SPATIAL VARIATION AND VEGETATION DYNAMICS IN THE COASTAL LOWLAND ECOSYSTEM, HAWAII VOLCANOES NATIONAL PARK

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INTRODUCTION

The coastal lowland is one of six major ecosystems in Hawaii Volcanoes National Park (HAVO). Its boundaries are defined by the coastline on the south side of the Park, the western Park boundary at the Great Crack (near the Kona Highway), the eastern Park boundary near Kalapana (and Queen's Bath), and inland by the 1000 feet (305 m) contour line. The inland topographic boundary corresponds to an air temperature isohyet of 22°C. Defined in this way, the lowland area lies in a warm tropical zone, which here has an altitudinal variation in annual mean temperature from about 24°C (at sea level) to 22°C (at 305 m). The western and eastern Park boundaries moreover coincide approximately with the rainfall isohyets of 1250 mm and 1500 mm, respectively. They encompass an area with a Mediterranean rainfall pattern, i.e., wet season in the winter months and a distinct drought season in the summer months (mid-May through September).

Among the six major Park ecosystems, the coastal lowland ecosystem is unique in the degree of past human use and destruction by feral animals, particularly the feral goat (*Capra hircus* L.). Today it is the ecosystem with the greatest number of exotic plants, particularly in terms of areal coverage.

The question of restoration of this ecosystem has always been an important concern of Park management. Control was exercised for many years through annual goat drives, eventually culminating in 1972 to 1974 in a near-elimination of goats from the area by means of a systematic fence-building project. Control of exotic plants has been another concern, then planting of native species, and very recently a formal prescription was given for restoring three restricted areas at the coast, Halapē, Keauhou Landing, and 'Āpua Point (Smith 1980).

In 1964/1965 I was involved in mapping the Park's vegetation for the preparation of an atlas (Doty & Mueller-Dombois 1966). For map interpretation I drew five topographic vegetation profiles, four of which extended into the coastal lowland. On this basis I recognized six major structural (or physiognomic) vegetation types: woodland, shrubland, grassland with low shrubs (chamaephytes), grassland, very sparse grass cover, and very sparse tree cover.

The underlying causal factors for this vegetation pattern were considered to be the rainfall gradient and dry-season effects, and the spatial variations in soil and substrate. The other causal factors considered were the past human use by the Hawaiian colonizers and the subsequent intensification of herbivory by the feral goats. For investigating the influence of the goats I suggested the construction of experimental exclosures.

SUCCESSION IN EXPERIMENTAL EXCLOSURES

One exclosure was established at Kūkalau'ula in 1968, two others on Pu'u Kaone in 1971. Vegetation development in these exclosures has been monitored since summer 1971, and two papers (Mueller-Dombois & Spatz 1975; Mueller-Dombois 1979) have given the results through 1976. A new paper gives the data through 1980 (Mueller-Dombois 1981). I will briefly review the development in and around these exclosures.

The Kūkalau'ula Site

This site was formerly mapped as a mixture of sparse annual grassland with the pantropical annual *Eragrostis tenella* (L.) Beauv. ex R. & S. as the dominant species. *Heteropogon contortus* (L.) Beauv. ex R. & S., the Hawaiian pili grass, formed a scattered component in the cracks of pāhoehoe lava. There were also denser patches of the perennial short-grass *Chrysopogon aciculatus* (Retz.) Trin. and the carpet-forming Bermuda grass, *Cynodon dactylon* (L.) Pers. The latter two grasses provided for the dominant cover on the fine ash soil which occurred as a discontinuous, shallow layer overlying the lava. There was also a high percentage cover of rock outcrop. In 1971, two years after the exclosure was built, *Chrysopogon* and *Eragrostis* occurred only sporadically in the exclosure, while particularly *Eragrostis* was still dominant outside with about 30% surface cover. Another dominant surface cover outside was rock (15%), barren soil (10%), and litter (15%), which together occupied about 40% of the area. Bermuda grass also occupied about 30% cover outside but still also over 20% inside the exclosure.

