalura and the indigenous

Carex macloviana and the fern Pteridium aquilinum var. decompositum. Apart from a clear separation of these nine species into 3 abundance groups, the curves indicate generally the same population trends, i.e. a relatively rapid numerical increase till 8 months (Feb.) after scalping and then numerical stability for the rest of the year. The rather sudden increase from September through February correlates with an increase in the month-to-month rainfall. The only instable species appears to be Epilobium oligodontum, which decreased in frequency toward the dry month of June, indicating either a seasonal response or mortality from competition. Further detail is shown in APPENDIX 1.

b) Changes in a Holcus-dominated stand. - The frequency trends recorded on the second scalped plot (no. 11) are shown in FIG. 4. Here, the three endemic species (Deschampsia, Panicum, Sisyrinchium) were relatively unimportant, while the exotic grass Holcus lanatus was very important with near 80% frequency in February through June. However, Holcus showed only the same frequency trend as in the other plot (no. 4). The indigenous sedge Carex macloviana was quite abundant in this second plot (no. 11). Further detail is recorded in APPENDIX 2.

The low frequency of Deschampsia in this second plot (no. 11, FIG. 4) can be explained by the dominance of the former occupants and surrounding species. Plot 4, with high Deschampsia invasion, was in an almost undisturbed native Deschampsia-Panicum community, while plot 11, 20 m away, was surrounded by a formerly pig-disturbed vegetation of Holcus, Carex macloviana, Festuca megalura, Epilobium oligodontum, Hypochaeris radicata and Rumex acetosella, with little Deschampsia and Panicum (TABLE 3).

Cover changes on the scalped plots. - TABLE 3 gives the cover on plots 4 and 11 before treatment. It can be seen that plot 4 had by far the greater cover of endemic species (from 61.5 to 76.9%), while plot 11 had by far the greater cover of exotic species (from 77 to 93.8%). TABLE 3 also shows that Holcus lanatus

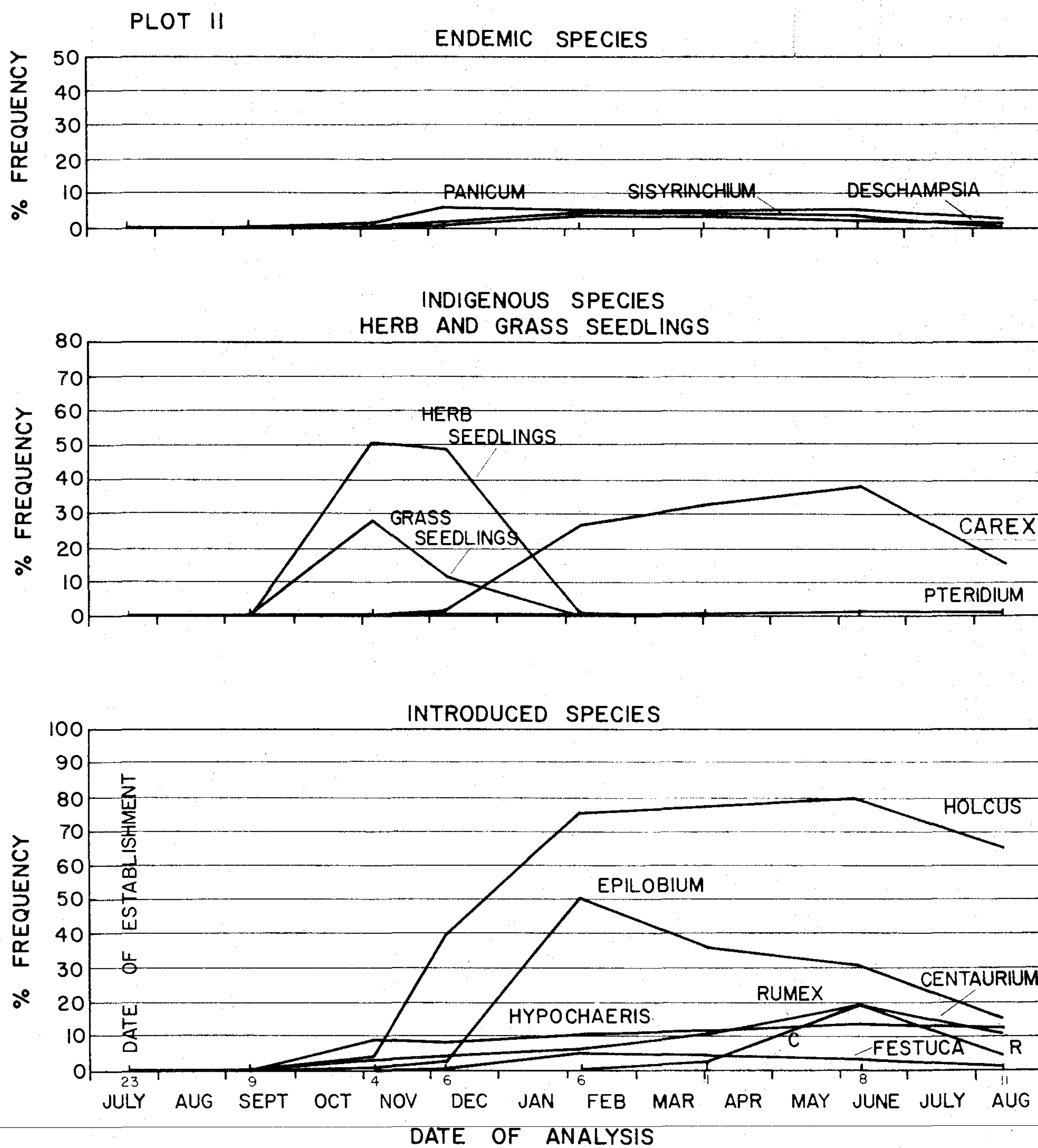

FIG. 4. Site 1 frequency curves for scalped plot no. 11 surrounded mainly by exotic species.

TABLE 3. Percent cover by species at site 1 in plots 4 (June 8, 1971) and 11 (July 23, 1971) before treatment.

	Species	Plot no. 4		Plot no. 11	
		a	b	a	b
E	Deschampsia australis	53.0	71.4	2.4	8.4
E	Panicum tenuifolium	8.5	5.5	0.8	2.4
I	Carex macloviana	1.5	--	--	3.4
X	Holcus lanatus	29.4	21.3	75.0	59.2
X	Hypochaeris radicata	2.1	0.3	3.2	3.6
X	Epilobium oligodontum	0.8	0.5	14.0	4.0
X	Rumex acetosella	--	--	1.6	0.6
X	Festuca megalura	--	--	--	9.6
E = endemics total		61.5	76.9	3.2	10.8
I = indigenous total		1.5	--	--	3.4
X = exotics total		32.3	22.1	93.8	77.0
Total plant cover		95.3	99.0	97.0	91.2

a plot half that was afterwards scalped

b plot half that was afterwards dug

in plot 4, on the segment that was afterwards scalped, had a relative cover (i.e. (29.4/95.3) x 100) of 30.1%. FIG. 5 portrays the cover curves for the same plot (no. 4). After one year, Holcus lanatus had already a greater relative cover, namely 52.1% (i.e. 12.4% Holcus cover out of 23.8% total cover, see FIG. 5*, introduced species, June 1972). For the native Deschampsia, this relation in cover was less favorable. Before initiation of the experiment, the relative cover of Deschampsia was 55.6% (i.e. (53/95.3) x 100, plot 4 a, TABLE 3), while a year after the start of the experiment, Deschampsia was reduced to 10 % (i.e. (2.4/23.8) x 100, FIG. 5, endemic species). This trend was paralleled by the second endemic grass Panicum tenuifolium.

Compared to the frequency curves, the cover curves show more variation, for example for Holcus lanatus and Hypochaeris radicata (compare FIG. 5, introduced with FIG. 3, introduced). The greater variation in some of the cover curves is understandable, since cover measures not only the occurrence of a species, but also its shoot expansion and reduction. The fluctuations were not great enough to note specific reasons such as seasonality, browsing or competition among the plants. In general the cover curves follow the same trend as the frequency curves, i.e. they show an increase with the early part of the rainy season and thereafter a levelling-off for most of the individual species. In contrast, the total plant cover curve shows a steady increase from zero in September (i.e. 3 months after scalping) to more than 30% in June 1972 (i.e. one year after scalping).

FIG. 6 portrays the cover curves for the scalped plot (no. 11) that was formerly occupied by a Holcus-dominated community (TABLE 3). As expected, Deschampsia shows less cover here, than in the Deschampsia-surrounded plot

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* The original data for FIG. 5 are recorded in APPENDIX 3.

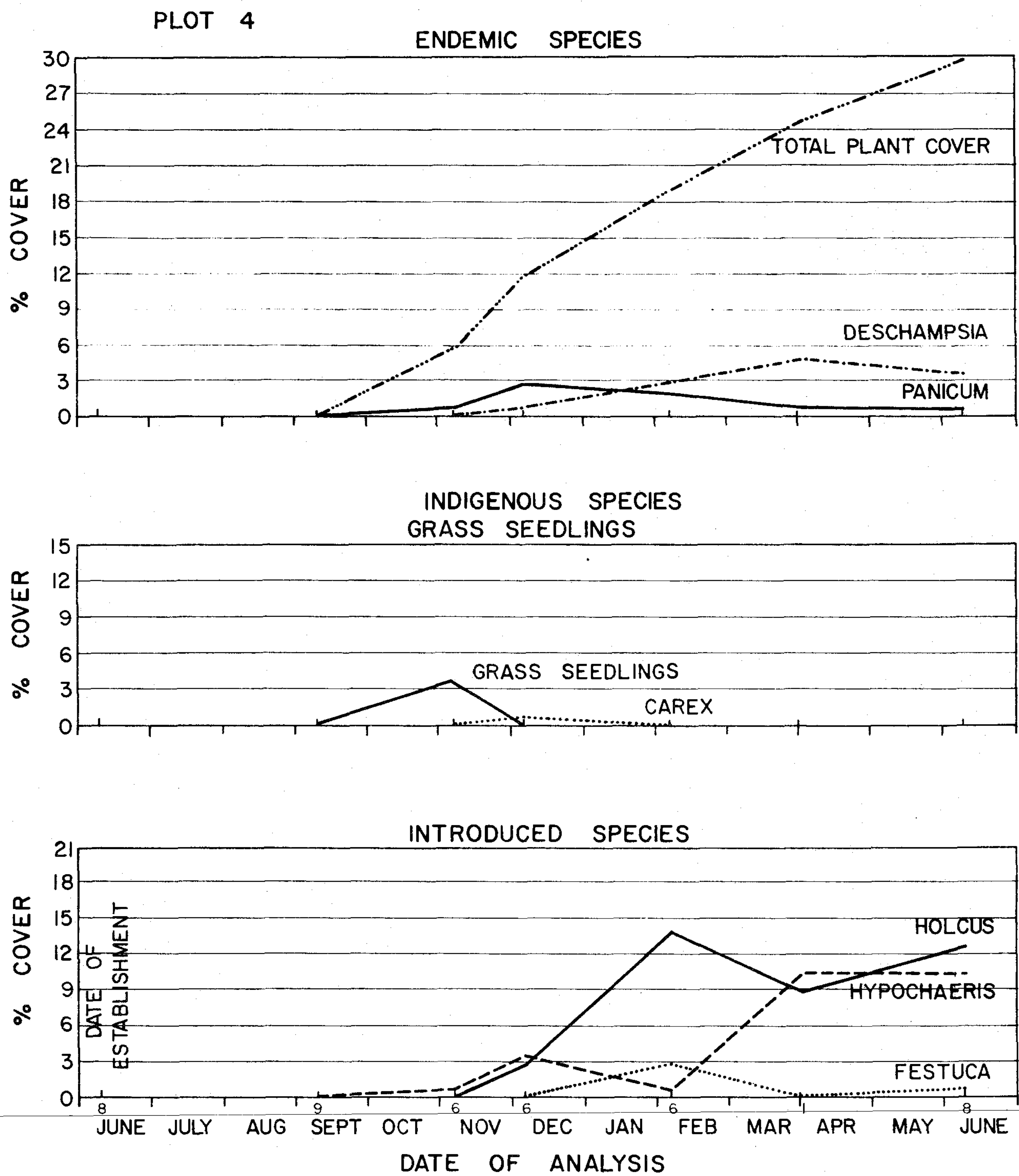


FIG. 5. Site 1 cover curves for scalped plot no. 4.

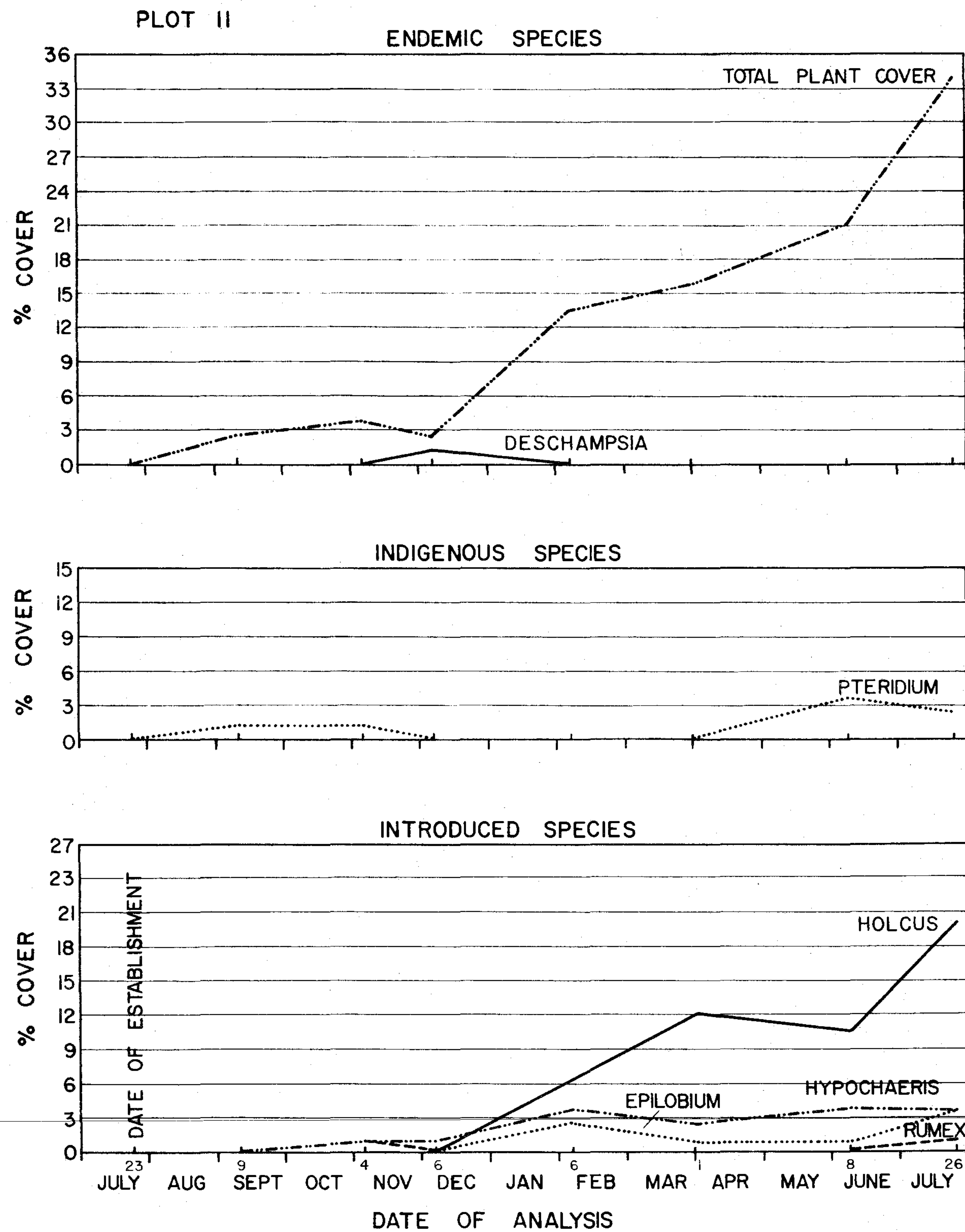


FIG. 6. Site 1 cover curves for scalped plot no. 11.

