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ECOLOGY OF THE SILVERSWORD

ARGYROXIPHIUM SANDWICENSE DC. (COMPOSITAE)

HALEAKALA CRATER, HAWAII

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE
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By

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In particular, I wish to thank former Park Naturalist Ralph Harris and the Haleakala National Park Staff for their encouragement, advise, and cooperation during my four-year study.

FRONTISPIECE

Flowering Silversword 1.5 m high
Silversword Loop 1971

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CHAPTER I

LITERATURE REVIEW

The literature on *Argyroxiphium sandwicense* DC., an endemic composite of remarkable evolution and adaptation to the severe Hawaiian alpine milieu, will be presented in three parts. The first seeks to describe the giant rosette plants of the tropical alpine in terms of their life form and environment. A taxonomic and anatomical survey of the Hawaiian Madinae follows. Finally the meager literature dealing directly with the ecology of *A. sandwicense* on Haleakala closes the review.

Giant Rosette Plants of the Low Latitude Alpine

On open, low latitude alpine slopes in several parts of the world, a life form having large, often tomentose, succulent leaves arranged in compact rosettes can be found. These "giant rosette plants" (Hedberg 1964) are typified by the composite genera *Senecio* in the African , *Espeletia* in the Andean, *Anaphalis* in the Indonesian, and *Argyroxiphium* in the Hawaiian alpine regions (Billings and Mooney 1968, Walter 1971). Although timberline the lower boundary of the alpine zone is an ecotone of gradual transition from closed forest to scattered low shrubs in the tropics, and therefore poorly defined (Fosberg 1959, Mueller-Dombois 1967, Troll 1957), the following will show that there is general agreement in the literature on the climatic and edaphic conditions found in the low latitude alpine regions throughout the world.

Solar radiation at all wavelength is high in the alpine because there are fewer molecules of air per unit volume to scatter and absorb radiant energy (Tranquillini 1964). The most conspicuous protection against high isolation and desiccation is the dense whitish pubescence of some rosette plants. Whitishness may be caused by reflection of all light wavelengths from trichomes that possess flattened lens-shaped cross-sections (Carlquist 1957). A flat felt-like pubescent covering may be produced by trichomes with articulated basal cells (Hare 1941).

Although ultra-violet radiation has long been suspected as an important ecological factor for montane plants, there have been few studies done under natural field conditions which would establish the relative importance of this type of raidation. Caldwell (1968) found little change in plant growth and development for one growing season in a temperate alpine community over which plastic film filters were used to exclude ultra-violet radiation. He found no statistically significant differences in either ultra-violet albedo or filtration capacities of alpine and lowland plants in Colorado.

Unlike the high latitudes, the tropic alpine regions have little variation in the mean monthly temperature between the coldest and warmest months. Differences of less than 7°C were reported by Budowski (1966) Peru, and Reber (1959) and Britten (1962) in Hawaii. However, the high insolation and low heat capacity of the thin, dry alpine air creates large diurnal changes during which frosts every night have been encountered in the Andes (Walter 1971) and the afroalpine belt (Hedberg 1964). On Haleakala's summit, unpublished U.S. Weather Service data from 1957 to 1969 indicate that subzero temperatures can be expected any day of the year.

Lacking seasonal adaptations such as bud dormancy and leaf abscission, giant rosette plants probably survive best if they are not subjected to frosts lasting more than a day or two. Shoot meristems are insulated within rosettes which may even fold inward at sunset in some species (Walter 1971). Hedberg (1964) measured a temperature of +1.8°C in the center of a rosette when the ambient air temperature was -4.0°C. The large thin-walled cells in the stem cortex of arborescent rosette composites (Carlquist 1966a) are sometimes insulated by sheaths of dry dead leaves (Hare 1941, Hedberg 1964).

In the tropics, the alpine zone is located above moisture-bearing clouds and receives little rain (Salt 1954, Blumenstock and Price 1967, Walter 1971). For example, rainfall on Haleakala decreases from a maximum of 10,000 mm at 1000 m elevation on the windward face to less than 760 mm on the summit (Britten 1962). Hedberg (1964) noted an increase in xeric characters of related species with altitude in Africa and South America. Some of the xeric characteristics of Senecio leaves described by Hare (1941) are:

1. greater development of the hypodermis,
2. decrease in the mesophyll air space,
3. decrease in the size of lower epidermal cells, and
4. increase in the number of trichomes per surface area.

On Mauna Kea and Mauna Loa, plant density is related to exposure to clouds and fog (Hartt and Neal 1940, Mueller-Dombois 1967).

Therefore in the low-rainfall alpine zone, fog-drip from trees and shrubs may increase groundwater significantly. For example, Ekern (1964) measured a gain of 30% over a 3-year period beneath a Norfolk Island pine on Lanaihale summit, Lanai at 837 m elevation.

The thick tap roots of acaulescent rosette plants of Africa and South America can withstand frost heave associated with solifluction, a condition frequently found in fine-textured alpine soils (Hedberg 1964). Dendroid Senecios are adapted to frost heave by the production of tough fibrous roots in the early juvenile stages (Hare 1941). The succulent roots that appear later in the water-retaining humic surface soil are the principal absorbing organs, whereas the role of the fibrous roots is primarily mechanical.

Summarizing, the giant rosette plants have features well adapted to the intense solar radiation, large diurnal temperature changes, and the dry air of the low latitude alpine climate.

The Hawaiian Madinae

The silverswords (*Argyroxiphium*) and their Hawaiian relatives (*Dubautia* and *Wilkesia*) belong to the subtribe Madinae (Compositae, tribe Heliantheae), a group consisting mostly of small annuals inhabiting open dry areas of western california (Carlquist 1959b). The Madinae are called tarweeds because of their resinous hairs (Carlquist 1965). The Hawaiian species are large perennials found in a wide range of ecological niches (Carlquist 1966a, 1966b). The rosette form, in particular, exhibits features of adaptive radiation typical of composites on large oceanic islands (Carlquist 1965, 1970).

Many weed species of composites "have small fruits with very good dispersal mechansims, and are thus unusually well reppesented on islands" (Carlquist 1965). The tarweeds are characterized by ray achenes enclosed in sticky bracts which may become attached to bird feathers. However, Argyroxiphium has shorter pappus scales than the mainland tarweeds. Carlquist (1966b) attributes this to the unimportance of long distance dispersal once the original immigrant became established in Hawaii.

The composites have evolved into rosette tree forms not only in Hawaii, but also on many other oceanic islands (Carlquist 1965). Whether insular or tropical alpine, they are basically herbaceous and retain juvenile characteristics throughout their lives. Some tnedencies listed by Carlquist (1966a) in low latitude insular species are:

1. continual cambial activity because of small seasonal temperature variations,
2. lack of strong selection for mechanical elements, and
3. parenchymatous tendencies in rosette forms.

Fosberg (1948) postulated that a single immigrant gave rise to the 61 species and varieties of the Hawaiian Madinae. It may have been a herbaceous annual transported from California as a seed attached to the feathers of a bird. Instead of dying back each winter, a rosette plant could grow continuously in the relatively milder maritime climate. Enclosing rosette leaves would be sufficient protection for the continuously active apical bud because temperature extremes are only of short duration. Thus the annual seedling stage may be bypassed

(Carlquist 1966a). In the absence of browsing herbivores, there would be no selection against increased succulence and leaf size (Carlquist 1965).

Madia sativa Molina is an example of a tarweed insular colonizer now establishing itself in Hawaii. Found from British Columbia to the Straits of Magellan, it was apparently first reported in Hawaii growing on sun-scorched cinder within Haleakala Crater in 1927 (Degener 1940). Eighteen years later Mitchell (1945) noted a slight increase in its range. Thus in *M. sativa* we have a tarweed colonizer adapted for a dry habitat, an adaptation which may have enabled *Argyroxiphium* and *Dubautia* to evolve in the Hawaiian alpine regions (Carlquist 1970).

The shrubby tarweeds (section Fruticosae, genus *Hemizonia*) found on the offshore islands of Lower California are examples of a more advanced stage of adaptive radiation. They have evolved from continental herbaceous annuals into several species characterized by a loss of seasonal growth in the milder maritime climate (Carlquist 1965). Presently found only on dry coastal areas, *Hemizonia* may move inland and cover a wide range of habitats in the future.

Asa Gray (1852) was the first to relate the genus *Argyroxiphium* to the Madinae of California. However Skottsberg (1930) and Keck (1936) favored connections to the Southern and Southwestern Pacific species. An extensive study by Carlquist (1959b) on the comparative anatomy and cytology of the Madinae tends to support Gray's viewpoint. Carlquist listed eight characters of the capitulum shared by members of the Madinae in California and Hawaii.

In Hawaii, the close interrelationship of the endemic genera Argyroxiphium, Dubautia, (= Railliardia) and Wilkesia has never been disputed. In the polymorphic Hawaiian Madinae, there is a tendency to merge genera: Wilkesia into Argyroxiphium, and Railliardia into Dubautia (Keck 1936). Hybrids are found among species (Keck 1936) as well as at the generic level, i.e. Argyrautia (Sherff 1944). An example of the latter was encountered by the writer during the Summer of 1969 on Haleakala (Kobayashi 1973). Gross external features, internal anatomical details, and plants grown from seed all point to an intergeneric hybrid between A. sandwicense and D. menziesii (A. Gray) Keck.

Dubautia, the most successful genus in terms of species and number, varies from herbaceous forms to the only truly woody species in the Madinae (Carlquist 1959b). Identical glandular trichomes, certain features of the leaves, floral bracts and style reveal its close affinity to the foliar structure of Argyroxiphium (Carlquist 1959b). Wilkesia found only on Kauai, was judged to be an advanced form of A. grayanum and was merged with Argyroxiphium by Keck (1936). Carlquist thought it was highly unlikely that Wilkesia's simple foliar features could be derived from Argyroxiphium's leaves which are unique in the Madinae. He argued that on the basis of leaf characters, wood anatomy, and inflorescence types, the three genera are clearly distinct (Carlquist 1957, 1959a, 1959b).

Argyroxiphium, probably first collected by David Douglas about 150 years ago (Degener 1945), was introduced into botanical nomenclature as Argyroxiphium by De Candolle in 1836. The name is derived from the Greek roots for "silver" and "sword" in reference to the foliage of the type species *A. sandwicense* DC. The Hawaiians named the plant *ahinahina* -- extremely gray -- since metals were unknown to them (Carlquist 1970). Some salient features of this genus excerpted from Degener (1957) are:

> Robust perennial herbs with woody stems simple or branched. Leaves brilliantly silver to gray-pubescent, entire, linear to linear-lanceolate, in cross section somewhat triangular. Heads arranged on large raceme, entire plant dying after seeding in simple stemmed species but in branched species only fertile branches doing so.

Argyroxiphium is divided into the densely pubescent silverswords (3 or 4 spp.) and glabrous to pubescent greenswords (3 spp.). All except *A. sandwicense* and *A. kauense* are rare and grow below 2,400 m in moist foggy areas. The foliar anatomy of *A. sandwicense* usually found on dry cinder, and *A. caliginii* of the Puu Kukui Bog can be correlated with their habitats (Carlquist 1957). The trichomes of the former are denser with thicker walls, and their distal ends are more flattened in cross section. The epidermal cells have a more prominent cuticle and are not thin-walled as in *A. caliginii*. Hydathodes, an adaptation to high air humidity and saturated soil conditions, present in *A. caliginii* and certain afroalpine giant rosette species (Hare 1941) may be recent adaptations because xeric features shared by all *Argyroxiphium* species point to a common ancestor adapted to a dry alpine habitat (Carlquist 1970). Specifically one feature, hydrophilic gels in the mesophyll may "aid survival in a xeric habitat, and is quite neutral in a mesic situation" according to Carlquist (1957).

Haleakala's common silversword *A. sandwicense*, the subject of the present research, may be a separate species, *A. macrocephalum*, as first circumscribed by Asa Gray (1852). Carpenter (1959) reported that a plant grown from the seed of a Hawaii Island silversword had distinctly longer, more flexible leaves than the Haleakala plants. If this plant was not *A. kauense* (Degener 1957; synonym *A. sandwicense* var. kauense, Rock and Neal 1957), then it appears that Haleakala's plants should be kept as a separate species rather than a variety of *A. sandwicense* as reduced by Hillebrand (1888).

In summary: the Hawaiian Madinae may have evolved from an annual tarweed transported from the West Coast as an achene attached to the feathers of a bird. The large succulent-leaved rosette form of insular and tropical alpine composites may be due to the retention of juvenile characteristics in an environment lacking seasonal changes and browsing herbivores. Although *A. sandwicense* is the only one of 6 or 7 species of *Argyroxiphium* found in the dry alpine zone of the Hawaiian Islands, xeric features shared by all species point to a common ancestor similar in form to *A. sandwicense*.

Argyroxiphium sandwicense on Haleakala

According to some accounts, "The Haleakala silverswords were so abundant during the late 19th Century so (sic) as to make the hillside look like winter or moonlight" (Degener 1930). Alexander (1870) also described a part of the crater floor now almost devoid of plants as, "sprinkled with myriads of silverswords, many of which were in full bloom, presenting a magnificent sight." Estimates of the number of plants have ranged from less than 100 in the Crater (Degener 1930) to "perhaps 10,000" for the entire Haleakala National Park (Badaracco 1963). Actual censuses of individuals were made only twice, both on centrally located Ka-Moa-o-Pele cinder cone (Lamb 1935b, Badaracco 1962), a net increase of 53% (1,470 to 2,248) in 27 years.

