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Technical Report 35

THE VEGETATION AND ENVIRONMENT IN THE CRATER DISTRICT OF HALEAKALA NATIONAL PARK

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October 1980

UNIVERSITY OF HAWAII AT MANOA
NATIONAL PARK SERVICE Contract No. CX 8000 7 0004
Contribution Number CPSU/UH 020/Final

ABSTRACT

A vegetation map of the Crater District of Haleakala National Park was produced at a scale of 1:24,000 which can be used as an overlay of the United States Geological Survey (USGS) topographic quadrangle maps. Fifty-three structural-floristic communities were mapped which were grouped into four structural vegetation-types (forest, scrub, grassland, and high altitude desert). Areas were calculated for each community using an electronic planimeter. The total area mapped was 7544.8 ha (18,643 acres).

Topographic vegetation profiles were constructed which show changes in vegetation-types in relation to climatic gradients. Also, matching correlations were observed between certain substrates and community-types.

Phytosociological analyses of relevé (vegetation sample) data by the synthesis table technique and the dendrograph technique resulted in ecologically meaningful groupings. Both analyses produced similar groupings though detailed comparison of the results of the two methods revealed interesting minor variations. Some relevés were left ungrouped. These were interpreted as unique community types within the sampling area.

The hypothesis that the community-types that are characteristic of other tropical alpine and subalpine ecosystems occur in the Crater District of Haleakala National Park was partially supported by the map units and phytosociological analyses of the relevé data. Ericaceous (pūkiawe-type) scrub, tussock grassland, and high altitude desert occur as mappable vegetation units. Only arborescent and rosette life-forms did not occur as mappable units. However, a rosette life-form, Argyroxiphium sandwicense DC. (silversword), does occur in the study area and may have had a wider and more abundant distribution in the past.

The hypothesis that the vegetation map of the Crater District of Haleakala National Park has similar vegetation units and vegetation-types as those mapped by Mueller-Dombois and Fosberg (1974) for the tropical alpine and subalpine ecosystem on the slopes of Mauna Loa in Hawaii Volcanoes National Park was supported by a comparison of the two maps.

Variation of the vegetation within the study area was associated with variations in climate, substrate, mechanical influences, and the effects of exotic plant species. Climate diagrams confirmed the tropical high mountain character of the study area, while they also illustrated the considerable variation of climate within the Crater as well as its seasonal variation. It was concluded that the diurnal (daily) frost boundary, as indicated by the vegetation, should be used to define the lower limit of the alpine zone in tropical high mountain areas. This conclusion implies that the subalpine zone be defined as those areas below the diurnal frost boundary and above the montane forests and grasslands.

RECOMMENDATIONS

1. Feral goats are a serious, disruptive force on almost all the vegetation and environment of the Crater District. These animals should be eliminated from the Park by building a barrier fence around all but the eastern side of the district perimeter. On the eastern boundary the fence should penetrate the rain forest for at least one quarter mile. Once the fence is completed all feral goats in the district should be removed or destroyed.

2. Feral pigs have extensively damaged much of the northern boundary of the Crater District. These animals are not resident within the Park. They should be prevented from foraging in the Park by constructing and maintaining a suitable barrier fence.

3. All campsites and cabin areas should be managed to prevent any further degradation of the environment around the sites. Some sites, particularly at Palikū, should be restored.

4. The māmane forest in the central and eastern segments of the Crater appear to be diminishing without any signs of regenerating. This problem should be evaluated and corrective management action taken where necessary.

5. Pu'u Nianiau is a severely degraded area. A restoration management plan should be formulated and implemented.

6. Serious consideration should be given to removing all exotic plants around Park buildings and restoring the native vegetation in these areas.

7. Implement management programs to eradicate kikuyugrass, gorse, castor bean, Maui pā'makani, and blackberry from the Crater District.

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INTRODUCTION

In planning to produce a map of the distribution of vegetation in the Crater District of Haleakala National Park and to relate the observed vegetation patterns to environmental factors certain questions have to be answered. First, what environmental conditions and plant communities can be expected in a tropical alpine and subalpine ecosystem? Second, what have other researchers found from their studies in Haleakalā? Finally, what methods should be used to accomplish the stated objectives of this study? A survey of the literature, therefore, was undertaken to seek the desired information.

This literature review begins with a discussion of tropical alpine and subalpine areas throughout the world. Environmental factors that are ecologically important in the tropical alpine and subalpine zones are first surveyed. This discussion leads into a review of the problems encountered in altitudinal zonation on tropical high mountains. Finally, the plant community types that are typical of tropical alpine and subalpine areas are reviewed.

Next, studies concerned with various aspects of the Crater District of Haleakala National Park are examined. The section begins with a discussion of the geography of the study area. Next, the physical environment is described with discussions of the geology, soils, and climate. Descriptions of the flora and fauna of the area illustrate the biotic resources. Finally, a review of ecological studies in the Crater District shows that little research has been addressed to this tropical alpine and subalpine ecosystem as a whole.

This survey of the literature (Whiteaker 1979) has shown that in different tropical alpine and subalpine ecosystems similar plant communities have been described at equivalent elevations. This similarity is the result of certain environmental factors which have had a similar evolutionary impact on plants in spite of their geographic isolation. Characteristic community-types of these tropical high mountain areas are ericaceous (pūkiawe-type) scrub, tussock grassland, arborescent and rosette life-forms, and high altitude desert. A general hypothesis was proposed which states that these same community-types that have been described for other tropical alpine and subalpine ecosystems occur in the Crater District of Haleakala National Park.

Mueller-Dombois and Fosberg (1974) have published a large-scale vegetation map for Hawaii Volcanoes National Park on the island of Hawai'i. The Park includes the summit of Mauna Loa at 3968 m (13,018 ft) and extends to the southeast coastline of Hawai'i. Thus it includes an alpine and subalpine ecosystem on the upper slopes of Mauna Loa. Since it was planned for this study to use structural-floristic map unit symbols similar to those used for the map of Hawaii Volcanoes National Park, a second hypothesis was proposed. This hypothesis states that, wherever similar substrates and climatic conditions occur, the vegetation map of the Crater District of Haleakala National Park will have similar vegetation units and vegetation-types as those mapped by Mueller-Dombois and Fosberg (1974) for the tropical alpine and subalpine ecosystem on the slopes of Mauna Loa in Hawaii Volcanoes National Park.

To test these hypotheses, the objectives of this study were two-fold, the second building upon the first. The first objective was to produce a large-scale vegetation map that indicates the vegetation of the Crater District of Haleakala National Park using structural-floristic map unit symbols similar to those used for Hawaii Volcanoes National Park by Mueller-Dombois and Fosberg (1974). Mapping was to be accomplished using aerial photographs and subsequent ground proofing in the field. These vegetation units were then to be verified and quantified using relevés (vegetation samples) placed throughout the study area and the data were to be analyzed statistically.

The second objective was to associate the mapped vegetation patterns with environmental factors observed or measured in the field during the releve analysis. Also, environmental data were to be assembled from both published and unpublished sources. Topographic vegetation profiles and climate diagrams were to be constructed to illustrate the relationships observed.

This study was also intended to be a base for future research and park managment. Mueller-Dombois and Ellenberg (1974) give several ways vegetation maps may be useful during different stages of an ecological investigation of an area. Maps can be used as a framework for research since the vegetation of an area is subdivided into relatively homogeneous units. Maps can provide a basis for distributing sample plots that may be used to describe the floristic content of the established units, test the validity of the subdivisions, or verify the boundaries drawn on the map. Sample plots can also be adequately distributed in the sense of geographic distribution and vegetation variation with the use of a map. Maps can also aid in classifying vegetation since mapping the vegetation will test the classification by forcing the investigator to accommodate all variations in his scheme. Maps based strictly on existing vegetation form a documentation "frozen" in time and thus can be used as a base for subsequent succession studies or other changes. Maps can be used to show the distribution of a specific vegetation unit by areal shading or by dots on the unit being investigated. Maps based on currently existing vegetation can be compared to environmental maps and can thereby aid in the causal analytical research of plant communities. Finally, maps can be used for applied purposes if the vegetation units reflect the factors of their habitats closely and thereby provide the basis for the production of habitat maps. These habitat maps can in turn be used to show the suitability of an area for particular purposes, such as forestry, species reintroduction, etc.

Larson (1969) edited a report that includes a simple vegetation map at a scale of approximately 1:62,500 for the Haleakalā Crater area that distinguished only four types of vegetation based on form: shrub, marginal rain forest, shrub-savannah, and scattered shrub and barren areas. The production of detailed vegetation, soil, topographic, and climatic overlay maps was recommended as needed research. The following study is one step towards the fulfillment of that need.

LITERATURE REVIEW
TROPICAL ALPINE AND SUBALPINE AREAS

Ecologically Important Environmental Factors

Tropical alpine and subalpine areas in the world are subject to a number of common environmental factors in spite of their biogeographic isolation. Higher radiation intensity especially at the short-wavelength (blue) end of the electromagnetic spectrum, for example, is a characteristic common to all these high altitude areas. This higher intensity is related to their topographic positions which are above the general screen of oxygen, dust, water vapor, clouds, and carbon dioxide. These materials are retained in the lower atmosphere by the inversion layer where they absorb or reflect solar radiation. The evolution of flat, silver, or grey hairs on the leaves of several alpine species is seen as an adaptation to withstand this radiation by increasing the albedo of the plant (Carlquist 1970).

In alpine and subalpine areas, the decrease in temperature with increasing elevation is described as an important environmental factor. This relationship between temperature and elevation contributes to a certain altitudinal zonation on different tropical high mountains (Hedberg 1951). Also, although tropical areas are known for their very limited seasonal variation in temperature, diurnal (daily) variation in temperature is an important ecological factor. A remarkable diurnal fluctuation of temperature occurs in high mountains where, characteristically, the heating of the surface is intense during the day and cooling is rapid during the night. This has been termed by Hedberg (1957) "winter every night and summer every day." Coe (1967) suggested that such a temperature regime must be an important selective factor in the evolution of the tropical mountain flora.

A related factor which has been described as important in almost all tropical alpine areas is the occurrence of night frost. The frost and thaw cycle results in the sorting of soil particles by size. This, in turn, produces stone rings or stone strips on slopes. Because of the steady decrease of temperature with elevation and the diurnal temperature fluctuation as noted above, frost may occur almost every night of the year above a certain elevation. On Mauna Loa in Hawai'i, the diurnal frost boundary was observed to occur at approximately 2600 m (8600 ft) and to coincide with the boundary of a vegetation community-type (Mueller-Dombois 1967). In South America, the boundary between Puna, a seasonally dry area of the southern high Andes, and alpine desert is defined as the elevation where frost occurs each night (Troll 1966). This elevation is a little below 4000 m (13,000 ft) in these mountains (Walter 1971). Natural selection favors those plants that can adapt their growth forms to tolerate daily freezing. These adaptations are predominantly expressed as megaphytic (large bodied) and rosette life-forms (Troll 1958; Coe 1967), but also other life-forms, for example, cushion plants.

Altitudinal Zonation

The use of the word alpine presents a problem in the altitudinal zonation of tropical mountains. In temperate regions, the lower limit of the alpine zone is clearly defined by a well-marked tree line. In tropical high mountain areas, however, such a tree line is often absent and is replaced by a gradual transition from montane forest to a park-like vegetation which gradually merges into a heath-type or moorland vegetation. A few attempts have been made to define this zone by species distribution but this criterion is also imprecise due to topographical microhabitats (Coe 1967). Troll (1958) recommended replacing the term alpine with nival and subnival, terms which correspond to above and below the permanent snow line, respectively. Wade and McVean (1969) adopted subnival from Troll when they compared the vegetation of the upper elevations of Mt. Wilhelm in New Guinea with the vegetation of high mountain areas north of the Antarctic Circle. However, Coe (1967) points out the term alpine is still very much a part of the literature and can be used in the broader meaning of "high mountain" when applied to tropical areas.

Altitudinal zonation in the tropics is also complicated by its three-dimensional character which involves not only temperature relations associated with latitude and altitude, but also precipitation. The sequence of vegetation types in the high Andes corresponds with a moisture gradient going from the Paramos in the north to moist Puna, dry Puna, thorn Puna, and finally desert Puna in the south (Troll 1966). High mountain areas in East Africa have been arranged in order of wetness which is said to account for the differences between equivalent altitudinal zones (Hedberg 1951). The definition of wetness, however, can also present a problem and should be defined in terms of the number of humid months rather than according to average annual precipitation. The morphology, stature, and structure of tropical alpine vegetation can be correlated with the pattern of rainfall (Troll 1958). The temporal distribution of precipitation and its relationship to temperature in determining the climate of an area can be viewed graphically by the use of the climate diagram method of Walter (1963).

The problem of defining altitudinal zonation on tropical high mountains, then, is three-fold. First, the upper limits of forests and trees, usually well definable in temperate areas, is not always clearly indicated on tropical mountains. Illustrative of one aspect of this problem are the tree-like, herbaceous forms growing at high elevations. They would be considered trees when classified by height but they are clearly related to herbaceous species. Second, the life-form of many woody species of tropical mountain plants changes from trees to bushes and low shrubs in adaptation to climatic severity. If such species are the uppermost trees, it becomes difficult to demarcate the treeline. Such a species in Hawai'i is māmane (Sophora chrysophylla (Salisb.) Seem.). Last, the ecological conditions of the forest and tree limits are not well-defined. Decreasing temperature with increasing altitude, of course, accounts for the basic zonation, but temperature is also important in precipitation effectiveness (incident precipitation relative to soil moisture that is available to plants). Local variations in elevation of the timber line, if recognizable, indicate that factors other than temperature and rainfall are also involved. Such factors include frequency of mist and clouds, frequency of frost and thaw, exposure to local winds, physical properties of the different substrates, and relative exposure to biotic influences such as herbivory (grazing, browsing, etc.) (Troll 1958). Substrate age and geologic history are other factors.

Plant Community Types

Similar plant communities have been described at equivalent elevations in different tropical alpine and subalpine environments. This resemblance is the result of certain outstanding environmental factors which had an evolutionary impact resulting in similar plant life-forms. Characteristic community-types of these tropical high mountain areas include ericaceous (heath-like) scrub; tussock (bunch grass) grassland; arborescent (tree-like) and rosette life-forms; and high altitude desert. However; differences are observed between areas due to a complex of local factors that are peculiar to any given area.

Ericaceous Scrub

The ericaceous scrub community-type can be generally described as consisting of evergreen, globose-shaped shrubs, many of which are in the families Ericaceae (includes 'ōhelo) and Epacridaceae (includes pūkiawe). High mountains of East Africa have an "ericaceous belt" in common whose similarity is indisputable despite physiognomic (physical appearance) differences related to climatic and edaphic (substrate) factors (Hedberg 1951). The "upper alpine belt" on Kilimanjaro was described as characterized by members of the Ericaceae family 0.5 to 1.0 m tall (Walter 1971). Salt (1954) calls the "heath formation" the most common plant cover on the same mountain and recognized six floristic communities related to slope and substrate within this formation. On Mt. Kenya, the "Ericaceous zone" has been recognized as being composed of three habitat types that are related to substrate (Coe 1967). On the much more humid Ruwenzori, the vegetation of the Ericaceous belt has been termed a "heath forest" which was divided into two floristic types, one dominated by species of Erica and the other dominated by species of Philippia occurring at higher elevations than the Erica-dominated type (Ross 1955).

In South America, three of the nine life-forms characteristic of high altitude areas of the Andes included evergreen scrub with dense foliage of small scale-like or rolled leaves, evergreen broadleaf scrub, and scrub with woolly leaves (Troll 1966). In the Puna, a seasonally dry area of the southern high Andes, two provinces were distinguished of which one, the "puna province," was characterized by nanophanerophytes (dwarf trees < 2 m tall) near 1 m tall with the Compositae (daisy family), Solanaceae (nightshade family), and Verbenaceae (includes Lantana) being the most important families forming two floristic communities (Cabrera 1966). In the Paramos, a continuously humid area of the northern high Andes, a "subparamo" formation occurring above the timber line forest has been described as consisting of shrubby species composed of genera common to other tropical high mountain areas (Cuatrecasas 1966).

The ericaceous community-type is also present in several high mountain areas of Asia. On Reunion Island in the Indian Ocean, ericaceous vegetation dominated by Philippia montana was composed of three main plant communities whose physiognomy and floristic structure were closely related to edaphic factors (Cadet 1974). In the Himalayas, dwarf rhododendron and juniper dominate communities up to about 5200 m (17,000 ft) elevation. These communities were divided by Swan (1961) into wet and dry types. Also, a "shrub rhododendron" community was recognized at lower elevations. In the high mountains of Malaysia, Ericaceae often dominate in scrub-forests and in the alpine heath (van Steenis 1934-35, 1962). On Mt. Wilhelm in New Guinea, Wade and McVean (1969) note that species of both Ericaceae and Epacridaceae are characteristic elements of the alpine and subalpine scrub communities.

In Hawai'i, this community-type also contains a significant and sometimes dominant epacridaceous (similar to or in the plant family Epacridaceae) element from the genus Styphelia (pūkiawe). Krajina's (1963) xerophytic (drought tolerant) scrub zone has been differentiated into three vegetation cover-types on Mauna Kea (Mueller-Dombois & Krajina 1968). On Mauna Loa, this community-type is represented by four described vegetation-types and several large-scale map units (Mueller-Dombois & Fosberg 1974).

Tussock Grassland

Another community-type characteristic of tropical high mountains is composed of tall bunch grasses known as tussock grasses. These tussocks are about 0.5 to 1.0 m or more tall, have about the same diameter, and look somewhat like sedge hummocks. The leaves are sclerophyllous (stiff and/or hard) and persist for long periods after dying and turning yellow. Genera that have tussock grass species include Festuca, Deschampsia, Danthonia, Stipa, Calamagrostis, and Andropogon (Walter 1971).

In the East African mountains, "tussock grasslands" are identified as one of five community-types occurring in the "alpine belt" (Hedberg 1951). On Kilimanjaro, a sedge and grass community is found on flat and wet ground and is mixed with a shrub species on gentle slopes in a "bog formation" (Salt 1954). A typical tussock grassland on peaty soil is described as the dominant vegetation cover of the lower alpine belt (Walter 1971). Tussock grasses cover by far the larger part of the surface of the "alpine zone" and occur in flat, damp bogs and in open spots on weathered and eroded ridges in the "lower alpine zone" of Mt. Kenya (Coe 1967).

In South America, the Paramo is characterized by tall bunch grasses with scattered shrubs and arborescent life-forms according to prevailing edaphic factors (Cuatrecasas 1966; Walter 1971). Further south, in the Puna, the "high-andine province" has been described as characterized by xerophytic caespitose (drought adapted bunch) grasses (Cabrera 1966). Thus, "tussock-like bunch grasses" have been included as one of the nine major life-forms characteristic of the high Andes (Troll 1966). In the Himalayas, a "xerophytic alpine" association on slopes and scree areas includes tussock grasses (Swan 1961). Grassland is also one of two community-types of alpine areas in Malaysia (van Steenis 1962). Wade and McVean (1969) describe both alpine and subalpine tussock grasslands on Mt. Wilhelm, New Guinea.

In Hawai'i, tussock grasslands have been described on the island of Hawai'i with native grasses dominant on Mauna Loa and introduced grasses dominant on Mauna Kea (Mueller-Dombois & Krajina 1968). The ecology of the tussock grassland on the northeast outer slope of Haleakalā has been studied in some detail (Forehand 1970).

Arborescent and Rosette Life-forms

Equally typical of tropical high mountains are arborescent plants that can be separated into two types based on growth form. Woolly rosetted species with tall, thick, and sparsely branched trunks are referred to as "woolly-rosetted" plants. Lower growing species with a single rosette and having candle-like woolly inflorescences are referred to as "woolly-candle" plants (Troll 1966). Although many authors have noted these peculiar growth forms, little work has been done to learn what factors or roles are associated with these modifications. It has been suggested by Coe (1967), however, that the rosette habit is related to the inhibiting effect on elongation of internodes produced by daily temperature changes and that this habit of growth functions in several ways to protect the plant from temperature extremes.

This life-form is represented by species of *Senecio* and *Lobelia* on the high mountains of East Africa and in the highest parts of Ethiopia (Troll 1958). On Kilimanjaro, these same two genera characterize an "upper alpine belt" (Walter 1971), and *Senecio* spp. also form communities in association with broken rock faces in the "heath formation" on the same mountain (Salt

1954). On Mt. Kenya, several species of both Senecio and Lobelia form communities in both the lower and upper alpine zone. The presence of one of these species, Senecio keniodendron, defines the upper alpine zone (Coe 1967). Thus, Hedberg (1951) identifies an "arborescent Senecio forest" as one of five major community-types common to all the high mountain areas of East Africa. These giant, woody Senecios and Lobelias of East Africa have been studied with regard to their evolution, morphology, and the biogeography of related species, especially as related to the taxonomy of these plants. Mabberley (1973, 1974a, 1974b, 1975) wrote a series of articles on these aspects which also include discussions on non-alpine species.

In South America, the Paramo vegetation includes stands of the woolly-rosetted species of the genus Espeletia (Cuatrecasas 1966; Walter 1971). Also occurring in the high Andes are species of woolly-candle plants from the genera Lobelia and Lupinus (Leguminosae) in the Paramos of Colombia and the Puna of Peru. Species of the genus Puya (Bromeliaceae) occurring in the Puna of Bolivia also form woolly-candle plants (Troll 1958). In Asia, Anaphalis javanica (family Compositae) which occurs in the high mountains of Malaysia corresponds to the woolly-rosetted form and the woolly-candle form is represented by Saussurea (family Compositae) and Crepis (family Compositae) in the Himalayas (Troll 1958; Walter 1971).

In Hawai'i the woolly-candle form is represented by several species of Argyroxiphium, the silverswords and greenswords. Thought to be widely distributed at one time on the high mountains of both Maui and Hawai'i (Ruhle 1959; Mueller-Dombois & Krajina 1968; Larson 1969), the silverswords are now very restricted in their distribution and have been entirely eliminated in most areas due to the activities of humans and introduced feral grazing animals (Ruhle 1959; Mueller-Dombois & Krajina 1968; Larson 1969).

High Altitude Desert

At very high elevations on tropical mountains, environmental conditions become so extreme that vascular plant cover becomes sparse or absent altogether, and soil and vegetation formation processes proceed very slowly. These areas are therefore referred to as alpine stone deserts or, more generally, high altitude deserts. The dominant environmental factor that determines the extent of this community-type is nightly frost which makes plant invasion and establishment difficult (Troll 1966). On Kilimanjaro in East Africa, there is a gradual transition from ericaceous heath vegetation to an "alpine desert" at about 4250 m (14,000 ft) with plants growing in sheltered positions and having a total plant cover of less than 5% (Salt 1954; Walter 1971). On Mt. Kenya, the "nival zone" is described as a region of recent glacial retreat with the earliest stages of plant colonization. Plants are small in number, stunted, and invariably grow in sheltered situations (Coe 1967).

In Bolivia, South America, few plants occur above 4700 m (15,400 ft) due to the daily occurrence of night frost (Troll 1966). In the Paramo region of the northern Andes, a "super-paramo" vegetation-type has been described above 4500 m (14,700 ft) elevation which was characterized by the scarcity of plants growing on the sandy and gravelly soil of that zone (Cuatrecasas 1966). In the high Himalayas of Asia, two of six ecological zones described were an "aeolian zone" and an "alto-alpine zone." In the aeolian zone, organisms that live on wind blown debris exist but no flowering plants are present. In the alto-alpine zone, flowering plants grow only at the bases of rocks (Swan 1961). On the high mountains of Malaysia, the "alpine zone" was described as a stone desert with mosses, lichens, and a few grasses and sedges (van Steenis 1934-35).

On Mauna Loa in Hawai'i three vegetation cover-types were described as high altitude desert communities or habitats. These were named a vegetationless stone desert, a Racomitrium moss desert, and a Vaccinium-Styphelia ('ōhelo-pūkiawe) low-scrub desert. The corresponding vegetation cover-types on Mauna Kea were described as a stone desert with occasional crustose lichens, an Agrostis-Trisetum grass desert, and a Styphelia low-scrub desert (Mueller-Dombois & Krajina 1968). The vegetation-types on Mauna Loa are also reflected in map units on a large-scale vegetation map of Hawaii Volcanoes National Park (Mueller-Dombois & Fosberg 1974).

In conclusion, it can be seen from the above comparisons of tropical alpine and subalpine ecosystems that tropical high mountain communities are structurally similar and are characteristic of basic ecological zones determined by factors related to increasing elevation, such as decreasing temperature and the associated frequency of night frost, changes in air pressure, and changes in radiation climate. However, differences in physiognomy (physical appearance) and altitudinal range of similar plant communities are observed and these are a function of a complex of local factors superimposed on the elevational factors. These factors include amount of precipitation, frequency of cloud mist, slope, chemical and physical properties of the soil and bedrock, and biotic factors, particularly the plant species present in the area.