A striking contrast was the presence of four bunch grasses--*Andropogon glomeratus* (Walt.) BSP., *Hyparrhenia rufa* (Nees) Stapf in Prain, *Sporobolus africanus* (Poir.) Robyns & Tournay, and *Tricholaena* (= *Rhynchelytrum*) *repens* (Willd.) Hitch.--which occurred inside but not outside the exclosure. A similar difference was shown by three low-shrub (chamaephyte) species--*Cassia leschenaultiana* DC., *Indigofera suffruticosa* Mill., and *Waltheria indica* L. (= *americana* L.)--which outside the exclosure occurred only as sporadic seedlings.

The most surprising event at Kūkalau'ula was the early appearance of the endemic legume vine, Canavalia kauensis St. John, which in four years attained its maximum cover of 51.1% in the 700 m exclosure. After four years, in spring of 1972, Canavalia declined inside the exclosure. In 1974, its cover was down to 11%. In 1977, cover increased again to 25%, then in spring of 1980 it was down again to 4.2%. However, Canavalia has not become unimportant. The vine extended its area-coverage in 1974 by climbing over the exclosure fence. In 1976, it already had 1% cover outside and in spring of 1980, this 1% cover had increased to nearly 25% cover.

However, Canavalia is not spreading uniformly over the area. Its distribution is patchy. It grows outward in certain directions from few established seedlings which, when mature, may cover areas of about 100 m in size. These patches of individuals then die back after a certain number of years (ranging from 3-5 years) and new patches develop adjacent to the old ones.

The Pu'u Kaone Site

This site was mapped in 1965 as closed Chrysopogon-Cynodon grass cover. At that time the Pu'u Kaone grassland was also a typical short-grass cover resembling an overgrazed pasture. The soil is deep, fine sandy loam without any significant rock outcrop.

Two exclosures were built in 1971 on Pu'u Kaone, a narrow, long exclosure of 10 x 100 m size similar to the one at Kūkalau'ula, and a larger, square exclosure of 100 x 100 m (1 ha) size. The 10 x 100 m exclosure was monitored for both inside and outside changes, the other only for inside changes.

Goat browsing pressure was drastically controlled at Pu'u Kaone in 1972 resulting in equal development of the vegetation both inside and outside the exclosures. Within four years, Chrysopogon aciculatus was reduced from a dominance of 3% to sporadic traces. Bermuda grass also declined gradually, while the bunch grasses Hyparrhenia rufa and Tricholaena (= Rhynchelytrum) repens increased each from less than 1% to about 25% cover in five years. The thick-mat forming molassesgrass, Melinis minutiflora Beauv., became the third dominant grass with likewise about 25% cover in five years. Other important cover contributors were the two chamaephytes, Cassia leschenaultiana and Indigofera suffruticosa. The latter increased from less than 1% to 16% in five years.

The large exclosure showed similar changes, notably a decrease in Bermuda grass and an increase in molassesgrass. Among woody plants, koa-haole (Leucaena leucocephala (Lam.) de Wit) played an important role and showed an increase from 1% to 16% despite repeated control efforts by the National Park Service (NPS) to reduce its spread.

The endemic legume vine, *Canavalia kauensis*, did not come up in any of the exclosures at Pu'u Kaone. However, two *Canavalia* patches developed in the Kaone area, one mauka of the large (1 ha) exclosure and another in a draw, about 200 m NE of the other exclosure. In addition, another apparently indigenous vine, the morning glory (*Ipomoea congesta* R. Br.), formed large patches in various areas over the dense tall-grass-chamaephyte cover.

Thus, within a few years in both the Kūkalau'ula and Pu'u Kaone areas, the vegetation had developed from a low-growing short-grass cover to a tall-grass-chamaephyte cover with patches of indigenous vines. The succession appeared to be more or less arrested in this life-form combination in 1976 (Mueller-Dombois 1979).

VEGETATION DEVELOPMENT ELSEWHERE

It would be misleading to generalize from these two study areas a similar and uniform vegetation development for the whole coastal lowland ecosystem.

The map (Fig. 1) will give an indication of the spatial heterogeneity and complexity that occurs throughout the coastal lowland.