Removal of plants by visitors and browsing by goats may be the main causes of the decline until 1929 when a permanent ranger position was established by the National Park Service (Ruhle 1959). Earlier, it was customary to bring down whole plants as proof of a visit to the summit (Missionary Herald 1829, Bryan 1915). On the front page of the Honolulu Advertiser Feb. 23, 1911, a photograph shows Maui's entry in the Washington's Birthday Annual Floral Parade: a touring car completely covered with large mature silverswords, even to plants fastened to wheel spokes. Even today, vandalism goes on constantly though sometimes the guilty ones are apprehended (Anonymous 1971).

The impact of browsing by goats is not as clearly defined as the effect of vandalism. Conflicting opinions were voiced by qualified observers interviewed by Lamb (1935a). Silverswords may not be eaten in preference to other plants because in January 1947, the easily identifiable leaves of the silversword were not found in the stomach contents of 33 goats (Yocum 1967). Shooting by Park personnel has reduced the number of goats from over 4,000 twenty years ago to presently about 600 mostly found around the crater rim (Yocum 1967, Larson 1969). Since the crater floor has always had the highest number of plants (Alexander 1870, Lamb 1935a, Powers 1938, Anonymous 1945, Badaracco 1962), browsing by goats may not be significant under the present hunting restrictions and the present range of the silversword.

On Haleakala, A. sandwicense usually remains in a sessile rosette form for 7 to 20 years (Ruhle 1959). Generally there is one shoot meristem produced per plant that becomes a floral raceme during the summer culminating in the death of the plant (Frontispiece). Therefore the silversword may be a typical seed plant whose flowering-to-seedling stages are relatively important in its life cycle (Pelton 1953). The number of plants that flower each year may vary from zero (personally observed in 1970) to 815 (Hjort 1941). Other than prolonged drought (Lamb 1935a), no reason for this variation has been given.

Although thousands of seeds are produced by one plant (Degener 1930), seed-set and long-term viability were reported to be poor. Knutson (1968) dissected and examined 700 seeds and found that only 5% contained viable embryos; however Park Naturalist Ralph Harris found 257 out of 500 seeds of the 1967 crop contained embryos (Harris 1968). His attempts at germinating two-year old seeds were not successful.

The great destruction of maturing seeds by insect larvae was noted over a century ago by Hillebrand (1854). Of the six endemic insects found only on the Haleakala silversword (Swezey 1954), a phycitid moth Rhynchephestia rhabdotis Hampson and a tephritid fly Tephritis cratericola Grimshaw are particularly destructive (Swezey and Degener 1928, Degener 1930, Lamb 1935b). Maggots and caterpillars of these insects feed on the developing seeds and may eliminate all but a few seeds in a capitulum according to Degener (1930). To prevent oviposition, Lamb (1935b) bagged individual capitula and erected mesh tents over entire plants. The results were inconclusive: eggs were laid before the capitula were bagged and the tents were damaged by vandals and high winds (Lamb 1936).

Siegel et al (1970) found that one-year old seeds germinated best when subjected to a 8-25°C cycle (27% germination) and a constant 25°C (14% germination) in the laboratory. Inhibitors were found in the seedcoat and inflorescences. They concluded that, "Narrow temperature range, low heat resistance of dormant seeds, and chemical inhibitors contribute to poor field germination of seeds."

During the past few decades, the silverswords have numbered at least a few thousand on Haleakala, the number flowering being highly variable from year to year. Under the protection of the Park Service, vandalism and browsing have been greatly reduced. Two host-specific insects are particularly destructive to silversword seeds. Although thousands of achenes are produced by a single plant, poor seed fertility, low resistance to temperature extremes, and inhibitors in the seedcoat may contribute to poor field germination.

CHAPTER II

ECOLOGY OF THE SILVERSWORD

ARGYROXIPHIUM SANDWICENSE DC. (COMPOSITAE)

HALEAKALA CRATER, HAWAII

ABSTRACT

Argyroxiphium sandwicense DC. is an endemic composite of the alpine zone in Hawaii. Western man and his herbivores have restricted its present distribution mostly to the cinder cones and lava flows within Haleakala Crater, Maui. Here the silversword is able to sustain a high regeneration rate under dynamic substrate conditions that eliminate all but a few exotic and endemic species.

Long-term field measurements of environmental parameters, and growth cabinet experiments on germination and seedling survival established the following optimal conditions. Germination and seedling survival depend on a temperature not exceeding about 30°C, and the relatively high moisture content of a stable sandy substratum completely covered by cinder fragments no thicker than about 5 cm. The maintenance of the thin complete cover over an area larger than a hectare for a period of a few decades, is best met by a shelf of agglutinates supplying tabular fragments which slide over a sloped sandy germination layer. The slope angle is about 35 degrees; low enough to stabilize the sandy layer, yet steep enough to be slightly unstable for tabular fragments. A thin cover is maintained by removal of fragments at the foot of the slope by wind and water during winter storms.

Vandalism and browsing are probably not important under the protection of the Park Service, but root breakage by trampling may become a problem with further increase in visitors. Seed damage by insects may not be important as previously reported, but confirmation awaits further investigation during a good flowering season.

INTRODUCTION

Among the endemic plants which evolved in the isolated oceanic Hawaiian Archipelago, few are better known to botanists and laymen alike than Argyroxiphium sandwicense DC. the Haleakala silversword (hereafter referred to as the silversword). With its brilliantly silver ball of leaves arranged in a sessile rosette and surmounted by a massive raceme of lavender capitula, the silversword is a striking example of evolution and adaptation in the subtropical alpine milieu (Frontispiece). Formerly abundant at all alpine elevations in Hawaii, the species has been reduced by man and his introduced herbivores until now it is numerous only in a 15 sq-km area in Haleakala Volcano, Maui. Today this nearly barren area of cinder cones and lava flows within the crater is still relatively untouched because of strict National Park control and access only on foot and horseback, or by helicopter. Consequently silversword populations within Haleakala Crater offer the increasingly rare opportunity of studying nearly all the individuals of a Hawaiian endemic plant species in a large, comparatively undisturbed environment.

Certain stages in the life cycle of the silversword pose problems of adaptation to its natural environment. The plant usually remains as a sessile rosette for 7 to 20 years (Ruhle 1959) after which the single shoot meristem produces a terminal raceme culminating in the death of the plant. Generally no side branches are produced as in other species of Argyroxiphium (Degener 1930, Carlquist 1970); thus the silversword is a typical seed plant whose seed and seedling stages are relatively important parts of its life cycle (Pelton 1953). The number of plants that flower during the summer season may vary from zero to several hundred, the triggering stimulus of which is still uncertain. Although thousands of seeds are produced, only 5% are reported to contain viable embryos (Knutson 1968). Another problem is the great destruction of maturing seeds by insect larvae noted as early as 1854 by Hillebrand (1854). Two insects found only on the silver-sword may eliminate all but a few seeds in a capitulum according to Degener (1930). The seed itself is extremely sensitive to high temperatures (Siegel et al 1970), and was reported to have a viability of less than two years by Harris (1968). Paradoxically, the juvenile and mature stages are highly adapted to long life in the desert-like environment of the crater floor (Carlquist 1970).

The distribution of silversword populations within the crater also raises questions relative to the physical environment. Although most plants seen from the trails appear to be on red slopes intercepting the tradewinds coming from the northeast, dense clusters are also found on dark cinder exposed to other directions. The red color of cinder is due to iron oxidation during and immediately following eruption (Macdonald 1967), and probably not because of weathering as implied by Ruhle (1959). Chemical weathering is low on cinder cones at high elevations according to Wentworth and Macdonald (1953).

The present research will be conducted in the following manner:

1. An extensive preliminary survey of the entire range of the silversword on Haleakala will be made, and
2. a study site will be selected for developing a hypothesis

on the factors governing germination and seedling survival.

3. Then the hypothesis will be verified by field and laboratory experiments, and

4. finally the hypothesis will be used to explain the past and present distribution of plants on Haleakala Crater.

A broad, comprehensive program is necessary because only two studies -- both brief and preliminary -- are available on the ecology of the silversword (Siegel *et al* 1970; Lamb 1935a, 1935b, 1936).

The endemic genera *Argyroxiphium*, *Dubautia*, and *Wilkesia* belong to the subtribe Madinae (Compositae, tribe Heliantheae), a group consisting mostly of small annuals inhabiting open dry areas of the California coast (Carlquist 1959b). The single immigrant giving rise to the 61 species and varieties of the Hawaiian Madinae (Fosberg 1948) may have arrived as a seed, either windblown or attached to the feather of a bird. According to Carlquist (1966b), pappus scales, plumose bristles, and ray achenes enclosed in sticky bracts found in some American tarweeds may aid seed dispersal by birds. The Hawaiian Madinae are so closely interrelated that hybrids are found not only among species (Keck 1936), but even at the generic level (Kobayashi 1973).

Argyroxiphium, probably first collected by David Douglas (Degener 1945), was introduced into botanical nomenclature by De Candolle in 1836, and consists of 6 or 7 species (Stone 1967). The name was derived from the Greek roots for "silver" and "sword" in reference to the foliage of the type species *A. sandwicense* DC. All except

A. sandwicense and *A. kauense* grow below 2,400 m in moist foggy surroundings. Certain xeric features found in all species of *Argyroxiphium* such as water-storing pectic compounds in the mesophyll, suggest that the genus is derived from a dry alpine plant resembling the Haleakala silversword (Carlquist 1970).

THE STUDY AREA

Geology

Haleakala Crater is the summit depression of Haleakala, a shield volcano 3,060 m high which forms all of East Maui, an area of about 1,400 sq-km. The depression is formed by the coalescence of two ampitheater-headed valleys: Keanae Valley (Koolau Gap) draining to the north, and Kaupo Valley draining to the south (Stearns 1942). The floor of the depression, 11 km from east to west and 3 km from north to south, is about 460 m below the crater rim and consists of rough aa flows and cinder and spatter cones up to 200 m high. These cones extend along a southeast rift zone from Hanakauhi Peak on the north rim, across the depression to the summit, and down to La Perouse Bay at sea level. The Bay was formed as a consequence of the last volcanic activity on Maui between 1786 and 1793 (Oostdam 1965). Silverswords are found mostly within the crater growing on the cones and flows of the Recent Hana Volcanic Series shown in Fig. 1. Only scattered individuals and very small populations grow on the crater rim and outer slopes which consists of the older Pleistocene Kula Volcanic rocks partially covered by windblown cinder from the Hana Series.

Cline (1955) classified Haleakala's substrate as regosols and lithosols, soils having little or no profile development. He stated that Haleakala cinder and ash, a sandy-textured regosol, have characteristics that depend primarily on the nature of the parent material. For example, the variation in color of cinder from dark brown to red and yellow is due to iron oxidation during and directly after the formation of cinder cones (Macdonald 1967).

Climate

The climate near the summit depends on the temperature inversion layer at 2,000 m which accompanies the northeast tradewinds present 50 to 70% of the time (Blumenstock and Price 1967). Above 2,000 m the air is generally clear and dry during the morning hours because orographically lifted moisture-bearing clouds are suppressed by the inversion. Cloud photos taken almost daily for one year (Ekern 1953) show that frequently towards noon, the inversion is overriden by clouds that are pushed upslope by the tradewinds, first into Koolau Gap and then into Kaupo Gap. As a consequence, the average annual precipitation varies from 2,000 mm at 2,100 m in the Koolau Gap to 800 mm at 3,000 m on the summit (Fig. 2). At the Ranger Station (2,130 m) where precipitation has been measured since 1939, the average annual figure is 1,300 mm, the minimum 450 mm in 1962, and the maximum 2,300 mm in 1948.

According to unpublished U.S. Weather Service records filed at the Honolulu Regional Office, the greatest changes in temperature on Haleakala are found at the summit where the mean yearly maximum and minimum temperatures are 14 and 4°C respectively. Freezing temperatures have been recorded for every month of the year. For example, September -- the month with the highest mean temperature of 10°C -- had a minimum of -2°C in 1958. The highest maximum recorded on the summit was 23°C in July 1961.

VEGETATION

The cinder cones and aa flows on which the silverswords are found are collectively called "scattered shrub and barren areas" by the Park Service (Larson 1969) (see Fig. 1 and 2). In these areas the vegetation never forms a closed cover of more than a few square meters. The only widespread exotic plants are *Rumex acetosella* L. and *Hypochaeris radicata* L., both annuals conspicuous only during their summer flowering seasons. Shrubs are mostly *Dubautia menziesii* (A. Gray) Keck, *Styphelia tameiameiae* (Cham.) F. Muell. and *Silene struthioloides* Gray. Dominant grasses are the native *Agrostis sandwicensis* Hbd. and *Deschampsia nubigena* (Hbd.) Hitchc. Cryptogams are mostly represented by the ferns *Pellaea ternifolia* (Cav.) Link and *Asplenium trichomanes* L. found in rock crevices and under overhanging ledges.