HALEAKALĀ CRATER

Geography

Haleakala National Park is located in the southeastern part of the island of Maui in the Hawaiian Archipelago, at latitude 20°45'N and longitude 156°12'W (Fig. 1). This eastern part of the island is formed by the large shield volcano of Haleakalā. The study area is the Crater District which incorporates Haleakalā Crater, small adjacent segments of the outer slopes, and portions of two broad erosional depressions, called gaps.

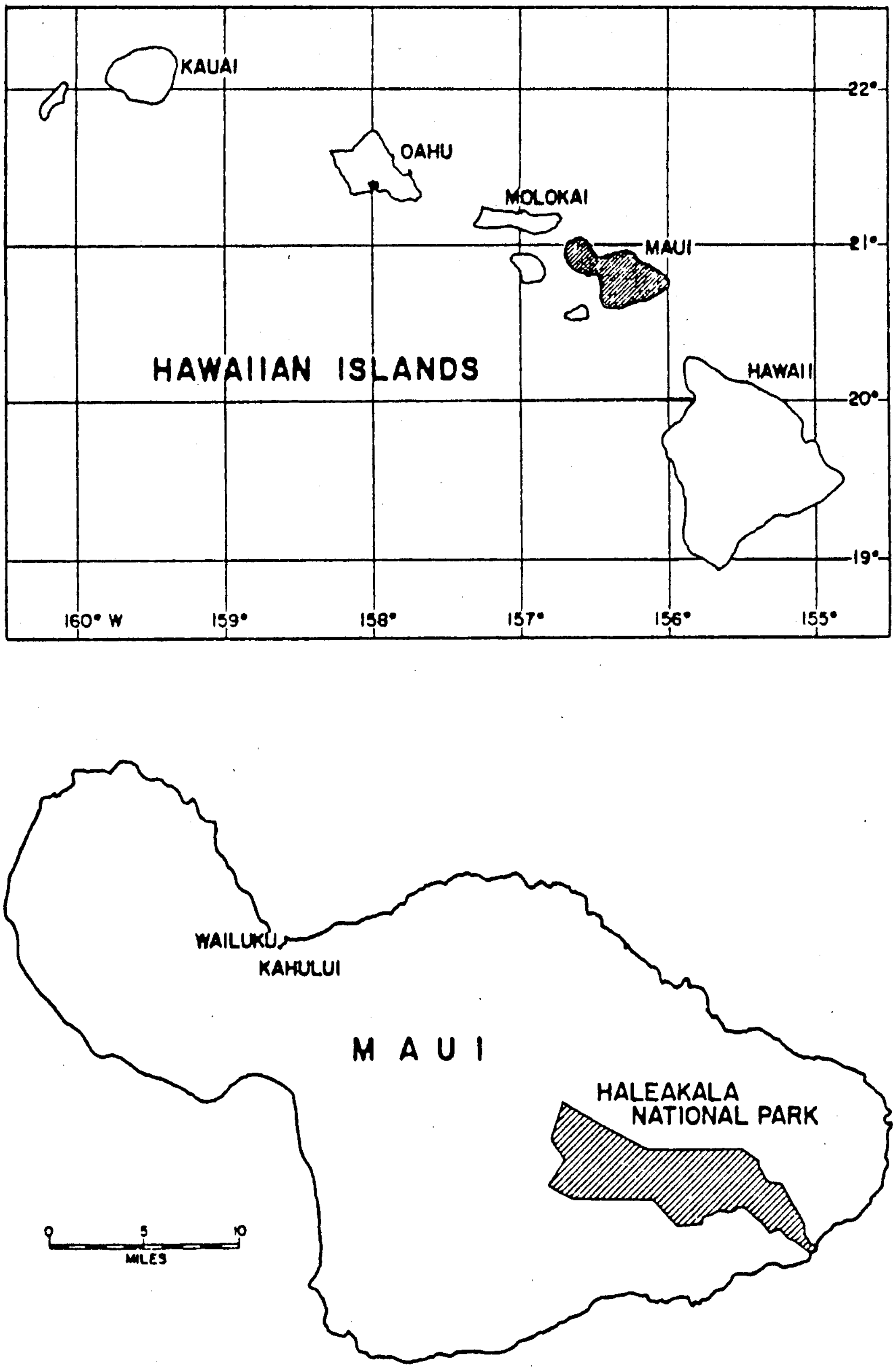


FIGURE 1. Map showing location of Haleakala National Park in reference to the Island of Maui and the Hawaiian Islands.

Ko'olau Gap faces northeast and opens into Ke'anae Valley which runs to the ocean. Kaupō Gap faces south and opens into the pastureland of Kaupō Ranch. Kīpahulu Valley, lying east of the study area and facing southeast, was excluded from this study since it will be described in a separate series of studies.

Structures on the northwest outer slope include the Park Headquarters, the stables, the Red Hill observatory, the old Civilian Conservation Corps Camp, the visitor center, and various scientific facilities located near the summit. Three visitor cabins are inside the Crater. These are Hōlua Cabin at the west end near Ko'olau Gap, Kapalaoa Cabin on the south central Crater floor, and Palikū Cabin at the extreme eastern end. A ranger cabin is also at the east end near Palikū Cabin. Access to the Crater District is by a narrow, winding, 19 km (12 mile) mountain road (State Highway #378) which ascends the northwest slope of Haleakalā and connects to standard highways leading to the rest of the island of Maui. The Crater District is 45 km (28 miles) from the city of Kahului and 48 km (30 miles) from Wailuku (county seat). Elevations in this portion of the Park range from 1144 m to 3055 m (3760-10,023 ft) above sea level.

Geology

Haleakalā Crater, 12.1 km (7.5 miles) long, 4.0 km (2.5 miles) wide, and up to 915 m (3000 ft) deep, is the large eroded summit depression of Haleakalā. A general history of the geological formation of Haleakalā has been given by Macdonald and Abbott (1970) and can be found in various other sources (Ruhle 1959; Larson 1969). The mountain was formed by three series of volcanic activity from Haleakalā Volcano. The first two are known as the Honomanū volcanic series which occurred during the Tertiary (65 million-2.5 million years before present), and the Kula volcanic series which occurred during the Pleistocene (2.5 million-15,000 years before present). These two volcanic series built up a large symmetrical shield volcano, much like Mauna Kea and Mauna Loa on Hawai'i, whose summit may have been up to 915 m (3000 ft) higher than the present crater rim.

At the end of the Kula eruption series, volcanic activity became infrequent or perhaps ceased. Water began to cut deeply into the mountainsides forming valleys all around. Ke'anae, Kaupō, Kīpahulu, and Waiho'i valleys became particularly large eroded areas and they still exist today in essentially this form. Ke'anae and Kaupō streams had the shortest and steepest courses and eventually cut into the very center of the mountain. Continued erosion resulted in these two valleys fusing into a single huge eroded depression that extended across the entire mountain top, divided only by a low, narrow ridge.

In geologically recent times, i.e., within the last 15,000 years, the third period of volcanic activity began. This series of lavas and cinder cones is known as the Hāna volcanic series. These lava flows covered the east and west slopes of the volcano and the floor of the depression. Great lava flows pushed through Ko'olau and Kaupō gaps to the sea. The ridge that divided the two great valleys is masked by large flows and cinder cones. The most recent eruption, estimated to have occurred about 1790, was on the southwest rift and is represented by two bare, black flows above La Pérouse Bay.

Soils

As would be expected from the recency of volcanic activity on Haleakalā, soils are young and relatively undeveloped. Almost all the soils of Haleakalā have been classified (Larson 1969) as lithosols (rock) or regosols (cinder and ash), with some latosolic soils (brown forest soils) occurring near the Park's northwest boundary being the only intrazonal (differentiated) soil in this section of the Park (USDA, Soil Conservation Service 1955). Maps of the distribution of various soil types in the area are available from the Soil Conservation Service's Soil Survey (1972). These maps are based primarily on reconnaissance survey mapping units for the Park and indicate an ash, cinder, rock, or rock outcrop substrate or rough mountainous terrain for almost all of the Crater area. Soil classification and data for the area are very incomplete and general in nature and offer little useful information for ecological studies.

Climate

The climate in Haleakalā varies greatly with dry, moderately warm summers and cool, wet windy winters being characteristic. At Haleakalā Ranger Station, mean monthly temperature ranges from 9.6°C (49°F) in February to 13.4°C (56°F) in August, a difference of only 3.8°C (7°F). Cloudy conditions are typical during midday all year. Snow has been recorded in the summit area in the winter, but only rarely (Larson 1969).

The climate of the area has been described by Blumenstock and Price (1967). It is greatly influenced by the temperature inversion layer which accompanies tradewinds, which are present 50% to 70% of the time. The inversion layer is a result of a slight increase in temperature which may extend several hundred feet upslope before the temperature begins once more to decrease upward, as is usual in the atmosphere. When present, the height of the inversion layer varies from day to day, but it is usually between 1525 m and 2130 m (5000-7000 ft) elevation. The inversion layer suppresses the vertical movement of the air thus restricting cloud formation to the zone beneath the inversion.

This boundary also results in a relative humidity generally below 40% above the cloud layer and occasionally as low as 10% or even 5%.

The upper slopes of the high mountains are considered to receive some of the lowest amounts of precipitation in the State (Blumenstock & Price 1967). Average annual precipitation does, however, vary greatly within the Park. Ko'olau Gap at 2100 m (6890 ft) elevation, averages 2000 mm (79 in.) precipitation while the summit averages only 800 mm (31.5 in.) at 3000 m (9842 ft) elevation (Kobayashi 1973). Detailed rainfall and temperature records for the area are scarce and fragmentary. Taliaferro (1959) includes mean minimum, mean maximum, and median rainfall figures by month for only two stations within the Park boundary. Four rain gauges and seven temperature shelters were maintained for 14 months (December 1970-February 1972) on the Crater floor in connection with a study of the silversword populations occurring there (Kobayashi 1973). Mr. Bernard Meisner of the University of Hawaii Meteorology Department is in the process of collecting rainfall and temperature data to update climatic maps for the State. Some information for the Crater area was obtained from computer tapes and more information may become available when research efforts are concentrated on the island of Maui.

Flora

The Hawaiian Islands are the most remote high volcanic islands in the world. They are virtually alone in the center of the North Pacific, being almost 4000 km (2500 miles) from North America to the east and 5635 km (3500 miles) from the Marianas Islands to the west. The closest high volcanic islands, the Marquesas, lie 3220 km (2000 miles) to the south (Carlquist 1970). Thus dispersal to Hawai'i had to be over large distances of ocean, since geological evidence indicates that no closer land existed even during earlier periods. This isolation has allowed the relatively few successful arrivals to evolve seemingly strange adaptations to fill niches (role of an organism in the ecosystem) left unoccupied by the usually continental occupants that were less successful at long distance dispersal (Carlquist 1970).

Therefore, many alpine plants typical of other high mountain regions in the world are absent from Haleakalā. Many of the plants on Haleakalā are representatives of north temperate zone groups. This is not surprising since the cooler temperatures of higher latitudes occur only at higher elevations in the Hawaiian Islands. North temperate zone taxa represented in Hawai'i include *Fragaria* (strawberry), *Artemisia* (wormwood), *Silene*, *Vaccinium*, and the Madiinae, the subtribe of Compositae including *Argyroxiphium* and *Railliardia* (na'ena'e, kūpaoa) (Carlquist 1970; Carr 1978). Similarly, some genera show affinities to south temperate zone groups such as *Coprosma* (pilo), *Santalum* (sandalwood), *Wikstroemia* ('ākia, false 'ōhelo), and probably *Sophora*. Another characteristic is that many high-altitude genera in Hawai'i occur also at lower elevations. These include *Styphelia*, *Dodonaea* ('a'ali'i), *Santalum*, and *Sadleria* ('ama'u ferns) (Carlquist 1970).

The Crater District flora also includes several exotic species introduced by man and his domestic animals. These introductions have resulted in native species losing ground to invading forms with up to 100% alteration in flowering plant species composition in some areas. Some of the more obvious and widespread of these genera include *Eupatorium* (pāmakani), *Hypochaeris* (hairy cats-ear), *Oenothera* (evening primrose), *Pennisetum* (grass), *Pinus* (pines), *Rumex* (docks & sorrels), and *Eucalyptus* (eucalypts). A list of exotic species has been compiled for the Park (Larson 1969).

The flora of the Crater is fairly well known because of studies focusing on the special adaptations mentioned above and the native species and species associations that occur in the area. Examples of candidate endangered native species found in the study area include *Viola tracheliifolia* Gingins, *Geranium arboreum* Gray, and *Stenogyne crenata* Gray. Detailed plant lists for the Crater District that include habitat notes are being compiled in a three-year resources basic inventory study by the Cooperative National Park Resource Studies Unit of the University of Hawaii (CPSU/UH) (Berger et al. 1976; Stemmermann et al. 1979). Since this study includes both vascular and non-vascular plants plus comments on each species (e.g., endemic, exotic, distribution, abundance, etc.), it is a significant expansion of the floristic knowledge of the area over previous works that only include species that are common or typical of the area (Skottsberg 1931; Mitchell 1945; Ruhle 1959; Hubbard & Bender 1960; Carlquist 1970). A detailed plant list has been compiled for the northeast outer slope of Haleakalā by Henrickson (1971). However, this area, although closely related to the Crater floristically, is only marginal to the study area of this paper.

Fauna

The Park is rich in insects most of which are endemic species very limited in their distribution. Many are associated with specific endemic plant species and are highly vulnerable to extinction. Of the introduced insects in the area, the large blowflies which breed in the carcasses of goats are the most conspicuous since they are a considerable nuisance (Ruhle 1959). The CPSU/UH Resources Basic Inventory (RBI) also includes a survey of the insect species of the Crater area (Berger et al. 1976; Stemmermann et al. 1979).

The bird life of the Crater includes several species in the endemic Hawaiian family Drepanididae. These include the 'Apapane (*Himatione sanguinea*); the 'I'iwi (*Vestiaria coccinea*); and the Maui 'Amakihi (*Loxops virens wilsoni*). Other native birds common in the Park include the Hawaiian Goose or Nēnē (*Branta sandvicensis*) once near extinction but now recovering through a restoration program; the White-tailed Tropicbird or Koa'e-kea (*Phaethon lepturus dorotheae*); the Golden Plover or Kōlea (*Pluvialis dominica*); and the Hawaiian Owl or Pueo (*Asio flammeus sandwichensis*) (Ruhle 1959; Larson 1969). Also native is a ground nesting seabird, the Hawaiian Dark-rumped Petrel or 'Ua'u (*Pterodroma phaeopygia sandwichensis*), an endangered species which has been the subject of some sporadic studies (Larson 1967) and census counts by National Park Service (NPS) personnel, Mssrs. J. Kunioki and J. Kjargaard. The biology of this species is now being intensively studied by Mr. T. Simmons of the University of Washington CPSU.

Introduced bird species are quite numerous and more commonly seen than native birds. These include the Japanese White-eye (*Zosterops japonicus*); Ring-necked Pheasant (*Phasianus colchicus*); Chukar (*Alectoris chukar*); House Finch (*Carpodacus mexicanus*); Skylark (*Alauda arvensis*); Mockingbird (*Mimus polyglottus*); Barn Owl (*Tyto alba*); California Quail (*Lophortyx californicus*); and House Sparrow (*Passer domesticus*) (Ruhle 1959)..

There are no mammals native to the Hawaiian Islands with the exceptions of the Hawaiian Bat (*Lasiurus cinereus semotus* (H. Allen)) (Larson 1969) and the Hawaiian Monk Seal (*Monachus schauinslandi* Matschie). When Polynesians arrived in Hawai'i, they brought pigs, dogs, and rats which probably established feral populations that extended into the Park. After Captain Cook's arrival, many mammals were brought in including goats, pigs, cattle, horses, sheep, cats, dogs, mice, and rats. Also, mongooses were imported with the intention of controlling the rat population. Horses, sheep, and cattle though once feral, no longer occur as wild populations in the Park (Ruhle 1959; Larson 1969).

The feral goat is the most obvious mammmal in the Crater District and once numbered into the thousands (Larson 1969), causing much damage to the vegetation and thereby speeding erosion. The goat population was studied by Yocum (1967) as to its distribution and ecological relationship to the Crater District's environment. The National Park Service has made some limited progress in the control of the introduced mammal populations through controlled shooting of goats and pigs and trapping of dogs, cats, mongooses, and rodents (Larson 1969).

Ecology

There have been few ecological studies in the Crater region, and of those that have been undertaken none addressed the ecology of Haleakalā Crater as a whole. A vegetation map has been produced at a scale of approximately 1:62,500 that distinguished only four types of vegetation based on its structural character: scattered shrub and barren areas, shrub, shrub-savannah, and marginal rain forest (Larson 1969). Several plant communities have been identified for the northeast outer slope of Haleakalā which are similar to communities found within the Crater. Although floristic composition was discussed in the text of the paper (Vogl 1971), the units were again based primarily on structural character and were identified as tussock grassland, alpine bog, heath-scrub, cloud forest, and montane rain forest. In a related study (Forehand 1970), the phytosociology of the tussock grassland community-type composed mainly of Deschampsia was studied. In her structural-floristic analysis Forehand used 21 sample stands to obtain percent frequency, percent cover, and density per acre for all species. She defined five "site-types" within this community. The five site-types were the level grassland site-type, the sloping grassland site-type, the heath ecotone (subdivision of ecosystem by Forehand) site-type, the fern ecotone site-type, and the mid-ecotone site-type. Also, the effect of pig digging was noted and soils data were collected.

Other studies have been concerned with the ecology of specific organisms found within the Crater. The silversword (Argyroxiphium sandwicense DC.), once common throughout the Crater and on the outer slopes of Haleakalā (Ruhle 1959; Larson 1969), has had its range restricted to cinder cone areas on the western crater floor and to a small area, now enclosed and specially protected by the National Park Service on the outer slope (Kobayashi 1973). This dramatic decline in the population is commonly attributed to vandalism by humans and to grazing pressure by feral goats (Ruhle 1959; Larson 1969). The ecology of the silversword in what is left of its range has been thoroughly studied by Kobayashi (1973) in a Ph.D. dissertation at the University of Hawaii. He found that the silversword is well-adapted to its remaining habitat in Haleakalā since it has xerophytic (drought resistant) features such as tomentose (densely covered with matted, wool-like hairs) succulent leaves and an ability to sustain regeneration under the dynamic substrate conditions found on larger cinder cones that eliminate all but a few exotic or endemic species.

The distribution, density, and ecology of the Crater's feral goat population has been studied by Yocum (1967). The goats' effect on the vegetation and substratum erosion was summarized as:

a. Overgrazing of the native plants.

b. Elimination of some native plants, thus eliminating ground cover.

c. Disturbance of the soil by sharp hooves.

d. Complete elimination of plants from saddles, hogback ridges, goat trails, and along the rim of the Crater by feeding or loitering herds of goats.

e. Pawing of the ground by billies before lying down.

f. Increased erosion by rainfall of soils disturbed by goats.

h. Slides started by grazing goats.

i. Slides started by goats of all ages playing on the exposed cinders and basalt.

j. Slides started by rocks dislodged by feeding goats.

The most dramatic examples of goat and pig accelerated erosion occur on the flat tops of Pōhakupalaha and Kuiki, east of Palikū. In these areas several acres of exposed rocks are dotted here and there with mesa-like clumps of soil showing that at one time these areas were covered with six or more feet of topsoil held in place by native shrubs and grasses (Yocum 1967).

THE VEGETATION AND ENVIRONMENT IN THE CRATER DISTRICT OF HALEAKALA NATIONAL PARK

METHODS

Mapping

Reconnaissance

A preliminary reconnaissance was carried out during the CPSU/UH Crater District Resources Basic Inventory (RBI) expedition of June 14 through June 26, 1976. Plant names were learned with the help of the other members of the party so that most species could be identified on sight. Notes were taken on possible vegetation units in the areas visited on daily field trips which covered almost the entire area to be mapped. This work was facilitated by trips to the ridge summits from which large areas of the Crater were visible. This allowed a familiarization with the topography of the area and the distribution of the vegetation. Subsequent to this initial period of reconnaissance, a logical breakdown of the vegetation into structural units was developed. These units were used for preliminary mapping on aerial photographs.

Map Preparation

A set of 12 black-and-white aerial photographs that covered the area to be mapped were obtained from the Agricultural Stabilization and Conservation Service (USDA 1954 series). The aerial photograph scale was 1:12,000 since the final map was to be an overlay for the standard USGS quadrangle maps (scale 1:24,000). The scale of aerial photographs used for mapping should be at least twice as large as the scale planned for the printed map (Küchler 1967). Vegetation boundaries were drawn on transparent overlays over the photographs using the structural units developed during the reconnaissance of the area. These units were then field checked for accuracy and further notes were taken on their floristic composition. An attempt was made to visit all the mapped units so that information on each unit would be as complete as possible since aerial photographs show only the surface layer of the vegetation (Küchler 1967). The classification and boundaries of the units were modified as field observations deemed necessary. Thus, enough information was collected during this first stage of field work to produce a preliminary vegetation map for the Crater District.

To produce a preliminary vegetation map, boundaries were hand drawn on the USGS quadrangle maps. By using the field notes taken during the ground proofing, the original structural vegetation units used during preliminary mapping were translated into symbols corresponding as closely as possible to the structural-floristic symbols used in the vegetation map of Hawaii Volcanoes National Park (Mueller-Dombois & Fosberg 1974).

Aerial photographs contain scale distortions (termed relief displacement) due to elevational changes in the topography. However, distortions are minimal in 1:12,000 scale enlargements of NASA false infrared color air photographs due to the high altitude from which they were taken and the greater stability of the aircraft at that altitude. It was, therefore, decided to transfer the vegetation boundaries onto overlays on six of these photographs with adjustments based on field notes from a second summer's field work. Also, observations on these better quality photographs allowed further interpretation since different vegetation-types often showed variations in color.

These new overlays were photographically reduced to a scale of 1:24,000 resulting in six transparent positives at the same scale as the USGS maps. A very small amount of relief displacement yet remained in these positives. This error was corrected by altering the transparent positives using known topographic features on the quadrangle maps. These adjustments were made to give the best possible representation of the true position of the vegetation boundaries. The adjustments, therefore, were not necessarily uniform in direction or amount throughout the entire map nor even within a single transparent positive. The vegetation boundaries were then traced on yet another overlay. This pencil tracing was again traced in ink. The vegetation units were then labeled using a Varityper photographic typesetting machine and photographed again. Thus, a final vegetation map was produced that is approximately planimetrically correct at a scale of 1:24,000 and can overlay a composite of the USGS quadrangle maps of Haleakala National Park Crater District.

Quantitative Data Collection

Relevé Data

The sampling of the plant communities was planned according to the relevé (vegetation sample) method as described by Mueller-Dombois and Ellenberg (1974). First, the sites were selected using the hand-drawn, preliminary vegetation map. A total of 40 relevés were chosen: 15 in scrub communities, 15 in grassland communities, five in forest communities, and five in high altitude desert communities. This distribution was thought to reflect the quantitative occurrence of these community-types in the Park, except for the high altitude desert. These desert areas, although extensive, contained very little vegetation to sample. The relevés were placed in as even a geographic distribution as possible throughout the area to be mapped.

Since the Crater District is a high mountain region on an isolated oceanic island group, the flora is relatively poor in numbers of species. Therefore, it was decided to use certain empirical values for the size of the relevés based on the structure of the vegetation, rather than performing a minimal area analysis for each vegetation-type. Thus, the relevés chosen for grassland communities were 100 m^2 (10 X 10 m); 200 m^2 (10 X 20 m) for scrub communities; 400 m^2 (20 X 20 m) for forest communities; and 400 m^2 (20 X 20 m) for high altitude desert communities.