Habitat Types

First of all, there are basic habitat variations which are the result of important substrate differences and additional differences in the spatial distribution of rainfall.

In terms of substrate variations, one can recognize four important types as follows:

1. Palis with 'a'ā rock-rubble, including other 'a'ā flows. These occur throughout the area from east to west.

2. Pāhoehoe lava on level or somewhat sloping ground. This substrate or landform type is the most dominant in the area and includes at least four significant variations:

   (a) very recent: -- flows that descended into the lowland from Mauna Ulu between 1969 and 1974. These cover now a significant portion of the eastern half of the coastal lowland. They extend in width from west of 'Āpua Point to Ka'ena Point;

(b) highly permeable but not very recent: -- flows with similarly low water retention as (a) but not so recent in origin. These occur often with raw, coarse ash overlays in pockets, south of the Ka'ū Desert between the Kūkalau'ula and Pu'u Kaone areas;

(c) with fine soil in the cracks or fissures;

(d) with fine soil in pockets extending beyond the cracks.

Both (c) and (d) occur throughout the area from east to west. They form the most widely-spread substrate types.

3. Discontinuous, shallow ash blanket deposits over lava rock with up to 50% rock outcrop. This substrate type is typical of the Kūkalau'ula site. Another area occurs mauka of Kū'ē'ē Ruins, and some sites in the eastern lowland may also belong to this substrate type.

4. Continuous, deep ash deposits without any significant rock outcrop. This substrate type has two variations:

(a) brown sandy loam, Pāhala ash deposit [typical for the Pu'u Kaone site];

(b) gray-black coarse sandy ash dunes [a small area SE of Kūkalau'ula].

Substrate types 2c and 2d are the most dominant and widely spread types throughout the coastal lowland and substrate type 4 represents the most localized.

Rainfall is not uniformly distributed over the area as shown by the mean annual rainfall isohyets (from Taliaferro 1959, somewhat modified) which are plotted on the vegetation map (Fig. 1). Substrate type 2b (highly permeable pāhoehoe between Kukalau'ula and Pu'u Kaone) coincides with the area of lowest rainfall of about 500 mm per year. The substrate porosity appears to attenuate the desert-like vegetation aspect of this area.

It is of some interest to note that rainfall increases toward both the eastern and western Park boundaries of the coastal lowland. The rainfall pattern coincides to some extent with the current distribution of broomsedge (*Andropogon virginicus* L.), which is found at the east and west sides of the coastal lowland but does not occur in any significant quantity throughout the central area.

Old versus New Vegetation Map Patterns

In the 1974 vegetation map report (Mueller-Dombois & Fosberg 1974), which was based on 1954 air photos and the 1966 Atlas map (Doty & Mueller-Dombois 1966), the following seven major vegetation types in the coastal lowland were recognized:

1. Eragrostis tenella grassland, with two variations: r(E) & E(r)--where r = rock surface; E = Eragrostis; r(E) means that barren rock surface dominates; E(r) means that grass cover of Eragrostis dominates over rock surface, i.e., with over 50% cover;

2. Heteropogon contortus grassland, with three variations: r(H), H(r), & H--where symbol positioning has the same meaning as before [H alone means Heteropogon cover is dense or closed rather than open as in H(r)];

3. Heteropogon contortus grassland with low shrubs or woody chamaephytes: H(ls)--where ls = lowland scrub;

4. Widely scattered 'ōhi'a (Metrosideros collina (J. R. & G. Forst.) Gray polymorpha (Gaud.) Rock and lama (Diospyros ferrea (Willd.) Bakh.) on 'a'ā lava and on some areas of coarsley broken or faulted, massive pāhoehoe: r(M) & r(M-D) --where M = Metrosideros; D = Diospyros;