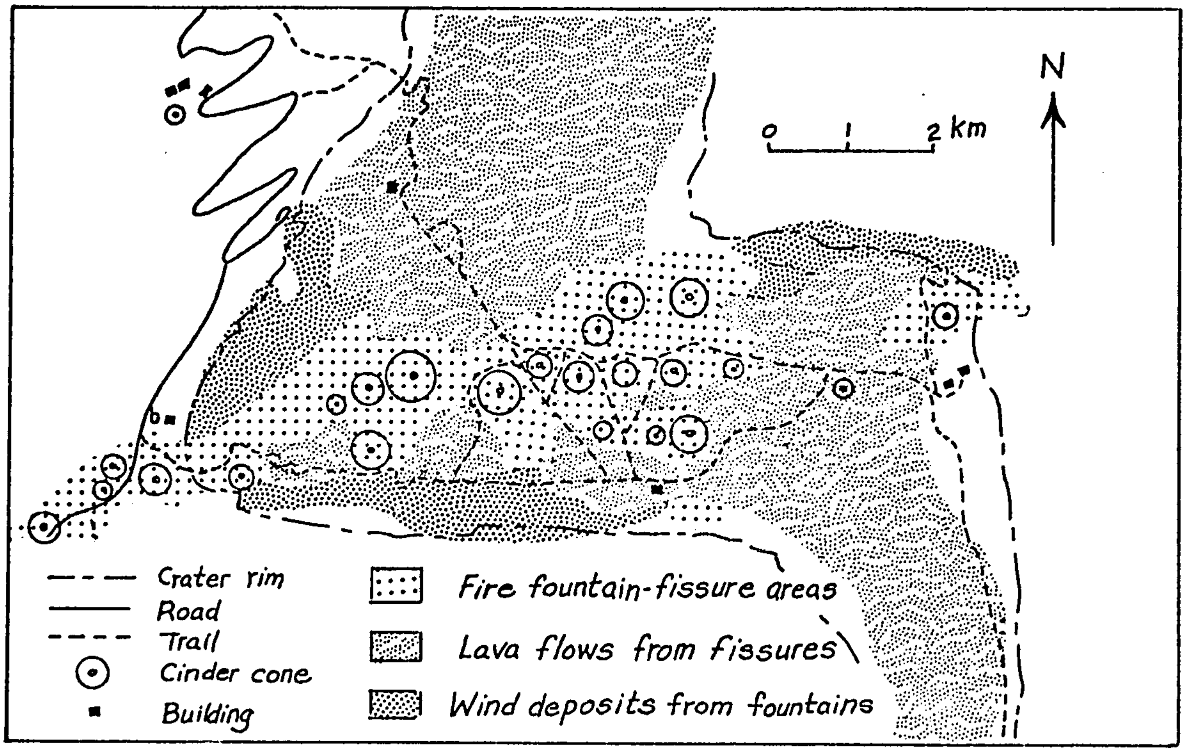


Fig. 1. -- Geologic and Man-made Features, Haleakala Crater Simplified from Stearns and Macdonald 1942.

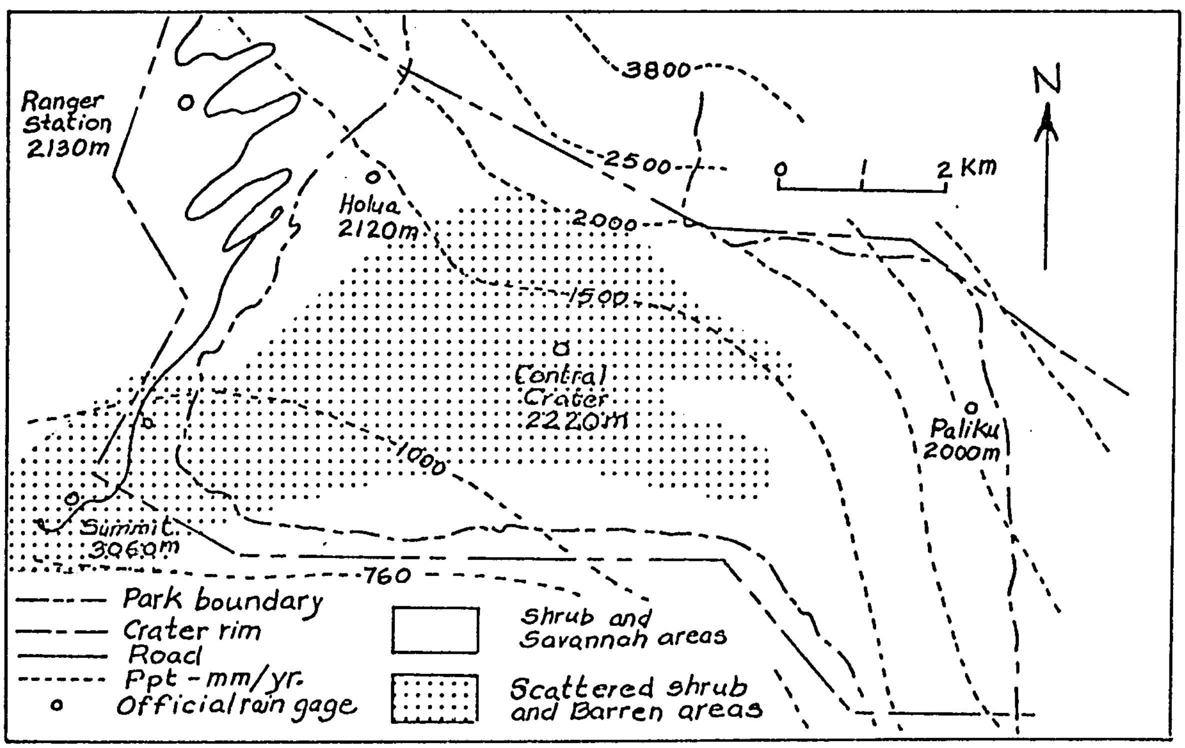


Fig. 2. -- Precipitation and Vegetation, Haleakala Crater Modified from Larson 1969.

MATERIALS AND METHODS

Meteorological Measurements

Most of the silverswords are found on the cinder cones and young lava flows of the western half of the crater floor. No temperatures have been recorded for this area of about 15 sq-km, and one 8-inch non-recording rain gage irregularly serviced a few times per month is the only source of past and present meteorological data.

To remedy this lack of weather information, bi-monthly maximum and minimum temperatures 5 dm above the ground were taken between December 1970 and February 1972. Cotton Belt weather shelters were constructed to 2/3 scale, equipped with Six's pattern thermometers and backpacked to four sites within the crater (Fig. 3).

Bi-monthly precipitation and fog-intercept data were also taken during the same time period. According to Ekern (1964), interception of tradewind clouds by vegetation may increase groundwater by at least 30%. To evaluate fog-intercept, an omni-directional wire harp was designed with a vertical cross-sectional area equivalent to a spherical plant of 12.5 cm (5 inches) crown diameter (Fig. 4). At each of seven locations, a pair of 9-cm gages, one with and one without a harp, were serviced by measuring the water levels with a ruler, emptying the gages, and adding a few drops of oil to retard evaporation.

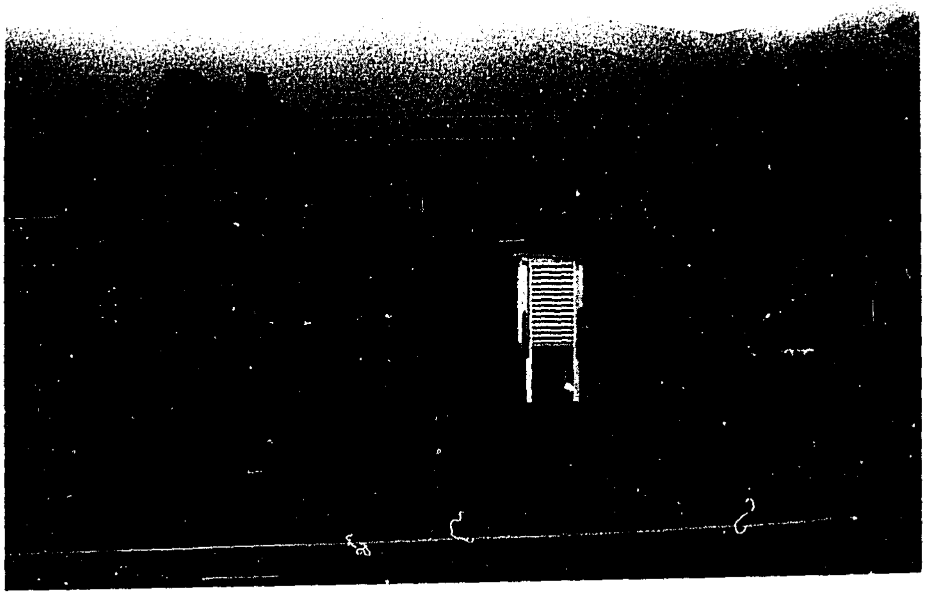


Fig. 3. -- Typical instrumented site. Instrument shelter 3, gage pair 4 at Ka-Moa-o-Pele 1970. Ka-Moa-o-Pele's high regeneration pop. 37 in mist, left background

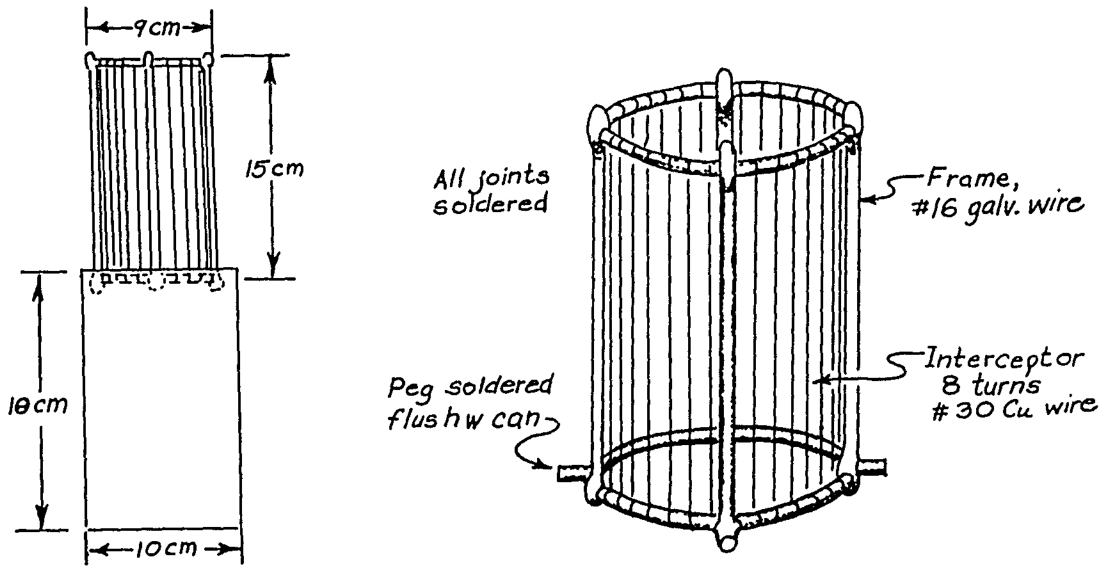


Fig. 4. -- Fog-intercept gage construction details

Census of Silverswords on Haleakala

The status of the silversword has always been a subject of conflicting accounts by the public press (Anonymous 1945, Hoyt 1969) as well as by qualified observers (Lamb 1935a). Since only one assessment which was 33 years old is available on the distribution and abundance of plants on Haleakala (Powers 1938), a comprehensive survey was needed to place this writer's ecological study on a firm foundation.

Research was initiated during the Summer of 1969 by a survey on foot of the entire known range of the species on Haleakala. This included the western slope from 2,200 to 3,000 m (7,000 to 10,000 ft), the perimeter of the crater rim, and the entire crater floor down into Koolau and Kaupo Gaps. The number of plants in three growth stages, and the location and approximate area of all populations of more than 25 plants were tabulated and drawn on 7.5 minute maps. For comparative purposes, the growth stages are the same as those of early investigators who counted plants on Ka-Moa-o-Pele cinder cone only (Lamb 1935b, Badaracco 1962). These stages are:

1. less than 20 cm (8 inches) crown diameter,
2. greater than 20 cm crown diameter, and
3. number flowered during 1969 and 1971.

None flowered during 1970 and only one in 1972. Plants were counted from a distance not exceeding 100 m using a 6X binoculars. Therefore small plants in large populations are probably underestimated, but large plants and flowering individuals are accurately tallied because of their smaller number and conspicuous appearance.

Preliminary Measurements on Ka-Moa-o-Pele

Ka-Moa-o-Pele cinder cone was selected for intensive study because:

1. silverswords of all age classes were represented,
2. it was the only location where plants had been previously counted in clearly demarcated areas which could be recounted,
3. a variety of substrate conditions was available, and
4. the cone was exposed to weather from all directions due to its symmetry, large size, and central location.

Lamb divided Ka-Moa-o-Pele into six census areas following natural ridge contours, and tallied plants according to their growth stages. His 1935 work was repeated by Badaracco in 1962 and this writer in 1971.

Elevational transect in a high regeneration area. -- To investigate the conditions related to high regeneration, three pits were dug along an elevational transect through a census area containing a high density of juvenile plants. Pit profiles were described by conventional soil survey procedures (Soil Survey Staff 1962). Temperatures of the air, substrate surface, and substrata were measured with a thermistor probe transducer connected to a wheatstone bridge. Windspeed was read on a hand-held manometer, and relative humidity was determined by a sling psychrometer. Sand-textured material from each pit was collected and the percent moisture on a dry weight basis determined by the oven-dry method. Field capacity was found by saturating a sample, allowing it to drain overnight in an air-tight container, and then determining the percent moisture.

Stability of the substrate material was assessed by first measuring the slope angle with the clinometer of a Brunton compass and comparing it with the angle of internal friction determined by triaxial compression tests on samples submitted to Walter Lum Associates of Honolulu, Soils Engineers.

Substrate characteristics of Ka-Moa-o-Pele's census areas. -- In order to compare the substrates of the six areas, the following six characteristics were selected.

1. Scree state

Cinder cones are formed by the relatively quiet action of free gas effervescing in magma rising in the throat of the main vent (Stearns and Macdonald 1942). Towards the end of the eruption, effervescence may decrease and a layer of agglutinates may form on the rim of the cone (Wentworth and Macdonald 1953). This layer having the appearance of a "ruff" on bare, slightly eroded cones was given the name Pohaku-o-Hanalei (wreath of stones) by the native Hawaiians. If present, this layer may supply mass-wasted cinder fragments to the slope below, and running water rarely seen on porous cinder (Stearns and Macdonald 1942) may remove fragments at the foot of the slope during winter storms. Thus geomorphological processes on bare cinder cones in Hawaii are similar to those on scree slopes of recently glaciated continental regions (King 1966).