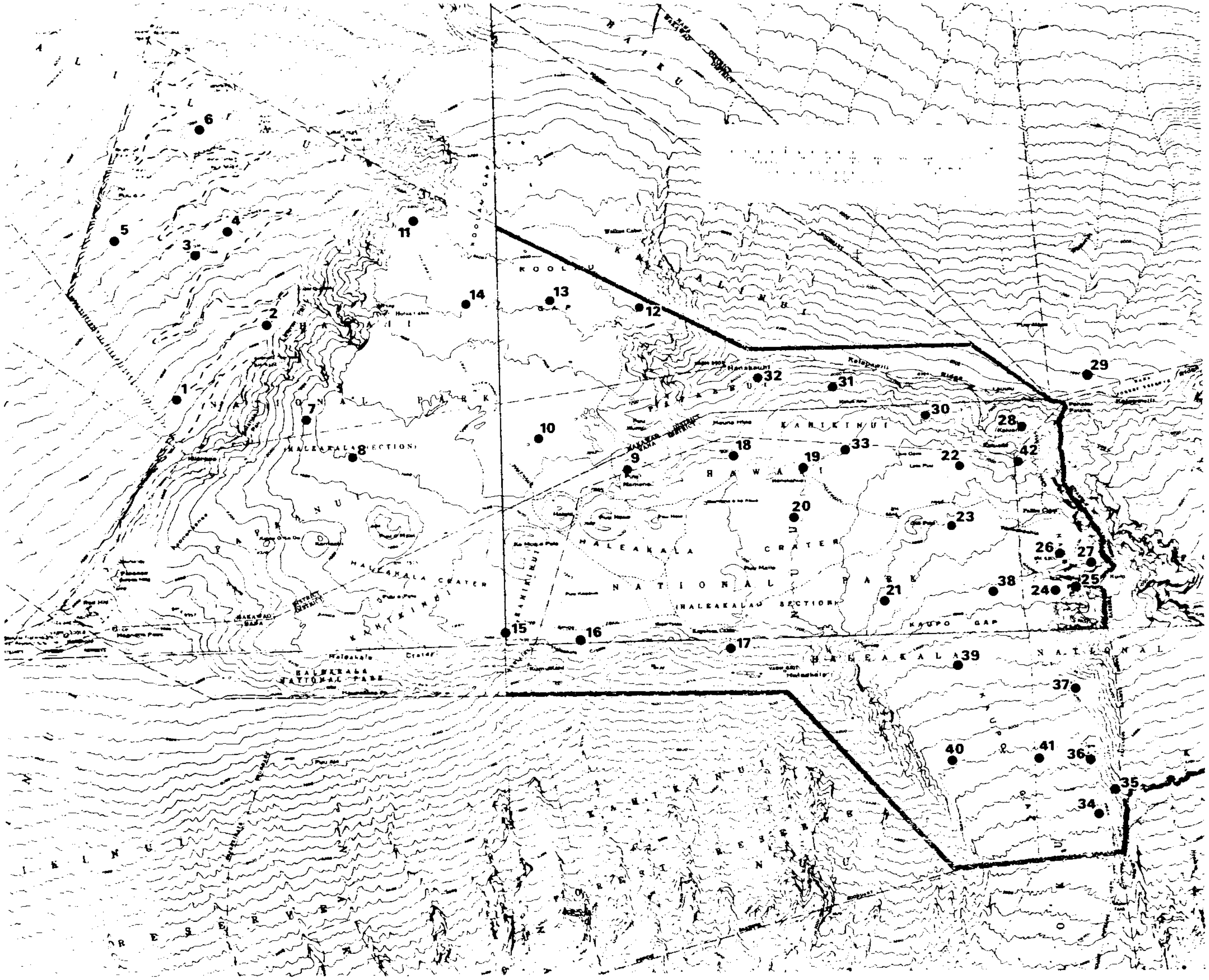
The field work for this segment was accomplished between June 3 and August 21, 1977. Each relevé was established at the planned location using a pair of cloth meter tapes. However, where the slope was excessively steep, the area had to be evaluated using a less formal but equivalent sample site. This latter approach was necessary at only three sites (relevés 25, 27, & 35). Certain environmental parameters were recorded on the printed data sheets. These were elevation using an altimeter, slope using an Abney level, and aspect using the walls of the Crater for orientation since magnetite in the area (e.g., Kuiki & Red Hill) produced distorted compass bearings. The location of the site, the relevé number, the substrate type, community-type as mapped on the preliminary map, the size of the relevé, and the stratification of the vegetation were also recorded. Additional remarks were recorded wherever relevant.

A complete species list was compiled for the relevé site in layers defined by height. Some species occurred in more than one layer and were therefore recorded more than once in a single releve. The quantity of each species in each layer was estimated using the Braun-Blanquet cover-abundance scale (Mueller-Dombois & Ellenberg 1974). Also, the life-form of each species was recorded using the Raunkiaer system (Mueller-Dombois & Ellenberg 1974). Appendix I gives a complete species list, by plant family, of plants found in relevé sites.

Two additional relevés were established to make the sampling more complete, one in a grassland community (relevé 7) and one in a scrub community (relevé 42). Relevé 7 was added to sample an open Deschampsia grassland on a scree slope on the inner west rim, since no relevé had been planned to sample this community. Relevé 42 was added to sample a vegetation unit that was added as a result of dividing a community, based on field observations, that appeared as a single unit on the preliminary map. Thus, the total number of relevés for the study was increased to 42 (Fig. 2).

Soil pits were planned at 10 of the relevé sites. They were selected in areas that were thought to have soil rather than a rock or cinder substrate so as to make a soil pit description possible. The soil pits were planned to have as even a geographic distribution as possible and to be representative of the communities occurring in the area. At each of the chosen sites, a pit was dug with a shovel to a depth at which a hard pan or rock layer was encountered. The total depth of the pit was measured and the horizontation of the soil was described including

FIGURE 2. Locations of relevé (vegetation sample) sites in the Crater District of Haleakala National Park. North is to the left.



each layer's color, texture, structure, and depth. A soil sample was taken from each soil pit for later analysis. One of the planned sites (relevé 38) was too rocky to dig a pit for a description of the soil profile, but a soil sample was taken. Thus, a total of nine soil descriptions were recorded and a total of 10 soil samples were taken.

Relevé Data Analyses

In a study of species distributions it is desirable to have an analytical methodology to objectively evaluate the distribution patterns. These methods should be of proven usefulness and be easily applicable to the relevé (vegetation sample) data collected in the field. It is also desirable that computer analysis techniques be utilized because of the large data base and the need for uniformity in the analysis. For these reasons, the synthesis table technique and the dendrograph technique described by Mueller-Dombois and Bridges (1975) were chosen.

Dendrograph Technique

A dendrograph is a two-dimensional diagram which displays the mutual relationships among a group of objects whose pairwise similarities are given. It differs from the usual dendrogram in that between-group similarities are calculated and displayed by scaling the distances along the X-axis. This scaling is in addition to the within-group similarities which are shown along the Y-axis of all dendrograms and dendrographs.

The data from the relevé sheets were entered into the computer. The dendrograph program of McCammon (McCammon & Wenniger 1970) was used because of its flexibility and tested usefulness. First, a matrix of similarity indexes is calculated using five methods of calculation resulting in five matrices: Jaccard, Gleason's modification of Jaccard, Spatz, presence/absence Sørensen, and quantitative Sørensen (Mueller-Dombois & Ellenberg 1974). Second, all percent indexes of similarity values are converted into metric distance values by the arc-cosine transformation. This transformation changes high similarity values into low distance values and vice versa. This transformation avoids the problem of averaging percentage values.

The construction of the dendrograph using the McCammon program is based entirely on the similarity matrix, so that the dendrograph is a mathematically derived display of the content of a similarity matrix. This derivation is accomplished by a computation cycle that, first, searches the matrix for the lowest arc-cosine value, which corresponds to the highest index of similarity value. The lowest arc-cosine value identifies the two relevés that are most similar in their quantitative species content. The computer then averages all distance values of these two relevés, thus reducing the similarity matrix by one column.

Then the computer again searches the entire matrix for the lowest distance value, which may be found either among the previously calculated values or among the new average values. Average values are again calculated, and the computation cycle is repeated in this way until all relevés are clustered. After the entire network of output clusters is established, the dendrograph is printed. Five dendrographs were produced in this way which correspond to the five methods of calculation of the indexes of similarity.

Synthesis Table Technique

The same relevé data used in the dendrograph technique were analyzed using the Ceska and Roemer (1971) program because of its unique flexibilities and its proven usefulness on the local computer. This program is a close simulation of the manual Braun-Blanquet synthesis table technique (Mueller-Dombois & Ellenberg 1974). The objective of the program is the extraction of those species groups from the table which optimally differentiate corresponding groups of relevés.

Group formation involves two processes which are repeated: selection of species which typify a group of relevés, and selection of relevés which are characterized by a certain group of species. Two rules are employed during the analysis. Species have to occur in at least X% of the relevés which are to be typified and they must not occur in more than Y% of all remaining relevés (rule I). Relevés are only considered to be members of the typified group if they contain X% of the typifying species (rule II). The several X/Y options examined were 50/10, 50/20, 66/10, 66/20, and 66/33. Formation of groups proceeds from species with higher constancies to species with lower constancies. First, a preliminary group is formed coinciding with the occurrence of a single initiating species. This group is then successively modified by alternating the application of rules I and II until a stable combination of species and relevés is achieved. The species groups formed in this way are listed together with a table containing these groups ordered according to size of groups and mean within-group similarity. This order can be subsequently rearranged for a better presentation of the analysis without changing the species combinations.

Since omnipresent species do not contribute any information to the differentiation of vegetation units, this program rejects species that are present in all or nearly all of the relevés. These species that are rejected at the start of the analysis are those that are present in 66% or more of the relevés under comparison, an arbitrarily set limit that conforms to a general norm used in phytosociological work. Species that occur in not more than two relevés also are not used in the analysis. Also, if a species cannot be grouped with at least a second species according to rule I, it is rejected as a "single species." Omnipresent species, low-constancy species, and single species appear at the end of the final table as ungrouped species.

Soil Analyses

Organic Carbon

Organic carbon was determined by a modification of the Walkley (1935) and Black (1965) methods using acid dichromate digestion. This method involves the oxidation of organic matter by potassium dichromate. The reaction is stimulated by the heat generated when two volumes of concentrated sulfuric acid are mixed with one volume of the 1N potassium dichromate solution. The excess dichromate is determined by titration with standard ferrous sulfate solution and the amount of organic matter oxidized is calculated from the amount of potassium dichromate reduced. Multiplication by a factor of 1.724 gives organic matter as a percent of oven dry weight of soil. Three replicates of each of 10 soil samples were analyzed.

pH

Soil pH was measured electrometrically using a Beckman Phasar-I digital pH meter. Equal volumes of soil and deionized water were mixed and left to stand for 24-hours to allow for an equilibrium to be established. The pH meter was calibrated using standard solutions of both pH 4.0 and pH 7.0. Readings were taken for three replicates of each of 10 soil samples.

Field Capacity and Permanent-Wilting Percentage

Field capacity and permanent-wilting percentage were determined using pressure plates, a standard laboratory technique. Soils were placed in rubber retaining rings and placed on the pressure plates. The plates were covered with water to wet the samples from below and left to soak overnight. Excess water was drained off and the pressure plates were placed in a pressure chamber. An extraction pressure of 0.1 bar was used for field capacity while an extraction pressure of 15 bars was used for permanent-wilting percentage. The samples were allowed to remain in the pressure chambers until the water content was stable. The samples were transferred to soil cans, weighed, oven dried, and weighed again. Moisture content was calculated as a percentage of oven dry weight. Three replicates for each of 10 soil samples were tested at each extraction pressure.

RESULTS AND DISCUSSION
VEGETATION MAP AND PROFILE DIAGRAMS

Vegetation Map

The final form of the vegetation map consists of labeled vegetation units outlined on a clear plastic overlay to a composite of the USGS quadrangle maps that cover the Crater District of Haleakala National Park. Copies of this final map are on file at Western Regional Headquarters of the National Park Service, San Francisco; Haleakala National Park Headquarters, Maui; and the Cooperative National Park Resource Studies Unit in the Department of Botany, University of Hawaii at Manoa, Honolulu. The map is presented here as a simple fold-out map sheet (see pocket on inside of back cover).

The communities are labeled on the map using a combination of symbols derived from generic names, plant cover designations, vegetation structure, substrate, or other predominant surface feature. Symbol combinations usually contain a front symbol of letters indicating the more obvious vegetation or surface features and an attribute symbol added in parentheses after the front symbol to indicate a finer variation within those features (Mueller-Dombois & Fosberg 1974). A total of 19 symbols were used to construct the map units which appear on the vegetation map (Table 1).

The mapped vegetation has been classified into 53 structural-floristic communities that are grouped into four structural vegetation-types (Table 2). Forest communities were defined as those areas in which the tallest vegetation layer was composed of woody vegetation greater than or equal to 5 m (16 ft) in height with at least 30% crown cover. Scrub communities were defined as areas in which the uppermost vegetation layer was composed of woody species greater than 0.3 m (1 ft) but less than 5 m in height with a crown cover exceeding 30%. Grassland communities were defined as areas in which grass species had more than 30% cover while the cover of woody species was less than 30%. High altitude desert communities were defined as areas having less than 30% total plant cover. Cover was defined as the vertical projection of the crown or shoot area of a species to the ground and expressed as a percent of the reference area (Mueller-Dombois & Ellenberg 1974). Closed cover was defined as 60% or more cover. Open cover was defined as 30-60% cover. Sparse cover was defined as less than 30% cover. These cover designations were applied to a single layer of the vegetation. For example, a community may be termed an open cover forest community with a closed cover shrub layer composing the understory.

Areas for the vegetation communities mapped at 1:24,000 (Table 3) were determined using an electronic planimeter. The total area mapped was 7544.8 ha (18,643 acres). Scrub communities had the largest total area of 3691.7 ha (9122 acres). Forest communities had the smallest total area of 164.9 ha (407 acres). In terms of area, the most common map unit was those

TABLE 1. Explanation of map symbols used for vegetation unit descriptions in the Crater District of Haleakala National Park.

Symbol	Explanation
Ac	*Acacia koa*
c	closed (>60% cover) used only in combinations
cin	cinder
D	*Deschampsia australis*
Dd	*Dodonaea eriocarpa* (individuals of tree stature)
Eu	*Eupatorium adenophorum*
Hl	*Holcus lanatus*
it	introduced trees (*Eucalyptus*, *Pinus*, etc.)
M	*Metrosideros collina*
mx	mixed grasses (*Holcus*, *Anthoxanthum*, *Poa*, etc.)
My	*Myrsine lanaiensis*
ns	native shrubs (Styphelia, Vaccinium, Coprosma, etc.)
o	open (30-60% cover) used only in combinations
Pe	*Pennisetum clandestinum*
r	rock (commonly pāhoehoe or 'a'ā lava)
Ru	*Rubus hawaiiensis*
Sd	*Sadleria cyatheoides*
So	*Sophora chrysophylla* (individuals of tree stature)
(xy)	symbol in parentheses indicates scattered or sparse cover (<30%) or as an understory of or matrix between the vegetation of the front symbol, used only in combinations

TABLE 2. Symbols and names of mapped vegetation units in the Crater District of Haleakala National Park.

Map Symbol	Community Name
Forest communities	
cM	closed Metrosideros forest
cDd-My	closed Dodonaea and Myrsine forest
cDd-Ac	closed Dodonaea and Acacia forest
oM	open Metrosideros forest
oM(ns)	open Metrosideros forest with a native scrub understory
oM-My(Sd)	open Metrosideros and Myrsine forest with much Sadleria in the understory
oDd(M)	open Dodonaea forest with scattered Metrosideros individuals
oDd-So	open Dodonaea and Sophora forest
oAc(mx)	open Acacia forest with a mixed grass matrix
oM-So(ns)	open Metrosideros and Sophora forest with an understory of native shrubs
it	introduced trees (Eucalyptus, Pinus, etc.)
Scrub communities	
cns	closed native scrub on substrates of various particle size
cns(mx)	closed native scrub with a mixed grass matrix
cns-mx	closed native scrub with a closed cover mixed grass matrix
cns(r)	closed native scrub on a rock substrate
ns	open native scrub on substrates of various particle size
ns(cin)	open native scrub on a cinder substrate
ns(r)	open native scrub on a rock substrate
ns(mx)	open native scrub with a mixed grass matrix
ns-mx	open native scrub with a mixed grass matrix having open to closed cover
ns-mx(Sd)	open native scrub with an open to closed mixed grass matrix and scattered Sadleria ferns
ns-mx(r)	open native scrub with an open mixed grass matrix on a rock substrate
ns(So-mx)	open native scrub with scattered Sophora trees and a mixed grass matrix
ns(r-cin)	open native scrub on a rock and cinder substrate
ns(mx-r)	open native scrub with a matrix of mixed grasses and exposed rock
ns(D)	open native scrub with a Deschampsia grass matrix

TABLE 2--Continued.

Map Symbol	Community Name
Scrub communities (con't.)	
ns-D	open native scrub with a Deschampsia grass matrix having open to closed cover
ns-r	open native scrub with a matrix of exposed rock having nearly equal cover
cRu-mx	closed *Rubus* patch with a closed mixed grass matrix
cEu(mx)	closed *Eupatorium* patch with a mixed grass matrix
Grassland communities	
cD	closed *Deschampsia* grassland
cD-Hl	closed *Deschampsia* and *Holcus* grassland
cHl-D(ns)	closed *Holcus* and *Deschampsia* grassland with scattered native shrubs
cHl(D)	closed *Holcus* grassland with scattered *Deschampsia* tussocks
cHl	closed *Holcus* grassland
Pe(Hl)	closed *Pennisetum* grassland with scattered *Holcus*
cmx	closed mixed grass grassland
oD	open *Deschampsia* grassland
oD(ns)	open *Deschampsia* grassland with scattered native shrubs
oD(So)	open *Deschampsia* grassland with scattered *Sophora* trees
mx	mixed grasses
mx(ns)	mixed grasses with scattered native shrubs
mx(So)	mixed grasses with scattered *Sophora* trees
mx(Sd)	mixed grasses with scattered *Sadleria* ferns
High altitude desert communities	
cin	barren cinder
cin(ns)	barren cinder with scattered native shrubs
cin(D)	barren cinder with scattered *Deschampsia* grass tussocks
r-cin	barren rock and cinder
r-cin(ns)	barren rock and cinder with scattered native shrubs
r-cin(D)	barren rock and cinder with scattered *Deschampsia* grass tussocks
r(ns)	barren rock with scattered native shrubs
r(ns-mx)	barren rock with scattered native shrubs and mixed grasses
r-ns	barren rock with native shrubs

TABLE 3. Total area mapped by vegetation-types and map units in the Crater District of Haleakala National Park.

		Map Unit	Area	
			Hectares	Acres
STRUCTURE	Forest	cDd-My	19.09	47.18
		cDd-Ac	10.71	26.46
		cM	2.06	5.09
		oM	42.81	105.77
		oM(ns)	23.76	58.72
		oM-So(ns)	4.82	11.91
		oM-My(Sd)	4.19	10.36
		oDd(M)	8.39	20.73
		oDd-So	4.19	10.35
		oAc(mx)	21.35	52.76
		it	23.53	58.14
		Total	164.90	407.47
	Scrub	cns	407.76	1007.57
		cns(mx)	611.55	1511.12
		cns-mx	141.75	350.27
		cns(r)	278.66	688.57
		ns(cin)	59.34	146.62
		ns(r)	537.34	1327.74
		ns(mx)	588.65	1454.53
		ns(So-mx)	14.12	34.89
		ns(r-cin)	284.81	703.76
		ns(mx-r)	167.49	413.87
		ns(D)	131.28	324.40
		ns-D	35.04	86.58
		ns-mx	199.54	493.06
		ns-mx(Sd)	80.74	199.50
		ns-mx(r)	81.42	201.18
		ns-r	48.50	119.83
		ns	16.60	41.02
		cEu(mx)	1.91	4.73
		cRu-mx	5.18	12.79
		Total	9122.03	3691.68
	Grassland	cD	80.58	199.12
		cD-Hl	21.45	53.00
		cmx	0.63	1.56
		cHl	17.11	42.29
		cHl(D)	11.89	29.39
		cHl-D(ns)	14.58	36.02
		Pe(Hl)	12.70	31.38

TABLE 3--Continued.

				Area	
		Map Unit		Hectares	Acres
STRUCTURE	Grassland	oD		168.11	415.40
		oD(ns)		57.01	140.87
		oD(So)		5.14	12.71
		mx(So)		32.78	81.01
		mx(Sd)		6.31	15.60
		mx(ns)		111.23	274.85
		mx		29.04	71.76
			Total	568.56	1404.96
	High Altitude Desert	cin		1015.59	2509.48
		cin(ns)		61.72	152.51
		cin(D)		110.91	274.06
		r-cin		1119.46	2766.15
		r-ns		2.34	5.78
		r-cin(ns)		157.80	389.93
		r-cin(D)		103.29	255.22
		r(ns)		450.97	1114.34
		r(ns-mx)		97.59	241.15
			Total	3119.67	7708.62
			TOTAL	7544.81	18643.08

areas where the rock and cinder substrate was the dominant surface feature (r-cin). This single unit had a total area of 1119.5 ha (2766 acres), larger than the total for forest and grassland communities combined. In terms of frequency, the most common community was open cover mixed grasses with scattered native shrubs mx(ns). This community was mapped 15 times but had a total area of only 111.2 ha (275 acres). The most common map unit, in terms of area, with significant vegetation cover (>30%) was closed native scrub with a mixed grass matrix cns(mx). This community covered 611.6 ha (1511 acres) of the study area.

Profile Diagrams

Three topographic vegetation profiles were constructed to aid in the interpretation of the map units. The courses of these profiles are shown on a reference map of the Park (Fig. 3). These courses were chosen to cross as much of the study area as possible while illustrating as much of the range in vegetation-types and environmental variables as possible. Profile 1 (Fig. 4) runs from the Park boundary at Pu'u Nianiau on the northwest outside slope at 2087.5 m (6849 ft) to Kilohana on the west rim of the Crater at 2926.1 m (9600 ft). Profile 2 (Fig. 5) runs from Kilohana, across the crater floor, to the east rim of the Crater above Palikū Cabin (1945 m/5850 ft) that separates Haleakalā Crater from Kīpahulu Valley at 2133.6 m (7000 ft). Profile 3 (Fig. 6) runs from the southern Park boundary in Kaupō Gap at 1158.2 m (3800 ft) up over Kalapawili Ridge at 2484 m (8150 ft) to the northern Park boundary on the north outside slope at 2316.5 m (7600 ft).

In profile 1 (Fig. 4), a decrease in both mean annual precipitation and mean annual temperature are associated with the increase in elevation. An apparent effect of the temperature gradient can be seen at about 2590.8 m (8500 ft) where the vegetation becomes very sparse and can be termed a high altitude desert. This change may be associated with the diurnal (daily) frost boundary, above which freezing temperatures occur at ground level every night of the year. A similar association occurs at approximately this elevation on Mauna Loa on the island of Hawai'i (Mueller-Dombois 1967).

In profile 2 (Fig. 5), an increase in mean annual temperature is associated with the decrease in elevation. An increase in mean annual precipitation is associated with the west to east orientation. The increase in rainfall is related to greater exposure to the effects of the predominant northeast trade winds. These factors result in a gradual increase in cover and stature of the vegetation from low growing very sparse vegetation (high altitude desert) through several variations of scrub communities to a low-stature rain forest.