5. Lowland scrub [ls], with two variations: open and closed;

6. Lowland forest [lf], also with two variations: open and closed;

7. Salt spray and other strand communities.

On the 1980 map (Fig. 1), which is based on 1977 air photos and field-map work from 1977 through 1980, only the first three grassland types have changed significantly. The Eragrostis tenella grassland has changed to Tricholaena (= Rhynchelytrum) repens grassland with woody chamaephytes; the chamaephytes include usually three species, namely Cassia leschenaultiana, Indigofera suffruticosa, and Waltheria indica. The Heteropogon contortus grassland likewise has changed to a Tricholaena grassland with chamaephytes. This means that formerly further differentiated units have become more homogenized in this case. The former Heteropogon grassland with chamaephytes also has changed into Tricholaena grassland with chamaephytes. But in some parts of the eastern lowland it has changed to open lowland scrub with Tricholaena repens and Andropogon virginicus, while in the central section from 'Āinahou to Pu'u Kaone it has changed in much of the area to a Hyparrhenia-Melinis grassland with chamaephytes.

Thus we may note a massive takeover by Tricholaena, the Natal redtop, which on the earlier map was restricted as a dominant type-forming grass to the western lowland outside the Park (near the Kona Highway). We may also note the totally new appearance of Hyparrhenia rufa as a dominant grass cover, which now forms a major grassland type in the central section of the lowland area. A further change worthy of note is the universal abundance of the woody chamaephytes, which formerly were rare in the western lowland section.

Apart from the floristic changes there has been a significant change in the life-form assemblage of the plants. Shortgrasses, such as Chrysopogon aciculatus and Eragrostis tenella, and mid-sized grasses, such as Cynodon dactylon and Heteropogon contortus, have been displaced by taller-growing grasses, such as Andropogon virginicus, Hyparrhenia rufa, Melinis minutiflora, and Tricholaena repens, with Andropogon only in certain higher rainfall areas. The reason for the restriction of Andropogon appears to be its phenological rhythm (Sorenson 1980) which is out of phase with the Mediterranean rainfall seasonality of the coastal lowland.

Significant appearances of vines have been noted so far only at the Kūkalau'ula and Pu'u Kaone sites.

DISCUSSION

Further information gained from the coastal lowland study can be discussed in relation to two questions: What sort of relationship exists (1) between the major habitats and vegetation patterns, and (2) between the structure and dynamic processes of the coastal lowland vegetation.

Correlation of Habitat and Vegetation Patterns

The four major substrate types and their variations have their effect on the vegetation primarily through their differences in soil-water relations.

The palis with 'a'ā rock rubble, including other older 'a'ā flows, are the primary habitats for the taller-growing trees such as 'ōhi'a and lama. In the eastern lowland they also commonly support the kukui tree (Aleurites moluccana (L.) Willd.) and some of the now rarer endemics such as Alphitonia ponderosa Hbd., Antidesma pulvinatum Hbd., Bobea timonioides (Hook. f.) Hbd., Erythrina sandwicensis Deg., Rauvolfia remotiflora Deg. & Sherff in Sherff, Xylosma hawaiiense Seem., and others. (In some cases, taller-growing trees are also found on pāhoehoe substrates which are hollow beneath the surface or which are coarsely broken or faulted. The relationship seems to be one of available root space for the larger tree roots and a protection from rapid water loss from the root zone.) The density of trees on both these substrate types is generally very low. However, there is a relationship of tree density to the rainfall gradient on the 'a'ā substrate type. Stocking is very sparse where the rainfall is under 1000 mm per year. Denser forest groves occur in areas where the rainfall exceeds 1000 mm per year.

The pāhoehoe substrate is the primary habitat of the lower-stature life-forms, the grasses, woody chamaephytes, and shrub-sized trees. Here, their density is related to the four substrate variations.

The "very recent" and the "highly permeable" variations support only extremely sparse plant growth and can be considered as edaphic deserts. The pāhoehoe lavas with fine soil restricted to cracks are generally more sparsely vegetated than those with fine soil extending beyond the cracks. The density of plant cover can often be used as an index for separating these two substrate variations, but there are usually no sharp breaks between them. Spatial variations in rainfall and past grazing intensity, moreover, interfere with plant denseness as an indicator of these two habitat variations. For example, the dense *Hyparrhenia* grass cover in the central section near the 'Āinahou Ranch area is partly on the same pāhoehoe with fine soil extending beyond the cracks as the sparser *Tricholaena*-dominated cover nearer to the coast, where rainfall is less.