(no. 4, FIG. 5). Also the cover of Holcus, which during the year was not very different, increased in June 1972 to more than 20% in the Holcus-surrounded plot (FIG. 6), while in the Deschampsia-surrounded plot (FIG. 5), the cover of Holcus was only about half that after one year. The total cover was similar, reaching about 34% after one year (FIG. 6). The original data are given in APPENDIX 4.

Cover changes on dug plots. - FIG. 7 shows the cover changes on the dug (1 x 5 m) sections of both plots no. 4 and no. 11. In addition, the cover of litter, barren soil and total plant cover are shown. In plot 4 the cover by litter was 100% to start with in June 1971 after the plot was dug up. It gradually broke down and covered about 60% surface after one year. In plot 11 the litter cover was only 70% to start with. It also lost about 40% during the year. There was more barren soil in plot 11 as shown on FIG. 7. In both the dug plot sections there was no measurable cover of the endemic grasses, Deschampsia australis and Panicum tenuifolium. Instead, Holcus lanatus grew very vigorously, reaching about 20-22% in both dug plots after one year. Also, the second exotic grass Festuca megalura grew extremely well on the dug plot 11 exceeding even Holcus in cover. This shows that a digging disburbance may favor the exotic grasses decidedly, even more than a scalping disturbance. After digging, the new species composition may be entirely exotic even where the stand was formerly occupied dominantly by endemics, as was the case in plot 4.

Succession at site 2

At this more central site in the mountain parkland ecosystem (at 1880 m) we had all of the naturally pig-disturbed plots (the large 3 x 5 m plot and the 5 line-intercept plots) and one artificially disturbed plot (no. 5, see TABLE 2).

The pattern in a naturally pig-disturbed area: a) Changes in an unevenly scarified grassland patch. - The large 3 x 5 m plot (FIG. 2) was established on

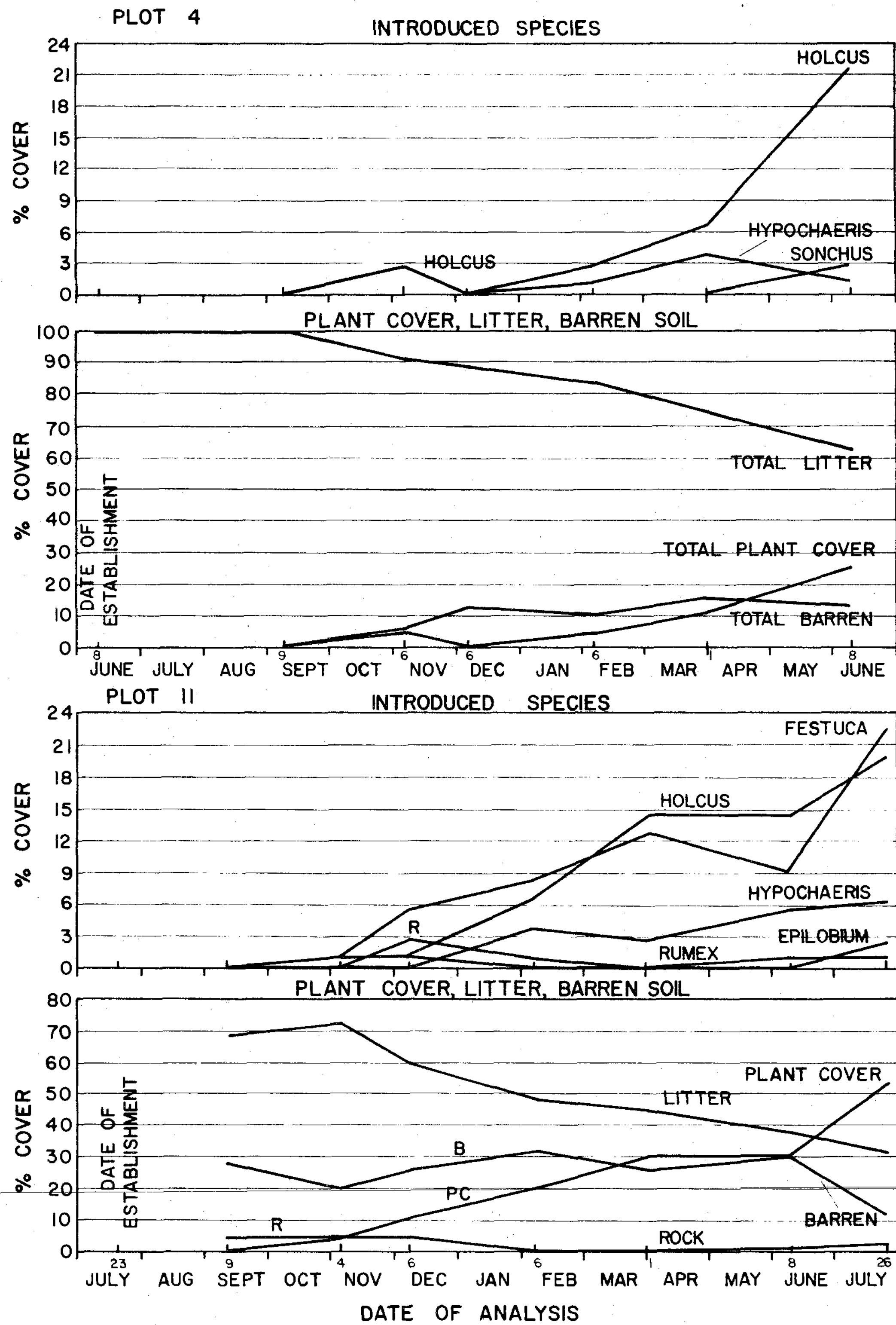


FIG. 7. Site 1 cover curves on dug plots (no's. 4 and 11).

an area that was heavily scarified by pigs in the center of the plot with much exposed soil showing. Litter from uprooted bunchgrass, primarily *Deschampsia australis*, was strewn about. At the plot margins occurred many remnant bunches of native species, *Deschampsia australis* (mainly), also *Panicum tenuifolium* and *Carex macloviana*. The proportion of *Holcus lanatus* was relatively small.

FIG. 8 shows the frequency changes that occurred on the 3 x 5 m plot from June 1971 to June 1972. The curves indicate that all species remained relatively stable through the year. The curves also show that the exotic *Holcus* was more dominant in frequency after one year than the native *Deschampsia*. (The data were extracted from APPENDIX 5).

The changes in plant cover are shown on a series of seven successive maps (FIG. 9 a-g). These maps were drawn from an area-grid composed of 15 contiguous one-square-meter-frame placements. The charting was done right after recording the frequency in each frame placement.

The maps drawn during each analysis show in detail the cover changes during the observation time. While the pattern was rather simple at the time of the first analysis in June 1971 (FIG. 9a), it became increasingly complex with each new analysis. In June 1971 the plot was dominated by large bunches of the endemic *Deschampsia* and *Panicum* and the indigenous sedge *Carex*. The bunchgrasses were more or less concentrated along the edge of the plot where they survived the pig digging which had taken place in the center of the plot prior to the study. In the disturbed center small *Holcus*, *Deschampsia* and *Panicum* plants were invading.

By September 1971 (FIG. 9b), the disturbed center was already crowded with many, small invading plants, native as well as introduced. Some had grown together to form mixed stands. Because of the beginning of the rainy season, a still more obvious change occurred in November (FIG. 9c). *Holcus*, especially, took

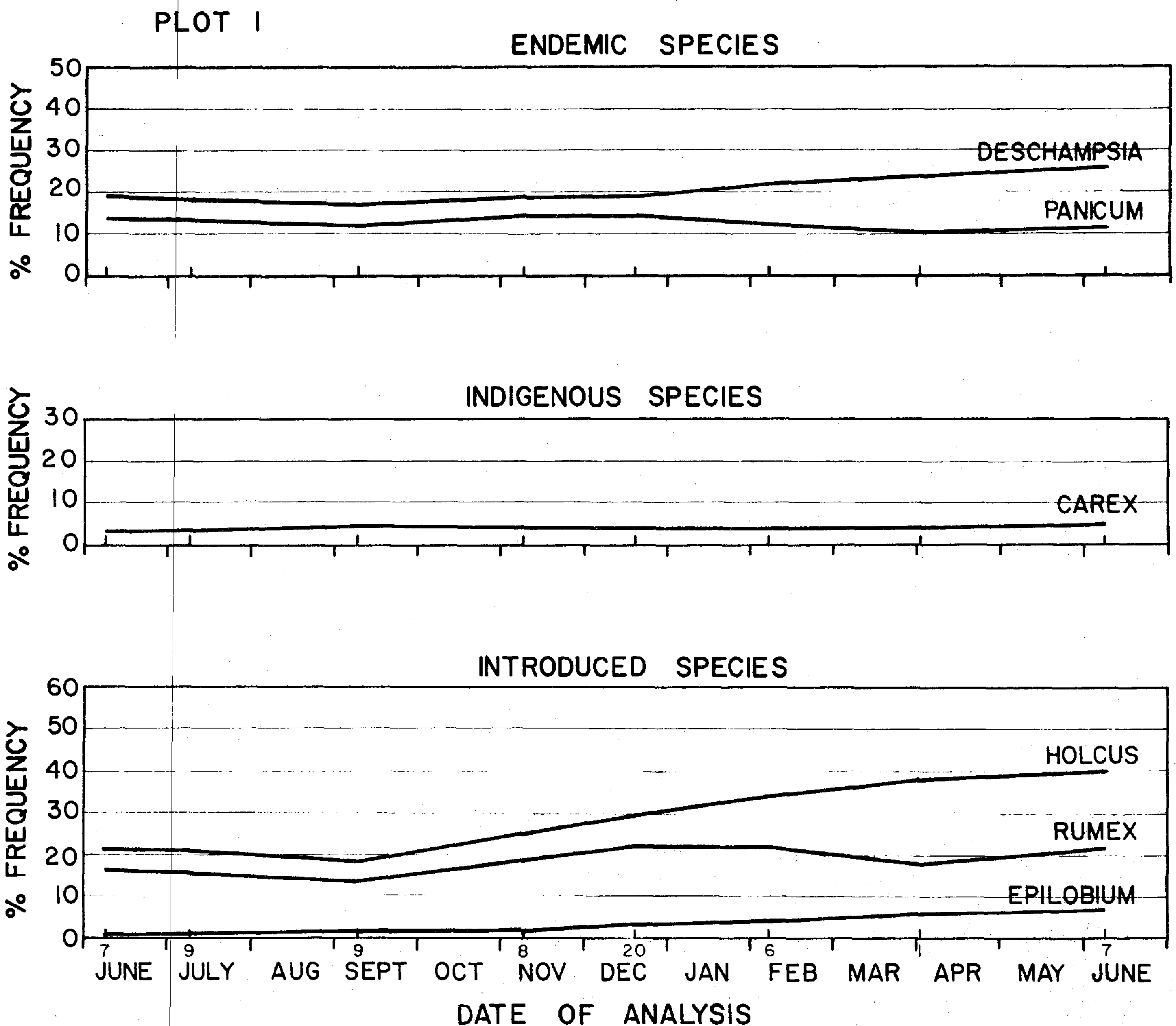


FIG. 8. Site 2 frequency curves of species growing on a naturally pig-disturbed place (plot no. 1).