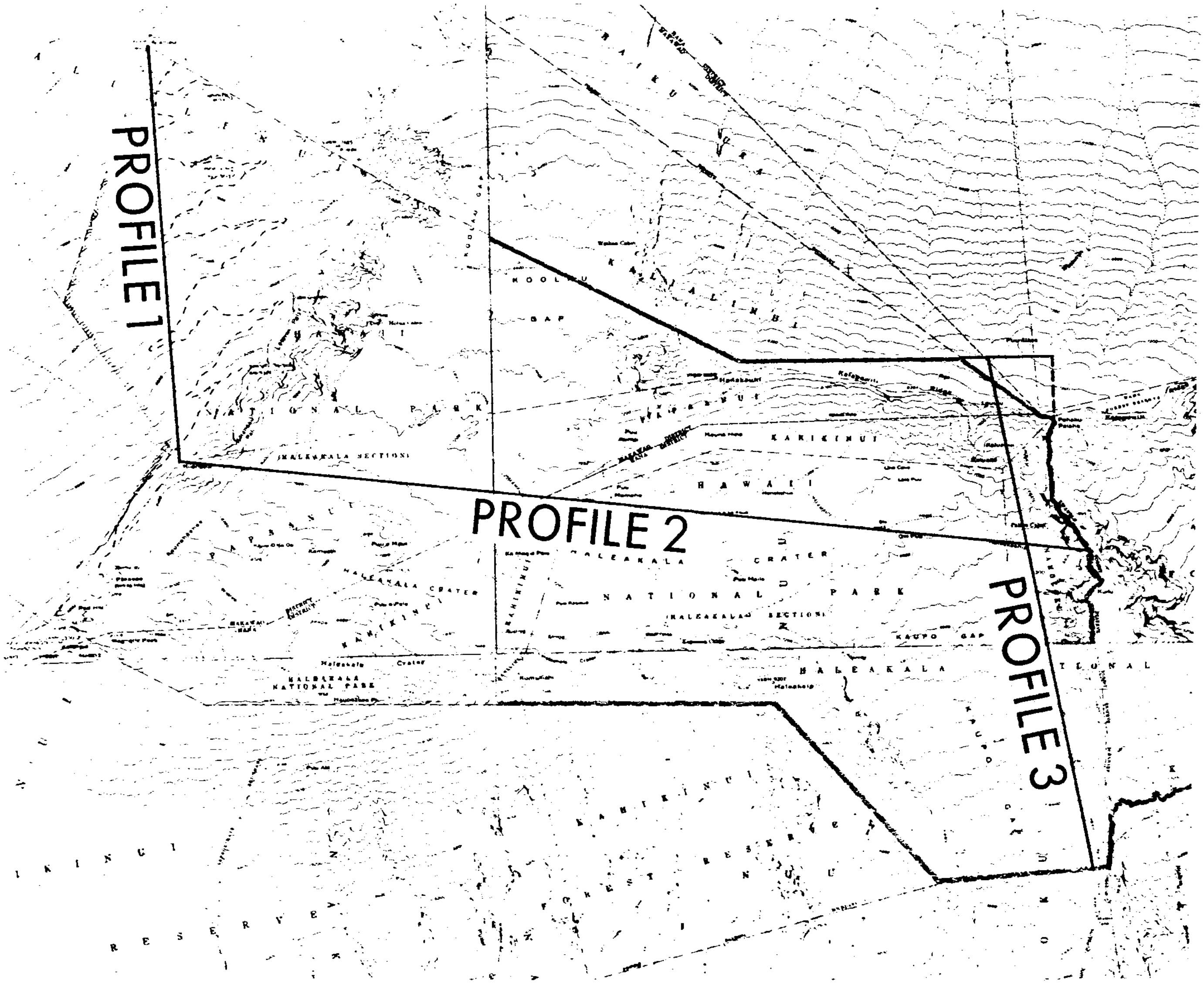
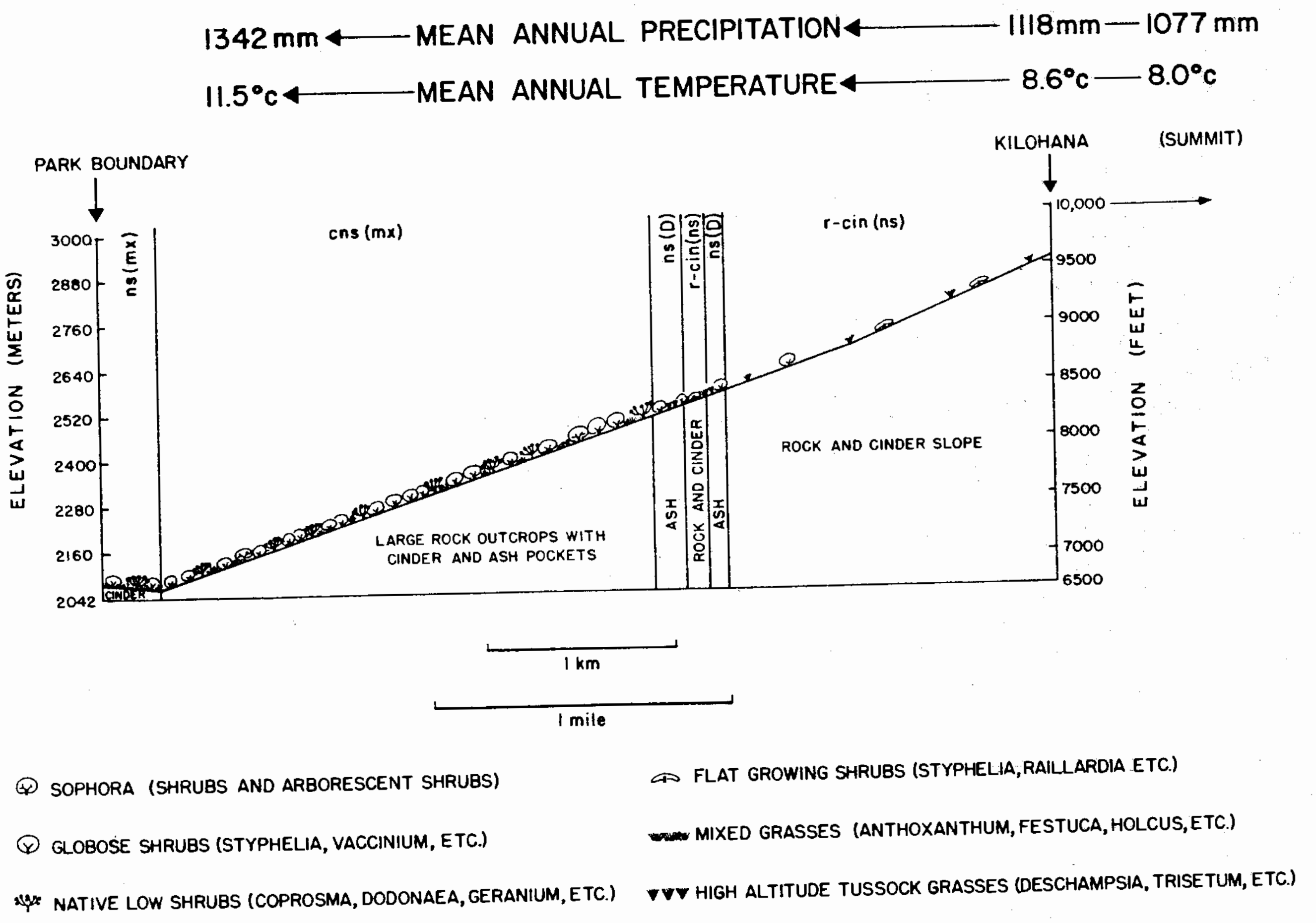


FIGURE 3. Courses of the topographic vegetation profiles of the Crater District of Haleakala National Park. North is towards the binding. Approximate scale is 1:77,000.

FIGURE 4. Topographic vegetation profile 1 of the Crater District of Haleakala National Park.



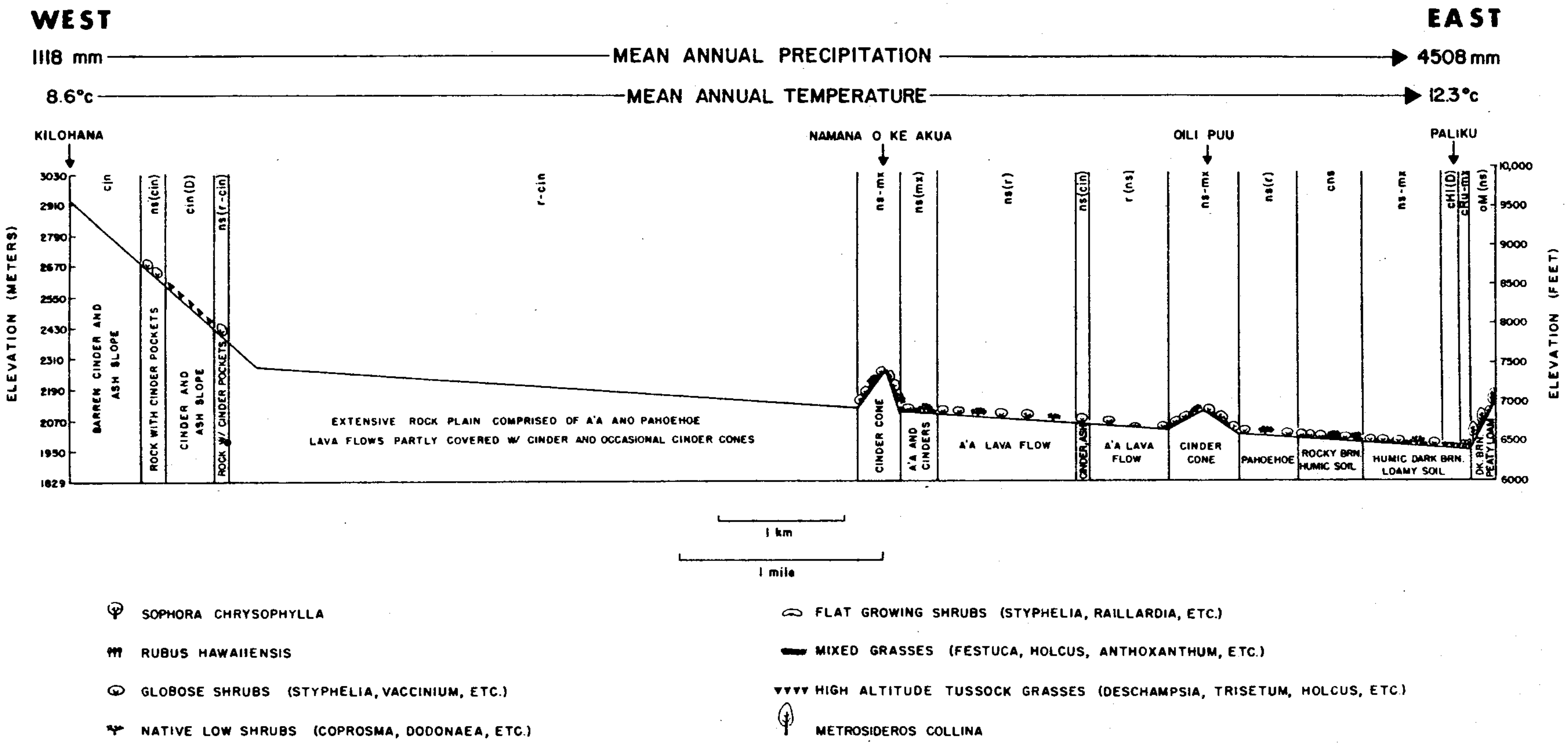
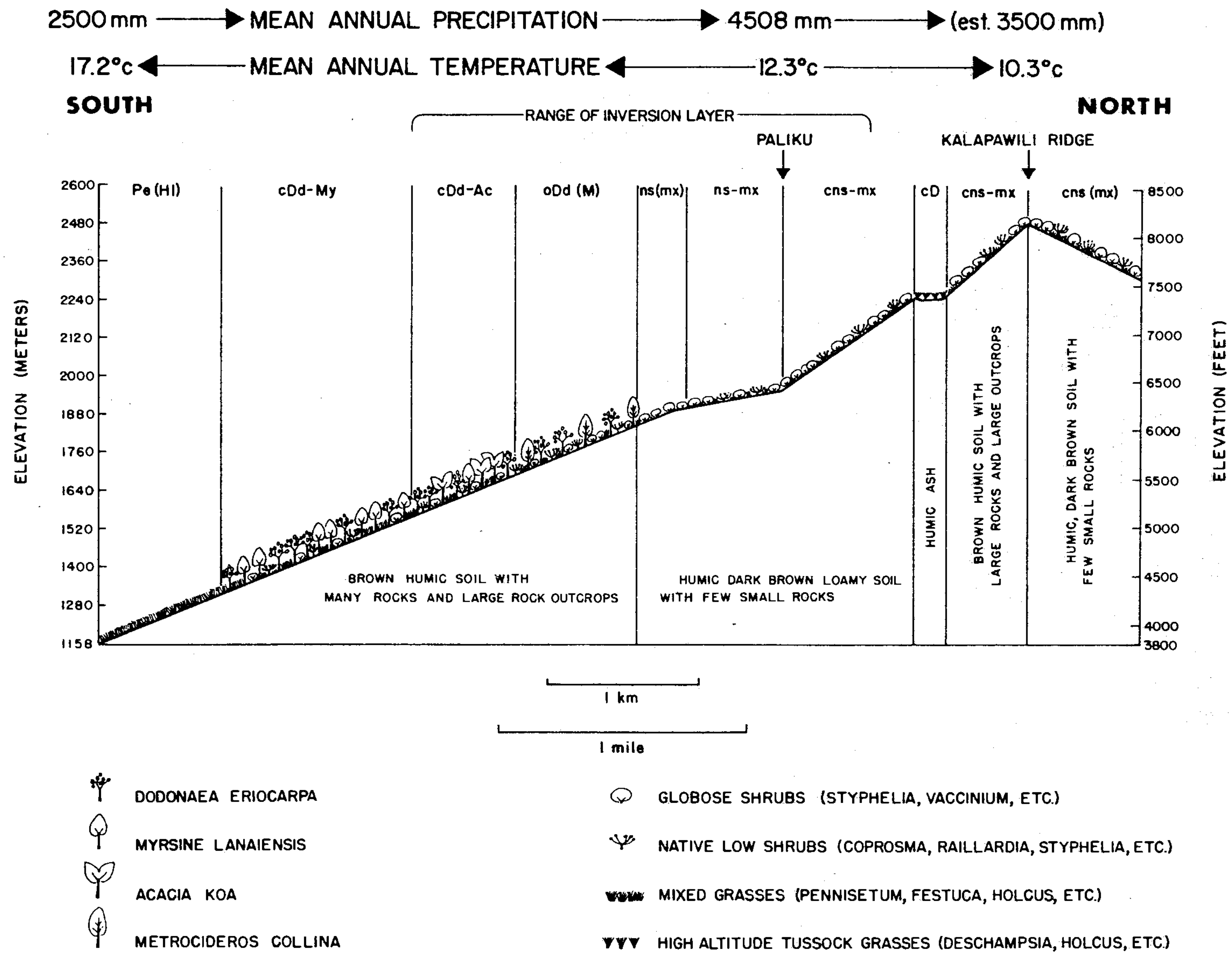


FIGURE 5. Topographic vegetation profile 2 of the Crater District of Haleakala National Park.

FIGURE 6. Topographic vegetation profile 3 of the Crater District of Haleakala National Park.



In profile 3 (Fig. 6), a decrease in mean annual temperature is associated with the increase in elevation, and an increase in mean annual precipitation resulting from greater exposure to the effects of the northeast trade winds is associated with the south to north orientation. The lower end of the profile also extends below the inversion layer which occurs between 1700 and 2300 m (5000-7000 ft) elevation (Blumenstock & Price 1967). This factor complex results in several forest communities between 1290 and 1890 m (4240-6200 ft) which are unique to this section of the study area.

These profiles also show the relationship between substrate and community-type. Matching correlations include open tussock grasslands on cinder and ash slopes, scrub communities with little or no grass matrix on rocky substrates, scrub communities with a grass matrix on moderately rocky cinder and ash-derived soils, and closed cover grasslands on deep, fine textured cinder and ash derived soils which occur on almost level ground. These correlations, of course, do not explain all causative relationships since soil and vegetation each influence the composition of the other with both being under the influence of the climate. The relationships between environmental factors and the vegetation patterns are further discussed below with the aid of these topographic vegetation profiles.

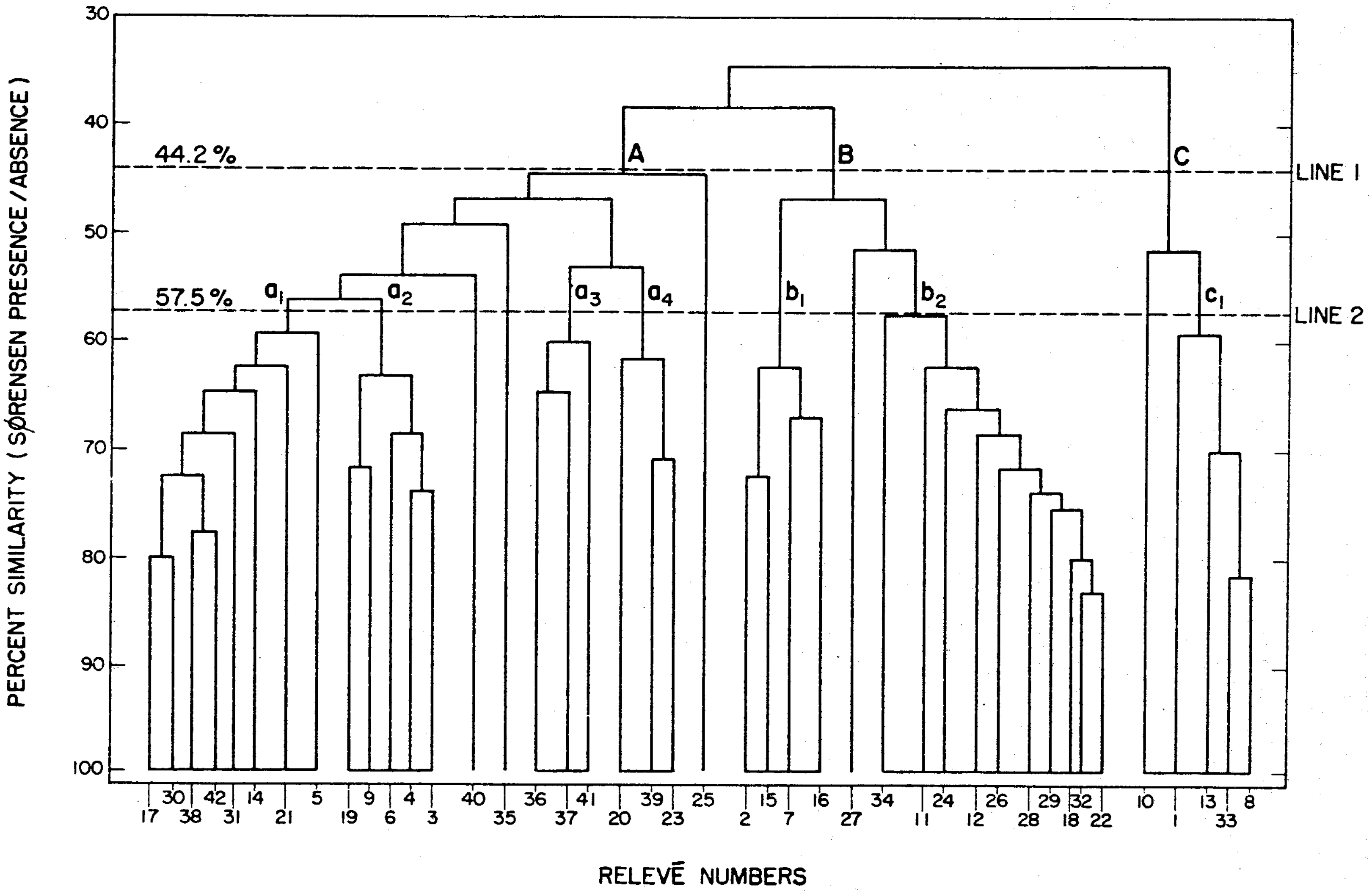
FLORISTIC COMMUNITY ANALYSES

Dendrograph Analysis

Five dendrographs were produced corresponding to the five matrices of similarity indexes associated with the five methods for calculation of the indexes of similarity. All five dendrographs produced similar groupings of the relevés (vegetation samples), but the dendrograph based on Sørensen's presence/absence method of calculation was thought to give the best results since it showed fewer inconsistencies in the groupings. Inconsistencies were considered to be the clustering of structurally and floristically dissimilar vegetation-types into the same group. These contradictions result from a particular calculation method overemphasizing one or more species common to several relevés. For example, forest, scrub, and grassland communities having obvious structural and floristic differences may be grouped together based on the high cover value of a single species in one layer, such as Holcus lanatus L. (velvetgrass) in the herb layer. The dendrograph which best fits the conclusions reached from other approaches (synthesis table technique and field assessment) is shown in Figure 7.

Two cut-off lines were used for the objective identification of dendrograph clusters. Since the purpose of this analysis was to identify ecologically meaningful clusters, the first line, line 1 in Figure 7, was drawn such that no relevés were left unclustered. This condition was fulfilled at a within-group

FIGURE 7. Dendrograph from Sørensen's presence/absence indexes of similarity for relevé (vegetation sample) data from the Crater District of Haleakala National Park.



similarity of 44% and identifies three major clusters (A, B, and C). These three clusters have the lowest similarity to one another. Line 2 in Figure 7 was drawn at a level that isolates seven more narrowly defined clusters with a minimum of single clusters. The seven clusters (a_1, a_2, a_3, a_4, b_1, b_2, and c) were isolated at a within-group similarity of 57.5% which left five relevés unclustered (40, 35, 27, 25, & 10), or only 12% of the total number of relevés.

The three lower-similarity clusters (A, B, C on Fig. 7) divide the vegetation into structural categories. Cluster A groups scrub and forest relevés, cluster B groups grassland relevés, and cluster C groups high altitude desert relevés. The seven higher-similarity clusters subdivide the lower-similarity clusters into finer vegetation-types. The five relevés not included in the higher-similarity clusters were left as single clusters since they are unique in the study area in some way.

Four subclusters and three unclustered relevés resulted from subdividing the broad woody vegetation group of cluster A. Cluster a_1 (relevés 17, 21, 30, 38, 5, 14, 42, & 31) represents native scrub communities characterized by *Styphelia* (pūkiawe) and Vaccinium ('ōhelo); cluster a_2 (relevés 3, 6, 9, 19, & 4) represents native scrub communities characterized by *Sophora* (māmane) and *Coprosma* (pilo); cluster a_3 (relevés 36, 37, & 41) represents forest and scrub communities with *Dodonaea* ('a'ali'i) trees in the tallest vegetation layer; and cluster a_4 (relevés 20, 23, & 39) represents native scrub communities with sparse (<30%) cover on rocky substrates. Relevé 35 is an open *Acacia koa* Gray (koa) forest community with many exotic species in the herbaceous layer which are not found elsewhere in the study area. Relevé 25 is an open, low stature *Metrosideros* ('ōhi'a) forest community. It is included in the woody community-type in the low-similarity clusters since the understory is dominated by shrub species. However, reference to the ungrouped species in Table 4 will show that this relevé contained species unique to the site. Relevé 40 is a scrub community dominated by pūkiawe (cluster a_1), but itis is located at a relatively low elevation and contains several species in the herbaceous layer that are unique within the study area.

The grassland communities (cluster B) were subdivided into two subclusters (which seem to be based on the presence or absence of velvetgrass) and one unclustered relevé. Cluster b_1 combines grassland relevés (2, 7, 15, & 16) in which velvetgrass is absent. Cluster b_2 combines grassland relevés (11, 12, 18, 22, 24, 28, 29, 32, & 34) in which velvetgrass is present. Relevé 27 is an open, low stature 'ōhi'a forest community. It was included in the grassland communities in the low-similarity clusters since its understory included two grass species of wide distribution within the study area, velvetgrass and *Deschampsia australis* Nees ex Steud. However, reference to the ungrouped species in Table 4 will show that this relevé contained species unique to the site.

Cluster c (relevés 13, 8, 33, & 1) combines all but one of the high altitude desert relevés in cluster C. Releve 10 is a high altitude desert community which contains only three species with less than 1% total cover and therefore this relevé is not qualitatively similar enough to be included in the high-similarity cluster (cluster c).

These results are summarized in Figure 8, in which the clusters and unclustered relevés were extracted to clarify the discussed vegetation-type relationships. Cluster designations appear on the left side of the figure, and relevé numbers along the top.

Synthesis Table Analysis

The Ceska and Roemer (1971) program produced five synthesis tables corresponding to the five inside-outside percentage combinations utilized. Of these, the 66/33 option was thought to give the best representation of the data since it produced the smallest number of relevés (vegetation samples) that did not contain a species group, thus it had the greatest number of relevés with some basis to group them into vegetation-types. This option resulted in eight species groups. The order of the relevés in the table were manually rearranged to more clearly show the distribution of these species groups. Rearrangement of the relevé order is a standard option of the program. The final synthesis table with both the grouped and ungrouped species is shown in Table 4, with the species groups within blocks of relevés outlined.

A summary chart (Fig. 9) was constructed from the data in Table 4, following a format developed by Mueller-Dombois and Bridges (1975), to further clarify the information displayed in the synthesis table. The species group numbers from Table 4 are listed on the left side of the chart in the same sequence as in the synthesis table. For drawing boundary lines, Mueller-Dombois and Bridges (1975) have suggested the criterion of having at least two group limits to indicate a boundary. However, in this study the analysis has resulted in much overlapping of group limits. Therefore, boundary lines were often drawn at the limits of one group using the knowledge of the vegetation gained while working in the field. A ninth species group was added which is composed of three nearly ubiquitous herbaceous species (Hypochaeris radicata L. [gosmore]; Deschampsia australis; and velvetgrass). The reason for this addition is discussed below.

Nine vegetation-types were identified and have been indicated on Table 4 and Figure 9. The first type is an open koa forest which is unique in the study area. It is the only vegetation-type represented by a single sample plot, relevé 35. The presence of species group 5 associates this type with the 'a'ali'i forest, but the koa forest lacks species group 6 and contains a number of ungrouped species (Table 4) that are found nowhere else in the study area.