On Ka-Moa-o-Pele, each census area consists of a well-defined inner or outer slope extending from the rim down to the foot or vent of the cone. Consequently each area was conveniently classified into one of the following four states employed by Thornes (1971) in describing scree slopes:

a. No supply, no removal: Static thickness of fragments.

b. Supply, no removal: dynamic accumulation of fragments.

c. No supply, removal: dynamic depletion of fragments.

d. Supply, removal: steady-state accumulation and depletion.

2. Surface fragment shape and percent cover

On Haleakala, silverswords are found on pyroclastic ejecta (= scoria) called "cinder" characterized by a vescicularity intermediate between heavier agglutinated clots of "splatter" and lighter-than-water "pumice" (Stearns and Macdonald 1942). Typically the specific gravity ranges from 0.5 to 2.1 and porosity from 30 to 80% (Macdonald 1967).

Cinder less than about 5 mm (0.2 inch) diameter (hereafter referred to as sand) appears to be readily moved and rounded by wind, water, and mass-wasting. Consequently sand fills the interstices between larger cinders on cinder cones and young lava flows. Black sands comprise most of the surface material banked against the inner crater walls and overlying older lava flows.

Cinder greater than 5 mm diameter (hereafter referred to as fragments) vary in shape from tabular to equiaxial pieces. Zingg's classification of pebble shapes wherein fragments of breadth-to-thickness ratio of less than 2:3 are tabular and those greater are equiaxial (Pettijohn 1957), was employed in estimating fragment shape and cover. In each of Ka-Moa-o-Pele's six census areas, a square-meter frame was placed on 10 subjectively chosen spots and the tabular and equiaxial fragments were estimated separately in 10 classes of percent cover.

3. Surface fragment thickness

In each census area, the thickness of the surface fragment cover was measured with a ruler in 100 subjectively chosen spots, and the data placed in one of four classes:

$<$2.5 cm, 2.5-5.0 cm (1-2"), 5.0-7.5 cm (2-3"), $>$7.5 cm

4. Percent sand moisture

Three samples in each census area were collected during one day and the percent moisture on a dry weight basis determined by the oven-dry method or by a Soiltest moisture tester. The tester measures the pressure of acetylene gas released by combining moist sand with calcium carbide.

5. Slope angle and exposure

Slope angle was measured to the nearest degree with the clinometer of a Brunton compass and verified by simple trigonometry involving elevation and distance scaled on 7.5 minute topographic maps.

Slope exposure of each census area was estimated with reference to the latitudinally oriented south crater wall, and placed in one of the eight cardinal compass directions. Visual estimations are necessary because conventional field compasses are unreliable in this region of high magnetite concentrations.

Laboratory and Field Experiments On Germination and Seedling Survival

Laboratory experiments -- All work was done in the environmental cabinets of the Soil Science and Botany Departments, U.H. utilizing the same sources of cinder substrate and silversword seeds. Cinder was collected from the best regeneration areas on Haleakala, air-dried and mixed in equal volumes, and sieved to separate the germination medium (less than 2 mm diameter) from coarser fragments. It was not necessary to sterilize the medium. For each experiment, seeds were drawn randomly from a batch of known viability combined from the undamaged seeds of 12 populations in 1971. Seeds were sown directly on the germination medium without presoaking.

1. Verification of the lethal germination temperature

Siegel et al (1970) found that seeds failed to germinate when exposed for eight hours or more at 35°C, and had the best response at 25°C. To verify their work, 500 seeds were kept at 400 ft-c of balanced constant illumination at each of four temperatures in this range. Seeds were sown on germination medium 1 cm thick maintained at field capacity in 125 ml flasks. Healthy and dying seedlings were counted at the end of 15 and 30 days.

2. Long-term viability of seeds

Viability of seeds collected in 1968 and 1969 was determined in late 1969 by microscope dissection of the achenes for the presence of embryos. Germination experiments were done at yearly intervals from 1969 to 1972 on random selections of five hundred 1968 and one thousand 1969 seeds, the selections being unequal because fewer seeds were available for 1968. The seeds were incubated at 100% relative humidity and 20°C on sand kept at field capacity. The number of germinants were counted at the end of 30 days.

3. Determination of substrate moisture adequate for seedling survival

Two hundred seeds were kept in a 400 ft-c, 20°C, 50% relative humidity atmosphere at each of five sand moisture values. In 500 ml beakers, seeds were sown on sand whose moisture content was predetermined by the oven-dry method. Then the seeds were covered by a thin layer of 2-5 mm diam cinder and the beaker weighed. Moisture was kept constant by frequent weighing of the beaker and replenishing of water lost by evapotranspiration. Seedlings were counted at the end of 15 and 30 days.

4. Effect of surface fragment thickness on germination and seedling survival

Two hundred seeds were kept at 400 ft-c, 20°C, 60% relative humidity atmosphere inder each of six thicknesses. The fragment size varied from 2-5 mm diam for a 6 mm thickness to 2-25 mm for 100 mm. The germination medium was maintained at field capacity in 500 ml beakers wrapped with opaque paper to prevent lateral growth of the seedlings. The number of seedlings that emerged through the fragments and opened their cotyledons were counted at the end of 15, 30, and 45 days.

5. Germination on red and black cinder

The wide variation in color of Hawaiian cinder is due to iron oxidation during and directly after the eruption (Macdonald 1967). Since red cinder appears to be associated with good regeneration in the field, a germination experiment was devised to see if this was actually the case. Three replicates of 100 seeds were sown on four different sand samples (2 colors x 2 locations). The sand was maintained at field capacity under 400 ft-c light intensity and 20°C, 100% relative humidity atmosphere. The number of germinants were counted after 30 days.

6. Effect of light intensity on seedling growth

On Haleakala, no silversword of any size has been seen under the crown of another plant (silversword or otherwise), or in the deeper shade of overhanging rocks. Since germination can take place in light or darkness (Siegel _et al_ 1970), survival of the seedling may depend upon a relatively high light intensity.

To test this proposition which may explain why silverswords are not found in the shrub-savannah zone, 300 seeds were kept at 21°C and 70% relative humidity at each of five balanced light intensities adjusted by a precalibrated Weston Model 603 illumination meter. Healthy seedlings were counted at the end of 15, 45, and 60 days.

Field experiments --

1. Maximum and minimum temperatures near the surface of various substrates

In November 1971, four sites were selected with the following surface material all about 3 cm thick:

a. red tabular fragments of the Hana Series

b. gray equiaxial fragments of the Hana Series

c. black wind-deposited cinder of the Hana Series

d. brown equiaxial fragments of the Kula Series

At each site, two square-meter plots on an exposed slope of less than 10 degs were marked off and the surface material removed from one plot. Maximum and minimum liquid-in-glass thermometers were buried with bulbs 3 cm within the surface material and 1 cm within the bared plot. Following accepted practice, thermometers were canted at 5 degs from the horizontal (U.S. Weather Bureau 1962), and fixed firmly in place with wire brackets.

During November 1971 to April 1972, all 16 thermometers were read and reset three times. This observation period coincides with the months seeds are dispersed from plants flowering during the previous summer.

2. Germination of seeds on various substrates

In November 1971, a gram of seeds containing an average of 420 achenes was strewn in each 1 x 1 m plot discussed in the previous section. Each plot was closely examined for germinants during the time the thermometers were serviced.

3. Rock movements on various substrates

The stability of the surface material was assessed by a method favored by geomorphologists (King 1966, Int. Geograph. Union 1967). In July 1971, 10 rocks 2.5 cm (1 inch) in diameter were selected on four types of substrates, marked with white paint, and aligned between two stationary stakes 1 m apart. Rock movement was measured four times during the course of one year by laying a straightedge between the stakes, then measuring the shortest distance between a rock and the straightedge.

Chemical Composition of Sand-textured Cinder

Cline (1955) classified the Hawaiian alpine regions as regosols and lithosols, soils having little or no profile development. He stated that Haleakala cinder and ash, a sand-textured regosol, has characteristics that depend primarily on the nature of the parent material.

To verify the low extent of chemical weathering in the cinder fragment parent material, three samples of fine-textured cinder were collected from each of two localities: the dark flow from Kamaolii and the red flow from Puu-o-Maui. The samples from each flow were air-dried, combined in equal parts by weight, pulverized with a mortar and pestle, and assayed for certain elements by Mr. Robert Suehisa of the Plant Physiology Department on an atomic absorption spectrophotometer. Then the most abundant elements of the two samples were compared to the analysis of rocks taken from the same flows by Macdonald and Powers (1968).

RESULTS

Meteorological Measurements

The maximum and minimum air temperatures of eight approximately equal intervals between Dec. 1970 and Feb. 1972 are tabulated in Appendix I for the two highest climatological stations on Haleakala, and the four weather shelters placed within the crater (see Appendix IV for locations). The data reveal an unexpected relation: the extremes encountered on the outer western slope between 2,000 and 3,000 m are typical of extremes at the same elevations on the western crater floor. Throughout the year, the shelter data differ only by a few degrees from U.S. Weather Service figures.

Precipitation, and fog-intercept plus precipitation were measured for the same eight intervals at seven locations, each with a pair of open and fog-intercept gages (Appendices II and IV). Open gage readings generally followed those of the official Central Crater 8-inch gage (see Fig. 2 for location) also listed in Appendix II for comparison. However fog-interception increased precipitation from four to more than 200%. In particular, Ka-Moa-o-Pele and Puu Kauaua received all of their water by fog-interception from April 16 to June 1, 1971. Both locations are in the most arid portion of the crater midway between Koolau and Kaupo Gaps.

Census of Silverswords on Haleakala

During a 3-year survey of the entire known range of the silversword on Haleakala, the number of plants in three growth stages, and the location and approximate area of all populations of more than 25 plants were tabulated and drawn on 7.5 minute maps (Appendices III and IV). The survey shows that more than 99% of the 43,000 plants counted were found in a 9 sq-km triangle whose baseline extends east-to-west from Magnetic Peak to Puu Kauaua. The Silversword Loop is the northern apex of this triangle which points into Koolau Gap. Fully 50% of the silverswords are found on the centrally located and most isolated cinder cone, Puu-o-Maui. Next in numbers are Ka-Moa-o-Pele, Puu-o-Pele, Puu Naue, and Puu Nole with 3,000 to 4,000 plants each. The only cluster of more than 25 plants counted outside of this triangle is population 58 at the Kalahaku Overlook that has 157 plants.

Perhaps the most important observation made during the survey is that only a few plants greater than about 5 cm (2 inches) crown diameter were found dead or dying of any cause. Apparently once a silversword survives the young juvenile stage, its life is terminated by flowering in most cases. The number of large dead plants were no more than a few hundred, thus the germination-to-young juvenile stages are probably most important since reproduction is mainly from seed. Later the production of lateral branches (tillering), previously thought to be rare by Degener (1930) but not by Lamb (1936), and the consequent effect on flowering will be discussed.

Only one source of information on the distribution of plants is available (Powers 1938). Powers qualitatively discribed the abundance of plants in 16 locations on Haleakala making it possible for comparisons to be made with present numbers at these locations. His comments and this writer's census subtotals for the 16 locations are listed side-

Table 1

Abundance of Silverswords
at 16 Locations, 1938 and 1969

Locations as stated by Powers 1938	Excerpts from Powers 1938	Census taken 1969(a)
1. Puu-o-Maui cone	A good many plants; with location 3, 2nd most abund.	22,000
2. Ka-Moa-o-Pele cone	Greatest number in any locality.	3,900
3. Red aa flow from Puu-o-Maui to S.S. Loop	A good many plants; with location 1, 2nd most abund.	1,900
4. Puu-o-Pele cone	A few good plants.	3,400
5. Kamoalii cone	None.	1,500
6. Puu Naue cone	A few plants.	3,400
7. Puu Nole cone(b)	A few plants.	3,000
8. Halalii cone	Relatively abundant.	44
9. Upper cliffs of palis on the western rim	Third most abundant.	180
10. Ka-Lua-o-ka-Oo cone	One plant.	0
11. Puu Maile cone	A few plants.	8
12. Lava field between Puu Maile and Puu Nole	A number of plants found scattered.	36
13. Puu Kauaua cone	A few plants.	7
14. North rim	Plants seen.	0
15. Kahuina-ka-One cone	A few plants.	7
16. Namana-o-ke-Akua cone	None.	0

a. When plants <20 cm and >20 cm are added together from Appendix III, the sum for large populations must be rounded-off because the accuracy of counting a large number of small plants is much lower than counting the fewer, more conspicuous large plants.

b. "Many plants" according to Badaracco 1963.

by-side in Table 1. Evidently locations can sustain a high number of plants (1 to 3), show an increase rapidly (4 to 7), drop in number (8 to 9) or remain virtually devoid of plants (10 to 16). Of the three locations maintaining a high number for the past 34 years (since 1938), past census figures are available for only one location, Ka-Moa-o-Pele (Lamb 1935b, Badaracco 1962). Therefore research was narrowed to investigation of the environmental conditions associated with sustained high regeneration on this cinder cone.

Preliminary Measurements on Ka-Moa-o-Pele

Lamb in 1935 divided Ka-Moa-o-Pele into six census areas following natural ridge contours (Figs 5 and 6). His counts were repeated by Badaracco and this writer in 1962 and 1971 respectively. Table 2 shows the change in number of plants since 1935 and 1962, and Table 3 lists the change in only juvenile plants since 1935. Figures for the 1962 juveniles are not available because Badaracco did not classify his plants according to size except in Area V. The data show that during the past few decades, Areas I and II have increased most rapidly in the total number of plants (Table 2), particularly in the juvenile class (Table 3). Thus these areas appeared to be suitable for investigating the edaphic conditions affecting seed germination and seedling survival.