SUCCESSION STAGES IN A PIG DISTURBED AREA ON MAUNA LOA EAST FLANK
PLOT D/H 1

ANALYSIS OF JUNE 7 1971

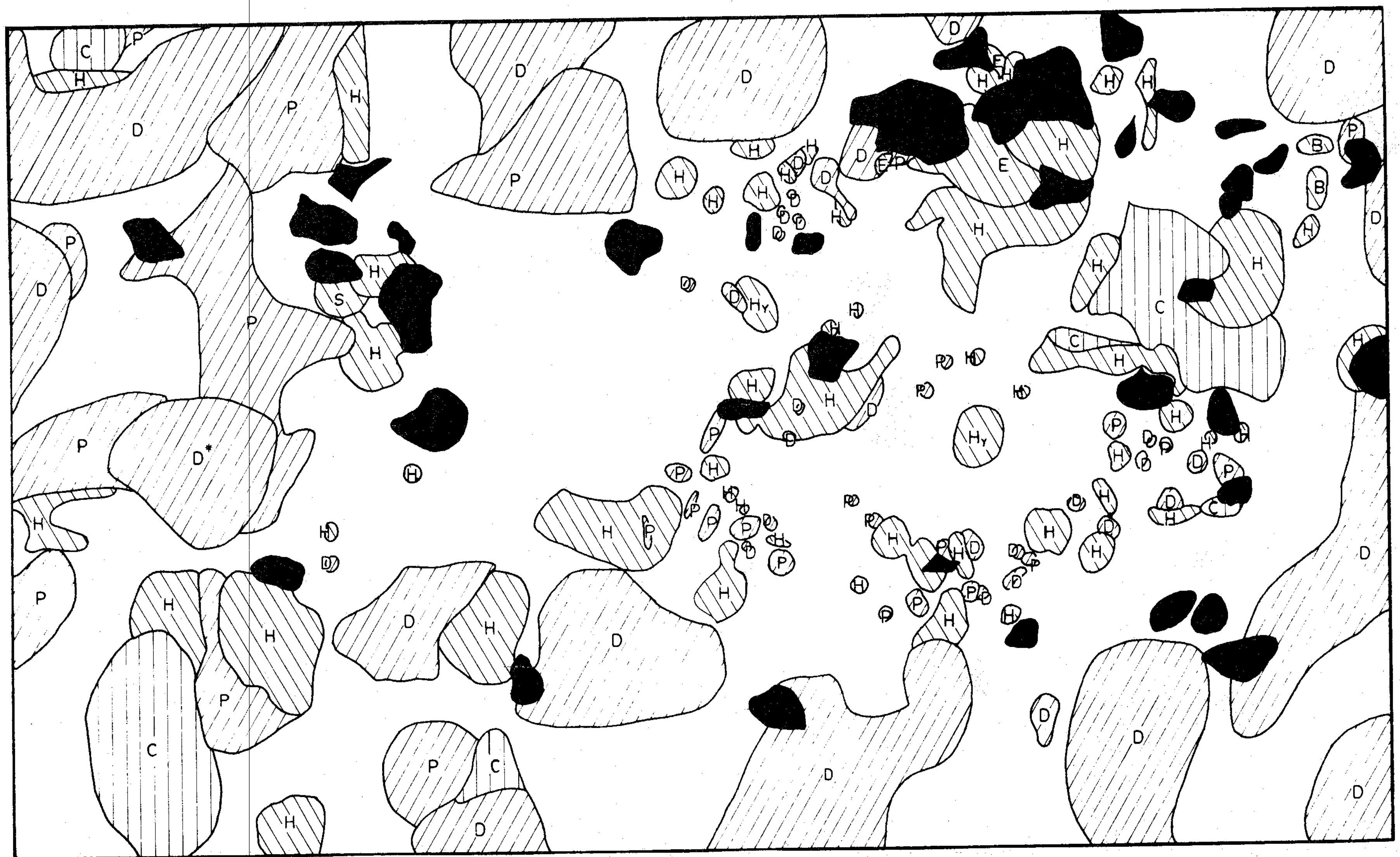


FIG. 9a

ANALYSIS OF SEPTEMBER 9 1971

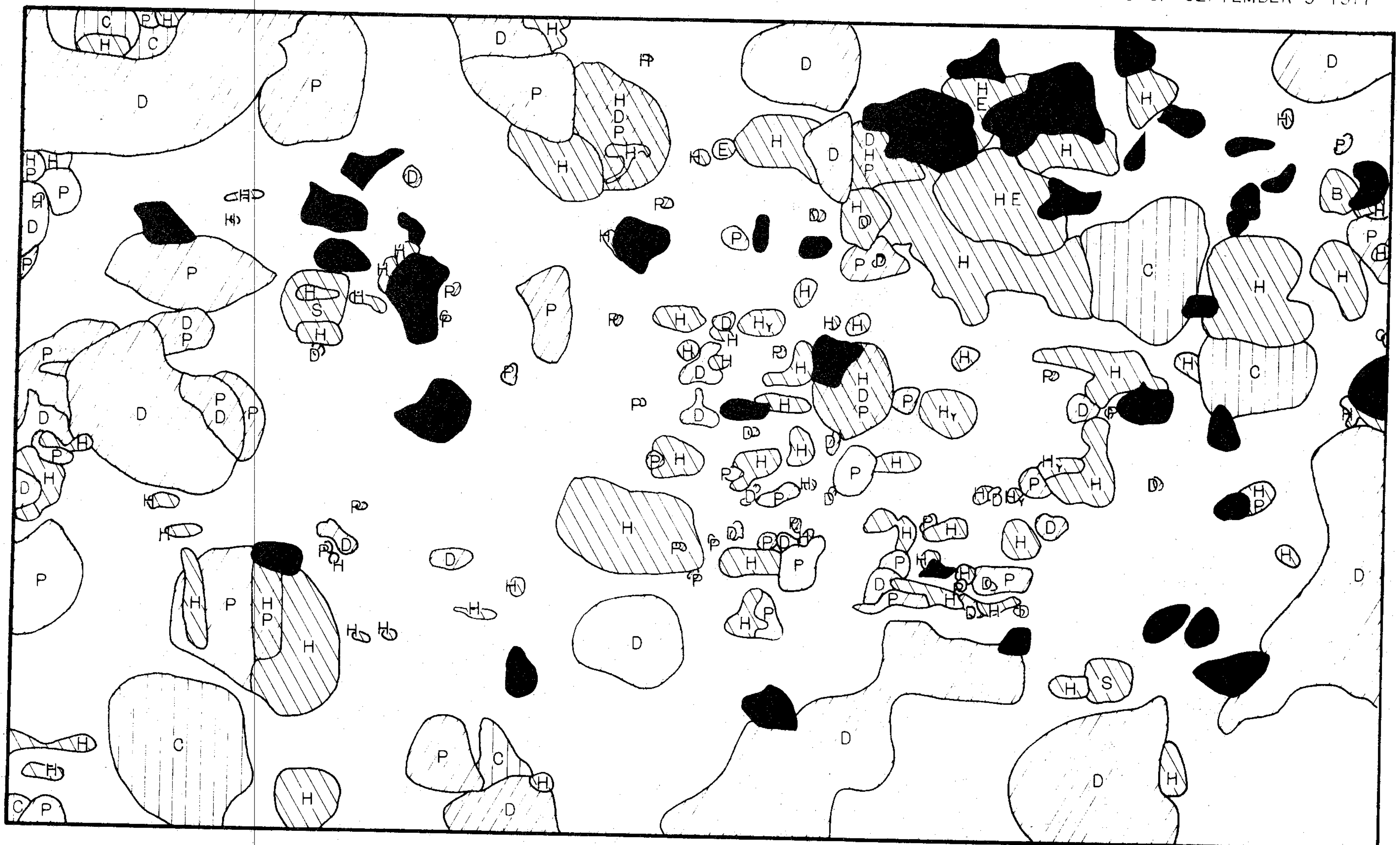


FIG. 9b

ANALYSIS OF NOVEMBER 8 1971

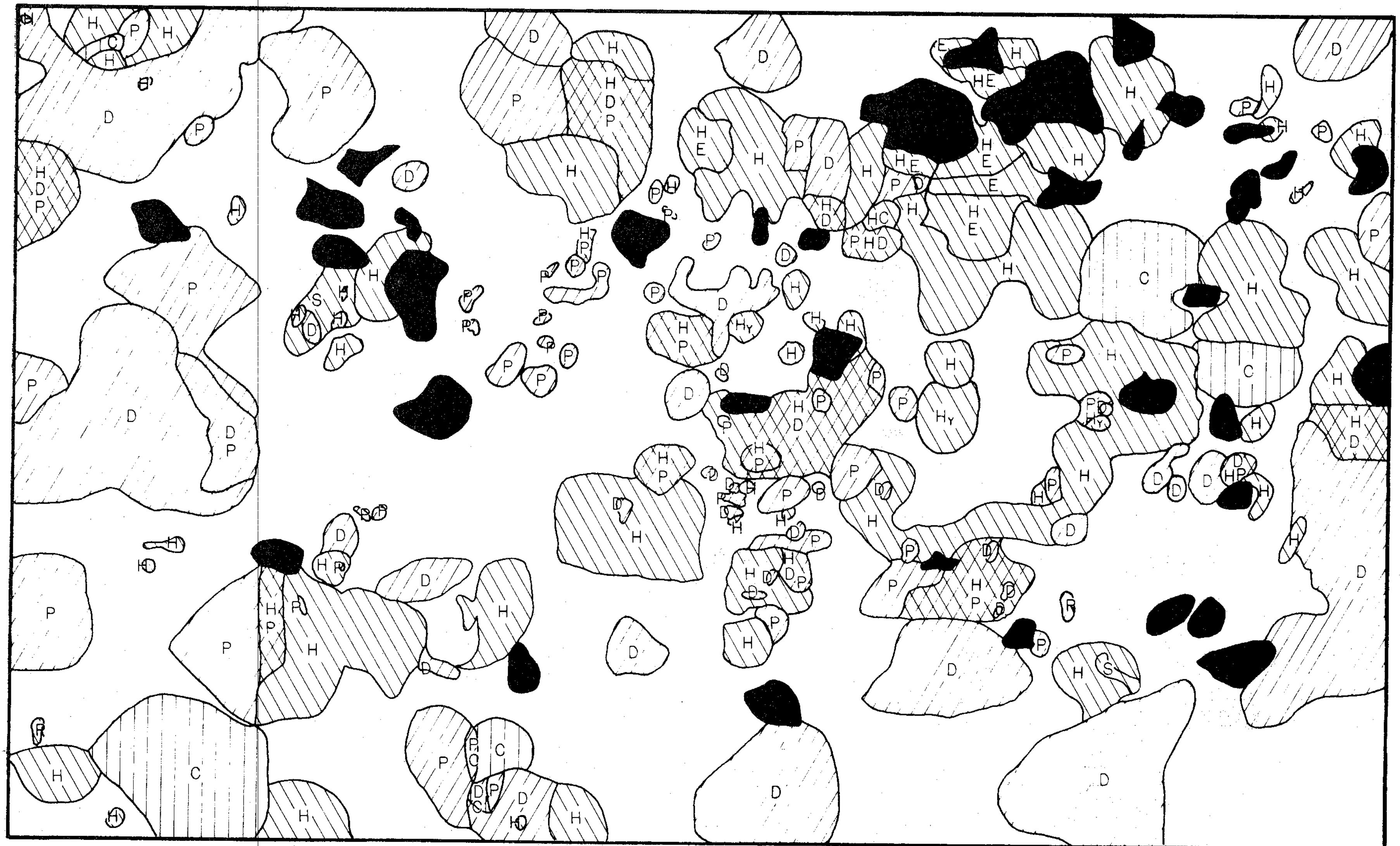


FIG. 9c

ANALYSIS OF DECEMBER 20 1971

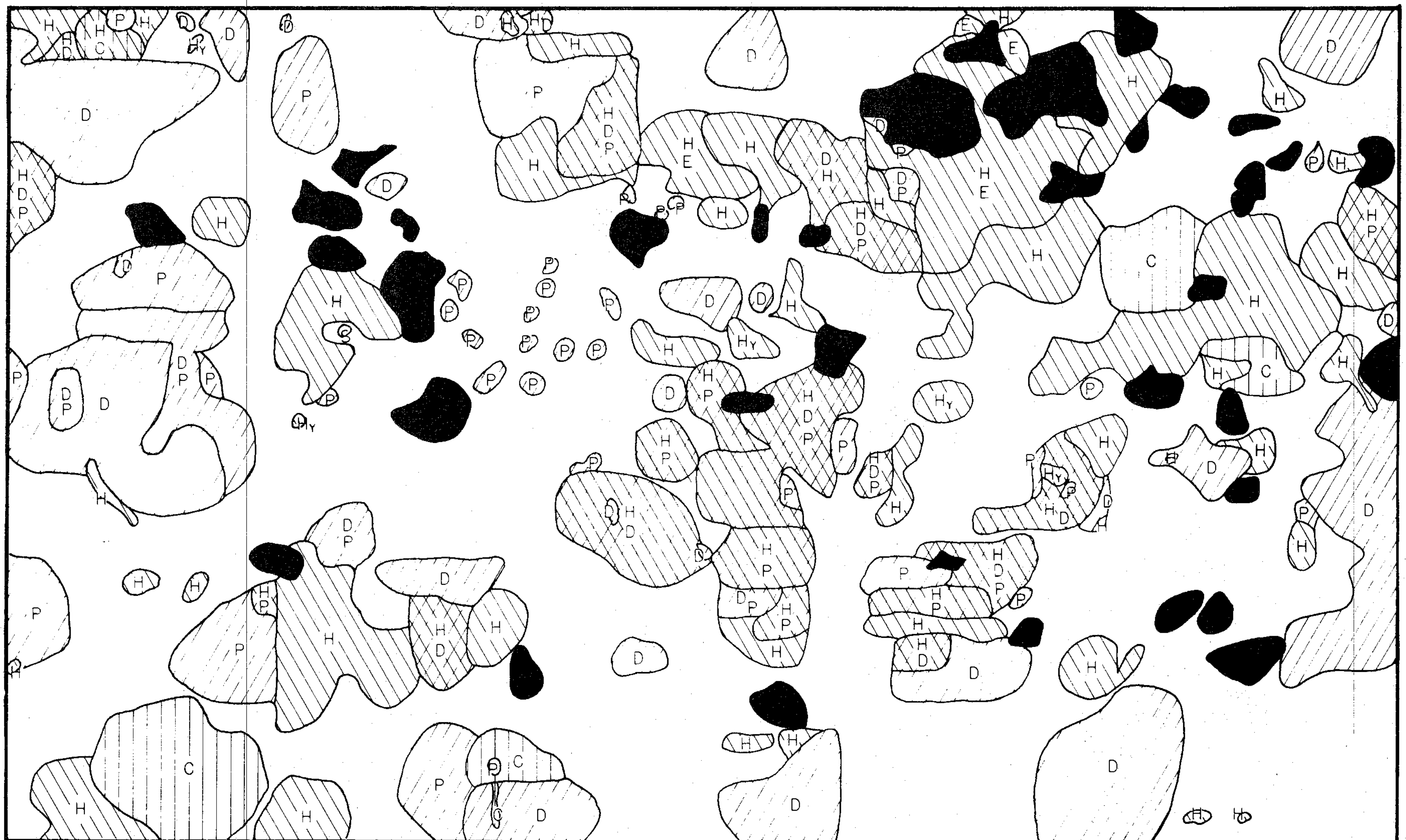


FIG. 9d

ANALYSIS OF FEBRUARY 6 1972

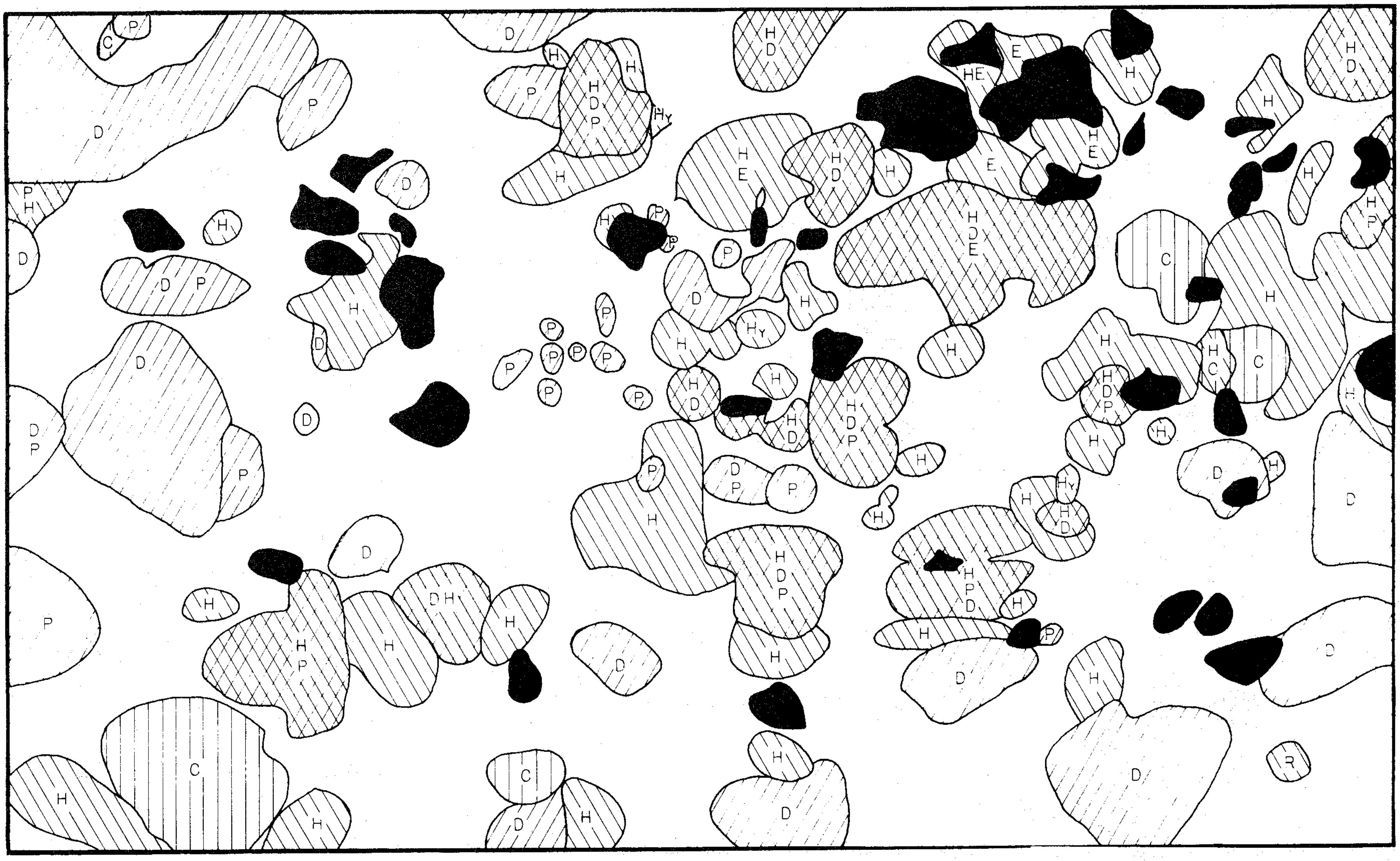


FIG. 9e

ANALYSIS OF APRIL 1 1972

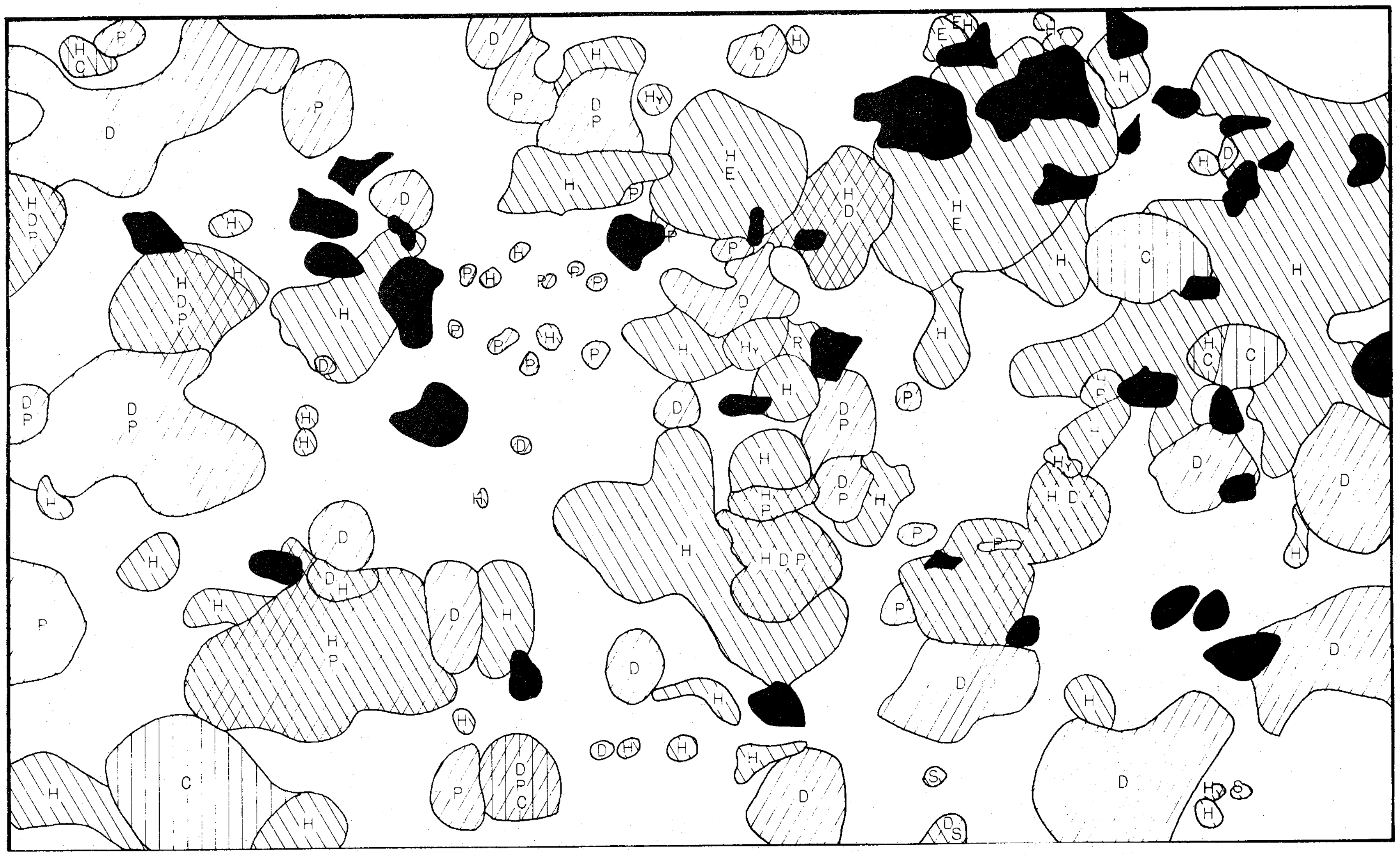


FIG. 9f

ANALYSIS OF JUNE 7 1972

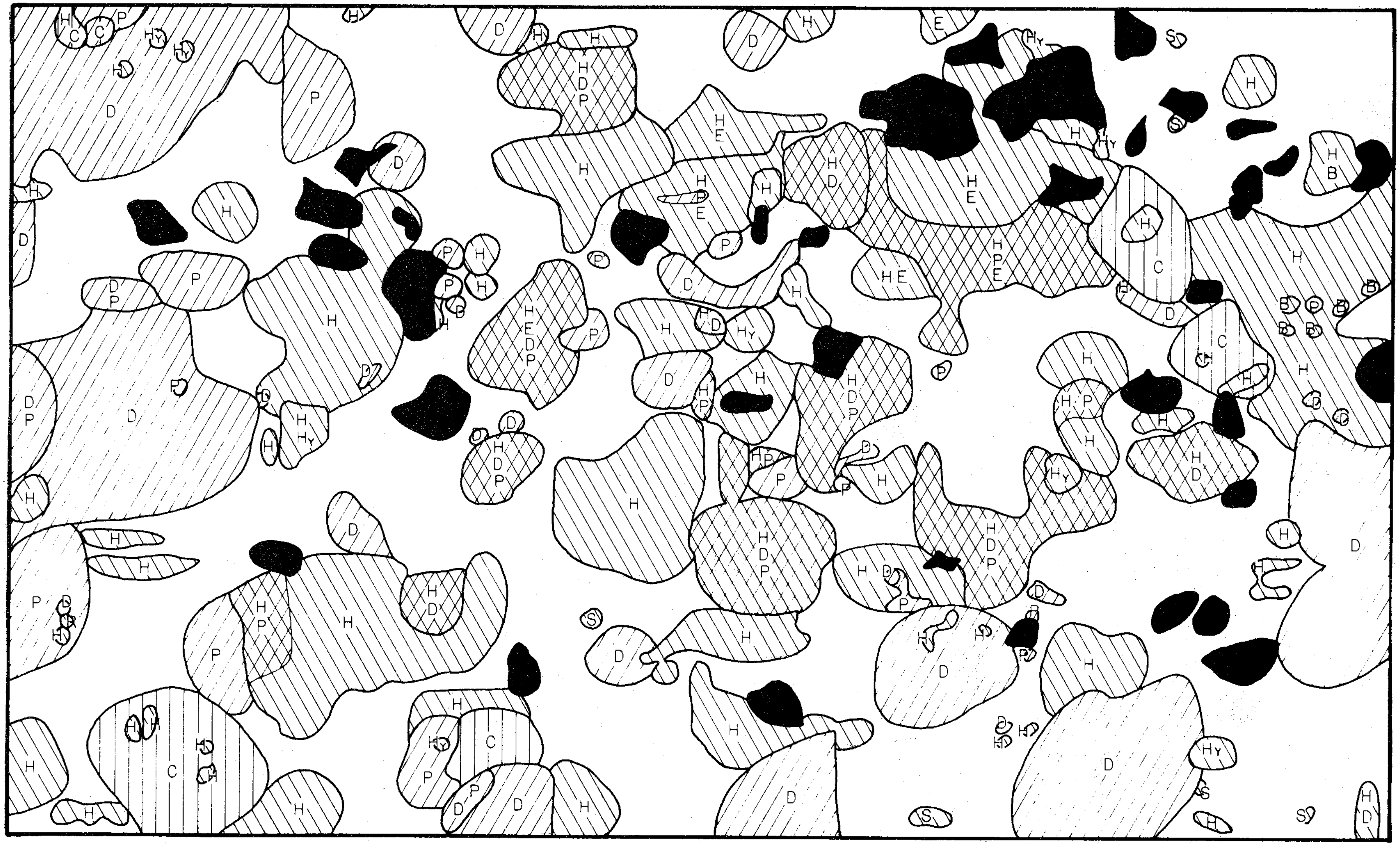


FIG. 9g

advantage of the rainfall by forming extensive patches in the disturbed center and by starting to penetrate into the surrounding grass bunches, forming mixed stands (cross-hatched on FIG. 9c) with the Deschampsia and Panicum. This trend continued throughout the analysis of December 20 (FIG. 9d) and February 6 (FIG. 9c). By the end of the wet season in April, the pig-disturbed center had recovered and was dominated by Holcus (FIG. 9f). The upper right corner of the map is almost exclusively covered by Holcus, which had been able to partially displace the bordering Deschampsia and Carex. At the last analysis on June 7, 1972 (FIG. 9g), the picture had changed greatly from that of the first analysis one year before (FIG. 9a). The formerly disturbed center of the plot had become covered by mostly mixed stands of Holcus, Deschampsia and Panicum. The edge was still dominated by bunches of Deschampsia and Panicum, but patches of Holcus were almost everywhere. An old Deschampsia bunch at the upper right corner had disappeared totally. The whole pattern had become much more complex, with considerable parts of the plot being covered by mixed stands.

The mapped cover was measured with a dot-grid and entered in APPENDIX 5. Here it is shown that Holcus was the most successful invader that almost doubled its coverage within a year (from 11% to 21.4%). Epilobium multiplied its meager 0.4% coverage in June 1971 to 2.2% a year later. The endemic species Deschampsia and Panicum fluctuated throughout the year, both declining during the wet and cool winter months from November through March. While Deschampsia could increase its final cover percentage a little, Panicum dropped from 6.7% to 5.3%. Carex remained more or less unchanged throughout the year.