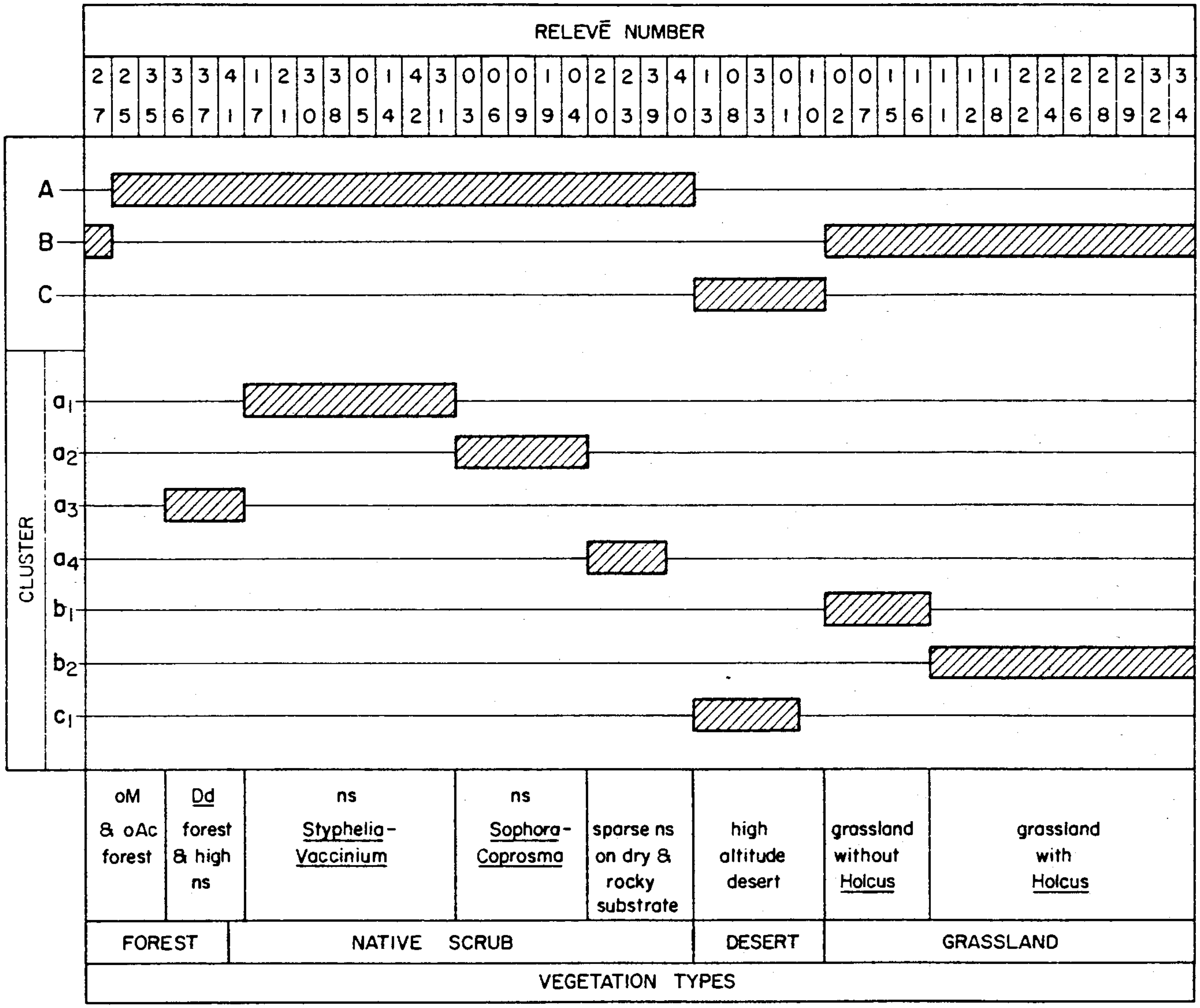


FIGURE 8. Summary chart of dendrograph clusters (Fig. 5) from Sørensen's presence/absence indexes of similarity of relevé (vegetation sample) data from the Crater District of Haleakala National Park.

TABLE 4. Synthesis table using the 66/33 option for relevé data from the Crater District of Haleakala National Park. Numbers in table refer to shoot or crown cover according to the Braun-Blanquet cover-abundance scale. 1=5% and numerous; 2=5-20%; 3=20-50%; 4=50-75%; 5=>75%; 6=small cover and few, 7=small cover and solitary

	Forest							Native Scrub															Desert					Grassland														
Vegetation Type	pA	oM		Dd				Sophora-Coprosma							Styphelia Vaccinium					on dry & rocky sub-strate			high altitude desert					with Pteridium							without Pteridium							
Relevé Number	35	27	25	36	37	41	38	20	42	19	09	05	06	03	04	17	21	30	40	39	23	14	13	08	33	10	01	02	18	22	24	31	32	34	07	11	12	15	16	26	28	29
SPECIES																																										
SPECIES GROUP 1																																										
Geranium cuneatum	-	-	-	-	-	-	-	-	-	-	-	-	6	6	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anthoxanthum odoratum	-	-	-	-	-	-	-	-	-	-	-	-	6	6	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SPECIES GROUP 2																																										
Fragaria chiloensis	-	6	6	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vaccinium berberifolium	-	2	6	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rubus hawaiiensis	-	6	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vaccinium calycinum	-	6	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Metrosideros collina	-	3	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Uncinia uncinata	-	6	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dryopteris paleacea	-	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SPECIES GROUP 3																																										
Coprosma montana	-	-	-	-	-	-	-	1	6	7	2	7	2	1	1	2	-	-	-	-	-	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sophora chrysophylla	-	-	2	6	-	-	-	2	6	2	2	6	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-	-	-	-	-	-	-
SPECIES GROUP 4																																										
Lysimachia sp.	-	-	6	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Myrsine lanaiensis	-	-	6	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

SPECIES GROUP 5

Eupatorium adenophorum	3	-	1	1	2	1	-	1	-	-	-	-	-	-	-	-	-	-	-	6	6	-	6	6	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dodonaea eriocarpa	1	-	1	2	3	2	2	6	7	-	-	1	-	-	-	-	-	-	-	6	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Osteomeles anthyllidifolia	-	-	-	1	1	6	1	6	-	-	-	-	-	-	-	-	-	-	-	6	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-

SPECIES GROUP 6

Pteridium aquilinum	-	1	1	1	1	1	1	-	1	2	2	6	1	1	1	1	1	1	6	-	-	1	-	-	-	-	-	1	2	6	1	1	2	6	3	-	-	2	-	-	-	-
Styphelia tameiameiae	6	2	-	2	2	2	2	2	2	7	1	1	2	2	2	3	3	2	5	2	1	2	6	-	-	-	1	-	-	-	-	2	-	7	-	-	-	-	-	-	-	-
Rumex acetocella	-	-	-	-	1	-	1	1	1	1	1	-	-	6	6	1	6	1	-	-	1	1	-	-	-	-	-	6	6	1	1	1	6	-	-	6	1	-	-	1	1	1

SPECIES GROUP 7

Cladonia leiodea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	6	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Stereocaulon vulcani	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	6	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Stereocaulon ramulosum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

SPECIES GROUP 8

Asplenium trichomanes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	6	6	6	6	7	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-
Tetramolopium humile	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	6	6	6	1	7	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

SPECIES GROUP 9

Hypochoeris radicata	1	6	6	1	1	1	1	1	1	2	6	6	1	1	6	1	1	1	1	1	6	6	6	6	6	-	6	6	1	1	-	1	6	6	6	-	6	6	6	-	6	1
Deschampsia australis	-	6	-	6	-	1	6	2	6	1	2	-	6	6	6	1	1	6	6	6	6	1	6	6	-	-	-	3	2	1	-	2	2	-	3	-	3	2	3	1	5	4
Holcus lanatus	3	6	1	2	2	1	2	1	2	4	1	1	1	1	-	6	-	2	1	-	1	-	-	-	7	-	-	-	1	5	5	1	6	2	-	2	4	-	-	5	1	2

UNGROUPED SPECIES

Vaccinium reticulatum	-	1	-	6	1	1	1	-	4	-	-	6	2	-	2	2	2	2	-	6	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pellaea ternifolia	-	-	-	-	-	-	-	1	-	-	-	1	-	-	6	6	6	6	6	1	1	1	6	6	1	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trisetum glomeratum	-	-	-	-	-	-	-	-	-	6	6	-	-	6	1	6	-	6	-	-	6	6	-	-	-	-	6	1	6	-	-	-	-	-	-	-	-	6	-	-	-	-
Luzula hawaiiensis	-	-	-	6	6	-	1	6	1	-	-	6	-	-	6	6	-	1	-	-	-	6	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	6
Festuca megalura	-	-	-	-	-	1	-	1	-	6	6	6	-	-	-	6	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-
Railliardia menziesii	-	-	-	-	-	-	-	-	6	-	1	-	-	6	1	-	-	-	-	-	-	1	-	6	1	6	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

TABLE 4--Continued.

Vegetation Type	Forest							Native Scrub															Desert					Grassland														
	oA	oM		Dd				Sophora-Coprosma							Styphelia Vaccinium					on dry & rocky sub-strate			high altitude desert					with Pteridium							without Pteridium							
Relevé Number	35	27	25	36	37	41	38	20	42	19	09	05	06	03	04	17	21	30	40	39	23	14	13	08	33	10	01	02	18	22	24	31	32	34	07	11	12	15	16	26	28	29
SPECIES																																										
UNGROUPED SPECIES (con't.)																																										
Epilobium cinereum	-	-	-	-	6	-	6	-	1	-	6	-	-	-	-	6	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-
Rhacomitrium lanuginosum	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	1	-	-	1	1	6	6	6	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Coprosma ernodeoides	-	1	-	-	-	-	1	-	1	-	-	-	-	-	-	6	1	6	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lythrum maritimum	2	-	1	1	1	6	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Carex wahuensis	-	-	-	-	6	-	-	6	-	-	-	-	6	6	7	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carex macloviana	-	6	-	-	-	-	-	-	-	6	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	6	-	-	-	-	-	-	-	-	6	-
Polypodium pellucidum	-	6	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	6	-	6	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lapsana communis	2	-	-	1	1	-	-	-	-	6	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Machaerina gahniaeformis	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	1	6	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sadleria cyatheoides	6	2	1	-	-	-	-	-	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Coprosma ochracea	1	-	1	1	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Asplenium adiantum-nigrum	-	-	-	-	-	-	-	7	-	-	6	-	-	-	-	-	-	6	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Agrostis sandwicensis	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	6	-	1	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Silene gallica	-	-	-	-	-	-	-	6	-	-	-	6	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Poa pratensis	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	2	-
Anagallis arvensis	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	6	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aira caryophyllea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	6	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sonchus oleraceus	6	-	-	6	-	-	-	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bromus rigidus	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-
Dactylis glomerata	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-

Polycarpon tetraphyllum	- - - - - - - - - - - - - - - - 1 - 1 -
Acacia koa	3 - - - 3 -
Verbena litoralis	6 - - - - 6 -
Cerastium vulgatum	- 6 -
Dryopteris parallelograma	- - - - - - - - - - - - 7 -
Gnaphalium sandwicensium	- 6 - - - - - - - - - - - - - - - - - -
Oenothera stricta	- - - - - - - - - 6 -
Gouldia hillebrandii	- - 6 -
Stenogyne crenata	- - - - - - - - - - - - - 6 -
Plantago lanceolata	- - - - - - - - - - - 1 -
Festuca dertonensis	- 6 - - - - - - - - - - - - - - - - - - -
Pleopeltis thunbergiana	- - 6 -
Polystichum hillebrandii	- - 6 -
Sanicula sandwicensis	- - - - - - - - - - 6 -
Microlepia speluncae	- - 6 -
Asplenium macraei	- - 6 -
Thuidium plicatum	- - 6 -
Athyrium microphyllum	- - 1 -
Peperomia erythroclada	- - 1 -
Danthonia semiannularis	- - - - - - - - - - - 6 -
Carex alligata	- - 6 -
Cheirodendron trigynum	- 6 -
Railliardia platyphylla	- 6 -
Astelia forbesii	- 6 -
Lycopodium venustulum	- 3 -
Elaphoglossum hirtum	- - 6 -
Sporobolus africanus	- 6 - - - - - - - -
Cyperus brevifolius	- 1 - - - - - - - -

TABLE 4--Continued.

Vegetation Type	Forest							Native Scrub															Desert					Grassland														
	bA	oM		Dd				Sophora-Coprosma							Styphelia Vaccinium					on dry & rocky substrate			high altitude desert					with Pteridium							without Pteridium							
Relevé Number	35	27	25	36	37	41	38	20	42	19	09	05	06	03	04	17	21	30	40	39	23	14	13	08	33	10	01	02	18	22	24	31	32	34	07	11	12	15	16	26	28	29
SPECIES																																										
UNGROUPED SPECIES (con't.)																																										
Dryopteris glabra	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pityogramma chrysophylla	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rubus rosaefolius	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nephrolepis exaltata	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dryopteris unidentata	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyperaceae sp.	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhynchelytrum repens	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bidens pilosa	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eragrostis variabilis	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pennisetum clandestinum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-
Convolvulaceae sp.	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pteris cretica	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lysimachia sp.	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Usnea rubicunda	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gnaphalium purpureum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cirsium vulgare	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Erigeron bonariensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Centaurium erythraea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cocculus ferrandianus	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Festuca sp.	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

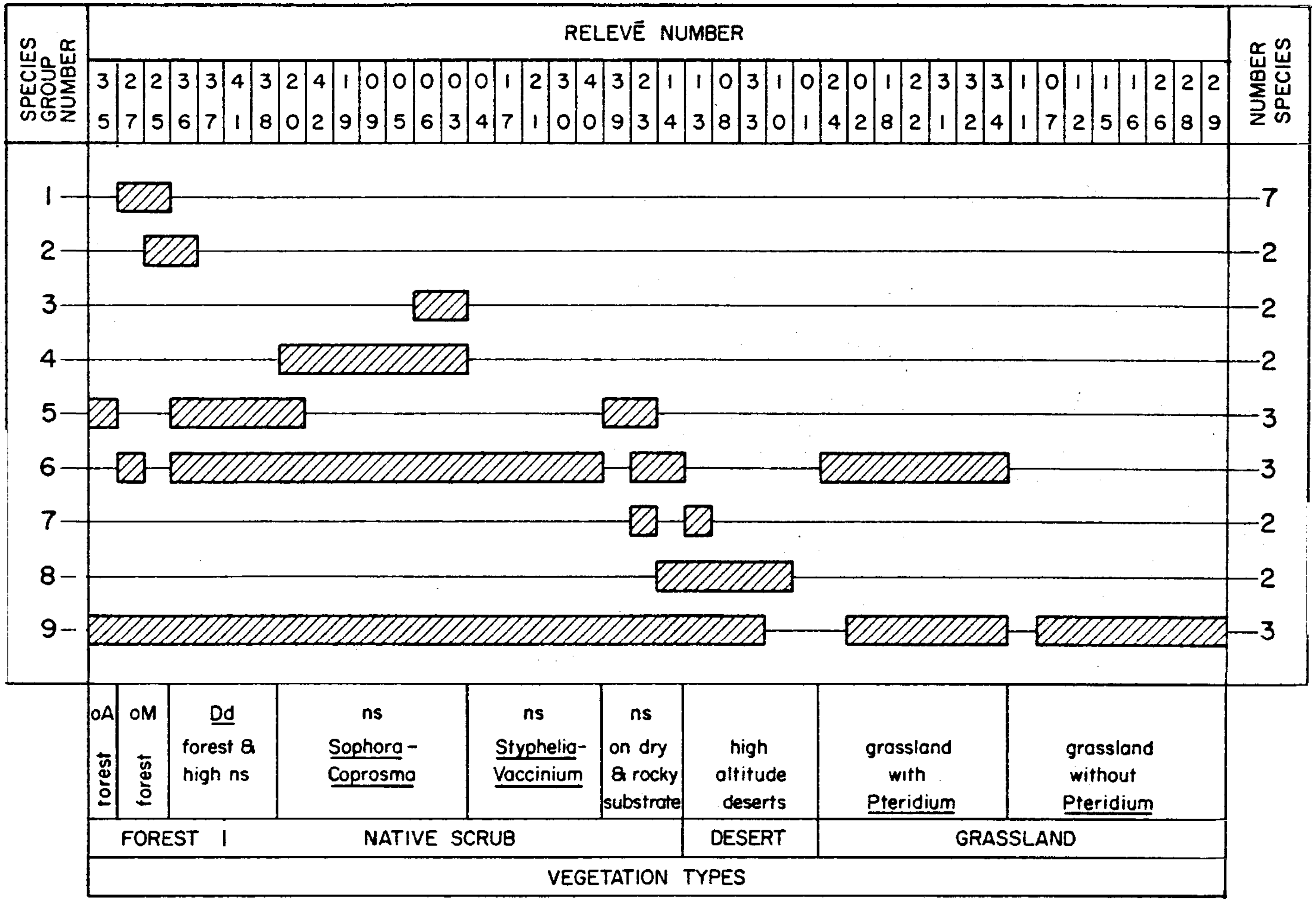


FIGURE 9. Summary chart of data from Synthesis Table (Table 4) using 66/33 option for relevé (vegetation sample) data from the Crater District of Haleakala National Park.

The next type is defined by species group 2 (*Fragaria chiloensis* (L.) Duch. [strawberry]; *Vaccinium berberifolium* (Gray) Skottsb. ['ōhelo]; *Dryopteris paleacea* (Swartz.) C. Chr.; *Metrosideros collina* (J. R. & G. Forst.) Gray; ['ōhi'a]; *Vaccinium calycinum* Sm. ['ōhelo]; *Uncinia uncinata* (L. f.) Kuek.; and *Rubus hawaiiensis* Gray ['ākala]) and includes relevés 25 and 27. These two sites are not identical, however, as indicated by the occurrence of species group 4 (*Lysimachia* sp. [kolokolokuahiwi] and *Myrsine lanaiensis* Hbd. [kōlea]) in relevé 25 and a number of species unique to each site listed among the ungrouped species (Table 4).

The third type is composed of forest and native scrub sites containing 'a'ali'i trees in the tallest vegetation layer. This type is represented by relevés 36, 37, 38, and 41, and is defined by the common occurrence of species group 6 (*Pteridium aquilinum* [bracken]; *Styphelia tameiameiae* (Cham.) F. Muell. [pūkiawe]; and *Rumex acetosella* L. [sheep sorrel]) and species group 5 (*Eupatorium adenophorum* Spreng. [Maui pā'makani]; *Dodonaea eriocarpa* Sm. ['a'ali'i]; and *Osteomeles anthyllidifolia* Lindl. ['ūlei]).

The first native scrub community-type can be termed a *Sophora-Coprosma* (māmane-pilo) association according to the composition of definitive species group 3 (*Sophora chrysophylla* (Salisb.) Seem. [māmane] and *Coprosma montana* Hbd. [pilo]) and the discussion of the association concept in Mueller-Dombois and Ellenberg (1974). This community-type includes relevés 20, 42, 19, 9, 5, 6, and 3. Relevés 6 and 3 comprise a variation of this type as indicated by the presence of species group 1 which includes only two species, *Geranium cuneatum* Hook. (hinahina) and *Anthoxanthum odoratum* L. (sweet vernal grass).

The fifth community-type identified can be termed a *Styphelia-Vaccinium* (pūkiawe-'ōhelo) association since pūkiawe is the only shrub species in species group 6, the only group present, and *Vaccinium reticulatum* Sm. ('ōhelo), an ungrouped species, occurs in four of the five relevés included in this type. These five relevés are 4, 17, 21, 30, and 40.

The sixth community-type includes three relevés (39, 23, & 14) that contain elements of several species groups from both the native scrub community-types and the high altitude desert community-type. These open to sparse cover native scrub communities occur on rocky substrates. They may be considered transitional between the native scrub and desert community types.

Next to be identified is the high altitude desert community-type represented by relevés 13, 8, 10, 33, and 1 whose dominant surface feature is rock and/or cinder substrate. This type is defined by species group 8 which contains two species adapted to these extreme conditions, *Tetramolopium humile* (Gray) Hbd. and *Asplenium trichomanes*.

The eighth community-type is grassland characterized by the presence of species group 6. The type is distinguished by the bracken fern since pūkiawe is only sparsely represented in these seven grassland relevés (2, 18, 22, 24, 31, 32, & 34).

The last community-type is grasslands distinguished by the absence of species group 6, and therefore bracken, and the presence of only species group 9 composed of three nearly ubiquitous herbaceous species: gosmore, velvetgrass, and Deschampsia australis. Relevés 7, 11, 12, 15, 16, 26, 28, and 29 represent this community-type.

Comparison of the Phytosociological Analyses

Both the synthesis table and the dendrograph analysis produced similar vegetation-types (Table 5). Relevés (vegetation samples) that are in the same community-type by both analyses can be thought of as a "core group" of sample plots that best illustrate the community-type. Such core groups include relevés 17, 21, and 30 for the pūkiawe-'ōhelo association and relevés 3, 6, 9, and 19 for māmane-pilo association. These core groups are underlined in Table 5. However, some variation exists in the relevés contained in corresponding vegetation community-types depending on the analytical technique. These relevés can be interpreted as intermediate or transitional between the two community-types in which a given relevé occurs. For example, relevé 38 occurs in the 'a'ali'i forest and native scrub community-type by the synthesis table analysis that used associated species groups, but occurs in the pūkiawe-'ōhelo association by the dendrograph analysis that uses the total qualitative similarity of the relevés. Therefore, relevé 38 can be interpreted as intermediate between these two community-types. This is presumably related to an intermediate position on one or more environmental gradients between the core group releves of the two types. Similar observations imply that relevés 4, 5, and 42 are the intermediate between the pūkiawe-'ōhelo association and the sparse native scrub type on dry, rocky substrates. The relevés that make up the high altitude desert type are identical for both analyses, as are the relevés that make up the open 'ōhi'a and koa types. However, the latter two community-types are lumped together in the dendrograph analysis.

Grassland communities were divided into two community-types by both analyses, but the basis for the division was not the same for both cases. The synthesis table analysis using associated species groups separated grasslands containing species group 6 from those without that group. In those relevés, this implies the presence or absence of bracken since pūkiawe, a shrub species, is rare or absent in these grassland relevés (Table 4). The distinction is presumably related to some complex of environmental variables, since no single variable can be correlated with the distribution of these community-types from the data collected in this study. The dendrograph analysis, using total qualitative

TABLE 5. Comparison of relevé (vegetation sample) grouping of the two phytosociological analyses of relevé data from the Crater District of Haleakala National Park. Core group relevés that occur in the same group by both analyses are underlined.

Group	Synthesis Table	Dendrograph
Acacia forest	35	25,27,35
Metrosideros forest	25,27	
Dodonaea forest and native scrub	36,37,41,38	36,37,41
Styphelia-*Vaccinium* association	17,21,30,4,40	17,21,30,5,14,31, 38,42
Sophora-*Coprosma* association	3,6,9,19,5,20,42	3,6,9,19,4
native scrub on dry & rocky substrates	23,39,14	23,39,20,40
grassland without *Holcus*		2,7,15,16
grassland with *Holcus*		11,12,18,22,24,26, 28,29,32,34
grassland without *Pteridium*	2,18,22,24,31,32,34	
grassland with *Pteridium*	7,11,12,15,16,26,28 29	

similarity, separated two groups which seem to be based on the presence or absence of velvetgrass since the species list of every relevé in cluster b_2 contains that species whereas it is absent from the species list of all the relevés in cluster b_1. This separation appears to be associated with a moisture gradient since all the relevés are mesic or wet sites. That is, velvetgrass seems to be unable to compete in dry situations.

Because each grassland community-type is so distinctively defined, no intermediate relevés could be identified. However, relevé 31 seems to be intermediate between a grassland community-type and a scrub community-type. The synthesis table analysis groups this relevé with grasslands while the dendrograph analysis groups it with scrub communities. Therefore, this relevé can be interpreted as a very open scrub community with a grass matrix or as a grassland community with scattered shrubs, as was indicated on the map.

These 10 groupings from the two phytosociological analyses distribute the mapped vegetation units into floristically distinguished community-types within four basic structural community-types. Within the forest community-type, koa, 'ōhi'a, and 'a'ali'i dominated subdivisions were distinguished. Ten of the 11 mapped vegetation units classified as forest fit these subdivisions (Table 2). The excluded unit was eucalyptus and pine plantation.

Within the scrub community-type there were four subdivisions. These were scrub areas dominated by 'a'ali'i, a pūkiawe-'ōhelo association, a māmane-pilo association, and scrub areas with open to sparse cover of mixed floristic composition on dry and rocky substrates. Nineteen mapped vegetation units were of the scrub community-type (Table 2), of which only two could not be included in one of these floristic subdivisions. These two were the closed Maui pā'makani scrub with mixed grasses and closed 'ākala scrub with mixed grasses. Both were of limited distribution (Table 3) and were not sampled.