Elevational transect in a high regeneration area. -- Initial elevational transects in Areas I and II showed that both have similar conditions: a red shelf of agglutinates that supply a cover of eroded cinder fragments to the slopes below (Figs 5-8). To investigate the

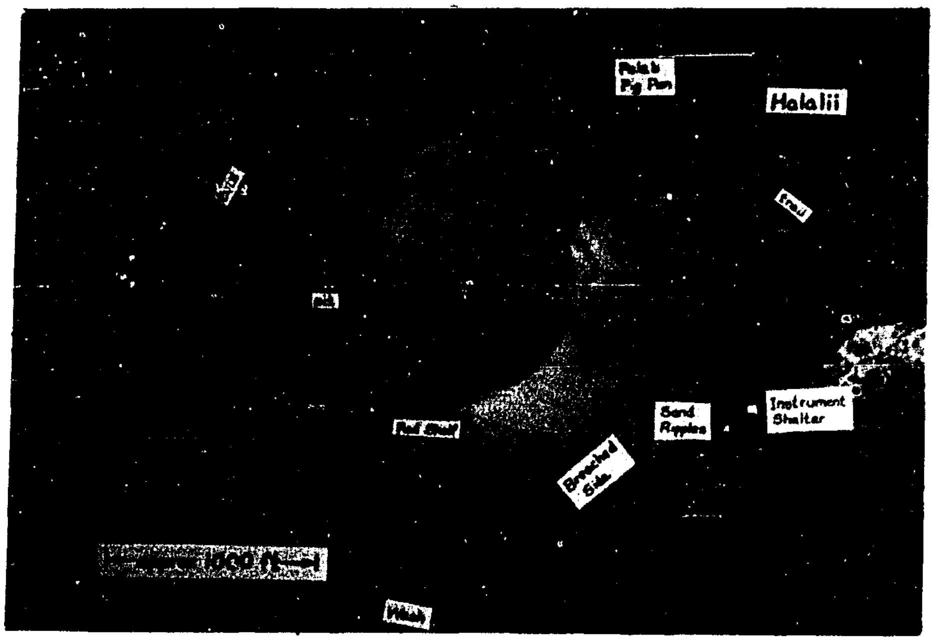


Fig. 5 -- Aerial plan view of Ka-Moa-o-Pele
USDA ASCS photo EKN 4CC 2/7/66

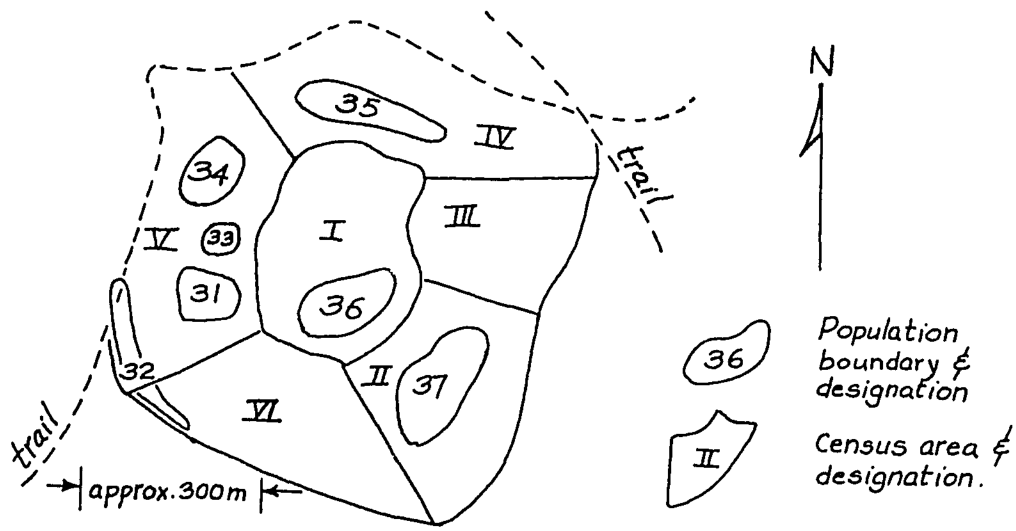


Fig. 6. -- Silversword populations and census areas on Ka-Moa-o-Pele cinder cone

Table 2

Census of All Plants
Ka-Moa-o-Pele

Counting area	Number of plants, all size classes		
	1935	1962	1971
I	319	550	1200
II	440	550	1230
III	35	50	6
IV	243	250	500
V	318	798	764
VI	115	50	290
Totals:	1470	1248	3990

Table 3

Censuses of plants less
than 20 cm crown diam.
Ka-Moa-o-Pele

Counting area	Number of plants, 20 cm crown dia	
	1935	1971
I	89	1020
II	170	1100
III	17	2
IV	89	470
V	212	663
VI	62	230
Totals:	639	3485

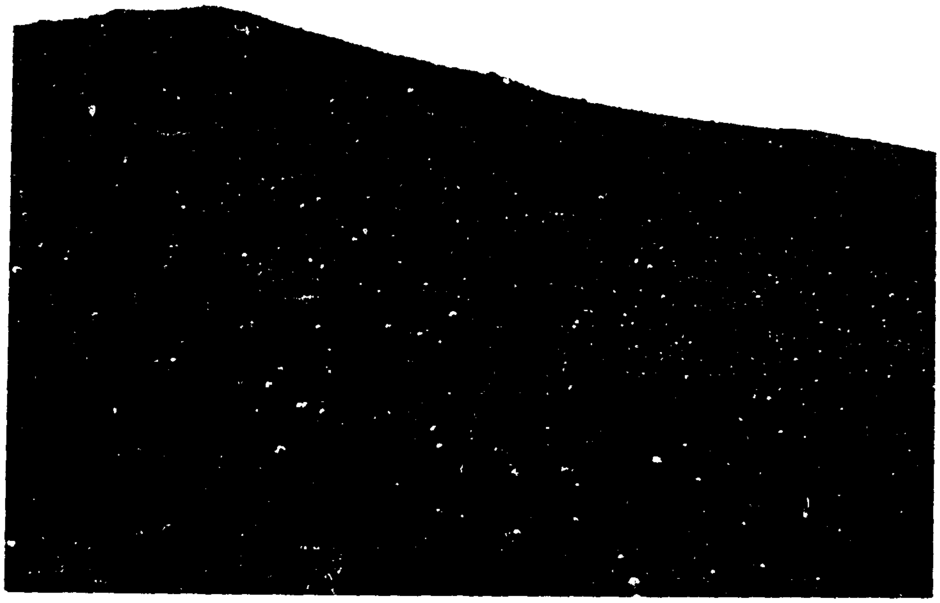


Fig. 7. -- High sustained regeneration over a large area: population 36, Area I, Ka-Moa-o-Pele 1969

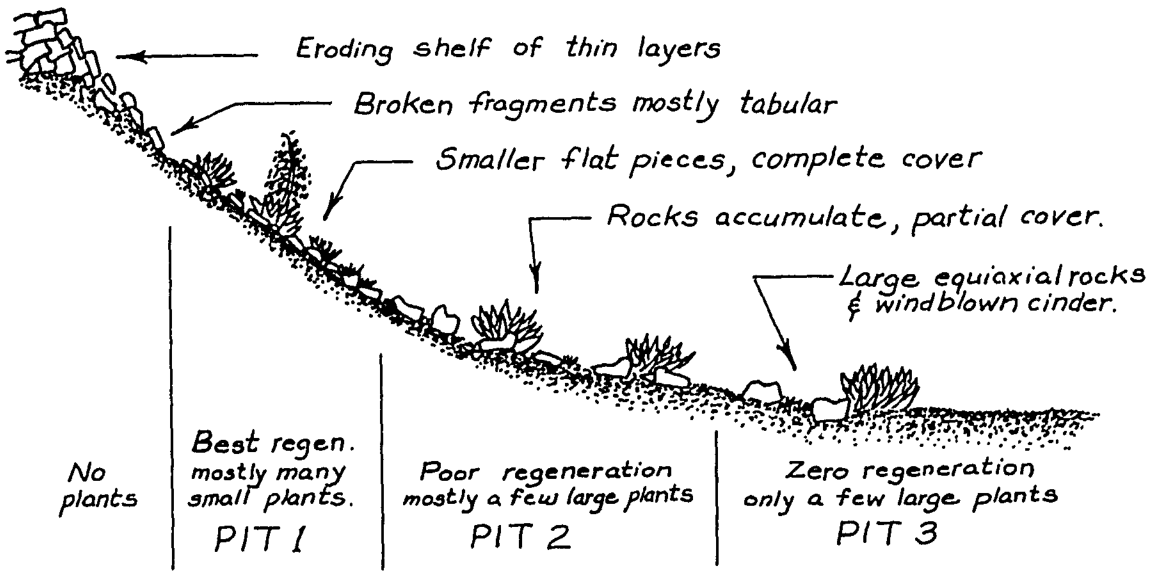


Fig. 8. -- Elevational transect of Area II, Ka-Moa-o-Pele. Also typical of Area I. 1969

subsurface conditions, vertical profiles were made along an elevational transect at high, poor, and zero regeneration sites (Table 4). The most notable characteristics of a high regeneration substrate profile was the presence of a very friable sandy substratum having a distinct upper boundary with a thin, complete surface layer of somewhat flattened cinder fragments (Fig. 9, 10). For the following three reasons, the sandy layer is immobile while the surface fragments slide at a constant rate not exceeding a few centimeters per year.

First of all, the surface presents a smooth pavement or shingle-like appearance (Fig. 7) suggesting that openings in the thin surface fabric made by any rolling equant rocks are repaired by the sliding motion of tabular rocks moved by gravity. A preponderance of translational rather than rotational motion is evident from the sharp linear boundary between the two layers and the distinct crusty texture of the unbroken sandy layer.

Secondly, even without a covering of fragments, the slope is stable from an engineering standpoint. Any breaks in the sandy middle layer will be filled by colluvium provided the maximum angle for slope stability is not exceeded appreciably. Otherwise in this dry, coarse material, the break will be enlarged by wind into a "blowout", a common occurrence on sand dunes denuded of vegetation (Oosting 1956). Soil mechanics theory predicts that for non-cohesive material such as sand, the slope becomes unstable at angles greater than the angle of internal friction defined as the arctangent of the shear stress divided by the normal stress (Smith 1968). The standard Mohr diagrams of Area I and II sand (Figs. 11 and 12) show the angle of internal friction to be

Table 4

Substrate Profile, Temperature, and Moisture Along an Elevational Transect
Area II, Ka-Moa-o-Pele, 9 AM June 25, 1969
At 1 m above ground: wind 6 mph, relative humidity 12%, temperature 20C

Location	Slope	Depth of Layer (cm)	Description of layer		Temp C	Pct moisture dry wt basis
Best regeneration site Pit 1 (a)	30-40° planar surface	0-5	Red rocks: somewhat flattened, all sizes 12 cm max. 100% cover.	At surface:	33	2
				Within layer :	30	
		5-10	Red sand: very friable distinct boundaries with adjacent layers.	1 cm in layer: (field capacity 21%)	27	10
		10-80	Mixture of upper layers.	At 25 cm depth:	22	6
Poor regeneration site Pit 2	10-20° somewhat concave surface	0-4	Red and gray rocks: various shapes, all sizes 12 cm max. 90% cov.			
		4-12	Red and gray sand: loose, somewhat indist. bound. with adj.layers.			
		12-80	Mixture of upper layers.			
Zero regeneration site Pit 3	0-5° somewhat irregular surface	variable	Gray rocks: subrounded and irregular, all sizes 25 cm max. 50% cover.	At surface:	34	
				Among rocks:	32	
				Under rocks:	30	
				Exposed sand:	48	2
		variable	Black cinder: sand blown from the north.	3 cm below rocks:	29	11
				3 cm in exposed sand:	46	3
		5-80	Mixture of upper layers.	15 cm in exp. sand:	24	5

a. For texture analysis of substrate, see Fig. 9.

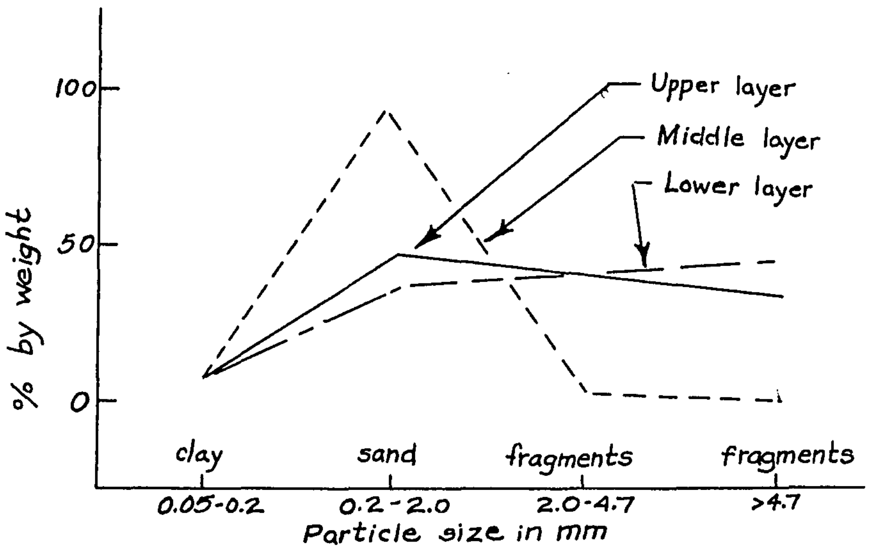


Fig. 9. -- Texture of substrate for Pit 1, a high regeneration site, Area II Ka-Moa-o-Pele