b) Changes in an area with different degrees of disturbance. - FIG. 10 shows the cover changes that occurred along five 10 m-long line-intercept transects. These were laid out next to the aforementioned 15 m^2 plot (no. 1) over

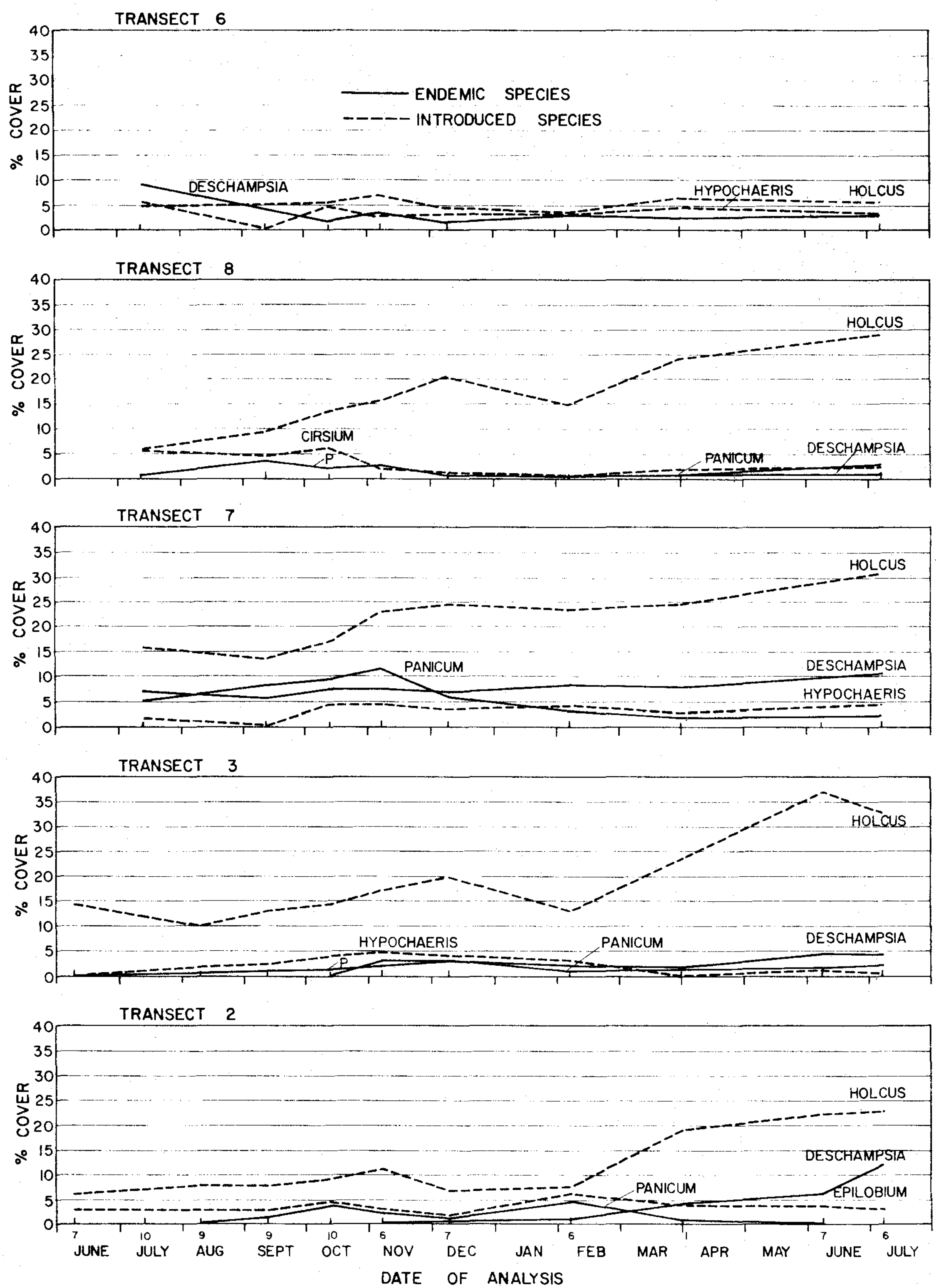


FIG. 10. Cover (%) along five line transects traversing differently disturbed segments of the grassland at site 2. Transects 2 and 3 are the least disturbed, transects 7 and 8 are more heavily disturbed and transect 6 is on the steeper part of a slope where goat and pig trampling was most severe.

differently disturbed sections of a gentle slope. This slope was not only disturbed by pig-digging, but also goats passed frequently causing disturbance by browsing and trampling. Trampling and trail-making was most conspicuous on the steeper part of the slope.

Along the less disturbed transects 2 and 3, the endemic Deschampsia and Panicum clearly increased their cover. Deschampsia, especially, showed that it has the potential to reoccupy as long as the factors causing disturbance are held in check. Nevertheless, Holcus was again the most successful species here.

The dominance of Holcus becomes more striking along transects 7 and 8, which were subject to more disturbance. While the cover of endemic plants remained about the same during the time of observation, Holcus increased its cover from 16% to 31% at transect 7 and from 6% to 29% at transect 8.

Transect 6, located on a steep slope frequently traversed by goats and pigs, was so continuously disturbed that even Holcus could just maintain its initial cover percentage. The cover of Deschampsia dropped from 8% to 3%. The total plant cover decreased from 23% at the beginning of the experiment to 13% at the end. (The raw data are shown in APPENDIX 6).

The pattern on an artificially disturbed plot. - A 1 x 10 m plot (no. 5, TABLE 2) was established in July 1971 next to the naturally pig-disturbed plot (no. 1). A 1 x 5 m section of the artificially disturbed plot was scalped and the other half was dug, thereby representing a replicate treatment to the two plots (no's. 4 and 11) discussed above under "Succession at site 1."

FIG. 11 shows the frequency curves on the scalped section of plot 5. These afford a direct comparison with FIG. 3 and FIG. 4 relating the scalped plots at site 1. There is a considerable similarity in the invasion pattern of FIG. 11 and FIG. 4. Both show a relatively high invasion rate of Holcus lanatus and

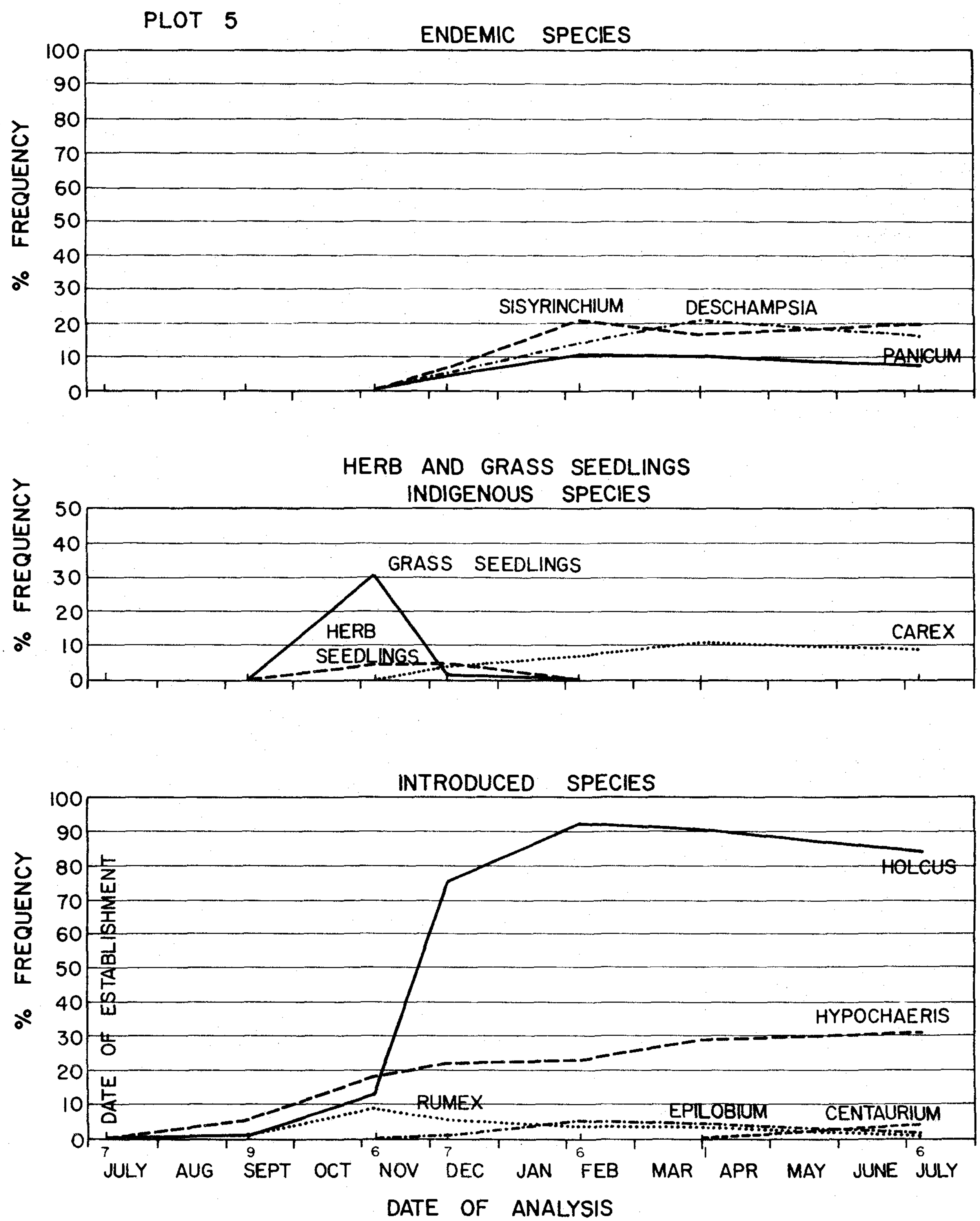


FIG. 11. Site 2 frequency curves for scalped plot no. 5 surrounded dominantly by exotic species.