The grassland community-type was subdivided into four floristic community-types. All 14 mapped vegetation units were included in the structurally defined grasslands.

The high altitude desert community-type was not subdivided by these analyses. All five relevés which sampled this community-type were grouped together by both analyses. Nine mapped vegetation units were included in this type (Table 2).

These analyses show that the Crater District of Haleakala National Park contains mappable vegetation units that can be grouped into floristic subdivisions of several of the community-types characteristic of tropical alpine and subalpine ecosystems. These are ericaceous (pūkiawe-like) scrub, tussock grassland, and high altitude desert. Only the tree-like (arborescent) and rosette life-forms do not occur as mappable vegetation units as they do in other tropical high mountain areas. However, a woolly candle-type species, the silversword (<u>Argyroxiphium</u> <u>sandwicense</u>

DC.), does occur in the study area but its distribution is limited to colonies in cinder cone areas and to an enclosure on the outside slope that is protected and maintained by the Park (Kobayashi 1973). Early accounts, however, describe this species as being common throughout the Crater as well as on the outside slope (Ruhle 1959; Larson 1969). Subsequently, the silversword has had its distribution in the area restricted due to vandalism by humans and grazing by feral goats (Ruhle 1959; Larson 1969; Kobayashi 1973). At one time, then, silverswords may have been a significant component of mappable vegetation units within the Crater District of Haleakala National Park. Thus, the first hypothesis proposed for this study is at least partially supported by the results, with a good probability that the undisturbed vegetation contained all four of the characteristic community-types.

In the vegetation map of Hawaii Volcanoes National Park (Mueller-Dombois & Fosberg 1974), two major vegetation-types were described for the alpine environment and three for the subalpine environment. In the alpine environment, the first type was a "*Racomitrium* moss desert" and was described as "old lava flows (rockland) with scattered moss colonies." In Haleakalā, a similar vegetation-type was found but was described as barren rock and cinder since most rockland areas in Haleakalā also include patches of cinders. In fact, the same moss species, *Racomitrium lanuginosum* var. *pruinosum* Wils., was found growing on the north to northeast faces of the otherwise barren lava, but covering less substrate than indicated for Mauna Loa. Other similarly barren areas of varying substrate types also occur in Haleakalā as can be seen by the map symbols and descriptions in Table 2. The second vegetation-type was a "*Vaccinium*-*Styphelia* lowscrub desert" and was described as "old lava flows with scattered low growing native shrubs." The associated map symbol was given as r(ns). On the Haleakalā vegetation map the same map symbol was used also to describe this same vegetation structure on slightly varying substrates (Table 2). Furthermore, it may be noted that the floristically derived community-types from the phytosociological analyses include a pūkiawe-'ōhelo association for the vegetation (Table 5).

The first vegetation-type described for the subalpine environment of Hawaii Volcanoes National Park was "open to closed globose scrub" usually "composed of several species ('ōhelo, pūkiawe, 'a'ali'i) aggregated into clumps." The associated map symbol was given as ns. This vegetation-type is quite common in Haleakalā and assigned the same symbol on the map along with several others that indicated floristic, structural, understory, and substrate variations (Table 2). The several species that occur in this vegetation-type in Haleakalā resulted in four floristic subdivisions (Table 5). The transitional relevés discussed above indicate the wide distribution of these species within this vegetation-type and therefore its mixed floristic character as implied for Mauna Loa.

The second type was described as "globose scrub with scattered *Metrosideros* trees." The associated map symbol was given as ns(M). A similar mapped vegetation unit in Haleakalā was oM(ns), described as an open 'ōhi'a forest with an understory composed of native shrubs (Table 2). The variation of the structure of these two similar vegetation-types may reflect substrate differences between the two mountains.

The last vegetation-type described for the subalpine environment of Hawaii Volcanoes National Park was an "open *Metrosideros* scrub-forest with scattered *Sophora* trees." The map symbol given for this type was oM(So-ns). A similar community found on Haleakalā was described as an open 'ōhi'a and māmane forest with an understory of native shrubs. The map symbol was oM-So(ns) (Table 2), very similar to the symbol for the community on Mauna Loa. Again, substrate differences between these mountains of different ages may account for the somewhat greater abundance of *Sophora* in the community on Haleakalā.

This comparison shows that the vegetation map of the Crater District of Haleakala National Park has similar vegetation units and vegetation-types as those mapped by Mueller-Dombois and Fosberg (1974) for the tropical alpine and subalpine ecosystem on the slopes of Mauna Loa in Hawaii Volcanoes National Park. Thus, the second hypothesis that was proposed for this study is supported by the results.

ENVIRONMENTAL RELATIONSHIPS

Vegetation communities in the Crater District are related to several environmental factors that vary considerably within the study area. These factors can be discussed by grouping them into four components: climate, substrate, mechanical influences, and exotic plant species.

Climate

Two climatic factors that are important in determining the distribution of vegetation communities are temperature and precipitation. Temperature data for two stations and precipitation data for four stations were obtained from Mr. B. Meisner of the University of Hawaii Meteorology Department who is collecting data to update climatic maps for the State. Precipitation data for a fifth station was obtained from the records of Haleakala National Park. These data were summarized into mean monthly values. Mean monthly temperature was calculated for three stations using the adiabatic lapse rate (standard decrease in temperature per unit increase in elevation) between the two stations for which data was available. Climate diagrams were constructed by the method of Walter (1963) for each of these five stations.

These portray the climates of sites with their characteristic within-year variations. Figure 10 shows the climate diagrams plotted on a map of the study area.

The mean annual temperature decreases with increasing elevation and varies from 8.0°C (46°F) at Haleakalā Summit at 3055 m (10,025 ft) to 17.6°C (64°F) in Kaupō Ranch just outside the Park boundary at 1088 m (3750 ft). Plants respond to different temperature regimes since the rates of their physiological processes are related to temperature, and different species have evolved which survive in different temperature regimes. An illustration of the vegetation's relationship to temperature occurs at the diurnal (daily) frost boundary (the elevation at which freezing temperatures occur at ground level every night of the year). Such conditions significantly decrease plant growth, accounting for the sparse cover, low stature vegetation. A transition to this type of vegetation occurs on the northwest outer slope at about 2600 m (8500 ft) as can be seen in profile 1 (Fig. 4). This is nearly the same elevation at which Mueller-Dombois and Krajina (1968) determined the summer diurnal frost boundary for Mauna Loa on Hawai'i Island by recording nightly low temperatures during the warmest month of the year (August). This diurnal frost boundary, indicated by the vegetation, provides a significant altitudinal zonation on tropical high mountains. The alpine zone can be defined as the area occurring below the diurnal frost boundary and above the montane forests or grasslands.

Mean annual precipitation varies from 1080 mm (42 inches) at Haleakalā Summit to 4510 mm (177 inches) at Palikū Cabin. This precipitation gradient is primarily a function of exposure to the effects of the northeast tradewinds and the height above the inversion layer. Clouds are pushed from the northeast into the Crater over the ridges and up through the gaps. Thus, precipitation decreases from northeast to southwest, as indicated by the climate diagrams and the mean annual figures on Figure 10. Structurally, the vegetation responds to increasing precipitation with increasing cover and stature, with forest community-types occurring in the wetter, eastern part of the study area (Fig. 5 & 6). The floristic composition of the vegetation communities may change as a function of the species adaptation to a certain range of moisture availability and/or competition. The more dominant or aggressive species indicate their optimal environmental relationships by their distribution, while others may be pushed out of their environmental optimum into more marginal habitats which they can tolerate (Mueller-Dombois & Sims 1966). This relationship can be observed in the Crater where 'ōhi'a forests occur in the wet northeast corner while 'a'ali'i forests occur in the more mesic southeast corner (Fig. 5 & 6).

Precipitation and temperature are related at any one site to define the climatic regime of that site. This relationship and the mean monthly variation of these factors can be observed on the climate diagrams of Figure 10. Each of the five diagrams shows a similar seasonal pattern of precipitation with the wettest months being December and January and the driest month June.

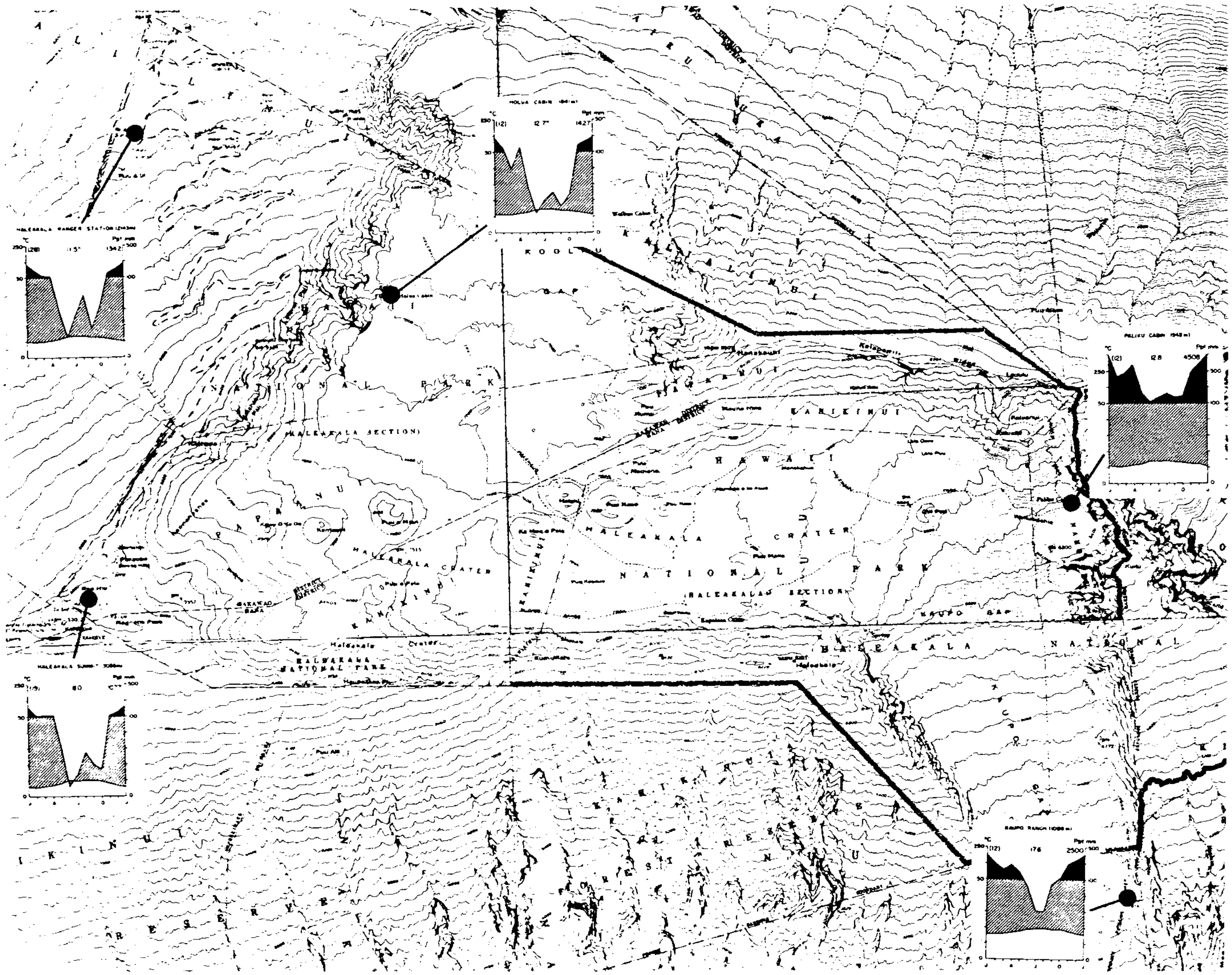


FIGURE 10. Climate diagrams and locations of stations for the Crater District of Haleakala National Park. North is towards the binding. Approximate scale is 1:77,500.

The mean monthly temperature curve shows very little seasonal variation indicating typically tropical insular climates at all elevations. The precipitation and temperature curves are related in that drought conditions are indicated when the mean monthly precipitation curve crosses below the mean monthly temperature curve. This occurs at three stations: Haleakalā Summit, Haleakalā Ranger Station, and Hōlua Cabin, but only for a short period in June. Therefore, the xeromorphic character of many of the species may be only partially correlated with the seasonal dryness of the climate, and probably is more closely related to the intense radiation and the large diurnal fluctuations in temperatures characteristic of the tropical high mountain climate.

Another climatic factor that may be significant in determining the structure and distribution of vegetation is fog drip. The prevalent northeast tradewinds push clouds over the north and east rims of the Crater and up through both Ko'olau Gap and Kaupō Gap, frequently creating foggy, damp conditions in these areas especially during the early morning and evening hours. Juvik and Perreira (1973) have demonstrated the importance of fog drip on Mauna Loa. There they found that fog drip added 65% precipitation to the rainfall in the treeline ecosystem at 2500 m (8200 ft) as measured from standardized cylindrical fog interceptors made from louvered aluminum shade screen and having a surface area of 2691 cm . A similar relationship can be expected for those areas on Haleakalā which are exposed to fog drip conditions, for example, the Palikū Cabin and Ko'olau Gap areas. Therefore, as the stature of the vegetation increases in these areas, it will likely increase the interception of moisture which should increase growth. Browsing animals which limit the growth of the plants should therefore be carefully controlled because they may indirectly reduce soil moisture on a permanent basis.

Substrate

The substrates of the Crater District consist of volcanic substances of geologically recent origin. Many areas, in fact, have substrates that can be described as pahoehoe lava, 'a'ā lava, cinder, ash, or a combination of these. Whatever soil occurs is poorly developed (soil here defined as the finely fractured product of long-term weathering processes on the geologic parent material). Thus, the raw geological environment determines the variation of the substrate.

Soil analysis results are summarized in Table 6. Data represent means and standard errors of means of three replicates for each sample in each test. Soil profiles had very little, if any, horizon development in the Crater. The detailed descriptions are given in Appendix II. The substrates which developed enough to be considered soils all seem to be derived from cinder and/or ash parent material. Some generalizations, therefore, can be made about these soils based on the soil pit descriptions. In

TABLE 6. Summary of soil tests on soils of the Crater District of Haleakala National Park. Figures are means and standard errors of the means of three replicates of each sample for each soil test. Available water = FC - PWP.

Relevé	Map Unit	Organic Carbon (%)	pH	FC (%)	PWP (%)	Available Water (%)
6	cns(mx)	11.25±0.25	5.9±0.01	161.33±3.34	104.27±0.64	57.06
9	ns(So-mx)	1.59±0.11	6.8±0.02	9.47±0.33	7.28±0.11	2.19
11	mx	7.55±0.98	6.0±0.02	74.30±1.79	40.30±0.14	34.00
24	mx(ns)	16.06±0.44	5.0±0.01	229.97±1.48	137.41±0.70	92.56
25	oM-So(ns)	18.58±3.15	4.3±0.01	114.31±1.09	111.38±1.05	2.93
27	oM(ns)	25.23±2.11	4.8±0.02	158.89±6.16	127.00±1.77	31.89
28	cD	15.49±0.95	5.0±0.04	103.59±2.89	57.09±1.10	46.50
29	cD	24.01±1.44	4.0±0.01	317.06±2.98	158.00±4.67	159.06
37	cDd-Ac	20.44±0.52	5.1±0.01	96.67±0.69	92.74±0.54	3.93
38	cns	14.55±0.56	5.6±0.02	60.13±3.27	51.03±0.16	9.10

NOTE: High values for field capacity and permanent wilting percentage can be compared to values for the Hydric Dystrandept of the Maile silt loam soil series on the island of Hawai'i (see text)(USDA, Soil Conservation Service 1976).

all but the dryest areas, a shallow A_1 horizon of organic material is present that is very densely ramified by roots and has a dark brown to black color. The A and B horizons were usually distinguished by an indistinct color difference with no definite boundary between them, the B horizon having a slightly lighter color. The color of these horizons ranged from dark brown to brown. Texture and structure were usually the same for both horizons since the cinder and/or ash parent materials resulted usually in a loam. Sometimes the soil had a sandy loam texture and a crumb structure but occasionally it was a structureless cinder and ash. The depths of these horizons varied from site to site. The soils usually contained many rocks. Rock outcrop was often the dominant substrate feature, while the soil was restricted to pockets only. It was possible to distinguish a C horizon in a few profiles but most B horizons were underlain directly by rock hardpan.

The 10 soil samples tested are characterized by a high organic carbon content and a moderately low pH (Table 6), that is, relatively acidic. In fact, these two soil characters show an inverse correlation; the higher the organic carbon content, the lower the pH (Fig. 11). Organic carbon content for these 10 samples ranges from 1.59% to 25.23% and has a mean of 15.48%. The pH ranges from 4.0 to 6.8 and has a mean of 5.2 (Although pH is a logarithmic scale, Daubenmire [1974] gives several reasons for treating pH arithmetically when applied to soils.). These figures are in agreement with those from other tropical high mountain regions. Coe (1967) tested soils from seven localities covering a wide altitudinal range on Mt. Kenya and found the pH to range between 5.0 and 6.5 with a mean of 5.4. Organic carbon content in the same area ranged between 7% and 12.59%. Cuatrecasas (1966), working in the Paramos region of the equatorial Andes, found the pH ranged between 3.7 and 5.4 and organic carbon content averaged 10.64%. The savannah and mountain parkland communities on Mauna Loa have an organic carbon content between 10% and 15% and the pH ranges from 5.5 to 6.5 (Mueller-Dombois & Bridges 1975). This characteristic of tropical high mountain soils is probably due to low temperatures and consequent low physiological activity of soil organisms which results in a slow chemical breakdown of organic matter (Coe 1967) with the consequent build up of humic acids. In Haleakala, these soil characteristics seem to be related to the relative wetness of each site. Increasing wetness is correlated with increasing organic carbon and decreasing pH. For example, the soil samples from relevés 9 and 11 (Fig. 2) which had a low organic carbon content and a relatively high pH (Table 6) are located in a relatively dry section of the Crater, as indicated by the climate diagrams (Fig. 10). The soil samples from relevés 27 and 29 (Fig. 2), however, which have a high organic carbon content and a relatively low pH (Table 6) are located in the northeast corner of the study area, the wettest and most vegetated section of the Crater District (Fig. 10). The tendency towards waterlogged soils further inhibits biological degradation of organic matter due to decreased oxygen concentrations and increases in acidity.

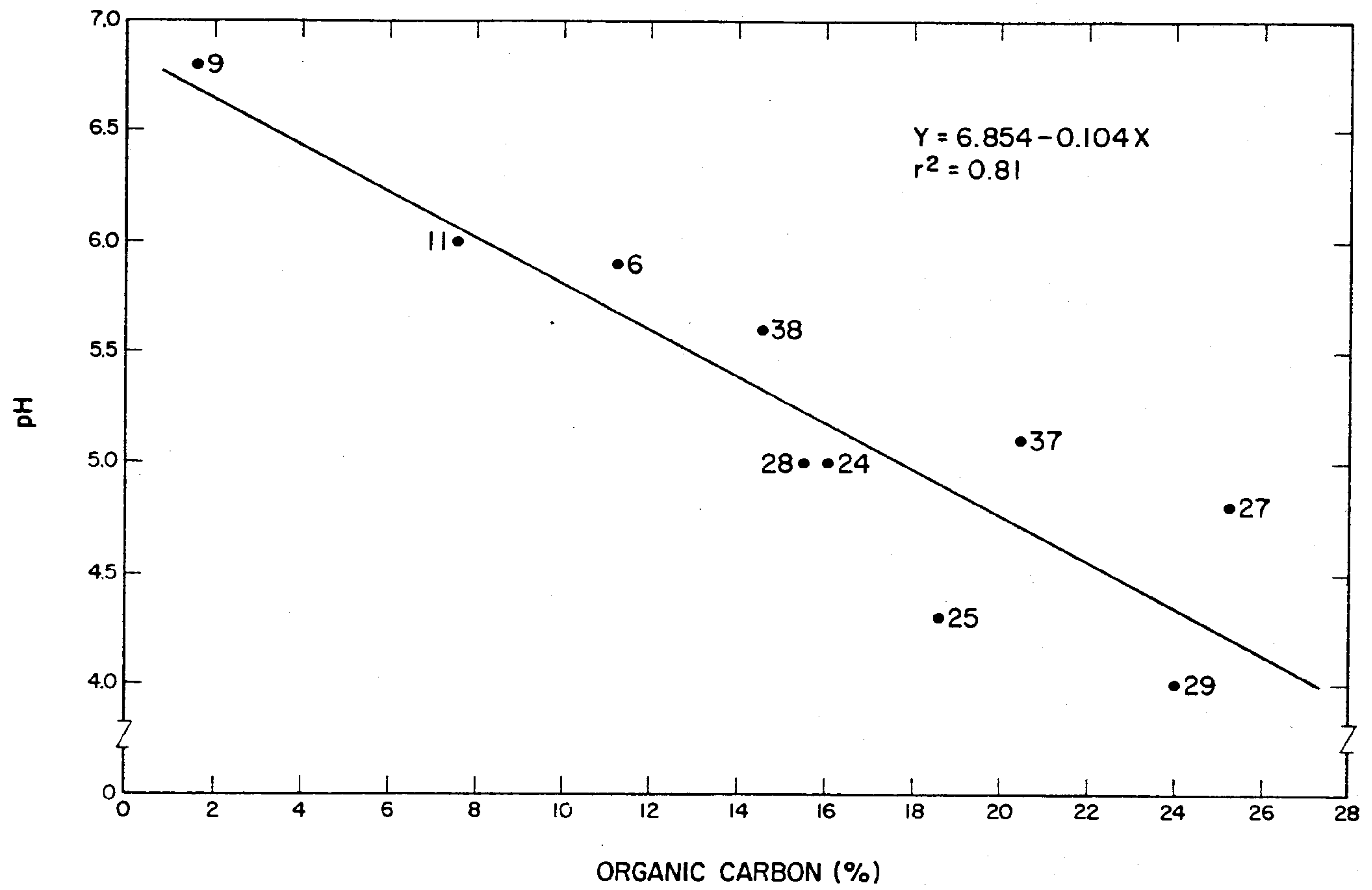


FIGURE 11. Inverse correlation of organic carbon content and pH for soils of the Crater District of Haleakala National Park.

Several of the soil samples tested show what may seem to be rather high values for field capacity and permanent-wilting percentage. These high values are a result of the water of hydration on oxides of iron and aluminum composing the amorphous clays of the Dystrandepts and Hydrandepts of Hawai'i. These soils are formed by rapid weathering of cinder and ash parent materials in areas of high rainfall. Comparable values for field capacity and permanent-wilting percentage are known for the Hydric Dystrandept of the Maile silt loam soil series on the island of Hawai'i (USDA, Soil Conservation Service 1976).

The variation in substrate in Haleakalā as determined by the age and character of the volcanic parent material can be viewed as a variation superimposed on the climatic regime defined by the temperature, precipitation, and amount of fog drip at any one site. Figure 5 shows a broad segment of rock and cinder substrate supporting a high altitude desert community-type. This vegetation is no doubt partially related to the relative dryness of the area and the extreme diurnal temperature variation as was proposed for the high altitude desert above the diurnal frost boundary on the northwest outer slope (Fig. 4). However, this area, which is below the diurnal frost boundary, can be contrasted with vegetated areas of similar elevation and dryness. Therefore, the relative recency of the substrate in the area must be an important influence on the vegetation-type that occurs there.

The variation in the native scrub community-type can be seen in Figure 5. 'Ō'ilipu'u, an old cinder cone, supports an open native scrub community with a grass matrix having nearly equal cover as the shrubs. To the immediate west there is a community with scattered native shrubs growing on a relatively recent 'a'ā lava flow that is the dominant surface feature of the site. Just east of 'Ō'ilipu'u is an open scrub community growing on a pāhoehoe lava flow that is old enough to be broken up to some extent. These three communities are adjacent to one another at nearly the same elevation, and have nearly the same mean annual temperature. Also, since they are adjacent to each other along the west-east rainfall gradient, they should have a similar mean annual precipitation. Thus, it is probable that the variation in the cover and structure of these three communities is related to the variation in the substrate. Such a relationship between community-type and substrate has been observed for other tropical high mountain areas. Coe (1967) describes three habitat types related to substrate in the "Ericaceous zone" of Mt. Kenya. On Mt. Kilimanjaro, Salt (1954) divides the heath formation into six floristic communities related to slope and substrate. The ericaceous vegetation of Reunion Island was separated by Cadet (1974) into three communities that were related to edaphic factors. Thus, the situation for Haleakalā is consistent with the observations in other tropical high mountain areas.