The discontinuous, shallow soil over lava rock (such as found at Kūkalau'ula) and the deep-soil habitat (such as found on Pu'u Kaone) currently support the same lower-stature plant life-forms (grasses, woody chamaephytes, & shrub-sized trees) as the pāhoehoe substrates. However, here the grasses form dense cover and are initially more vigorous than the woody plants. The latter, particularly the woody chamaephyte *Indigofera suffruticosa*, has become denser in the course of succession (as shown by the exclosure results), and the two exotic weed trees now on these habitats, *Leucaena leucocephala* and *Ricinus communis* L., appear to have the potential for becoming dominant.

Structural Complexity and Dynamic Processes

In terms of vegetation map units, the new map has been kept as simple as the earlier map. However, *Tricholaena repens* is now considered the dominant grass over much of the areas separated earlier into *Eragrostis* and *Heteropogon* types. Yet, within former *Heteropogon* grassland, some areas are now dominated also by *Hyparrhenia rufa* which earlier was not recognized as a vegetation-type forming grass.

An important phenomenon associated with the elimination of goats from the area has been an increase in floristic as well as structural complexity. An increase in floristic complexity means simply that there are now more plant species in the area than during its occupation by goats. The grasses that were dominant during goat occupation, such as *Chrysopogon aciculatus*, *Cynodon dactylon*, *Eragrostis tenella*, and *Heteropogon contortus*, are still present in the area; they are merely displaced on most sites from their earlier role as dominants. For example, *Heteropogon* is still found in patches and particularly along foot trails. Also, a number of new species have been added from surrounding areas and thus most of the coastal lowland sites have become floristically more diverse.

Associated with the increase in floristic complexity is a trend towards loss of dominance of single species and an increase in structural complexity. The increased structural complexity was brought about by the appearance of new plant life-forms, for example, the taller-growing bunch grasses and the vines that probably had only marginal positions during the era of goat occupation of the lowland. Molassesgrass, which was formerly considered a subdominant, is still a subdominant grass today. This does not mean that it has remained static. In fact it has spread to Kūkalau'ula and other areas in the western lowland where it was not seen before. However, this thick-mat forming grass does not appear as a continuous layer over very large areas of several hectares. It forms instead dense patches of various sizes, from a few to several hundred square meters. In these patches the grass is locally absolutely dominant. The boundary zones of these molassesgrass patches do not usually coincide with distinct differences in soil-substrate. Therefore, they are not habitat related. Instead, the molassesgrass patches create a mosaic pattern within grassland covers on otherwise uniform sites, as is shown similarly for the vines, *Canavalia kauensis* at Kūkalau'ula and *Ipomoea congesta* at Pu'u Kaone. I have seen molassesgrass patches age and deteriorate suddenly, then form huge masses of litter. These patches behave very much like the *Canavalia* vine as monitored in the Kūkalau'ula exclosure.

There seems to be initially a spatially restricted cohort development from seedlings which develop into mature plants through considerable lateral outgrowth and densification of foliage mass. After a few years these cohorts attain maturity and soon thereafter go into a senescing phase. During the latter phase, synchronized breakdown of the cohorts or patch communities may be triggered by environmental factors or biotic agents. In *Melinis* this may be soil water stress; in *Canavalia* it may be related to infestations of the black stink bug (*Coptosoma xanthogramma* (White)). The latter has been observed to form dense populations on dying *Canavalia* patches at Kūkalau'ula.

CONCLUSIONS

It can be concluded that the increase in floristic and structural complexity of the grassland sites after goat removal is associated with a new dynamic complexity. This dynamic complexity relates not only to the successional development following goat removal, but also to the seasonal changes in the phenology of the vegetation cover, both of which are well-documented. The additional dynamic phenomenon is also related to the particular mix of plant life-form types and their ecological behavior as determined in part by their life cycle characteristics. Most of the plant life-forms on the pahoehoe substrates are short-lived perennials. Their life-spans vary between species and may vary within species among populations on different substrates. For example, a population of molassesgrass on nutritionally well supplied substrates may become older than one on a nutritionally less well supplied site.