Hypochaeris radicata with a very low invasion rate of the endemic species *Deschampsia australis*, *Panicum tenuifolium* and *Sisyrinchium acre*. The former vegetation and the currently surrounding species composition of the plot (no. 5) at site 2 was similarly dominated by exotics as at plot 11 in site 1. Thus, the low invasion rate of *Deschampsia* on these plots is directly related to the meager presence of *Deschampsia* in the surrounding vegetation. At site 2, *Hypochaeris* sprouted initially from left-over roots soon after the plot was scalped, but in addition seed germination occurred after the first significant rainfall. *Holcus* reached a frequency of 90% in February, which was about 10% greater than its invasion at site 1.

FIG. 12 shows the cover curves for *Hypochaeris* and *Holcus*, which were the only two species attaining significant cover within a year on the scalped plot at site 2. A comparison with the two scalped plots at site 1 (FIG. 5 and 6) shows not much difference. At both sites (1 and 2) *Holcus* attained a cover between 10% to 20% on the scalped strips. The total cover at site 2 was only 27% after 1 year, while at site 1 it was from 30% to 35%.

On the dug part of the plot 5 (site 2) the cover after one year was extremely small, and consisted exclusively of introduced plants. The reason for such a paucity of cover was that pigs had visited the site several times, rooting in the dug part of plot 5, which seemed to be more attractive to them than the adjacent scalped part. (The original data for plot 5 is shown in APPENDIX 7).

Succession at site 3

At this lower elevation (1220 m) site we had two artificially disturbed plots (no. 9 and 10, TABLE 2) forming replicate treatments to those at site 1 and 2. However, site 3 is in a different ecosystem, the savanna grassland.

FIG. 13 shows the frequency curves of the invading species on the scalped

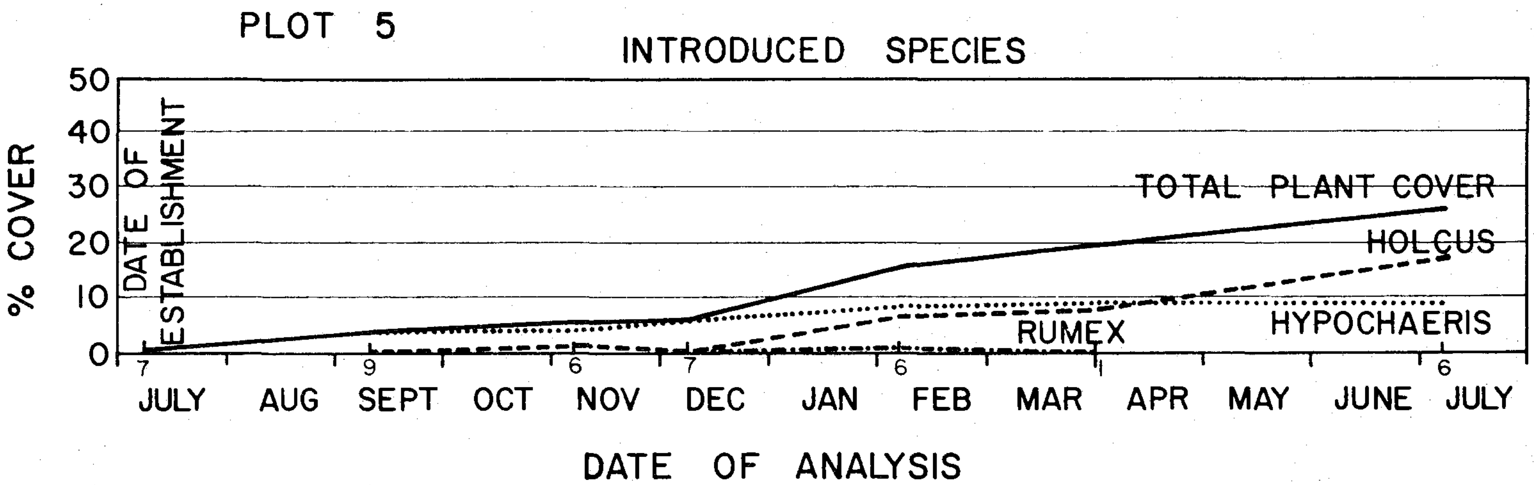
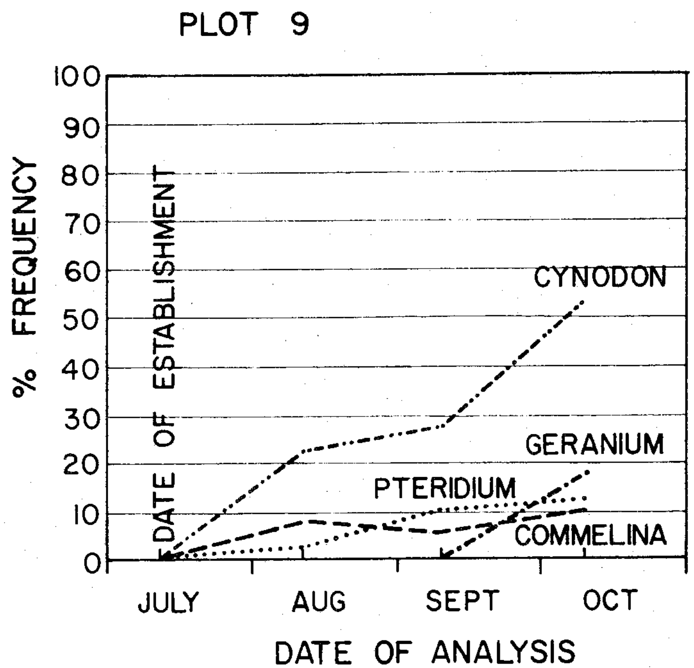


FIG. 12. Site 2 cover curves for scalped plot no. 5.



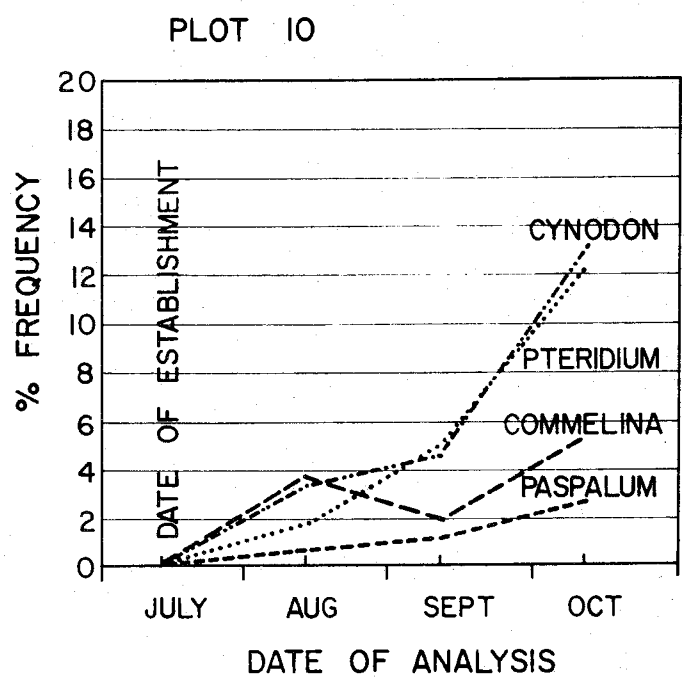


FIG. 13. Site 3 frequency curves for scalped plots no. 9 and 10. (Note difference in frequency scales).

parts of plots 9 and 10. The invasion on both plots was dominated by Cynodon dactylon, which sprouted soon after scalping from left-over roots. The great difference in Cynodon frequency (54% in plot 9 and 13% in plot 10) after 3 months in October was a function of the left-over roots. Geranium carolinianum started to germinate from seeds during September and October.

FIG. 14 demonstrates the increase in plant cover on the scalped section of each plot. The total plant cover increased rapidly in comparison to the scalped plots in the mountain parkland. There was also quite a change in species composition. Seasonal behavior was obvious in Cynodon and Pteridium aquilinum var. decompositum. Their cover reached a peak from October to December after which time it declined again. It is interesting that Holcus lanatus appeared as a late invader in October and then increased steadily in cover to become the most dominant species in both scalped plots. In terms of total cover, plot 9 was completely recovered after 7 months, while plot 9 was almost completely recovered after 8 months, with 93% in March. In comparison to site 2 (FIG. 12) and site 1 (FIG. 7), the recovery rate at site 3 was very much faster. This is understandable in view of the higher rainfall, deeper soil and warmer temperature at site 3 (TABLE 1).

FIG. 15 illustrates the cover changes on the dug sections of plots 9 and 10. Here the pattern was very different in so far as Commelina diffusa spread the fastest. It became dominant because of its superior ability to regenerate vegetatively from stolons. Cynodon dactylon was subdued by Commelina. Holcus lanatus was able to spread steadily to become the next dominant species after Commelina. Except for the endemic variety of Pteridium, no native species participated in the succession at site 3. Both plots showed a 100% plant cover within 6 to 7 months after the disturbance. (The raw data for FIG.'s 13, 14 and 15 were recorded in APPENDIX 8 and 9).

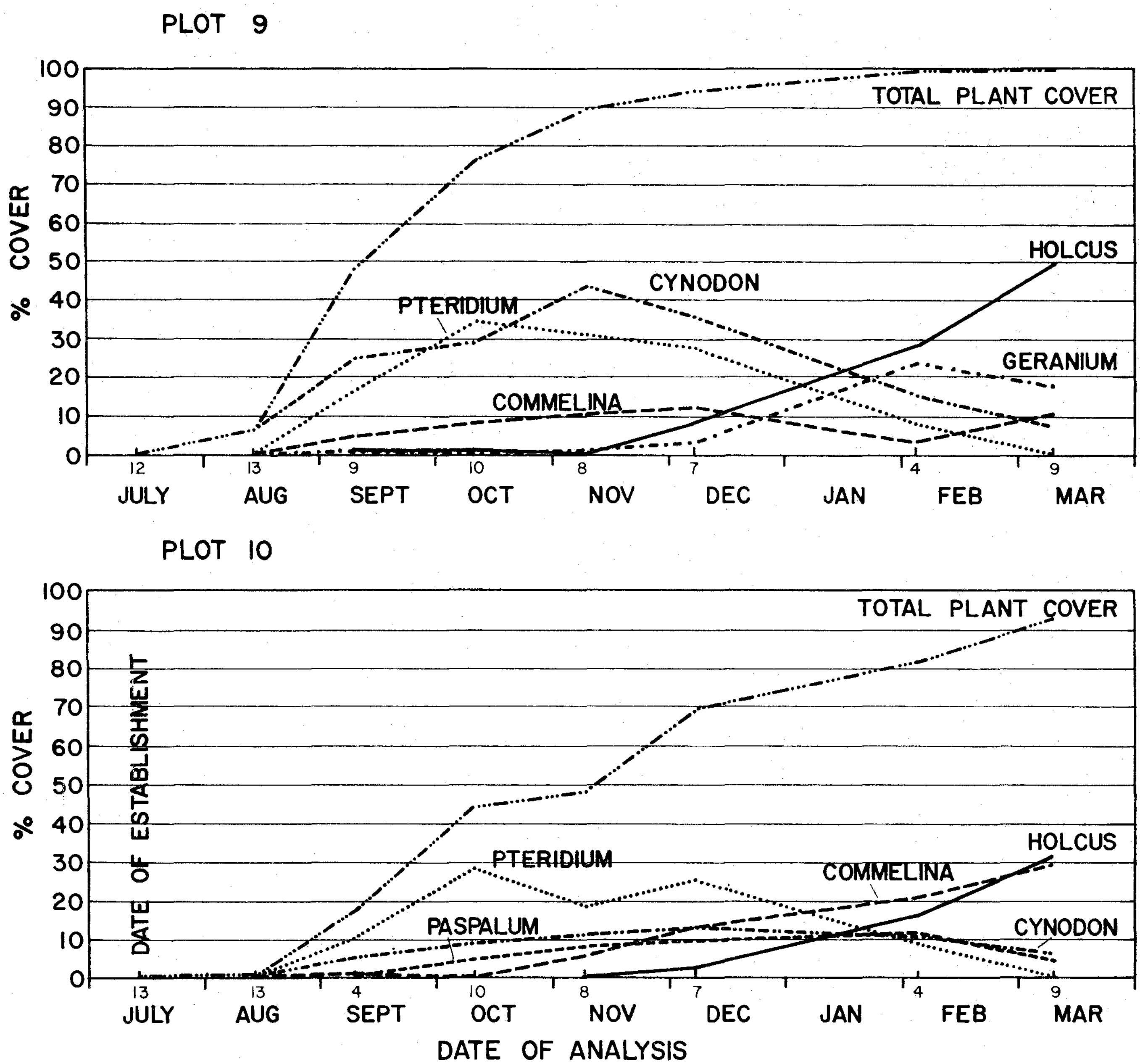


FIG. 14. Site 3 cover curves for scalped plots no. 9 and 10.