These observations make it tempting to try to predict or even map substrate types by the vegetation that it supports. However, changes in vegetation communities are not always correlated with obvious changes in substrate. Profile 3 (Fig. 6) shows several communities growing on very similar substrates. Releve descriptions of substrates, as used on the profile, indicate three forest communities, a closed native scrub and grass community, and a grassland community, all growing on brown humic soil with many rocks and large rock outcrops. Thus, it can be seen that although vegetation many times indicates a certain substrate type, other factors such as climate and various mechanical factors influence the distribution of vegetation, and these result in variation of vegetation-types within a given substrate type.

Mechanical Factors

The two most important mechanical factors influencing the vegetation in the Crater District are herbivory (grazing) and ground disturbance.

Herbivory in the form of cattle grazing has been a historical influence in the Park. Cattle ranches still border the Park on the north, west, and south. A special reservation in the land acquisition agreement of 1916 allowed cattle to graze within the Park but outside the Crater, and to cross the Crater to new pastures. Also, longhorn cattle grazed the Deschampsia grassland on the northeast outer slope. However, no cattle grazing has been practiced in the District in over 30 years (Forehand 1970; Haleakala National Park 1976). The extent and duration of the use of the District by cattle ranchers is not known, but cattle ranches have been established on Maui since the introduction of cattle by Captain Vancouver in 1793. Therefore, grazing in the area could conceivably have been extensive and over a fairly long period. This pressure would undoubtedly have the effect of reducing koa tree communities, as has been documented on the island of Hawai'i (Cuddihy 1978). Presently, grazing rights for Haleakalā Crater are held by van Tempsky and the Haleakalā Ranch Company.

The major herbivore presently in the Park is the feral goat (Capra hircus L.). Goats once numbered in the thousands in the Park, but now have been reduced by control measures to less than 1000 (Larson 1969). Yocum (1967) has enumerated the general effects of goat grazing on the vegetation of the Crater. Two plant species in particular exhibit those effects. Māmane displays unmistakable browse lines and limited reproduction in browsed areas but new growth is apparent where goats no longer feed. Silversword once covered sizeable areas of the crater floor and outer slope but now is found only in the arid crater center and in rocky refuges out of the reach of goats (Larson 1969). This restriction in distribution is attributed not only to direct grazing by goats but also to their trampling of the roots and general disturbance of the substratum (Kobayashi 1973).

A reduction in the goat population in the mountain parkland of Hawaii Volcanoes National Park resulted in expansion of koa colonies at a rate of 0.5 to 2.5 m per year into the surrounding grass matrix (Mueller-Dombois 1967). Although the goats did not completely eliminate sucker reproduction of koa, their browsing effects seemed to produce an abnormally dense stocking of suckers in a haphazard pattern (Spatz & Mueller-Dombois 1973). The 1975 Crater District Resources Basic Inventory expedition (Berger et al. 1976) observed that a stand of mature koa trees located in east Kaupō Gap at 1525 m (5000 ft) elevation produced no seedlings, although copious amounts of seeds are produced. Also, no root sucker reproduction was observed. It was their opinion that this complete lack of regeneration, in an area that had probably at one time supported a koa forest, is the result of intensive goat browsing.

Horses continue to graze in the Park during the activities of Park operations, outside horse concessions, and visitors taking Crater trips on horseback. The direct effect of this grazing is considered minimal (Haleakala National Park 1976). However, horse traffic may be responsible for the continued introduction of exotic plant species, since many of these species are found near pastures, stables, trails, and cabins. Propagules are probably carried on the hooves and legs of the animals, in the horse droppings, and in the hay and fodder.

Ground disturbances from feral pigs (Sus scrofa L.) are common mechanical influences in the wetter portions of the area. Pigs dig up the ground in search for food and the plant cover is generally killed by such treatment. Exotic species, particularly velvetgrass, gosmore, and sheep sorrel, invade the exposed areas and out-compete the germinating endemic and indigenous species. These changes plus other changes in the soil which further suppress the reestablishment of native species have been observed for the Deschampsia grassland on the northeast outer slope by Forehand (1970). Spatz and Mueller-Dombois (1972) also found that velvetgrass replaced Deschampsia australis in pig disturbed areas in the mountain parkland of Hawaii Volcanoes National Park. This replacement has been nearly complete in some areas of the Crater with velvetgrass having nearly 100% cover and Deschampsia only surviving in the form of rare, isolated tussocks (cHl grassland). Also, in some areas, the introduced grass Poa pratensis L. (Kentucky bluegrass) is associated with pig disturbed sites (Fig. 2, relevés 11 & 28).

Exotic Plant Species

Many species of exotic plants have become established in the Crater District. A list of most of these species was given by Larson (1969). The species list of the Crater District produced by the CPSU/UH includes exotic species and designates them as such (Stemmermann et al. 1979). These introductions are usually associated with the activities of man and his domestic animals.

They are distributed more densely near buildings, trails, and roads. In fact, the immediate surroundings of houses, offices, and cabins are islands of exotic plants which may serve as centers of distribution for these species. Conifers and exotic grasses are especially evident around the Park Headquarters, employee housing, and Hosmer Grove on the northwest outer slope. These areas together with the large planted conifer forest north of Hosmer Grove are large enough to be mappable units of introduced trees.

Several of these species are of particular concern to the ecology of the Crater. Velvetgrass is displacing the native grass *Deschampsia australis* in many grassland areas. As discussed above, this species is usually associated with feral pig activity but, once established, it maintains itself even in the absence of pig disturbance. Kentucky bluegrass has the same tendency to displace *Deschampsia*. This ability is most evident in the grasslands along Lau'ulu Trail and in the large grassland at the base of Halemau'u Trail. *Pennisetum clandestinum* Hochst. ex Chiov. (kikuyugrass) is an introduced grass that provides good grazing for cattle. This species occurs inside the Park near its southern boundary in Kaupō Gap. It has spread from the adjacent pastures of Kaupō Ranch. This grass is stoloniferous and forms thick, dense mats which prevent seedling establishment of other species. It has spread into the 'a'ali'i forest areas where observations suggest that seedlings of native species cannot establish themselves. This area may become a grassland dominated by an exotic species when the mature trees die. Kikuyugrass can also be found at the base of Halemau'u Trail.

Another stand-forming exotic is Maui pā'makani, a herbaceous to shrub-like member of the Compositae (Daisy family). It is dominant in areas large enough to be mapped and sufficiently common throughout the study area to be part of an associated species group on the synthesis table (species group 5). The presence of this species may be at the expense of native species. This plant is abundant in spite of the parasitic insect *Procecidochares utiles* Stone, introduced in 1944 to check its spread by infesting living plants with gall-forming larvae. *Ricinus communis* L. (castor bean) is a poisonous species which forms a small but dense stand in Kaupō Gap that could serve as a center of infestation.

Several other plant species have been noted to occur in the Park which may cause problems in the future. *Ulex europaeus* L. (gorse) was found near Park Headquarters. It is a spiny shrub which is considered an aggressive species with a potential for widespread distribution. It is currently under control but still present.

Cirsium vulgare (Savi) Tenore (bull thistle) has been found at Hōlua Cabin, on the east side of Ko'olau Gap, and in Kaupō Gap. It produces large quantities of wind-dispersed seeds which give this species the potential for rapid distribution.

Schinus terebinthifolius Raddi (christmas berry) has been found in Kaupō Gap. This species can be spread quickly by birds. It forms dense stands in other areas outside the Park.

Opuntia megacantha Salm-Dyck (prickly pear cactus) has also been observed in Kaupō Gap. This species has been a problem in other areas. A moth was imported whose larvae feed on this species. However, the thick growth of prickly pear in Ōma'opio, below the Kula area, still looks quite healthy and shows little effect of this biological control measure.

Several grass species were found in the area which have a potential for future large-scale invasion because of their aggressive nature. These species include sweet vernal grass; Bromus rigidus Roth (ripgutgrass); Dactylis glomerata L. (cocksfoot); Festuca rubra L. (red fescue); Paspalum orbiculare Forst. f. (ricegrass); and Sporobolus africanus (Poir.) Robyns & Tournay (African dropseed) among others.

Although the Crater is often considered a last stronghold for many native species, invasion of habitats by exotic species is a potentially serious resource management problem. Since 23 of the 53 mapped units were characterized by exotic species, non-native species have a significant impact on the vegetation of the Crater District.

SUMMARY AND CONCLUSIONS

The major focus of this study was the production of a vegetation map of the Crater District of Haleakala National Park at a scale of 1:24,000 which can be used as an overlay of the USGS 1:24,000 topographic quandrangle maps. Fifty-three structural-floristic communities were mapped which were grouped into four structural vegetation-types. These were forest, scrub, grassland, and high altitude desert communities. Areas were calculated for each community using an electronic planimeter. The total area mapped was 7544.8 ha (18,643 acres).

Topographic vegetation profiles were constructed which show changes in vegetation-types in relation to climatic gradients. Also, correlations were observed between substrates and community-types.

Phytosociological analyses of relevé (vegetation sample) data by the synthesis table and the dendrograph techniques resulted in ecologically meaningful groupings. Both analyses resulted in similar groupings. Detailed comparison of the groupings by the two methods revealed interesting minor variations. Some relevés were left ungrouped. These were interpreted as ecologically unique within the sampling area.

The 10 groupings from the phytosociological analyses distribute the mapped vegetation units into floristically distinguished community-types. Ten of 11 mapped vegetation units classified as forest fit into three floristically distinguished forest community-types. Four floristic community-types contained 17 of 19 mapped vegetation units classified as scrub communities. Fourteen mapped vegetation units classified as grasslands were distributed into two of four floristic community-types depending on the analysis technique. The high altitude desert community-type was not subdivided floristically by either analysis and included nine mapped vegetation units.

It was concluded that the Crater District of Haleakala National Park contains mappable units that can be grouped into floristic subdivisons of three of the four community-types characteristic of tropical alpine and subalpine ecosystems. These are ericaceous (pūkiawe-type) scrub, tussock grassland, and high altitude desert. Only arborescent and rosette life-forms do not occur as mappable vegetation units as they do in other tropical high mountain areas. However, the endemic woolly candle-type species, the silversword, has had its distribution restricted due to vandalism and grazing. At one time this species may have been a significant component of mappable vegetation units within the study area. Thus, the first hypothesis proposed for this study is at least partially supported by the results, with a good probability that the undisturbed vegetation contained all four of the characteristic community-types.

It was also concluded that the vegetation map of the Crater District of Haleakala National Park has similar vegetation units and vegetation-types as those mapped by Mueller-Dombois and Fosberg (1974) for the tropical alpine and subalpine ecosystem on the slopes of Mauna Loa in Hawaii Volcanoes National Park. Thus, the second hypothesis that was proposed for this study is supported by the results.

A discussion of environmental relationships of the vegetation showed that variation of the vegetation within the study area was associated with variations in climate, substrate, mechanical influences, and the effects of exotic plant species. Climate diagrams showed the tropical high mountain character of the study area, while they illustrated also the considerable geographic variation of climate within the Crater as well as its seasonal variation. It was concluded that the diurnal (daily) frost boundary should be used to define the lower limit of the alpine zone in tropical high mountain areas, as has been done by Mueller-Dombois and Krajina (1968) for Mauna Loa and Mauna Kea. This demarcation implies that the subalpine zone be defined as those areas below the diurnal frost boundary and above the montane forests and grasslands.

The 10 soil samples tested were characterized by high organic carbon content, low pH, and relatively high values for field capacity and permanent-wilting percentage. Several correlations between variation in substrate and variation in subcommunity-type may vary within a given substrate type. It was concluded that although variation of vegetation and substrate are often correlated, all aspects of the environment must be considered in assessing the distribution of vegetation. Thus, although difficult, it is possible to suggest what native community-type would occur in all severely disturbed areas.

The Hypothetical Pre-Cook Vegetation

The observations of the impact of mechanical factors and exotic plant species on the environment lead to the conclusion that the Crater has been severely altered since 1778. It can be considered a degraded ecosystem. It is therefore tempting to speculate about how the vegetation may have looked before the arrival of western civilization. The most obvious difference from the present vegetation would be the complete absence of the exotic species brought here since Captain Cook's arrival. One of the most widespread implications of this would be that Deschampsia australis, the dominant native grass in the area, may have dominated in grassland areas and in the grass matrix of other structural vegetation-types. In terms of the map, the symbol indicating velvetgrass (Hl) as a component of the vegetation would disappear and presumably be replaced by the symbol for Deschampsia (D). The same is implied for the mixed grass symbol (mx) and the symbol for kikuyugrass (Pe), although this last species may be replacing other vegetation-types as discussed previously. Map symbols for other exotic species that would be deleted include those for Maui pā'makani (Eu) and introduced trees (it).

The absence of grazing pressure by domestic and feral animals has several implications. The most obvious difference from the present situation would be that all vegetated areas would have had more cover. Even open scrub areas would not only have had somewhat increased woody crown cover but also increased cover for the grass matrix since the associated effects of goat grazing (Yocum 1967) would have been absent. Similarly, open Deschampsia grasslands on dry sites also may have had a more complete cover.

Observed reactions to grazing pressure and to the removal of grazing pressure on māmane (Larson 1969) and koa (Mueller-Dombois 1967; Berger et al. 1976; Cuddihy 1978) indicate that these two species probably were much more widespread at one time, each forming woody communities scattered throughout the Crater. In fact, the scattered occurrence of many native species in protected sites throughout the Park (Berger et al. 1976; Stemmermann et al. 1979) indicates that many areas probably had more diversified species compositions than at present. Ruhle (1959) refers to Rock (1913) when he describes Pu'u Nianiau near the Park entrance on the northwest outer slope as formerly being thickly covered with māmane and 'ākala and containing rarer associates which included Neurophyllodes sp. (a tree geranium), tree Railliardia, Argyroxiphium virescens Hbd. (greensword), and a tree lobelia, Clermontia haleakalensis Rock. Artemisia mauiensis

(Gray) Skottsb. (Maui wormwood), a silvery colored relative of sagebrush, probably had a much wider distribution and a higher proportion of cover in scrub communities since, although now rare, it can be observed growing vigorously in scrub areas that are protected from goats. The silversword at one time was probably distributed throughout the area, both inside the Crater and on the outer slopes (Ruhle 1959; Larson 1969; Kobayashi 1973). Therefore, it was once a more common component of the vegetation of the area.

The rare but geographically widespread occurrence of tree species may also have implications for the pre-Cook vegetation. These species include Pittosporum confertifolium Gray (ho'awa), Santalum haleakalae Hbd. (Haleakala sandalwood), plus the tree species noted above as formerly found on Pu'u Nianiau. These, together with a more extensive distribution and cover for mamane and koa, indicate that tree species probably had greater populations in the past. Greater tree population density may have taken the form of small stands of forest scattered throughout the study area on sites that are environmentally suited to their development. Such areas do exist, although probably now as relicts, for example, the small kipuka just south of 'O'ilipu'u.

Thus, what is now the Crater District of Haleakala National Park probably once supported a vegetation that had a more complete cover than at present except where limited by substrate or climatic factors. This vegetation was composed of undisturbed tussock grasslands dominated by Deschampsia australis, scrub communities composed of a wider diversity of species including the silvery Maui wormwood and silversword, plus small stands of forest scattered throughout the area composed of a variety of native trees.

Suggestions For Further Study

The above discussion of the hypothetical pre-Cook vegetation suggests that the autecology of both native and exotic species should be studied. Such studies would indicate the environmental optima and thus the areas where native species, now restricted in their distribution, probably grew at one time. Also, further study of the environmental relationships of exotic species may indicate limitations of these species that could be used to make more precise predictions of their future development in the Park. Species interactions, particularly between native and invading exotic species, should also be studied more fully. These results would aid the management of the Park to achieve its objective of restoration and maintenance of native ecosystems.

Successional studies of disturbed areas would also help in management decisions. In disturbed areas, the original environmental and biotic conditions may have changed. Thus, reintroduction of species formerly occurring on the site may meet with failure if the conditions are not well understood. A secondary succession of plant species may be necessary to restore the environmental conditions needed for the maintenance of the pre-disturbance ecosystem. This may be the case in many areas that have been eroded due to disturbance by feral animals.

The environmental factors that determine where a particular plant community occurs should also be studied. Some of these factors have been indicated in this study. However, detailed climatic and edaphic data are needed to fully elucidate the dynamics of the relationships between the plant communities and their environment. Of particular interest would be the climatological location of the diurnal frost boundary, its seasonal variation, and further elucidation of its effects on the distribution of both plant communities and individual plant species.

ACKNOWLEDGMENTS

This study was supported by National Park Service Contract CX 8000 7 0004 administered by the Cooperative National Park Resource Studies Unit (CPSU/UH), Department of Botany, University of Hawaii at Manoa. This support is gratefully acknowledged. I would also like to express my thanks to the following:

Ms. Puanani Frobel and Ms. Leesa Durham for their invaluable assistance in the field work conducted for this study.

Mr. Clyde Kanehiro, Mr. Ismael Trono, and Mr. Tamotsu Nakata for the drafting of the vegetation map and many of the figures.

Dr. Gerald Carr, Department of Botany, University of Hawaii at Manoa, for his advice concerning taxonomic nomenclature.

Dr. Tissa Herat, Dr. William Hoe, Mr. Paul Higashino, and Ms. Lani Stemmermann for their guidance in the identification of plant species.

Dr. Y. Kanehiro and Dr. R. E. Green, Department of Agronomy and Soils, University of Hawaii at Manoa, for their advice concerning soils testing and data.

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APPENDIX I

Species List of Plants Found in Relevé Sites

Species list of plants found in relevé (vegetation sample) sites in the Crater District of Haleakala National Park arranged by family. Nomenclature of the flowering plants follows St. John (1973). Nomenclature of the mosses follows Hoe (1974). Names of the other non-flowering plants are according to several unpublished sources that list validly published names. Meaning of symbols preceding species names: E = endemic, I = Indigenous, and X = exotic.

FAMILY
Scientific Name

FLOWERING PLANTS

Monocotyledons

CYPERACEAE
- E *Carex alligata* F. Boott
- I *Carex macloviana* var. *subfusca* (W. Boott) Kuek.
- E *Carex wahuensis* C. A. Mey.
- I *Cyperus brevifolius* (Rottb.) Hassk.
- E *Machaerina gahniaeformis* (Gaud.) Kern
- I *Uncinia uncinata* (L. f.) Kuek.

GRAMINEAE
- E *Agrostis sandwicensis* Hbd.
- X *Aira caryophyllea* L.
- X *Anthoxanthum odoratum* L.
- X *Bromus rigidus* Roth
- X *Dactylis glomerata* L.
- X *Danthonia semiannularis* (Labill.) R. Br.
- E *Deschampsia australis* Nees ex Steud.
- E *Eragrostis variabilis* (Gaud.) Hbd.
- X *Festuca megalura* Nutt.
- X *Holcus lanatus* L.
- X *Pennisetum clandestinum* Hochst. ex Chiov.
- X *Poa pratensis* L.
- X *Rhynchelytrum repens* (Willd.) C. E. Hubb.
- X *Sporobolus africanus* (Poir.) Robyns & Tournay
- E *Trisetum glomeratum* (Kunth) Trin. in Steud.

JUNCACEAE
- E *Luzula hawaiiensis* Buch. var. *hawaiiensis*

LILIACEAE
- E *Astelia forbesii* Skottsb.

Appendix I--Continued.

FAMILY
Scientific Name

Dicotyledons

ARALIACEAE
E *Cheirodendron trigynum* (Gaud.) Heller

CARYOPHYLLACEAE
X *Cerastium vulgatum* L.
X *Polycarpon tetraphyllum* (L.) L.
X *Silene gallica* L.

COMPOSITAE
X *Bidens pilosa* L.
X *Cirsium vulgare* (Savi) Tenore
X *Erigeron bonariensis* L.
X *Eupatorium adenophorum* Spreng.
X *Gnaphalium purpureum* L.
E *Gnaphalium sandwicensium* Gaud.
X *Hypochaeris radicata* L.
X *Lapsana communis* L.
E *Railliardia menziesii* Gray
E *Railliardia platyphylla* Gray
X *Sonchus oleraceus* L.
E *Tetramolopium humile* (Gray) Hbd. var. *humile*

EPACRIDACEAE
I *Styphelia tameiameiae* (Cham.) F. Muell.

ERICACEAE
E *Vaccinium berberifolium* (Gray) Skottsb.
E *Vaccinium calycinum* Sm.
E *Vaccinium reticulatum* Sm.

GENTIANACEAE
X *Centaurium erythraea* Rafn.

GERANIACEAE
E *Geranium cuneatum* var. *tridens* (Hbd.) Fosb.

LABIATAE
E *Stenogyne crenata* Gray

LEGUMINOSAE
E *Acacia koa* Gray
E *Sophora chrysophylla* (Salisb.) Seem.

Appendix I--Continued.

FAMILY
Scientific Name

Dicotyledons--(con't.)

LYTHRACEAE
X *Lythrum maritimum* HBK.

MENISPERMACEAE
E *Cocculus ferrandianus* Gaud.

MYRSINACEAE
E *Myrsine lanaiensis* Hbd. var. *lanaiensis*

MYRTACEAE
E *Metrosideros collina* (J. R. & G. Forst.) Gray

ONAGRACEAE
X *Epilobium cinereum* A. Rich.
X *Oenothera stricta* Ledeb. in Link

PIPERACEAE
E *Peperomia erythroclada* C. DC.

PLANTAGINACEAE
X *Plantago lanceolata* L.

POLYGONACEAE
X *Rumex acetosella* L.

PRIMULACEAE
X *Anagallis arvensis* L.
E *Lysimachia* sp.

ROSACEAE
E *Fragaria chiloensis* var. *sandwicensis* Deg. & Deg.
E *Osteomeles anthylidifolia* Lindl.
E *Rubus hawaiiensis* Gray var. *hawaiiensis*
X *Rubus rosaefolius* Sm.

RUBIACEAE
E *Coprosma ernodeoides* var. *mauiensis* St. John
E *Coprosma montana* Hbd.
E *Coprosma ochracea* Oliver var. *ochracea*
E *Gouldia hillebrandii* Fosb.

SAPINDACEAE
E *Dodonaea eriocarpa* Sm.

UMBELLIFERAE
E *Sanicula sandwicensis* Gray var. *sandwicensis*

Appendix I--Continued.

FAMILY
Scientific Name

Dicotyledons--(con't.)

VERBENACEAE
X *Verbena litoralis* HBK.

FERNS AND FERN ALLIES

ADIANTACEAE
I *Pellaea ternifolia* (Cav.) Link
I *Pteris cretica* L.
I *Microlepia speluncae* (L.) Moore
X *Pityrogramma calomelanos* (L.) Link

ASPIDIACEAE
E *Athyrium microphyllum* (Sm.) Alston
I *Dryopteris glabra* (Brack.) Ktze.
I *Dryopteris parallelograma* (Ktze.) Alston
E *Dryopteris unidentata* (Hook. & Arn.) C. Chr.
I *Dryopteris paleacea* (Sw.) C. Chr.
I *Elaphoglossum hirtum* var. *micans* (Mett.) C. Chr.
E *Polystichum hillebrandii* Carruth.

ASPLENIACEAE
I *Asplenium adiantum-nigrum* L.
E *Asplenium macraei* Hk. & Grev.
I *Asplenium trichomanes* L.

BLECHNACEAE
E *Sadleria cyatheoides* Kaulf.

DAVALLIACEAE
I *Nephrolepis exaltata* (L.) Schott

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

LYCOPODIACEAE
I *Lycopodium venustulum* Gaud.

POLYPODIACEAE
I *Pleopeltis thunbergiana* Kaulf.
E *Polypodium pellucidum* Kaulf.

Appendix I--Continued.

FAMILY Scientific Name
MOSSES
GRIMMIACEAE
I *Racomitrium lanuginosum* var. *pruinosum* Wils. in Hook. f.
THUIDIACEAE
E *Thuidium plicatum* Mitt. var. *plicatum*
LICHENS
CLADONIACEAE
E *Cladonia leiodea* Magn.
STEREOCAULACEAE
I *Stereocaulon ramulosum* (Sw.) Raeusch.
I *Stereocaulon vulcani* (Bory) Ach.
USNEACEAE
I *Usnea rubicunda* Stirt.