Moreover, population establishment and population breakdown may be synchronized among individuals or these processes may be non-synchronized. This depends on population-inherent factors as well as on those that operate from outside the population. In the coastal lowland ecosystem at least two short-lived perennials have shown synchronized population breakdowns, the vine Canavalia kauensis and the mat-forming grass Melinis minutiflora. I have noted similar phenomena in broomsedge locally in both the extreme west and east parts of the coastal lowland and in one case in Heteropogon contortus.

Such life-cycle dependent dynamic processes are difficult to detect because they are easily confused with seasonal behavior or with competitive elimination in successional development. They are detectable only through frequent revisits or continuous monitoring of an ecosystem. In the coastal lowland ecosystem these processes of population senescence and breakdown are of particular interest because they indicate localized increases in fire hazard wherever they occur. They also indicate a point in vegetation development where it is difficult to predict the next following development because our observation period is not yet long enough. Such dying populations may be replaced by its own kind or they may be replaced by other species, for example, Canavalia through Cynodon or Tricholaena or chamaephytes, in Kūkalau'ula, or Melinis also through Tricholaena or Hyparrhenia or Indigofera or a combination of these. This cyclic or oscillating development is characteristic for the current state of the grassland areas of the coastal lowland. This is why I have considered the present situation a state of arrest in successional development.

However, the senescing stages and breakdown patterns of local populations in the grass cover may also indicate a weak point in the natural maintenance of grasslands where woody plants could invade, if the seed sources of ecologically adapted tree species were available in the area. It is possible that the endemic shrub Osteomeles anthyllidifolia Lindl., and the two low-stature trees Canthium odoratum (Forst. f.) Seem. and Wikstroemia ?phyllyroefolia Gray, which still thrive in the eastern lowland, could establish in such situations if their seed was carried there.

No specific resource management recommendations are presented. Though it was concluded that a native shrub and two trees could thrive in the area, the implementation of any program to promote these species should be reviewed thoroughly.

LITERATURE CITED

Doty, M. S., and D. Mueller-Dombois. 1966. Atlas for bioecology studies in Hawaii Volcanoes National Park. Hawaii Botanical Science Paper No. 2. Republished in 1970 as Hawaii Agric. Expt. Sta. Miscell. Publication 89. 507 pp.

Mueller-Dombois, D. 1979. Succession following goat removal in Hawaii Volcanoes National Park. Pages 1149-1154 in R. M. Linn, ed. Proceed. First Conf. on Scientific Research in National Parks. USDI National Park Service Transactions & Proceed. Series No. 5. 1325 pp.

______. 1981. Vegetation dynamics in a coastal grassland of Hawaii. Vegetatio. (In press).

Mueller-Dombois, D., and F. R. Fosberg. 1974. Vegetation map of Hawaii Volcanoes National Park at 1:52,000. CPSU/UH Tech. Rep. 4 (Dept. of Botany, University of Hawaii). 44 pp.