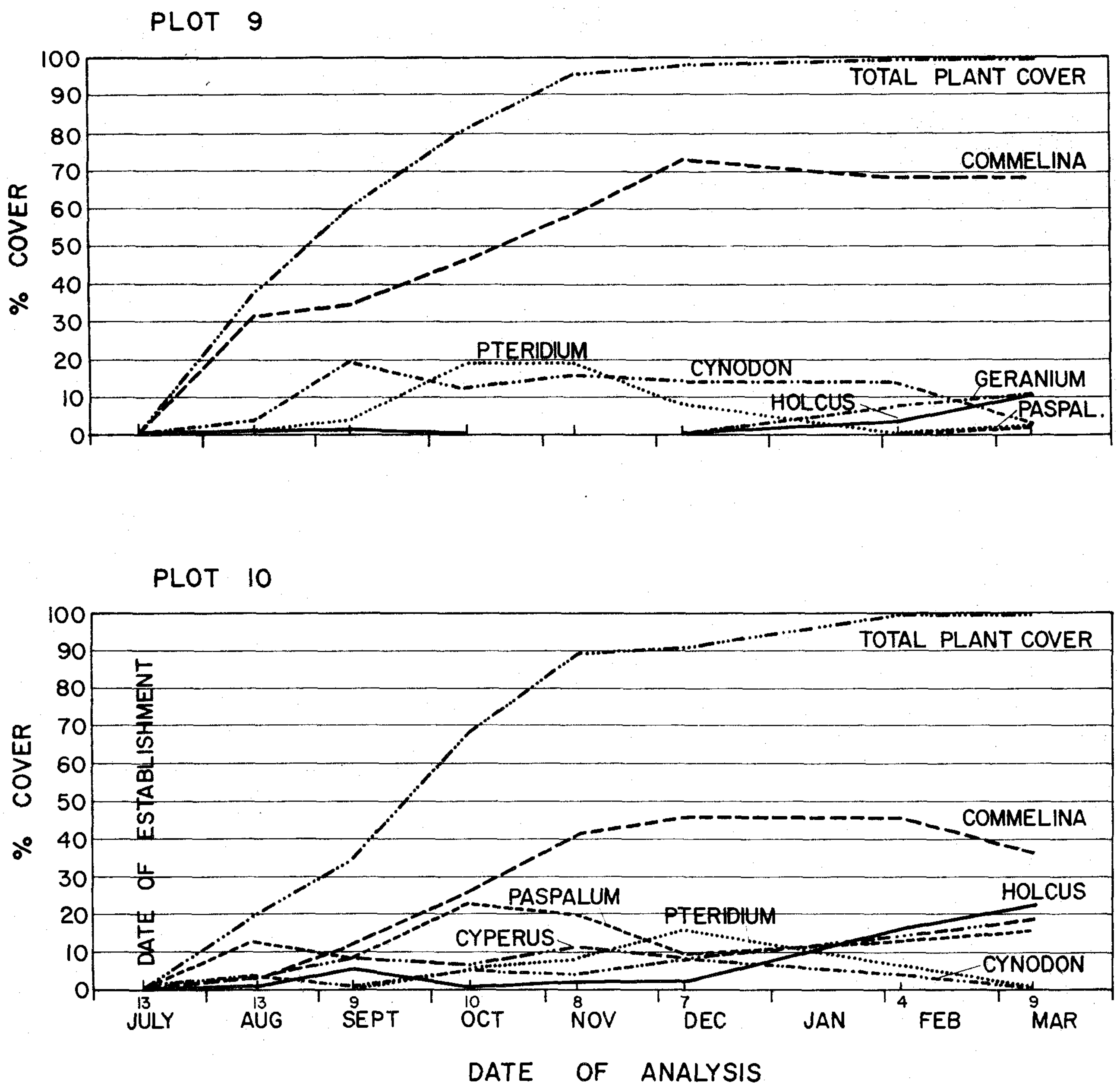


FIG. 15. Site 3 cover curves for dug sections of plots no. 9 and 10.

Invasion on plots cleared monthly

TABLE 4 shows the species that occurred at site 1 and site 3 in each three 1-m^2 plots. Only four species occurred at both sites (Holcus lanatus, Poa pratensis, Geranium carolinianum and suckers of the endemic tree species Acacia koa). The greater number of species was unique to either plot sets reflecting in part the environmental difference between sites 1 and 3 (TABLE 1). Moreover, the location chosen for plot-set 12 a, b, c at site 1 was in a rarely used horse corral that had no native grasses left.

On plot-set 12 (site 1) Dactylis glomerata, abundant in the surrounding horse corral, was the most commonly reappearing species after monthly clearings, with 23 out of a possible 39. Next in reestablishment capacity were Rumex acetosella, (20 times), then Holcus lanatus and Geranium carolinianum (both 11 times). Acacia koa suckers also resprouted frequently.

In the savanna grassland (site 3) the lush cover of Paspalum, Pteridium, Commelina, Cynodon and Holcus was reflected by the plants appearing in plots 13 a, b, c. Most often noted were Paspalum and Pteridium, but Cynodon, Commelina, Holcus and Cyperus were also common.

In combining the data of the two sites (in TABLE 4) it becomes apparent that Holcus was the species with the highest overall occurrence. It was very invasive at both locations. Paspalum was limited to site 3, where it was the most successful species in terms of short-term establishment. Even though it occurred in the area surrounding plot-set 12, Pteridium was absent on the plot-set itself, but was very aggressive in site 3 in the savanna grassland. Commelina and Cyperus, very frequent on plot-set 13, did not appear in the higher elevation site 1.

The results of koa sucker reproduction and those relating to the clipped half of the 1 x 2 m monthly treated plots will be discussed in another report of this series.

TABLE 4. Species appearances on site 1 and site 3 in two plot-sets each that were cleared every month, from June 1971 to June 1972.

Species	Site 1 (12 a,b,c)	Site 3 (13 a,b,c)	Total (out of 78)
Holcus lanatus	11	17	28
*Acacia koa	9	8	17
Poa pratensis	8	1	9
Geranium carolinianum	11	3	14
Dactylis glomerata	23	--	23
Rumex acetosella	20	--	20
Vicia sativa	6	--	6
Trifolium repens	3	--	3
Geranium disectum	3	--	3
Juncus bufonius	2	--	2
Festuca megalura	1	--	1
Hypochaeris radicata	1	--	1
Oenothera stricta	1	--	1
Paspalum dilatatum	--	28	28
*Pteridium aquilinum var. decompositum	--	26	26
Cynodon dactylon	--	23	23
Commelina diffusa	--	19	19
Cyperus brevifolius	--	14	14
Verbena litoralis	--	9	9
Sonchus oleraceus	--	5	5
Anagallis arvensis	--	1	1
Total species	13	12	21
No. species appearances	99	154	253

* native species

DISCUSSION AND CONCLUSIONS

The questions, do pigs play a major role in turning the native grass communities on Mauna Loa's east flank into communities which are dominated by introduced species, and how much do they change the composition of communities already dominated by exotics can be at least partially answered.

In the mountain parkland the two main competitors are the endemic grass *Deschampsia australis* and the exotic grass *Holcus lanatus*. Obviously, pig digging influences the plant composition of the reoccupying vegetation. Immediately following a disturbance, *Holcus* has the competitive advantage, and as was seen on plots 4 and 11 (site 1) repeated pig scarification can lead to a replacement of *Deschampsia*, and also of another endemic grass *Panicum tenuifolium*.

Of these two native species, *Deschampsia* was the more vigorous and to a certain extent was able to reoccupy the cleared strips. Much more sensitive, *Panicum* was almost eliminated after one clearing action.

It seems possible that *Deschampsia* might be able to become dominant over *Holcus* after a longer period of succession. This possibility is supported by the naturally pig-disturbed plot 1 (site 2) which showed a more advanced stage of succession. On this plot, in an area of older pig digging, *Deschampsia* was relatively more successful than on the plots that were newly dug up for the experiment. *Holcus* appears to establish more readily on open soil, but when it comes into competition with *Deschampsia*, the tall and dense-growing native may eventually become dominant over the exotic. The *Deschampsia* bunch indicated with an asterisk in the middle left of the first map sheet (FIG. 9a) may serve to support the hypothesis that this species may even be able to overgrow some adjacent *Holcus*. In the center of the last map sheet, *Holcus* colonies formed gradually from many small plants which were present at the beginning of the observations. They took advantage of the disturbed soil there and then later replaced a decadent bunch of Deschampsia. This Deschampsia bunch was decadent because it had been partly uprooted by pig-activity, but was left in place.

Weather is important also, as Holcus is favored by wet, cool conditions, and Deschampsia and Panicum are more competitive during the warm dry season.

As shown by plot 4 (site 1), Deschampsia regenerates quite aggressively if the surrounding community contains still a dominant proportion of Deschampsia. Thus, the seed source in the immediate surrounding is an important factor for the continued presence of this endemic grass. In contrast, on the same plot (no. 4), Holcus was an equally aggressive invader, in spite of a relatively low proportion of Holcus in the surrounding vegetation. This shows that Holcus is favored over Deschampsia with progressive soil disturbance.

However, it is also apparent that the native grasses are more successful on the scalped parts of the plots than on the dug parts, where the turned over bunches of grass still support more Holcus. The reason for this could be that the endemic species are better adapted to barren soil, like volcano ash deposits, as opposed to a soil covered with turned over grass bunches resulting from pig disturbance.

As long as the high levels of pig activity continue, this disturbance factor is strong enough to enable Holcus to gradually take over the grassland.

In the lower elevations, where the present grass communities are already totally composed of exotics (except for Pteridium aquilinium var. decompositum) the pig influence is not that alarming. As was pointed out already by Mueller-Dombois and Lamoureux (1967), pig-scarification can even lead to an establishment of trees. Koa suckering can be stimulated by pig scarification (Spatz and Mueller-Dombois 1972a). However, the influence varies between favorable and damaging so that pig-scarification does not add significantly in forest reestablishment.

Strict pig control measures are required in the mountain parkland if the native _Deschampsia-Panicum_ grassland is to be preserved in this ecosystem.

ADKNOWLEDGEMENTS

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APPENDIX 1. Frequency (%) for scalped plot no. 4 in site 1 at six recording dates. Plot established June 8, 1971.

	Sept. 9 71	Nov. 6 71	Dec. 6 71	Feb. 6 72	April 1 72	June 8 72
ENDEMIC						
Deschampsia australis	--	18.70	40.50	67.06	69.03	68.70
Panicum tenuifolium	--	18.49	35.95	26.23	22.06	22.06
Sisyrinchium acre	--	0.63	8.10	22.60	15.97	14.71
INDIGENOUS						
Pteridium aquilinum var. decompositum	0.41	0.63	0.71	--	--	0.21
Carex macloviana	--	--	0.95	4.90	5.67	3.99
INTRODUCED						
Hypochaeris radicata	0.82	11.13	15.95	24.30	27.10	27.10
Holcus lanatus	--	26.05	60.24	80.60	78.99	78.99
Epilobium oligodontum	--	0.63	10.00	37.74	30.46	22.48
Sonchus oleraceus	--	--	0.48	1.66	0.84	0.84
Gnaphalium purpureum	--	--	0.24	0.85	1.05	1.05
Festuca megalura	--	--	8.07	9.06	4.50	3.57
Conyza canadensis	--	--	--	--	--	0.63
Rumex acetosella	--	--	--	0.21	--	--
Styphelia douglasii	--	--	--	--	--	0.21
Centaurium umbellatum	--	--	--	--	1.05	6.30
MISCELLANEOUS						
Grass seedling	--	41.39	7.33	1.71	--	--
Herb seedling	--	30.88	10.71	--	--	--

APPENDIX 2. Frequency (%) for scalped plot no. 11 in site 1 at seven recording dates. Plot established July 23, 1971.

Species	Sept. 9 71	Nov. 4 71	Dec. 6 71	Feb. 6 72	April 1 72	June 8 72	Aug. 11 72
ENDEMIC							
Deschampsia australis	--	0.6	1.4	4.8	3.0	2.8	1.8
Panicum tenuifolium	--	1.2	6.6	5.4	5.2	6.0	3.8
Sisyrinchium acre	--	--	1.80	4.2	4.4	4.6	0.2
INDIGENEOUS							
Pteridium aquilinum var. decompositum	0.2	0.4	0.2	0.2	0.2	0.4	0.2
Carex macloviana	--	0.2	0.8	26.8	32.0	38.0	15.0
INTRODUCED							
Holcus lanatus	0.8	4.4	39.0	75.8	77.0	79.0	66.8
Epilobium oligodontum	0.6	0.6	2.8	50.2	36.6	31.2	15.8
Rumex acetosella	0.6	3.6	4.2	7.2	12.0	19.8	4.4
Hypochaeris radicata	--	9.0	8.6	11.6	12.8	14.0	12.8
Sonchus oleraceus	--	0.4	0.6	0.6	0.6	0.6	0.4
Festuca megalura	--	--	0.4	6.2	4.8	2.6	1.4
Centaurium umbellatum	--	--	--	--	2.6	19.8	10.2
Gnaphalium purpureum	--	--	--	--	0.4	0.6	0.2
MISCELLANEOUS							
Grass seedling	--	27.4	12.0	--	--	--	--
Herb seedling	--	50.4	48.0	0.2	--	--	--

APPENDIX 3. Cover (%) for scalped and dug parts of plot no. 4, site 1 at six recording dates.

Species		Sept. 9 71	Nov. 6 71	Dec. 6 71	Feb. 6 72	April 1 72	June 8 72
ENDEMIC							
Deschampsia australis	S	--	--	0.95	2.86	4.76	3.81
	D	--	1.33	--	--	--	--
Panicum tenuifolium	S	--	0.95	2.86	1.91	0.95	0.95
	D	--	--	--	--	--	--
Sisyrinchium acre	S	--	--	--	--	--	0.95
	D	--	--	--	--	--	--
Total endemic	S	--	0.95	3.81	1.91	5.71	5.71
	D	--	1.33	--	--	--	--
INDIGENOUS							
Pteridium aquilinum var. decompositum	S	0.95	--	0.95	--	--	--
	D	--	--	--	--	--	--
Carex macloviana	S	--	--	--	--	--	--
	D	--	--	--	--	--	--
Total indigenous	S	0.95	--	0.95	--	--	--
	D	--	--	--	--	--	--
INTRODUCED							
Hypochaeris radicata	S	--	0.95	3.81	0.95	10.48	10.48
	D	--	--	--	1.33	4.00	1.33
Holcus lanatus	S	--	--	2.86	13.33	8.57	12.38
	D	--	2.67	--	2.67	6.67	21.33
Epilobium oligodontum	S	--	--	--	--	--	--
	D	--	--	--	--	--	--

APPENDIX 3 Concluded.

Species		Sept. 9 71	Nov. 6 71	Dec. 6 71	Feb. 6 72	April 1 72	June 8 72
Sonchus oleraceus	S	--	--	--	--	--	--
	D	--	--	--	--	--	2.67
Gnaphalium purpureum	S	--	--	--	--	--	--
	D	--	--	--	--	--	--
Festuca megalura	S	--	--	--	--	--	0.95
	D	--	--	--	--	--	--
Conyza canadensis	S	--	--	--	--	--	--
	D	--	--	--	--	--	--
Rumex acetosella	S	--	--	--	--	--	--
	D	--	--	--	--	--	--
Styphelia douglasii	S	--	--	--	--	--	--
	D	--	--	--	--	--	--
Centaurium umbellatum	S	--	--	--	--	--	--
	D	--	--	--	--	--	--
Total introduced	S	--	0.95	6.67	14.28	19.05	23.81
	D	--	2.67	--	4.00	10.67	25.33
MISCELLANEOUS							
Grass seedling	S	--	3.81	--	--	--	--
	D	--	--	--	--	--	--
Herb seedling	S	--	--	--	--	--	--
	D	--	--	--	--	--	--
TOTAL							
Plant Cover	S	--	5.71	11.43	19.05	24.76	29.51
	D	10.00	4.00	--	4.00	10.67	25.33
Litter	S	--	4.76	--	--	--	1.90
	D	89.30	90.67	88.00	86.67	74.67	62.67
Barren	S	99.05	89.52	88.57	80.95	75.24	68.57
	D	10.70	5.33	12.00	9.33	14.67	12.00

S = scalped part of plot 4 (extracted for FIG. 5)
D = dug part of plot 4 (extracted for FIG. 7)

APPENDIX 4. Cover (%) for scalped and dug parts of plot no. 11, site 1 at seven recording dates.

Species		Sept. 9 71	Nov. 4 71	Dec. 6 71	Feb. 6 72	April 1 72	June 8 72	Aug. 11 72
ENDEMIC								
Deschampsia australis	S	--	--	1.33	--	--	--	--
	D	--	--	--	--	--	--	--
Panicum tenuifolium	S	--	--	--	--	--	--	--
	D	--	--	--	--	--	--	--
Sisyrinchium acre	S	--	--	--	--	--	--	--
	D	--	--	--	--	--	--	--
Total endemic	S	--	--	1.33	--	--	--	--
	D	--	--	--	--	--	--	--
INDIGENOUS								
Pteridium aquilinum var. decompositum	S	1.33	1.33	--	--	--	4.00	2.67
	D	--	--	--	--	--	--	--
Carex macloviana	S	--	--	--	--	--	--	--
	D	--	--	--	--	--	--	--
Total indigenous	S	1.33	1.33	--	--	--	4.00	2.67
	D	--	--	--	--	--	--	--
INTRODUCED								
Holcus lanatus	S	--	--	--	6.67	12.00	10.67	20.00
	D	--	1.33	1.33	6.67	14.67	14.67	20.00
Epilobium oligondontum	S	--	--	--	2.67	1.33	1.33	4.00
	D	--	1.33	1.33	--	--	--	2.67
Rumex acetosella	S	--	1.33	--	--	--	--	1.33
	D	--	--	2.67	1.33	--	1.33	1.33
Hypochaeris radicata	S	--	1.33	1.33	4.00	2.67	4.00	4.00
	D	--	--	--	4.00	2.67	5.33	6.67

APPENDIX 4 Concluded.