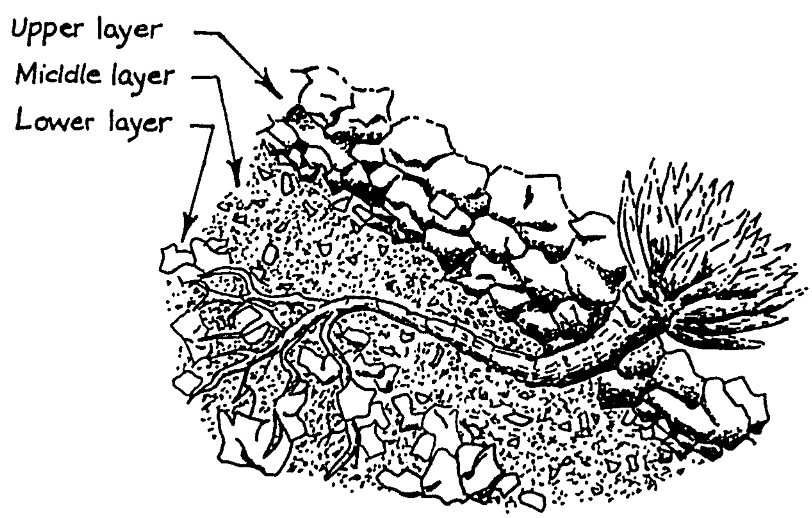


Fig. 10. -- Typical silversword near Pit 1, a high regeneration site, Area II Ka-Moa-o-Pele

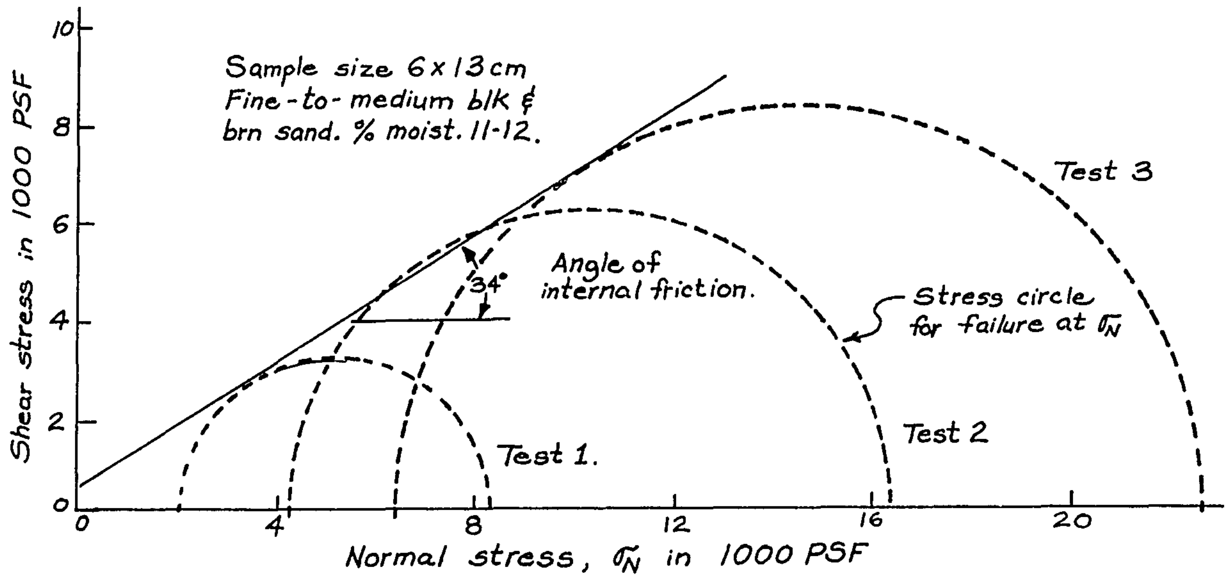


Fig. 11. -- Triaxial compression test on soil sample from Area I, Ka-Moa-o-Pele

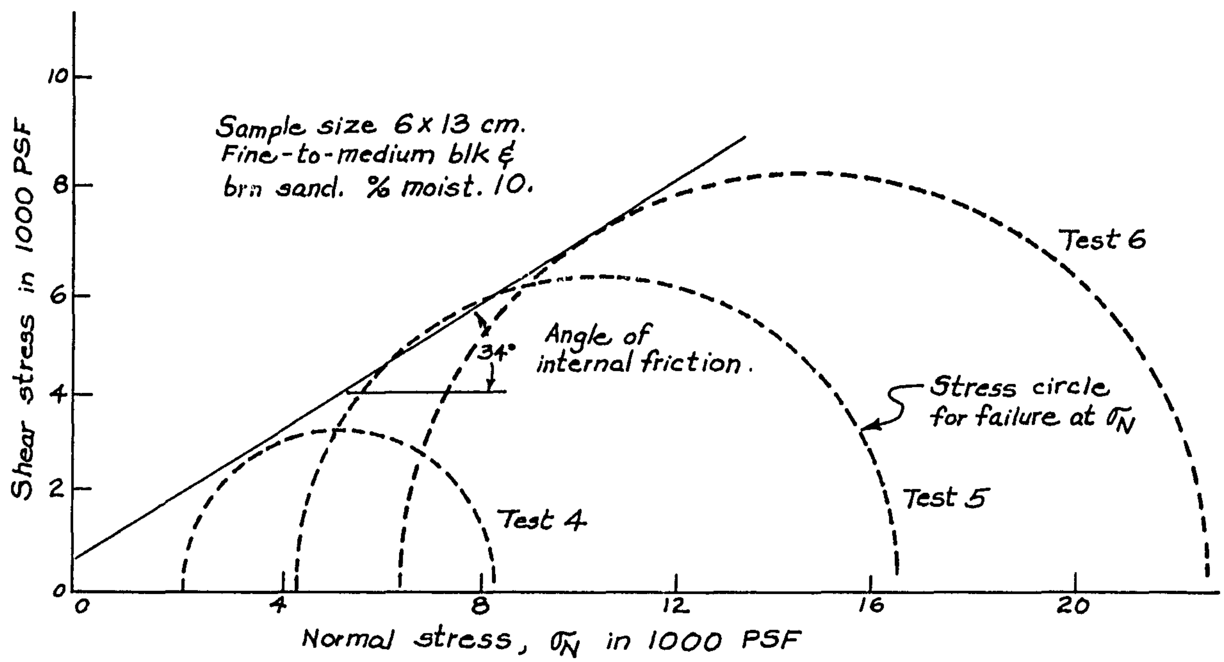


Fig. 12. -- Triaxial compression test on soil sample from Area II, ka-Moa-o-Pele

34 degrees. This is close to the measured slope angles of 36 degrees for Area I and 35 degrees for Area II. King (1966) indicated a 38 degree slope for granitic scree slopes, whereas Macdonald (1967) gave a slope of about 30 degrees for more erosive cinder.

The final reason for believing that the surface cover moves at a constant rate over an immobile sandy layer is found in the root morphology of the silverswords in Area I and II. All plants greater than 2 cm crown diameter in the high regeneration sites have a distinctive S-shaped bend in the primary root just below the transition zone (Figs 9 and 13). The midportion of this bend always located in the crusty layer, is straight, and about 3 cm long regardless of the crown size of the individual. By contrast, plants of poor regeneration sites on shallow slopes have straight, weakly developed primary roots (Fig. 13). Weaver (1919) and Fisher (1952) described plants with similar root morphology on sliding scree surfaces.

It appears that a seed landing on the surface would sift down to the crust, germinate and send its primary root downward. But while the root is still able to elongate, the shoot is pushed downslope by the pressure of cinder fragments until extensive lateral root development firmly anchors the plant. The S-shaped segment would retain a fixed length during the life of the plant.

In Area II, the surface layer has been moving at a constant rate for at least 10 years because the minimum life of a silversword is 7 years (Ruhle 1959) and flowered plants dead for several seasons possess this 3 cm length of root segment.

Temperature and moisture readings were taken near Pits 1 and 3 to

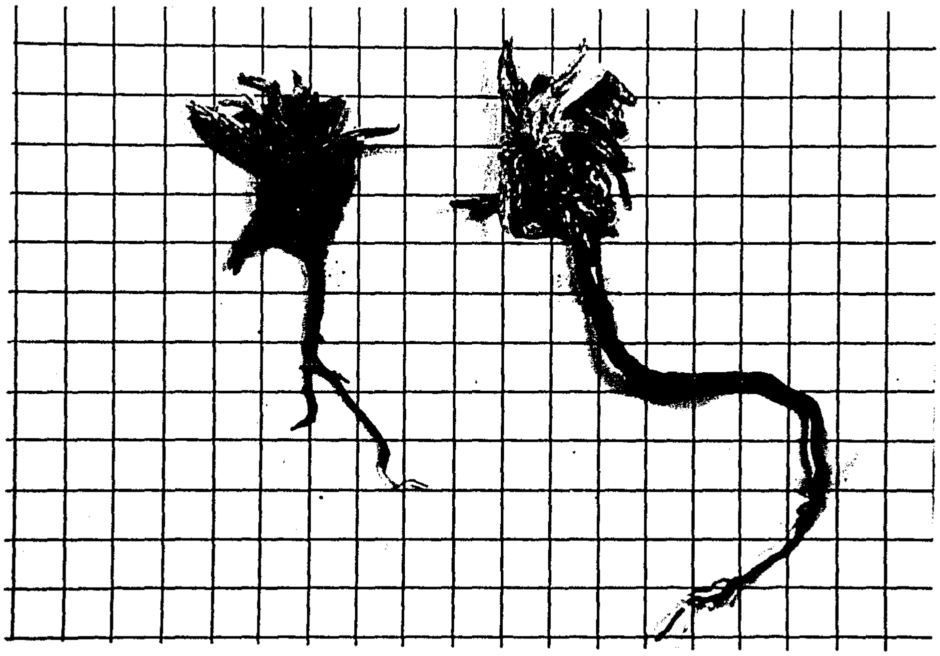


Fig. 13. -- Young plants from Area II, Ka-Moa-o-Pele
left - from poor regeneration 10 deg slope
right - from high regeneration 35 deg slope

see if they could be related to the profile differences of high and zero regeneration sites described in Table 4. Several temperature measurements were taken during a 30 minute interval on a clear cloudless summer day following a week of dry weather. The data revealed that by 9 AM surface fragments can approach, and exposed sand can greatly exceed the lethal germination temperature of 35°C found experimentally by Siegel _et al_ (1970). By contrast, an abrupt decrease in temperature, and a several-fold increase in moisture were encountered only a few centimeters below the surface of rock fragments. The stable sandy crust of Pit 1 was the shallowest layer in which the germination range of 8-25°C (Siegel _et al_ 1970) was approached. The surface and substrata of exposed sand have harsh conditions for germination: temperatures above 40°C and moisture contents of only a few percent.

In summarizing the substrate profile, temperature, and moisture data along the transect in Area II, we see that:

1. sustained regeneration over a broad slope during a period of several decades was related to the presence of a complete thin cover of fragments sliding over a stable crust of sand, and
2. the temperature and moisture conditions suitable for germination are not at the surface, but in this underlying crust.

Substrate characteristics of Ka-Moa-o-Pele's census areas. -- Substrate characteristics for high regeneration mentioned in the previous paragraph were verified for all of Ka-Moa-o-Pele by comparing additional measurements in each of the six areas to the plant counts of a corresponding area. Scree state was included as a characteristic because cinder cone slopes resemble scree surfaces where simultaneous addition and removal of sliding fragments establishes the most favorable conditions for maintaing a constant thickness of surface fragments (Thornes 1972). Thus the dynamic condition of Ka-Moa-o-Pele's slopes can be described by the four distinct scree states discussed earlier under MATERIALS AND METHODS.

The data of Table 5 show that the substrate characteristics of Pits 1, 2, and 3 of the elevational transect in Area II are reproduced by Areas I and II, Areas IV to VI, and Area III in that order. High regeneration (Area I and II) is related to an active supply and removal of fragments, a complete cover of mostly tabular fragments 2.5 to 5.0 cm thick, and a stable 36-degree sandy layer of relatively high moisture content. Moderate regeneration (Areas IV and VI) is generally characterized by the absence of a supply shelf, a partial cover of fragments, and high-to-low sand moisture content. Zero regeneration (Area III) has a favorable scree state, but is overlain by an 80% cover of windblown cinder having the lowest moisture content of any area listed in Table 5.

Areas IV and VI were purposely divided into sub-areas in Table 5 to introduce a variable not yet discussed in the RESULTS: the effect of surface fragment thickness on seedling survival. The eastern half of Area IV and all of Area VI excluding population 32 are almost devoid of plants. Probing of the cinder surface revealed that the sub-areas are the only places on Ka-Moa-o-Pele with a layer of fragments exceeding an average thickness of 7.5 cm (3 inches), thus raising the question of whether a seedling after germination is able

Table 5

Substrate Characteristics Under Ka-Moa-o-Pele's Silversword Populations

Area	Population designation (a)	Scree state (b) supply	Scree state (b) removal	Surface fragments shape & pct cover (c) tabular	Surface fragments shape & pct cover (c) equiaxial	Surf. frag. avg. thick. cm	Slope degs	Slope expos.	Sand moisture pct (d)
I	36	present	present	90	10	2.5-5.0	36	N	12
II	37	"	"	90	10	"	35	SE	10
III		"	"	10	20	"	30	SE	5
IV	east 35	present	absent	10	20	>7.5	28	NE	6
	west 35	absent	present	90	10	2.5-5.0	30	N	13
V	34	"	"	80	10	5.0-7.5	27	NW	10
	33	"	"	80	10	2.5-5.0	31	W	10
	31	"	"	70	20	"	37	W	9
	north 32	"	"	30	20	"	17	W	9
VI	south 32	"	"	30	20	5.0-7.5	16	SW	8
		present	present	10	90	>7.5	38	SW	10

a. Only populations with more than 25 plants have designations. Halves of Area IV differ in substrate and number of plants (see text). Boundary between Areas V and VI cross population 32 (see Fig. 4).

b. Supply refers to presence or absence of a shelf supplying cinder fragments to the slope below. Removal refers to the presence or absence of a wash removing fragments from the foot of the slope.

c. Cover estimated to the nearest 10% from the average of 10 quadrat placements. Percent of exposed cinder sand can be found as follows: e.g. Area III, 100-(10+20) = 70%.

d. Average of 3 samples, range within 1% sand moisture. All samples collected on July 15, 1971.

to grow through a cover thicker than about 5 cm.