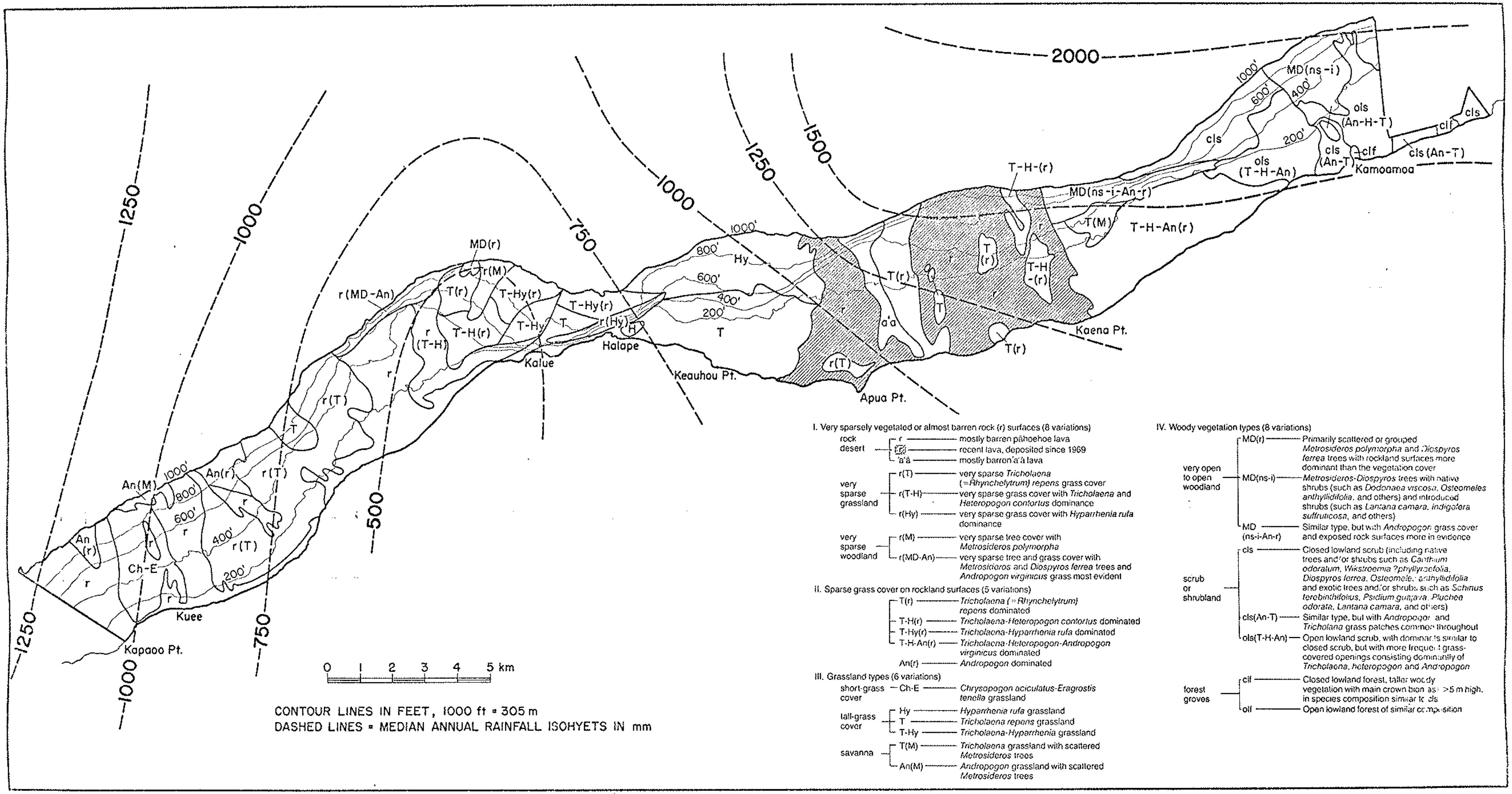
Mueller-Dombois, D., and G. Spatz. 1975. The influence of feral goats on the lowland vegetation in Hawaii Volcanoes National Park. Phytocoenologia 3(1): 1-29.

Smith, C. W. 1980. Proposed native ecosystem restoration program for Halape, Keauhou, and Apua Point, Hawaii Volcanoes National Park. CPSU/UH Tech. Rep. 28 (Dept. of Botany, University of Hawaii). 35 pp.

Sorenson, J. C. 1980. Phenology of *Andropogon virginicus* in Hawaii. M.S. Thesis in Botany, University of Hawaii, Honolulu.

Taliaferro, W. J. 1959. Rainfall of the Hawaiian Islands. Hawaii Water Authority, Honolulu. 394 pp.

VEGETATION MAP OF COASTAL LOWLAND ECOSYSTEM
HAWAII VOLCANOES NATIONAL PARK



BASED ON 1977 AERIAL PHOTOGRAPHS AND GROUND SURVEYS FROM 1977 THROUGH 1980. D. MUELLER-DOMBOIS.