Species		Sept. 9 71	Nov. 4 71	Dec. 6 71	Feb. 6 72	April 1 72	June 8 72	Aug. 11 72
Sonchus oleraceus	S	--	--	--	--	--	1.33	--
	D	--	--	--	--	--	--	--
Festuca megalura	S	--	--	--	--	--	--	1.33
	D	--	1.33	5.33	8.00	13.33	9.33	22.67
Centaurium umbellatum	S	--	--	--	--	--	--	1.33
	D	--	--	--	--	--	--	--
Gnaphalium purpureum	S	--	--	--	--	--	--	--
	D	--	--	--	--	--	--	--
Total introduced	S	--	2.66	1.33	13.34	16.00	17.33	31.99
	D	--	3.99	10.66	20.00	30.67	30.66	53.34
TOTAL								
Plant cover	S	2.66	3.99	2.66	13.34	16.00	21.33	34.66
	D	--	3.99	10.66	20.00	30.67	30.66	53.34
Litter	S	--	2.67	--	--	--	--	14.67
	D	68.00	72.00	58.67	48.00	44.00	37.33	32.00
Barren	S	98.67	93.33	97.33	86.67	84.00	78.67	50.67
	D	28.00	20.00	26.67	32.00	25.33	30.67	12.00
Rock	S	--	--	--	--	--	--	--
	D	4.00	4.00	4.00	--	--	1.33	2.67

S = scalped part of plot 11 (extracted for FIG. 6)
D = dug part of plot 11 (extracted for FIG. 7)

APPENDIX 5. Frequency (%) and cover (%) data for the 3 x 5 m plot (no. 1) at site 2.

Species		June 7 71	July 9 71	Sept. 9 71	Nov. 8 71	Dec. 20 71	Feb. 6 72	April 1 72	June 7 72
ENDEMIC									
Deschampsia australis	F	19.0	18.7	17.1	18.2	18.3	22.7	23.7	26.8
	C	16.1	--	16.1	16.1	14.5	16.4	15.6	17.8
Panicum tenuifolium	F	12.9	12.8	12.3	14.4	14.3	12.3	10.3	12.0
	C	6.7	--	7.6	9.5	8.3	4.9	3.9	5.3
Total endemic	C	**22.8**	**--**	**23.8**	**25.5**	**22.8**	**21.3**	**19.5**	**23.1**
INDIGENOUS									
Carex macloviana	F	3.2	3.3	4.1	3.9	3.9	3.9	4.1	4.9
	C	2.1	--	3.8	3.3	3.2	3.1	3.1	3.2
Pteridium aquilinum var. decompositum	F	--	--	--	--	--	--	--	--
	C	--	--	--	--	--	--	--	--
Total indigenous	C	**2.1**	**--**	**3.8**	**3.3**	**3.2**	**3.1**	**3.1**	**3.2**
INTRODUCED									
Holcus lanatus	F	21.1	20.6	18.8	25.2	29.5	34.0	37.9	40.3
	C	11.0	--	10.5	16.9	17.3	17.1	21.1	21.4
Rumex acetosella	F	16.2	15.5	13.5	17.9	22.1	21.9	17.6	22.1
	C	--	--	--	--	--	--	--	--
Epilobium oligodontum	F	0.9	1.0	1.7	1.7	2.8	4.0	5.5	6.9
	C	0.4	--	0.4	0.9	1.1	2.5	2.3	2.2
Hypochaeris radicata	F	0.2	0.2	0.5	0.9	1.3	1.3	1.5	2.8
	C	--	--	--	--	--	--	--	--
Bromus rigidus	F	0.4	0.3	0.2	--	--	--	--	2.1
	C	--	--	--	--	--	--	--	--

APPENDIX 5 Concluded.

Species		June 7 71	July 9 71	Sept. 9 71	Nov. 8 71	Dec. 20 71	Feb. 6 72	April 1 72	June 7 72
Senecio sylvaticus	F	0.8	--	0.6	0.7	0.2	1.9	2.1	2.7
	C	--	--	--	--	--	--	--	--
Conyza canadensis	F	--	--	--	0.1	0.5	--	--	--
	C	--	--	--	--	--	--	--	--
Cirsium volgare	F	--	--	--	0.2	0.3	0.4	0.3	0.4
	C	--	--	--	--	--	--	--	--
Total introduced	C	11.4	--	10.9	17.9	18.4	19.5	23.4	23.6
MISCELLANEOUS									
Grass seedling	F	--	--	--	--	4.1	--	--	--
	C	--	--	--	--	--	--	--	--
Herb seedling	F	--	--	--	34.0	0.7	--	--	--
	C	--	--	--	--	--	--	--	--
Total miscellaneous	C	--	--	--	--	--	--	--	--
TOTAL									
Plant cover	C	--	36.2	38.7	46.7	44.4	43.9	45.9	49.9

F = frequency data (extracted for FIG. 8)
C = cover data (extracted from map-sheets FIG. 9 a-g)

APPENDIX 6. Cover (%) measured by line-intercept method along five transects at 10 recording dates at site 2.

Species	June 7 71	Aug. 7 71	Sept. 9 71	Oct. 10 71	Nov. 6 71	Dec. 7 71	Feb. 6 72	Mar. 4 72	June 7 72	July 6 72
					TRANSECT 2					
ENDEMIC										
Deschampsia australis	--	--	--	--	0.2	0.7	1.0	4.5	6.3	12.0
Panicum tenuifolium	--	--	1.7	4.2	2.5	1.7	5.0	1.2	--	--
Total endemic plants	--	--	1.7	4.2	2.7	2.4	6.0	5.7	6.3	12.0
INTRODUCED										
Holcus lanatus	6.8	8.3	8.3	9.2	10.5	7.2	7.7	18.3	24.3	26.0
Rumex acetosella	0.5	0.5	0.3	0.5	1.7	1.5	0.2	1.5	2.5	1.0
Epilobium oligodontum	3.5	3.3	3.3	5.0	3.5	2.2	6.7	4.0	4.0	3.3
Hypochaeris radicata	--	--	--	--	0.2	--	0.2	--	--	--
Senecio sylvaticus	--	--	--	--	--	--	--	--	0.7	--
Total introduced	10.8	12.1	11.9	14.7	15.9	10.9	14.8	23.8	31.5	30.3
Rock	11.0	8.3	16.0	12.7	7.5	10.3	12.5	18.3	15.7	19.2
					TRANSECT 3					
ENDEMIC										
Deschampsia australis	--	--	--	--	3.0	3.0	2.3	2.0	4.6	4.0
Panicum tenuifolium	--	1.0	1.4	1.4	2.1	3.0	1.0	1.6	1.6	2.0
Total endemic plants	--	1.0	1.4	1.4	5.1	6.0	3.3	3.6	6.2	6.0
INTRODUCED										
Holcus lanatus	14.9	10.5	13.0	14.6	17.1	20.0	13.0	23.1	37.0	32.9
Rumex acetosella	0.3	0.4	--	--	--	--	--	--	--	0.4
Hypochaeris radicata	0.1	2.0	2.5	3.3	5.0	4.0	3.0	--	1.0	0.4
Senecio sylvaticus	1.3	1.5	1.6	1.4	1.7	--	0.7	--	--	--
Bromus rigidus	--	--	--	--	--	--	--	--	1.6	--
Cirsium vulgare	--	--	--	--	--	--	--	--	0.1	1.0
Total introduced plants	16.6	14.4	17.1	19.3	23.8	24.0	16.7	23.1	39.7	34.7
Rock	6.3	5.3	5.0	5.7	5.7	6.3	2.0	2.3	3.0	1.6

APPENDIX 6 Continued.

Species	July 10 71	Sept. 9 71	Oct. 10 71	Nov. 6 71	Dec. 7 71	Feb. 6 72	Apr. 1 72	July 6 72
ENDEMIC				TRANSECT 6				
Deschampsia australis	8.0	3.5	1.6	3.0	1.2	2.5	2.1	3.1
Panicum tenuifolium	0.1	0.1	0.1	0.1	--	0.1	0.1	1.0
Acacia koa var. hawaiiensis	--	--	--	--	--	--	0.1	--
Total endemic plants	8.1	3.6	1.7	3.1	1.2	2.6	2.3	4.1
INDIGENOUS								
Pteridium aquilinum var. decompositum	5.3	3.1	1.6	4.6	2.4	--	1.0	0.3
Total indigenous plants	5.3	3.1	1.6	4.6	2.4	--	1.0	0.3
INTRODUCED								
Holcus lanatus	5.0	5.0	5.5	7.0	4.2	3.7	6.5	5.5
Hypochaeris radicata	5.5	--	4.6	2.5	2.6	2.6	4.0	3.2
Senecio sylvatica	--	--	--	--	--	--	0.2	--
Cirsium vulgare	--	--	--	--	--	0.6	0.1	--
Total introduced	10.5	5.0	10.1	9.5	6.8	6.9	10.8	8.7
Rock	9.5	--	2.3	1.0	--	--	--	--
ENDEMIC				TRANSECT 7				
Deschampsia australis	7.3	6.0	7.5	7.5	7.0	8.3	7.8	11.0
Panicum tenuifolium	5.2	8.2	9.2	11.5	6.3	3.3	2.1	2.4
Sisyrinchium acre	--	1.0	--	--	--	--	--	--
Total endemic plants	12.5	15.2	16.7	19.0	13.3	11.6	9.9	13.4

APPENDIX 6 Concluded.

Species	July 10 71	Sept. 9 71	Oct. 10 71	Nov. 6 71	Dec. 7 71	Feb. 6 72	Apr. 1 72	July 6 72
INTRODUCED								
Holcus lanatus	16.0	13.5	17.1	22.7	24.2	23.8	24.4	30.6
Rumex acetosella	0.2	0.7	0.8	1.2	1.6	0.2	0.4	0.5
Hypochaeris radicata	2.0	--	4.0	4.0	3.0	3.8	2.6	4.5
Senecio sylvaticus	--	--	1.0	1.0	--	--	--	0.5
Cirsium vulgare	4.7	3.0	7.2	3.2	0.1	1.5	2.5	1.6
Verbena litoralis	--	--	0.6	0.6	0.2	--	--	0.2
Total introduced plants	22.9	17.2	30.7	32.7	29.1	29.3	29.9	37.9
Rock	7.5	--	10.0	9.0	9.5	5.2	9.0	7.5
Litter	--	--	--	3.5	--	--	--	--
				TRANSECT 8				
ENDEMIC								
Deschampsia australis	--	--	--	--	--	--	0.9	0.7
Panicum tenuifolium	0.5	3.2	2.0	2.7	0.2	--	0.5	2.3
Total endemic plants	0.5	3.2	2.0	2.7	0.2	--	1.4	3.0
INTRODUCED								
Holcus lanatus	5.9	9.0	13.5	15.8	20.6	15.0	23.9	28.9
Rumex acetosella	--	0.8	0.4	0.5	--	0.7	0.5	0.2
Hypochaeris radicata	1.4	--	1.0	--	1.2	--	--	0.9
Senecio sylvaticus	--	--	--	--	--	--	0.5	1.2
Cirsium vulgare	5.5	3.9	6.2	2.0	0.6	0.2	1.7	2.0
Verbena litoralis	0.1	0.8	0.5	0.2	0.5	0.9	2.7	0.1
Conyza sp. canadensis	--	--	--	--	--	--	--	0.3
Total introduced plants	12.9	14.5	21.6	18.5	22.9	16.8	29.3	33.6
Rock	10.0	--	5.6	5.7	5.4	6.7	9.7	1.2

APPENDIX 7. Frequency (%) and cover (%) data for the artificially disturbed plot 5 at site 2.

Species		Sept. 9 71	Nov. 6 71	Dec. 7 71	Feb. 6 72	April 1 72	July 6 72
ENDEMIC							
Panicum tenuifolium	F	--	--	4.6	11.0	10.0	7.0
	S	--	--	--	--	--	--
	D	--	--	--	--	--	--
Deschampsia australis	F	--	0.8	5.0	14.6	22.0	19.0
	S	--	--	1.3	--	--	1.3
	D	--	--	58.7	--	--	--
Sisyrinchium acre	F	--	--	7.0	20.2	17.0	15.8
	S	--	--	--	--	--	--
	D	--	--	--	--	--	--
Acacia koa var. hawaiiensis	F	--	--	--	--	--	0.2
	S	--	--	--	--	--	--
	D	--	--	--	--	--	--
Total endemic	S	--	--	1.3	--	--	1.3
	D	--	--	58.7	--	--	--
INDIGENOUS							
Carex macloviana	F	--	--	0.4	7.2	12.4	9.4
	S	--	--	--	--	--	--
	D	--	--	--	--	--	--
Total indigenous	S	--	--	--	--	--	--
	D	--	--	--	--	--	--
EXOTIC							
Hypochaeris radicata	F	6.0	19.4	22.6	27.0	28.0	30.2
	S	4.0	4.0	6.7	8.0	9.3	9.3
	D	--	1.3	--	--	1.3	1.3

APPENDIX 7 Continued.

Species		Sept. 9 71	Nov. 6 71	Dec. 7 71	Feb. 6 72	April 1 72	July 6 72
Holcus lanatus	F	1.6	13.4	75.8	92.6	91.4	85.2
	S	--	1.3	--	6.7	8.0	17.3
	D	--	--	--	1.3	--	1.3
Rumex acetosella	F	1.6	9.6	6.2	4.4	4.2	1.8
	S	--	--	--	1.3	--	--
	D	--	--	--	2.7	--	--
Epilobium oligodontum	F	0.2	--	2.0	6.4	5.0	2.0
	S	--	--	--	--	2.7	--
	D	--	--	--	--	--	--
Festuca megalura	F	--	--	--	4.8	--	0.6
	S	--	--	--	--	--	--
	D	--	--	--	--	--	--
Cynodon dactylon	F	--	--	--	0.2	--	--
	S	--	--	--	--	--	--
	D	--	--	--	--	--	--
Centaureum umbellatum	F	--	--	--	--	--	4.6
	S	--	--	--	--	--	--
	D	--	--	--	--	--	--
Conyza canadensis	F	--	--	--	0.2	--	0.2
	S	--	--	--	--	--	--
	D	--	--	--	--	--	--
Gnaphalium purpureum	F	--	--	--	--	--	0.2
	S	--	--	--	--	--	--
	D	--	--	--	--	--	--
Senecio sylvaticus	F	--	--	--	--	0.8	0.2
	S	--	--	--	--	--	--
	D	--	--	--	--	--	--
Total exotic	S	4.0	5.3	6.7	16.0	20.0	26.6
	D	--	1.3	--	4.0	1.3	2.6

APPENDIX 7 Concluded.

Species		Sept. 9 71	Nov. 6 71	Dec. 7 71	Feb. 6 72	April 1 72	July 6 72
MISCELLANEOUS							
Grass seedling	F	--	31.8	2.1	--	--	--
	S	--	1.3	--	--	--	--
	D	--	--	--	--	--	--
Herb seedling	F	--	4.8	4.6	--	--	--
	S	--	--	--	--	--	--
	D	--	--	--	--	--	--
TOTAL							
Plant Cover	S	4.0	5.3	8.0	16.0	20.0	28.0
	D	--	1.3	58.7	4.0	1.3	2.7
Litter	S	--	1.3	--	--	--	1.3
	D	58.7	61.3	--	49.3	40.0	45.3
Barren	S	96.0	92.0	92.0	84.0	80.0	70.7
	D	41.3	37.3	41.3	46.7	58.7	52.0

F = frequency % on scalped plot half (extracted for FIG. 11)
S = cover % on scalped plot half (extracted for FIG. 12)
D = cover % on dug plot half

APPENDIX 8. Frequency (%) and cover (%) data for artificially disturbed plot 9 at site 3. Established July 12, 1971.