Statement of the Hypothesis on Germination and Seedling Survival

The data of this writer and others presented thus far in the RESULTS appear to support the following hypotheses. Germination and seedling survival depend on a temperature not exceeding about 30°C, and the relatively high moisture content of a stable sandy substratum completely covered by cinder fragments no thicker than about 5 cm. On the other hand, the poorest germination is on, or in the upper few centimeters of unstabilized exposed sand where the lethal temperature of 35°C is easily attained and where the moisture content is relatively low.

For sustained high regeneration, the maintenance of the thin complete cover over an area larger than a hectare and for a period of a few decades, is best met by a shelf of agglutinates supplying tabular fragments which slide over the sloped sandy germination layer. The slope angle is about 35 degrees; low enough to stabilize the sandy layer, yet steep enough to be slightly unstable for tabular fragments. To prevent the surface layer from exceeding a thickness of about 5 cm which is detrimental to the survival of the seedling, fragments must be carried off by some agent of removal at the foot of the slope.

In the following section, the hypotheses will be verified under the controlled conditions of long-term laboratory and field experimentation.

Laboratory and Field Experiments on Germination and Seedling Survival

Verification of the lethal germination temperature. -- Seeds subjected to controlled temperature conditions had percentage germinations (Table 6) that agreed with Siegel et al's (1970) preliminary work and this writer's field measurements (Siegel et al found that after three weeks, seeds held at 25°C had 14% germination, and at the next increment of temperature, 35°C, the germination was zero). In Table 6, the writer's germinants for 28°C and 32°C decreased from 16% to 9% with a corresponding decrease in the ratio of healthy-to-dying plants. In the field (table 4), temperatures never exceeded 32°C within cinder fragments even under adverse hot dry summer conditions. Long-term temperature data taken during the season when seeds are dispersed by winter storms (Table 7) also substantiate the importance of surface fragments in reducing temperature: the maximum never exceeded 23°C within any type of fragment, whereas loose cinder and experimentally bared sand had maxima ranging from 31 to 47°C.

In November 1971, a gram of seeds containing an average of 420 achenes was strewn in each of the 16 square-meter plots in which the maximum-minimum temperatures were taken. As of April 1972, no germinants were seen. However, according to long-term viability data (Table 8), the seeds may germinate at any time during the next several years provided lethal temperatures are avoided by burial beneath surface fragments. Despite a high reduction in viability each year, four-year old seeds were still able to germinate in 1972.

Determination of substrate moisture adequate for seedling survival. -- Seeds under laboratory moisture conditions adequate for germination

Table 6

Percentage Germination of Silversword Seeds at Four Temperature Conditions

Temperature	After 15 days: Healthy	Dying	After 30 days: Healthy	Dying
20°C	17	0	26	0
24°C	13	0	20	0
28°C	11	0	10	6
32°C	3	0	4	5

Table 7

Maximum and Minimum Temperatures Within Various Substrates Nov. 11, 1971 to Apr. 4, 1972

		11/24-12/27 max/min °C	12/28-2/22 max/min °C	2/23-4/4 max/min °C
Haleakala summit, 3040 m Official Air Temperatures (a)		14/-2	12/0	18/-1
Surface material 3 cm thick, 2740 m:				
Red tabular fragments,	b	21/-1	18/-2	21/0
Hana series:	c	34/-2	36/-1	38/-2
Gray equiaxial fragments,	b	21/-3	19/0	23/-2
Hana series:	c	32/-2	35/0	40/0
Brown equiaxial fragments,	b	22/0	23/1	20/0
Kula series:	c	31/0	35/1	47/-2
Wind-deposited cinders	b	25/-3	34/-3	40/1
Hana series:	c	37/-3	38/-2	41/-1

a. Included for comparison with substrate temperatures.

b. Three centimeters within fragments or cinders.

c. One centimeter within sand exposed by removing surface material.

By contrast the upper layers of exposed cinder sand (Table 4), and areas of poor surface fragment cover (Table 5) had much lower moisture percentages. The experimental data of Table 9 show that below one-half field capacity, there is a sharp drop in germination. Thus Percent cinder cover and substrate moisture appear to be related to high regeneration. High regeneration Area I had a 100% cover with 12% moisture, whereas poor regeneration Area III had a 30% cover with only 5% moisture.

Effect of surface fragment thickness on germination and seedling survival. -- Experimental data on the percentage of seedlings surviving germination and growth through several fragment thicknesses (Table 10) agreed with the field data of Table 5. In poor regeneration areas, notably Area VI, the surface is covered by an average thickness in excess of 7.5 cm, whereas in other areas the cover is thinner than 5.0 cm. Under controlled conditions (Table 10), no seedling survived growth through a fragment thickness exceeding 5.0 cm.

Rock movements on various substrates. -- From the data discussed earlier on the stability of slopes and the shape of surface fragments, we would expect that the rock movement on steep slopes to be least on tabular fragments, moderate on equiaxial fragments, and greatest on wind-deposited cinder. The results of measuring rock movement for one year on four types of substrates (Table 11) tend to support this expectation: rocks on tabular or equiaxial fabric moved far less than those on wind-deposited cinder. The large movement of Kula Series rocks may be due to a high proportion of wind-deposited subrounded cinder at

Table 8

Percentage Germination
1968 and 1969 Seeds

	6/69	6/70	6/71	6/72
1968	25	15	9	4
1969		16	11	8

Table 9

Percentage Germination of Silversword
Seeds at Five Sand Moisture Conditions

Pct moisture on a dry weight basis	After 15 days	After 30 days
3 ± 1	0	0
7 ± 1	1	1
10 ± 2	4	14
15 ± 2	7	16
21 ± 2 (a)	13	22

a. Field capacity.

Table 10

Percentage Seedlings Surviving Germination and Growth Through Six Fragment Thicknesses

Fragment thickness (cm)	After 15 days	After 30 days	After 45 days
0.5	4	8	10
2.0	4	11	11
3.7	1	6	4
5.0	1	2	2
7.5	0	0	0
10.0	0	0	0

Table 11

Average Rock Movement on Various Substrates(a)
July 1971 to July 1972 - cm

Type of substrate	Location	July-Oct	Nov-Feb	Mar-Apr	May-July
Red tabular frag. Hana series:	Ka-Moa-o-Pele slope 28 degs	0.0	1.0	0.8	0.0
Gray equiax. frag. Hana series:	Ka-Moa-o-Pele slope 30 degs	0.0	3.5	2.0	0.8
Brown equiax. frg. Kula series:	Kalahaku Ovrlk slope 20 degs	0.0	7.8	6.5	5.4
Wind-deposited cinder, Hana series:	Ka-Moa-o-Pele slope 30 degs	0.8	8.0	14.0	2.5

a. Average of 10 rocks, each approximately 2.5 cm (1 inch) length selected at the sites.

Kalahaku Overlook and other places on the crater rim.

Chemical composition of sand-textured cinder. -- The Hawaiian alpine regions, including the cinder cones at high elevations, have little mechanical and chemical weathering of the volcanic parent material (Cline 1955, Wentworth and Macdonald 1953). Tezuka (1961) showed that lava flows of a Japanese island must weather to sand before species highly tolerant to low fertility levels can become established. To verify the low extent of chemical weathering of Haleakala cinder, sand samples from red and black flows were compared to rocks analyzed from the same locations (Table 12). Percent composition of elements (expressed as oxides) were about the same for the four analyses indicating little difference between red and black rocks and their subsequent erosion to sand.

A germination experiment was devised to see if the association of red cinder with high regeneration seen in the field was due to chemical differences accompanying iron oxidation. The results of the experiment (Table 13) revealed no significant difference at the 95% confidence level between the mean percent germinants on red and black sand when tested by the non-parametric rank-sum method (Cox 1967).

The experimental data presented thus far were in support of the hypothesis on the substrate conditions governing germination and seedling survival. The following will consider ecological factors affecting other stages in the life cycle of the Haleakala silversword.

Insect Damage to Silversword Seeds

For more than a hundred years insects have been blamed for the

Table 12

Chemical Composition of Rock and Sand
Percent Dry Weight

Element as an oxide	Dark flow from Kamaolii rock	Dark flow from Kamaolii sand	Red flow from Puu-o-Maui rock	Red flow from Puu-o-Maui sand
SiO_2	42.46	40.10	41.55	39.27
Al_2O_3	12.57	16.35	14.13	18.90
Fe oxides	14.88	14.91	15.35	15.19
K_2O	1.27	1.62	1.67	1.39
CaO	11.77	11.26	11.79	10.79
Na_2O	2.96	3.10	3.84	3.22
MgO	9.37	7.45	6.04	5.53

Table 13

Germination of Silversword Seeds
on Red and Black Cinder

	Percent germinants after 30 days Replicate 1	Replicate 2	Replicate 3
Red cinder sand:			
Puu-o-Maui	22	27	24
Ka-Moa-o-Pele	18	26	25
Black cinder sand:			
Kamoalii flow	20	19	25
Ka-Moa-o-Pele	23	20	29

decrease in the number of plants on Haleakala (Hillebrand 1854) despite the opposite conclusions of the only field study of infestation on the silversword (Lamb 1936). The three following considerations support Lamb, and will temper the generally accepted viewpoint.

The first is the observation by this writer and others that the insects most destructive to the silversword are the larvae of Rhynchephestia rhabdotis Hampson and Tephritis cratericola Grimshaw which feed on developing seeds (Swezey and Degener 1928, Degener 1930, Lamb 1935b). The insects are specifically associated with Argyroxiphium sandwicense (Swezey 1954), and their existence depends completely on food supply available only if the seeds are not completely eaten by their larvae. A time period sufficient to evolve such an insect behavior is suggested by the fact that six of the ten insects taken on A. sandwicense are not found on other plant species (Swezey 1954). Such relatively high numbers of associated insects were taken as an indication of long insular coevolution by Swezey (1925). Therefore under natural conditions, high insect infestation may not necessarily be detrimental to the existence of the silversword. However, long term studies during years when silverswords are flowering are needed to evaluate the disturbance introduced by non-native organisms into this symbiotic relationship.

The second consideration is that while examining hundreds of capitula in every flowering population of the 1969 and 1971 seasons, none were found with seeds completely destroyed by insects; thus raising the implication that seeds are always available despite heavy infestation. According to Table 14, the most heavily damaged popula-

Table 14

Insect Seed Damage and Seed Viability in Twelve Selected Populations - 1971

Population designation & location (Appen. III)		Pct seeds damaged by insects(a)	Pct viability of undamaged seeds(b)
6	Upper Sliding Sands Trail	50	21
11	Puu-o-Pele	90	39
20	Puu-o-Maui	80	31
29	Un-named cones	90	38
32	Ka-Moa-o-Pele	70	25
38	Ka-Moa-o-Pele outlier	20	19
40	Near official rain gage	10	18
41	Puu Naue	70	26
44	Buu Nole	70	24
52	Red flow from Puu-o-Maui	20	16
57	Silversword Loop	60	22
58	Kalahaku Overlook	70	28
	Arithmetic mean:	60	26

a. Mean estimate of 100 mature capitula in each population.

b. Number of embryos in 300 seeds drawn from a mixture of 10 capitula from each population (divided by 3 to give mean number).

tion (population 29 on the un-named cones) still had at least 3% of its viable seeds available for dispersal after the 1971 flowering season. Viable seeds survive because only the inner disc achenes are eaten, the outer disc and ray achenes -- often fertile -- are left intact.

The last point to consider is the relationship between the extent of insect damage and the size of the infested population: large dense populations suffer most while small isolated ones are the least damaged (compare Table 14 with Appendices III and IV). Since the large populations have remained large on the cinder cones and red flows for at least 100 years (Alexander 1870), high infestation does not necessarily lead to a drop in number. Even if the plants are reduced to "barely a hundred specimens" as in 1927 (Degener 1930), a highly unlikely event according to Lamb (1936), the small isolated populations may act as nuclei for the reestablishment of the large populations.

Effect of Light Intensity on Seedling Growth

On Haleakala no silverswords are found in deep shade, and few are in the shrub-savannah surrounding the scattered shrub and barren area where the plants are found almost exclusively (compare maps of Fig. 2 and Appendix IV). Hence survival of the seedling may depend on high light intensity, although germination is not light-inhibited according to Siegel _et al_ (1970) and this writer's experiment on the effect of surface fragment thickness. The results of a test on the effect of different light intensities on seedling growth were inconclusive (Table 15). From the data, the light compensation point lies between 100 and 300 ft-c which is below the minimum of 400 to 500 ft-c for sun

Table 15

Percentage Seedling Survival
at Five Light Intensities

Intensity ft-c	After 15 days	After 45 days	After 60 days
1000	7	9	9
300	8	8	8
100	8	5	3
27	8	6	3
12	9	4	2

plants according to Bonner and Galston (1952).

Effect of Browsing by Goats

In addition to hunting discussed earlier, there are two reasons why browsing by herbivores, thought important in the past (Bryan 1948) is presently probably insignificant in the ecology of the Haleakala silversword.

First of all the silversword is not eaten in preference to other plants according to 3 years of observation by this writer. Several times goats were seen eating Styphelia tameiameiae, consumed as a last resort according to Yocum (1967), within 200 m of mature silverswords. Goats have not visited the high density populations on Puu Nole easily seen only 600 m away across flat terrain from Namana-o-Ke-Akua cinder cone, one of the most heavily browsed areas in the Park. Also the easily identifiable leaves of the silversword were not among the nine plant species in the stomach contents of 33 goats shot in January 1947 (Yocum 1967).