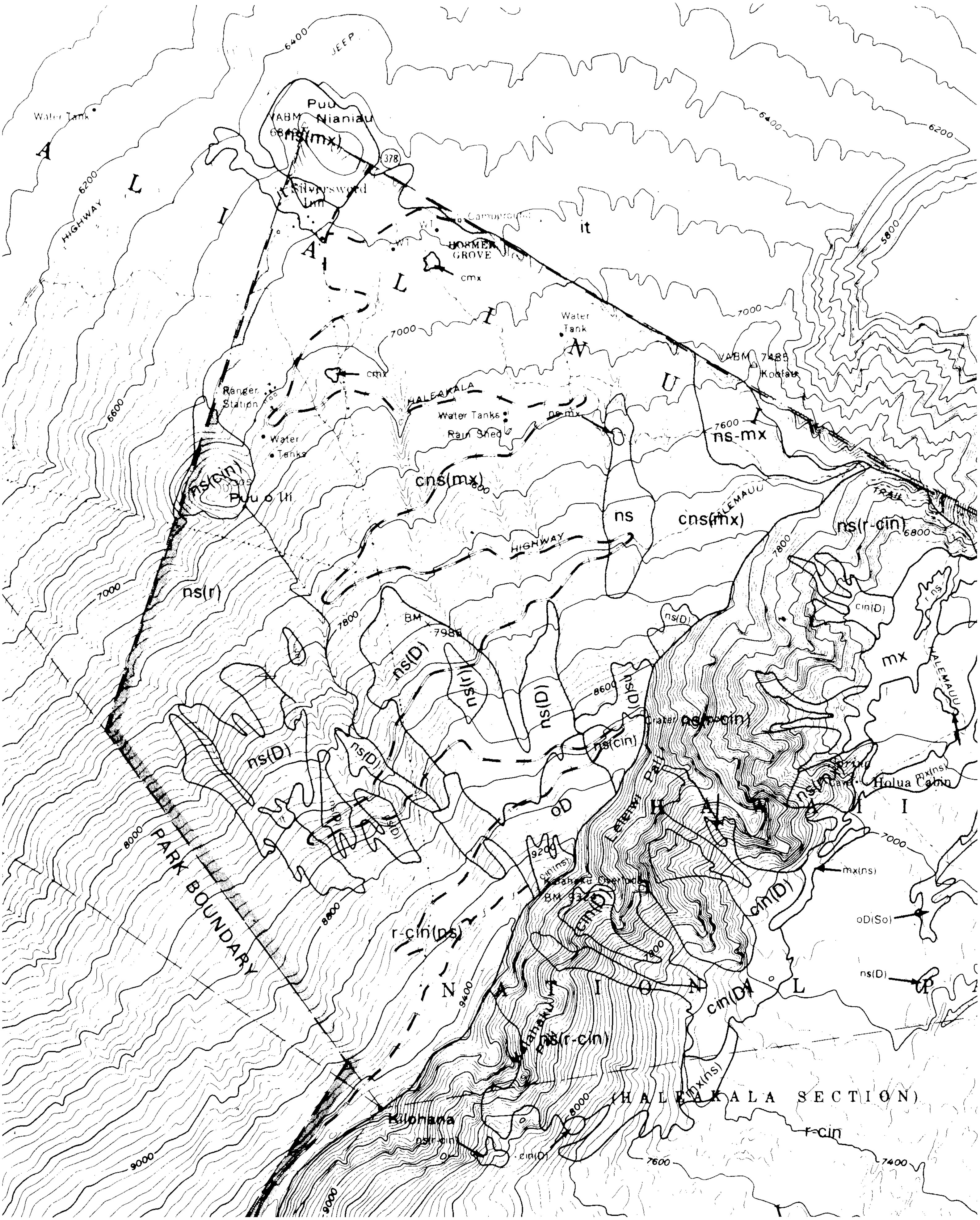
APPENDIX II

Soil Pit Descriptions

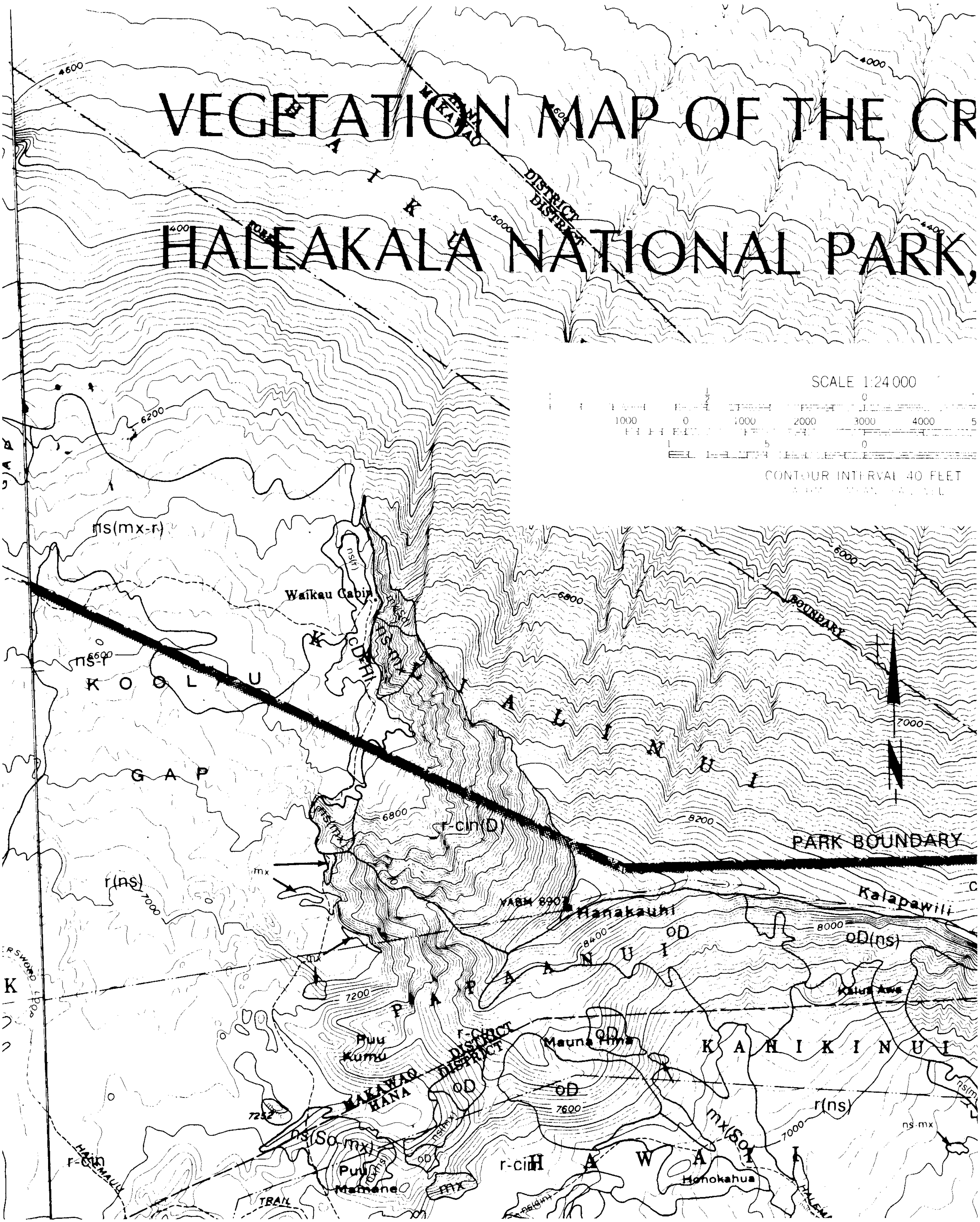
Soil pit descriptions from the Crater District of Haleakala National Park. All parameters are from field determinations.

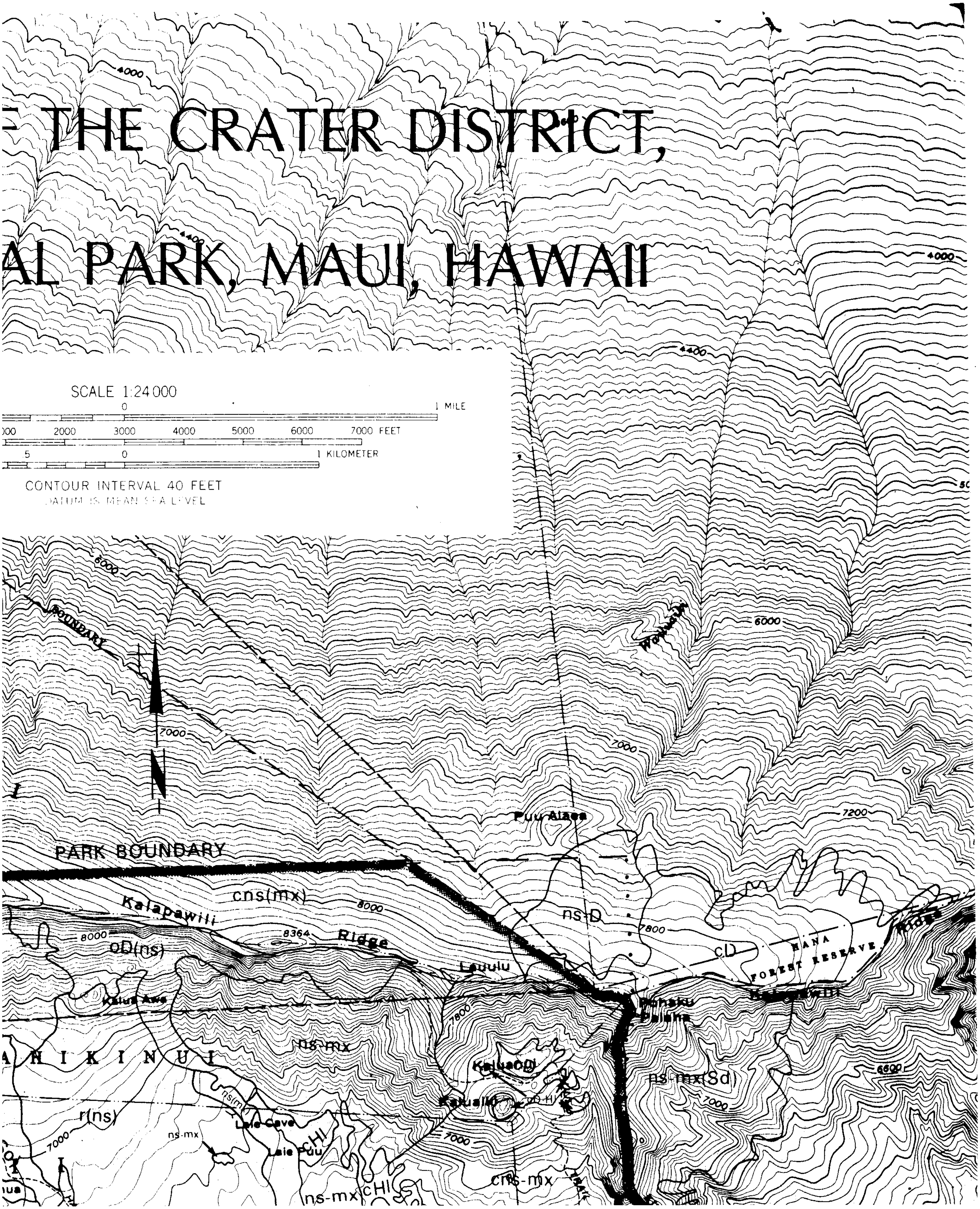
Releve # & Map Unit	Horizon	Depth (cm)	Color	Texture	Structure	Consistency
6	A_1	0-11	dark brown	loam	crumb	friable
	A	11-23	dark brown	loam	crumb	firm
cns(mx)	B	23-67	brown	loam	unstructured	firm
	C	67	yellow-brown	clay-loam	blocky	v. firm w/rocks
	maximum depth	72				
9	A	0-30	black	cinder	unstructured	friable
	B	30	black	cinder	unstructured	firm
ns(So-mx)	maximum depth	80				
11	A_1	0-13	yellow-brown	loamy-peat	crumb	friable
	A	13	dark brown	sandy-loam	unstructured	friable
cmx	maximum depth	82				
24	A_1	0-10	dark brown	loam	crumb	friable
	A	10-25	dark brown	loam	crumb	firm
mx(ns)	B	25	dark brown w/ yellow-brown patches	loam	blocky	firm
	maximum depth	60				

25	A	0-7	dark brown	loam	crumb	friable
	B	7-45	rust-brown	sandy-loam	crumb	firm
oM-So(ns)	C	45				compacted(rock)
	maximum depth	45				
27	A	0-18	dark brown	loamy-peat	crumb	friable
	B	18	rust-brown	loam	crumb	friable
oM(ns)	maximum depth	65				
28	A_1	0-10	grey-brown	peaty	crumb	friable
	A	10-23	black	loam	crumb	friable
cD	B	23-40	brown	sandy-loam	crumb	friable
	C	40	brown	sandy-loam	unstructured	firm w/rocks
	maximum depth	60				
29	A	0-10	black	loam	crumb	friable
	B	10-40	dark brown	loam	crumb	friable
cD	C	40	reddish-brown	clay-loam	blocky	compacted
	maximum depth	40				
37	A	0-11	dark brown	loam	crumb	friable w/rocks
	B	11	brown	loam	crumb	firm w/rocks
cDd-Ac	maximum depth	50				
38	-- too rocky for soil pit description --					
cns						


Water Tank
6400
JEEP
Puu Nianiau
VABM 6849
ns(mx)
378
6400
6200
A
L
6200
HIGHWAY
Silversword Inn
it
Campground
it
W.T.
W.T.
HOSMER GROVE
A
L
cmx
5800
I
7000
Water Tank
7000
N
VABM 7485
Koolau
cmx
U
Ranger Station
HALEAKALA
Water Tanks
ns-mx
6600
Water Tanks
Rain Shed
7600
ns-mx
ns(cin)
cns(mx)
Puu o Ili
ns
cns(mx)
HALEMAUU TRAIL
ns(r-cin)
6800
HIGHWAY
7800
7000
ns(r)
cin(D)
r-ns
7800
BM 7986
ns(D)
ns(D)
mx
ns(r)
HALEMAUU
ns(D)
8600
ns(D)
Crater
ns(r-cin)
ns(D)
ns(D)
ns(cin)
Leleiwi Pali
ns(r)
Holua Cabin
mx(ns)
oD
H
A
W
A
I
I
8000
PARK BOUNDARY
9200
7000
cin(ns)
Kalahaku Overlook
BM 9324
mx(ns)
cin(D)
cin(D)
oD(So)
8800
r-cin(ns)
7800
ns(D)
N
A
T
I
O
N
A
L
P
A
9400
cin(D)
cin(D)
Kalahaku Pali
ns(r-cin)
mx(ns)
(HALEAKALA SECTION)
8000
Kilohana
r-cin
ns(r-cin)
cin(D)
7600
7400
9000
9000

VEGETATION MAP OF THE CR
HALEAKALA NATIONAL PARK,





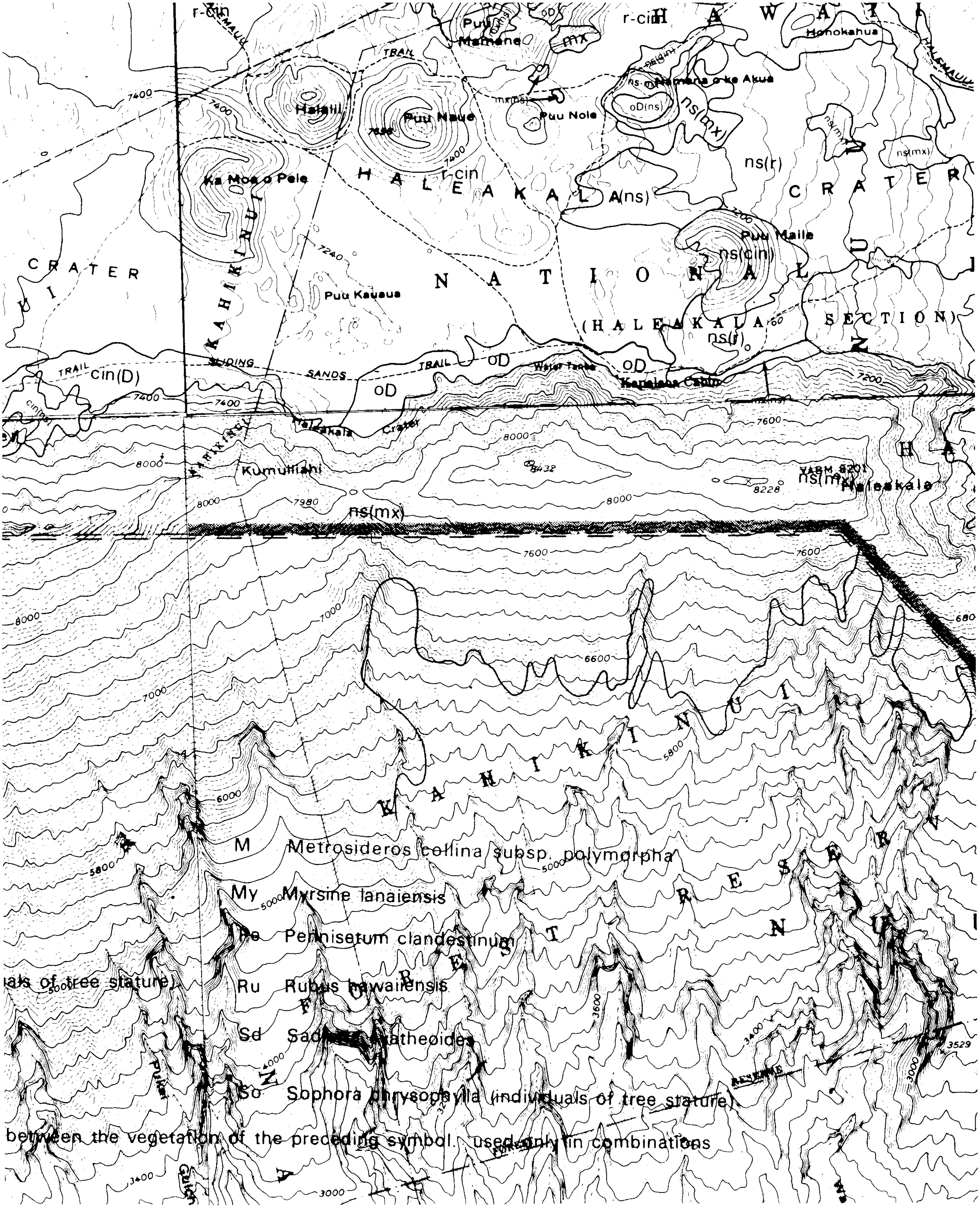
F THE CRATER DISTRICT,

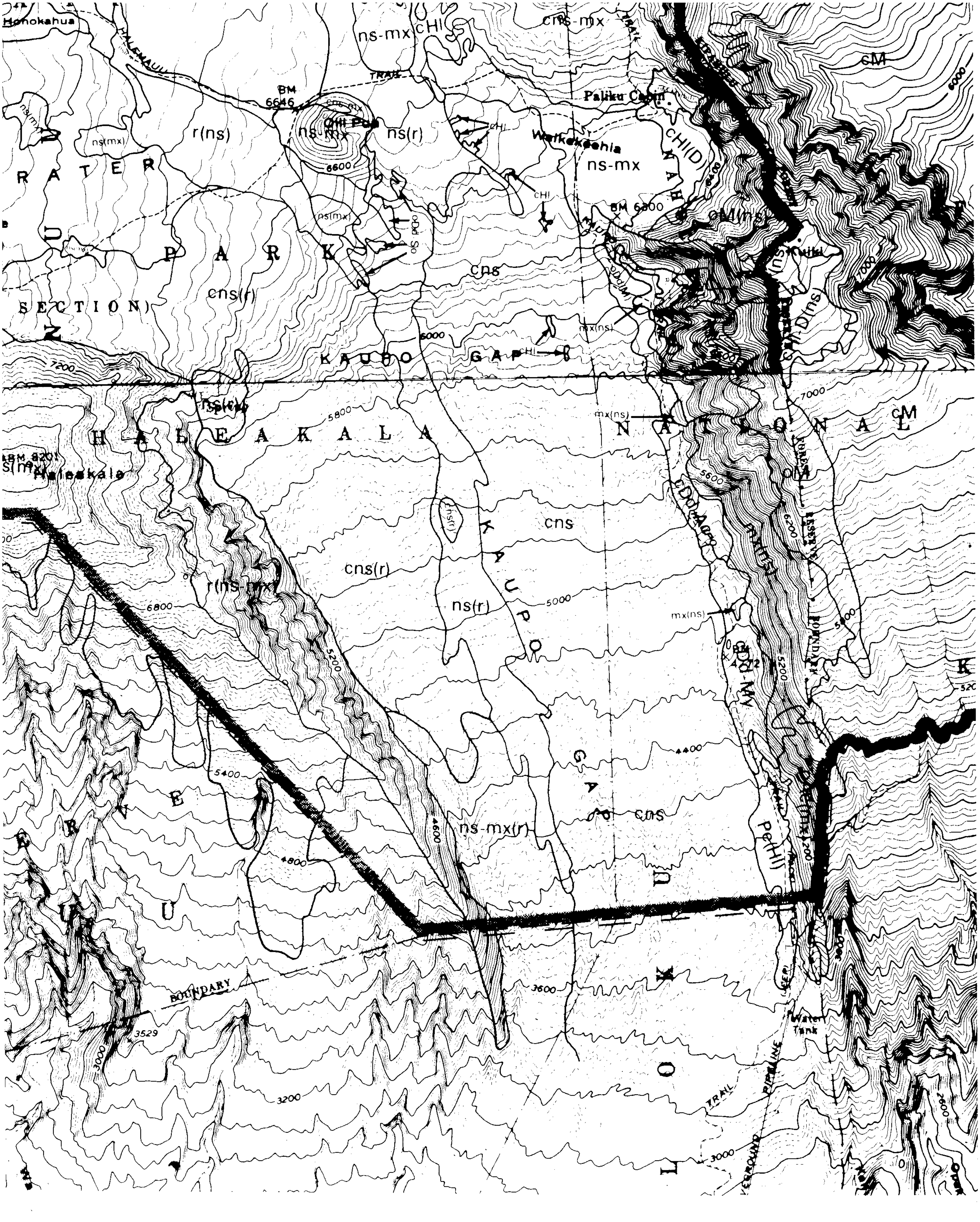
AL PARK, MAUI, HAWAII

KEY TO SYMBOLS

c	closed (>60% cover) used only in combinations	cin	cinder
o	open (30-60% cover) used only in combinations	Ac	Acacia koa
ns	native shrubs (Styphelia, Vaccinium, Coprosma, etc.)	D	Deschampsia australis
mx	mixed grasses (Holcus, Anthoxanthum, Poa, etc.)	Dd	Dodonaea eriocarpa (individ
r	rock (commonly pahoehoe or a'a lava)	Eu	Eupatorium adenophorum
it	introduced trees (Eucalyptus, Pinus, etc.)	Hl	Holcus lanatus

(ns) symbol in parenthesis are scattered, sparse (<30% cover) or as an understory of or matri


HAWAII
HALEAKALA NATIONAL PARK
(HALEAKALA SECTION)
CRATER
KAHIKINUI
KAHIKINUI FOREST RESERVE
Puu Mamane
Honokahua
Namana o ke Akua
Halalii
Puu Naue
Puu Nole
Ka Moa o Pele
Puu Kauaua
Puu Maile
Kumuiliahi
Kapalaoa Cabin
Water Tanks
Haleakala
SLIDING SANDS TRAIL
TRAIL
r-cin
mx
ns(mx)
oD(ns)
ns(r)
A(ns)
ns(cin)
oD
cin(D)
7400
7240
7600
8000
8432
8228
7980
VABM 8201
7000
6600
5800
6000
5000
4000
3600
3400
3000
3529
M Metrosideros collina subsp. polymorpha
My Myrsine lanaiensis
Pe Pennisetum clandestinum
…als of tree stature)
Ru Rubus hawaiiensis
Sd Sadleria cyatheoides
So Sophora chrysophylla (individuals of tree stature)
between the vegetation of the preceding symbol. used only in combinations


Honokahua
HALEMAUU
TRAIL
BM 6646
Oili Puu
ns-mx
cns-mx
cHl
ns(r)
r(ns)
ns(mx)
6600
CRATER
PARK
SECTION)
cns(r)
cns
Paliku Cabin
Waikekeehia
CHl(D)
ns-mx
BM 6300
cM(ns)
cM
6000
7000
KAUPO GAP
mx(ns)
7200
ns(r)
Spring
5800
HALEAKALA NATIONAL
BM 8201
s(mx)
Haleakala
cns
cns(r)
ns(r)
cns(r)
r(ns-mx)
6800
5600
mx(ns)
5200
5000
cM
KAUPO
BM 4712
K
4400
5400
RESERVE
GAP
ns-mx(r)
cns
4800
4600
Pe(Hl)
U
BOUNDARY
3600
KOKI
3529
3000
3200
Water Tank
TRAIL
PIPELINE
UNDERGROUND
JEEP
3000
2800