Species		Aug. 13 71	Sept. 11 71	Oct. 10 71	Nov. 8 71	Dec. 7 71	Feb. 4 72	Mar. 9 72
Cynodon dactylon	F	23.8	28.0	54.0	discontinued			
	S	0.1	0.3	0.3	0.4	0.4	0.2	0.1
	D	0.04	0.2	0.1	0.2	0.2	0.2	0.1
Pteridium aquilinum var. decompositum	F	4.2	10.6	14.0	discontinued			
	S	--	0.2	0.4	0.3	0.3	0.01	0.01
	D	0.01	0.04	0.2	0.2	0.1	0.01	--
Commelina diffusa	F	9.0	6.6	12.0	discontinued			
	S	--	0.1	0.1	0.1	0.1	0.04	0.1
	D	0.3	0.4	0.5	0.7	0.7	0.7	0.7
Lythrum maritimum	F	0.6	0.4	--	discontinued			
	S	--	--	--	--	--	--	--
	D	--	--	--	--	--	--	--
Seedling	F	2.0	0.8	22.8	discontinued			
	S	--	--	--	--	--	--	--
	D	--	--	--	--	--	--	--
Cirsium vulgare	F	--	0.2	4.0	discontinued			
	S	--	--	--	--	0.01	0.1	0.04
	D	--	--	--	--	--	--	--
Holcus lanatus	F	--	0.4	--	discontinued			
	S	--	0.01	0.01	--	0.1	0.3	0.5
	D	--	--	0.01	--	--	0.04	0.1
Geranium carolinianum var. australe	F	--	--	18.6	discontinued			
	S	--	--	--	0.01	0.03	0.2	0.2
	D	--	0.02	0.01	--	0.01	0.1	0.1
Ipomoea indica	F	--	--	0.2	discontinued			
	S	--	--	0.01	--	0.01	--	0.03
	D	--	--	--	--	--	--	--
Verbena litoralis	F	--	--	0.2	discontinued			
	S	--	--	--	--	--	0.03	0.04
	D	--	--	--	--	--	--	--

APPENDIX 8 Concluded.

Species		Aug. 13 71	Sept. 11 71	Oct. 10 71	Nov. 8 71	Dec. 7 71	Feb. 4 72	Mar. 9 72
Oxalis corniculata	F	--	--	0.2	discontinued			
	S	--	--	--	--	--	--	--
	D	--	--	--	--	--	--	--
Sonchus oleraceus	F	--	--	0.2	discontinued			
	S	--	--	--	--	--	--	--
	D	--	--	0.01	--	--	--	--
Modiola caroliniana	F	--	--	--	discontinued			
	S	--	--	--	0.01	0.03	--	--
	D	--	--	--	--	--	--	--
Paspalum dilatatum	F	--	--	--	discontinued			
	S	--	--	--	--	--	0.1	--
	D	--	--	--	--	--	0.01	0.04
Solanum nigram	F	--	--	--	discontinued			
	S	--	--	--	--	0.01	0.01	--
	D	--	--	--	--	--	--	--
Cyperus brevifolius	F	--	--	--	discontinued			
	S	--	--	--	--	--	--	--
	D	--	--	--	--	--	0.01	--
TOTAL: Plant Cover	S	0.1	0.5	0.8	0.9	0.9	1.0	1.0
	D	0.4	0.6	0.8	1.0	1.0	1.1	1.0
Litter	S	0.1	0.1	0.1	0.1	0.04	--	--
	D	0.4	0.3	0.1	0.03	--	--	--
Barren	S	0.8	0.4	0.1	0.03	0.01	--	--
	D	0.2	0.1	0.1	0.01	0.01	--	--

F = frequency % on scalped plot half (extracted for FIG. 13)
S = cover % on sclaped plot half (extracted for FIG. 14)
D = cover % on dug plot half (extracted for FIG. 15)

APPENDIX 9. Frequency (%) and cover (%) data for artificially disturbed plot 10 at site 3. Established July 12, 1971.

Species		Aug. 13 71	Sept. 9 71	Oct. 11 71	Nov. 8 71	Dec. 7 71	Feb. 4 72	Mar. 9 72
Cynodon dactylon	F	3.2	5.0	13.0	discontinued			
	S	1.3	5.3	9.3	12.0	13.3	10.7	6.7
	D	3.0	1.3	5.3	4.0	8.0	4.0	1.3
Pteridium aquilinum var. decompositum	F	1.8	5.8	12.4	discontinued			
	S	--	10.7	28.0	18.7	25.3	9.3	1.3
	D	--	--	5.3	8.0	16.0	6.7	1.3
Commelina diffusa	F	3.6	2.0	5.2	discontinued			
	S	--	1.3	--	6.7	13.3	21.3	29.3
	D	--	12.0	26.7	41.3	45.3	45.3	37.3
Paspalum dilatatum	F	0.8	1.2	2.8	discontinued			
	S	--	--	5.3	8.0	10.7	12.0	5.3
	D	13.0	8.0	22.7	20.0	9.3	13.3	16.0
Lythrum maritimum	F	0.2	--	--	discontinued			
	S	--	--	--	--	--	--	1.3
	D	--	--	--	--	1.3	--	1.3
Holcus lanatus	F	0.6	--	--	discontinued			
	S	--	--	--	--	2.7	17.3	32.0
	D	1.0	5.3	1.3	2.7	2.7	16.0	22.7
Seedling	F	0.6	--	19.2	discontinued			
	S	--	--	--	--	--	--	--
	D	--	--	--	--	--	--	--
Geranium carolinianum var. australe	F	--	--	3.0	discontinued			
	S	--	--	1.3	--	1.3	5.3	10.7
	D	--	--	--	--	--	--	--
Acacia koa var. hawaiiensis	F	--	--	0.2	discontinued			
	S	--	--	--	--	1.3	2.7	1.3
	D	--	--	--	--	--	--	--

APPENDIX 9   Concluded.

Species		Aug. 13 71	Sept. 9 71	Oct. 11 71	Nov. 8 71	Dec. 7 71	Feb. 4 72	Mar. 9 72
Oxalis corniculata	F	--	--	0.4	discontinued			
	S	--	--	--	--	--	--	--
	D	--	--	--	--	--	--	--
Cyperus brevifolius	F	--	--	--	discontinued			
	S	--	--	--	--	--	2.7	1.3
	D	3.0	8.0	6.7	12.0	8.0	14.7	18.7
Grass seedling	F	--	--	--	discontinued			
	S	--	--	--	1.3	1.3	--	--
	D	--	--	--	--	--	--	--
Ipomoea indica	F	--	--	--	discontinued			
	S	--	--	1.3	1.3	--	1.3	2.7
	D	--	--	--	--	--	--	--
Sonchus oleraceus	F	--	--	--	discontinued			
	S	--	--	--	--	--	--	--
	D	--	--	--	--	--	--	1.3
Verbena litoralis	F	--	--	--	discontinued			
	S	--	--	--	--	--	--	1.3
	D	--	--	--	--	--	--	--
TOTAL: Plant Cover	S	1.3	17.3	45.3	48.0	69.3	82.6	93.3
	D	20.0	34.7	68.0	88.0	90.7	100.0	100.0
Litter	S	9.3	1.3	1.3	4.0	6.7	5.3	1.3
	D	60.0	40.0	20.0	8.0	2.7	--	--
Barren	S	89.3	81.3	53.3	48.0	24.0	12.0	5.3
	D	20.0	25.3	12.0	4.0	6.7	--	--

F = frequency % on scalped plot half (extracted for FIG. 13)
S = cover % on sclaped plot half (extracted for FIG. 14)
D = cover % on dug plot half (extracted for FIG. 15)

APPENDIX 10. Species reappearance on three plots (12 a, b, c) cleared every month in site 1, from June 1971 to June 1972. First clearing May 1971.

		Months in 1971							Months in 1972						No.
Species	Plot	6	7	8	9	10	11	12	1	2	3	4	5	6	times
Rumex acetosella	a	-	-	-	+	+	+	+	+	+	+	+	+	+	10
	b	+	-	-	+	-	-	-	-	-	+	+	+	+	6
	c	-	-	-	+	-	-	-	-	-	-	+	+	+	4
Trifolium repens	a	-	-	-	-	+	+	-	+	-	-	-	-	-	3
	b	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	c	-	-	-	-	-	-	-	-	-	-	-	-	-	0
*Geranium carolinianum	a	-	-	-	-	+	+	+	+	+	+	-	-	+	7
	b	-	-	-	-	-	-	-	+	-	-	-	-	-	1
	c	-	-	-	-	-	-	-	+	+	-	+	-	-	3
Dactylis glomerata	a	-	-	-	-	+	+	+	+	+	-	+	+	-	7
	b	-	-	-	-	+	+	+	-	+	+	+	+	+	8
	c	-	-	-	-	+	+	+	-	+	+	+	+	+	8
*Acacia koa	a	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	b	-	-	-	-	+	+	+	-	+	+	-	-	-	5
	c	-	-	-	-	-	+	+	-	+	+	-	-	-	4
*Holcus lanatus	a	-	-	-	-	-	-	+	+	+	+	-	-	-	4
	b	-	-	-	-	-	+	-	-	-	-	+	-	+	3
	c	-	-	-	-	-	+	-	-	+	+	-	+	-	4
Vicia sativa	a	-	-	-	-	-	-	+	+	+	+	+	-	-	5
	b	-	-	-	-	-	-	-	-	-	-	-	-	+	1
	c	-	-	-	-	-	-	-	-	-	-	-	-	-	0
*Poa pratensis	a	-	-	-	-	-	-	-	+	+	+	+	+	-	5
	b	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	c	-	-	-	-	-	-	-	-	+	+	+	-	-	3
Oenathera stricta	a	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	b	-	-	-	-	-	-	-	-	-	+	-	-	-	1
	c	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Festuca megalura	a	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	b	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	c	-	-	-	-	-	-	-	-	-	+	-	-	-	1
Geranium disectum	a	-	-	-	-	-	-	-	-	+	-	+	-	-	2
	b	-	-	-	-	-	-	-	-	-	-	+	-	-	1
	c	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Hypochaeris radicata	a	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	b	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	c	-	-	-	-	-	-	-	-	-	-	+	-	-	1
Juncus bufonius	a	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	b	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	c	-	-	-	-	-	-	-	-	-	-	-	+	+	2
No. of species		1	0	0	3	7	10	9	9	14	14	14	9	9	

*species common to sites 1 and 3

APPENDIX 11. Species reappearnce on three plots (13 a, b, c) cleared every month in site 3, from June 1971 to June 1972. First clearing May 1971.

Species	Plot	Months in 1971							Months in 1972						No.
		6	7	8	9	10	11	12	1	2	3	4	5	6	times
Cynodon dactylon	a	+	+	+	+	+	-	-	-	+	+	+	-	-	8
	b	+	+	-	-	+	-	-	-	-	-	-	-	+	4
	c	+	+	+	+	+	+	-	+	+	+	+	+	-	11
Commelina diffusa	a	+	-	-	-	-	-	+	+	+	+	+	+	+	8
	b	+	-	-	-	-	-	-	+	+	+	+	+	+	7
	c	+	-	-	-	-	-	+	-	-	-	+	+	-	4
Paspalum dilatatum	a	+	+	+	+	+	+	-	-	+	+	+	+	+	11
	b	+	-	+	-	+	+	+	+	+	+	+	+	+	11
	c	+	-	-	-	-	+	+	-	+	+	+	-	-	6
Pteridium aquilinum var. decompositum	a	+	-	-	+	-	+	-	+	+	-	+	-	+	7
	b	+	+	+	-	+	+	+	+	+	-	+	+	+	11
	c	+	+	+	+	+	-	-	+	-	-	-	+	+	8
Cyperus brevifolius	a	+	-	+	-	-	-	-	+	+	+	-	+	-	6
	b	+	-	-	-	-	-	-	-	-	-	-	-	+	2
	c	+	-	-	-	-	-	-	+	-	+	+	+	+	6
*Holcus lanatus	a	-	-	-	-	-	-	+	+	+	+	+	+	-	6
	b	-	+	-	-	-	+	-	+	+	+	+	+	-	7
	c	-	-	-	-	-	-	-	+	+	+	-	+	-	4
*Poa pratensis	a	-	-	+	-	-	-	-	-	-	-	-	-	-	1
	b	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	c	-	-	-	-	-	-	-	-	-	-	-	-	-	0
*Acacia koa	a	-	-	-	-	+	+	+	+	+	+	+	+	-	8
	b	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	c	-	-	-	-	-	-	-	-	-	-	-	-	-	0
Sonchus oleraceus	a	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	b	-	-	-	-	-	-	-	+	+	+	-	-	-	3
	c	-	-	-	-	-	+	-	+	-	-	-	-	-	2
Verbena litoralis	a	-	-	-	-	-	-	-	-	+	-	-	-	-	1
	b	-	-	-	-	-	-	+	+	+	+	-	-	+	5
	c	-	-	-	-	-	-	-	+	+	+	-	-	-	3
Anagallis arvensis	a	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	b	-	-	-	-	-	-	-	+	-	-	-	-	-	1
	c	-	-	-	-	-	-	-	-	-	-	-	-	-	0
*Geranium carolinianum	a	-	-	-	-	-	-	-	-	-	-	-	-	-	0
	b	-	-	-	-	-	-	+	-	-	-	-	+	+	3
	c	-	-	-	-	-	-	-	-	-	-	-	-	-	0
No. of species		15	7	8	5	8	9	9	18	18	16	14	15	12	

*species common to sites 1 and 3

APPENDIX 12. Checklist of species by families. Citation of names follows Fosberg (1966, 1972). X = exotic species, E = endemic species, I = indigenous species.

POLYPODIACEAE

E *Pteridium aquilinum* var. *decompositum* (Gaud.) Tryon

GRAMINEAE

X *Bromus rigidus* Roth
X *Cynodon dactylon* (L.) Pers
X *Dactylis glomerata* L.
E *Deschampsia australis* Nees & Steud.
X *Festuca megalura* Nutt.
X *Holcus lanatus* L.
E *Panicum tenuifolium* H. & A.
X *Paspalum dilatatum* Poir.
X *Poa pratensis* L.

CYPERACEAE

I *Carex macloviana* D'urv.
X *Cyperus brevifolius* (Rottb) Hassk

COMMELINACEAE

X *Commelina diffusa* Brum. Filius.

JUNCACEAE

X *Juncus bufanius* L.

IRIDACEAE

E *Sisyrinchium acre* Mann

POLYGONACEAE

X *Rumex acetosella* L.

LEGUMINOSAE

E *Acacia koa* var. *hawaiiensis* Rock
X *Trifolium repens* L.
X *Vicia sativa* L.

GERANIACEAE

X *Geranium carolinianum* var. *australe* (Benth) Fosb.
X *Geranium dissectum* L.

OXALIDACEAE

X *Oxalis corniculata* (sensu lato) L.

MALVACEAE

X Modiola caroliniana (L.) G. Don

LYTHRACEAE

X Lythrum maritimum Hbk.

ONAGRACEAE

X Epilobium oligodontum Haussk
X Oenothera stricta Ledeb

EPACRIDACEAE

E Styphelia douglasii (Gray) F. Muell.

PRIMULACEAE

X Anagallis arvensis L.

GENTIANACEAE

X Centaurium umbellatum Gilib.

CONVOLVULACEAE

I Ipomoea indica (Burm) Merr.

VERBENACEAE

X Verbena litoralis Hbk.

SOLANACEAE

X Solanum nigrum L.

COMPOSITAE

X Cirsium vulgare (Savi) Airy-Shaw
X Conyza canadensis (L.) Cronq.
X Gnaphalium purpureum L.
X Hypochaeris radicata L.
X Sonchus oleraceus L.
X Senecio sylvaticus L.