Secondly browsing when reported, is usually infrequent and does not necessarily kill the plant because sometimes lateral branches develop with the removal of the apical meristem. Lamb (1935a) interviewed qualified laymen and scientists who reported no browsing or only isolated instances of browsing. Bryan's (1948) recollection of seeing hundreds of flower buds eaten out by goats ca. 1920 is the only account of heavy browsing encountered by this writer. The only plants reported to be browsed during the past four years were a cluster of 13 large plants within a quarter-hectare area on the western rim (population 60, Appendix III), a locale very low in forage and high in the number of goats (Yocum 1967). By November 1972, rebrowsing had killed the majority of the plants (personal communication, Laurence R. Guth, Park Ranger, Haleakala National Park). However several small plants nearby have survived removal of their apical meristem by the activation of lateral buds (Fig. 11). Since excavation of flowered plants abutting large ones by Lamb (1936) and this writer reveals that *A. sandwicense* is frequently multibranched and the branches may flower during different seasons, and since a high proportion of these plants are in areas frequented by goats (notably the western crater rim and the Silversword Loop), browsing may actually increase the seedcrop by causing an individual to flower repeatedly. Whether repeated browsing diminishes the seedcrop of an individual plant is not known because several years may lapse before reflowering occurs.

Two reasons have been given to show that for the past 40 years goat browsing has not been an important factor in the distribution and abundance of silverswords on Haleakala. (1) Goats do not prefer silverswords to other forage plants, and the animals are usually found outside of the silversword's present range. (2) The incidence of browsing is extremely low today, and browsing itself may even increase the seedcrop by the induction of lateral flowering branches.

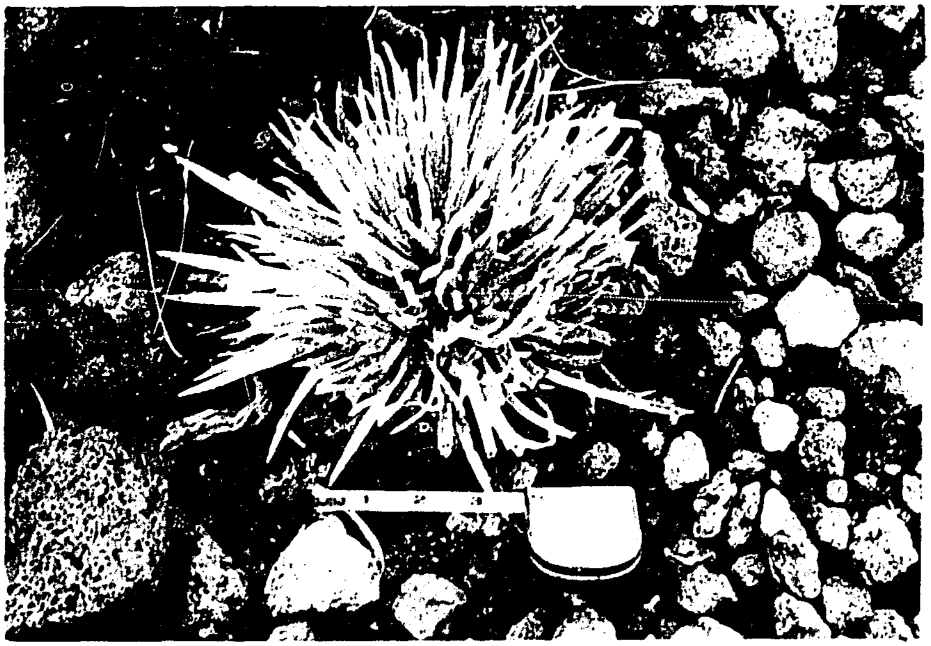


Fig. 14. -- Young silversword one year after browsing by goats. Complete removal of the single meristem produced many lateral ones. Near Kalahaku Overlook 1972. Scale in inches.

DISCUSSION

The alpine elevations of the Hawaiian Islands have few native species in common with other alpine areas, and appear to be more associated with the forest flora at lower elevations (Skottsberg 1930, Carlquist 1970). Typical subalpine plants such as Styphelia tameiameiae, Sophora chrysophylla, and Dodonaea eriocarpa are found on somewhat open ridges well within the forest zone. Also certain genera, notably Dubautia and Geranium, have closely related species growing on dry alpine cinder as well as within the cloud-shrouded rain forest.

The origin of the alpine flora is still uncertain. According to Skottsberg (1930), the cool open soil of Hawaii's highest summits should favor the continuous establishment of temperate weeds brought in by the wind and birds. Noting that the alpine flora was depauperate, vicarious, and 91% endemic, Skottsberg negated the importance of direct long distance dispersal and according to Stone (1967) inferred that the present alpine flora is simply a reduced derivative of a previous Hawaiian alpine flora. Stone placed the probable location of this earlier flora on Oahu or Kauai, now greatly reduced in elevation; but considered long distance dispersal still in operation. Although a strong proponent of wind and bird dispersal, Carlquist (1970) limited his views to the Madinae wherein "...the dry habitat preferences of tarweed ancestors probably have preadapted their descendents -- Argyroxiphium and Dubautia -- for alpine conditions."

The views of Stone and Carlquist are supported by the fairly recent introduction of Madia sativa Molina. This tarweed, widespread along the American Western Cordillera, was found by Degener (1940) almost 50 years ago on the sun-scorched cinders of the Haleakala Crater floor. Apparently brought in by birds and thriving because of preadaptation to a xeric cool climate, *M. sativa* may well have resembled the original immigrant giving rise to the 61 species and varieties of the Hawaiian tarweeds listed by Fosberg (1948).

Certain edaphic conditions in the Hawaiian alpine zone may limit the establishment of temperate plants even though they may be preadapted to cool temperatures and intense sunlight. The peaks in Hawaii are areas of recent vulcanism, and the substrate has undergone little mechanical weathering. For example, Hartt and Neal (1940) on Mauna Kea reported the coarse cinder as somewhat unstable and low in water retention.

The distribution of plant species on the youngest parts of Haleakala Crater attests to the severity of this environment. Only two exotic species *Hypochaeris radicata* and *Rumex acetosella* are widespread. These are well-adapted small annuals that set seed before the dry summer season. All other exotics from grasses to woody weeds (e.g. *Poa pratensis* L., *Eupatorium adenophorum* Spreng. etc.) are usually found only where stable pockets of clay and silt have accumulated. On the other hand, the endemic species are widespread, and display conspicuous xerophytic adaptations ranging from a thick cuticle in *Dubautia menziesii* to a whitish pubescence in *Argyroxiphium sandwicense*.

Much more difficult to assess is the microhabitat preference of a species. At one extreme, only *Gnaphalium sandwicensium* Gaud. appears able to germinate and grow through thick layers of cinder fragments.

On the other hand, only Silene struthioloides Gray can be found on the smooth hard-packed silty washes inundated by flash floods during winter storms. Other species grow on sites between these extremes; however no plant has been able to cope with a substrate consisting entirely of loose windblown cinder.

Edaphic Conditions and the Silversword

Virtually all of the silverswords (99%) grow on the nearly barren cinder cones and lava flows within the Crater away from the typical shrub-savannah of Hawaii's subalpine zone. Although most plants appear to be on red slopes intercepting the moist northeast tradewinds, dense clusters are also found on dark substrates facing other directions. Clearly then, edaphic conditions need to be evaluated along with more easily measurable ecological factors such as meteorological variables.

The cinder cone Ka-Moa-o-Pele was selected for intensive study because:

1. silverswords of all age classes were present,
2. a variety of substrate conditions was available, and
3. the cone is exposed to weather from all direction due to its symmetry, large size, and central location.

Preliminary measurements along an elevational transect in high regeneration areas, later expanded to quantitative studies encompassing all of the cinder cone, led to the following two-part hypothesis:

1. Germination and seedling survival depend on a stable sandy substratum having a temperature of less than 30 C and relatively high moisture content which is completely covered by fragments no thicker than 5 cm.

2. The maintenance of the substrate conditions stated above over an area of several square meters is best met by the constant supply and removal of tabular fragments sliding over the sandy substratum at an angle of about 35 degrees.

Features of the hypothesis were verified by a series of field and laboratory experiments. In growth cabinets, the minimum lethal germination temperature between 28-32°C agreed with Siegel et al (1970); in the field during the months when seeds are usually dispersed, the temperature remained below 24°C within cinder fragments and often exceeded 30°C for exposed sand. The minimum moisture requirement of laboratory germinated seeds -- one-half field capacity -- agreed with earlier field measurements under hot dry summer conditions. In the laboratory, the maximum thickness of fragments for seedling germination and survival was between 5.0 and 7.5 cm, thus verifying earlier measurements done on Ka-Moa-o-Pele. Finally the greater stability of a fragment cover to exposed sand-textured cinder was demonstrated by the measurement of rock movement over various sloped surfaces during the course of one year.

The hypothesized edaphic factors were shown to operate throughout the Crater by relating large-scale geomorphological features to silversword regeneration (Fig. 15), geomorphology being in turn linked to the hypothesis. This relationship will be discussed in the following pages under four degrees of silversword regeneration and with respect to: (1) large-scale geomorphological features, (2) the hypothesized substrate factors, (3) the present number of plants, and (4) the abundance of plants 38 years ago. The last two items are listed in Table 1, and constitute the only known comparison of past and present distributions for all of Haleakala.

1. Broad areas of high regeneration. -- Puu-o-Maui and Ka-Moa-o-Pele are breached cones with a prominent thin-layered shelf perched on the lip

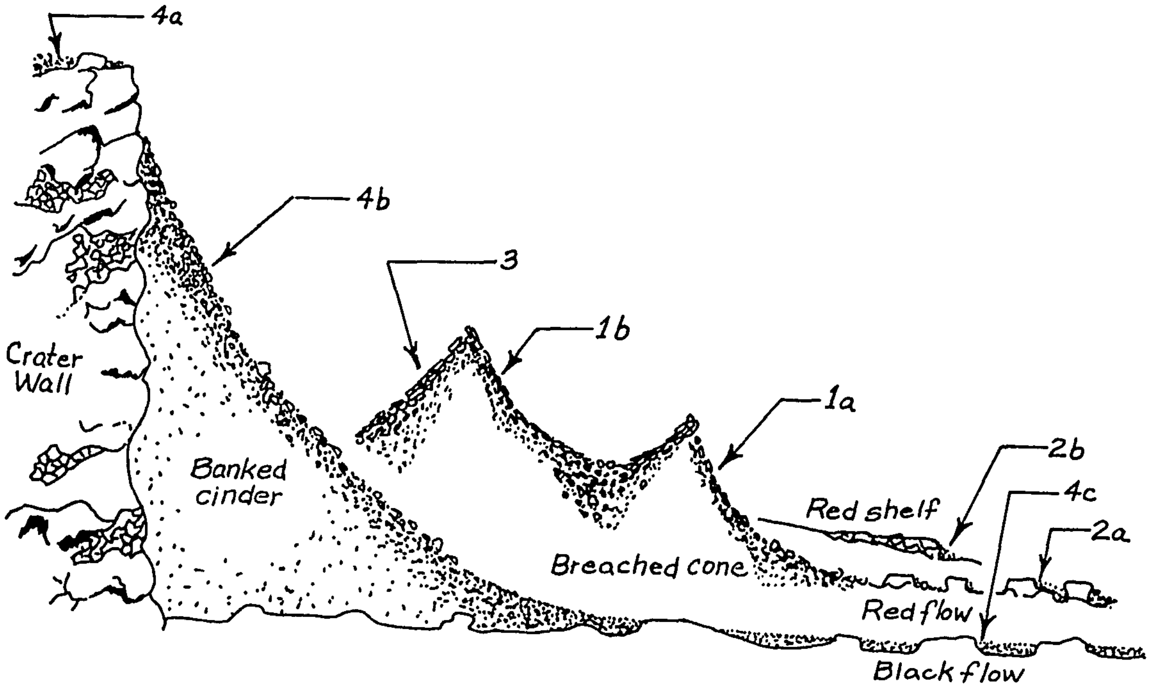


Fig. 15. -- Geomorphological features of Haleakala pertinent to silversword regeneration

1. Broad areas of high regeneration:
   a. outer slopes and trough of breached cones
   b. outer and inner slopes of red cinder cones

2. Small areas of high regeneration:
   a. foot of rafted boulders from breached cones
   b. windward edge of red flows

3. Moderate-to-low regeneration:
   agglutinates weathering <u>in situ</u> on slopes of cones, usually mixed with windblown cinder.

4. Low-to-zero regeneration:
   areas mostly covered by windblown cinder.
   a. crater rim - Kula Series basalt layers
   b. cinder banked against crater wall
   c. black flows

of the breach high above a wash (Figs. 5 and 16). A constant supply and removal of red tabular fragments over a long broad slope creates the uniform two-layer condition ideal for germination and seedling survival over an area of at least a hectare. Presently, populations 19, 20, 36 (Fig. 7), and 37 found on these slopes comprise 38% of the plants on Haleakala. According to Table 1, Powell in 1938 also thought the two cinder cones (locations 1 and 2) had the highest number of plants.

Almost all of the cinder cones have portions of their outer and inner slopes partially covered by fragments supplied by low red thin-layered shelves, sometimes almost completely eroded. Outer slopes are often broad and long with a wash at its base. Here the silverswords are usually dense (e.g. Puu-o-Pele pop. 11, 2,200 plants). However the inner slopes are broad but short with no discernable means of fragment removal and have fewer plants (e.g. Puu-o-Pele pop. 10, 900 plants). These populations comprise 35 to 45% of the plants on Haleakala and are mostly at locations 1, 2, and 4-7 in Table 1. Certain isolated cones such as Puu-o-Maui and Kamaolii are difficult to walk around; this may account for the discrepancies between past and present numbers at these locations.

2. Small areas of high regeneration. -- The curious pattern of small populations extending northeast from Puu-o-Maui on the map of Appendix IV can be explained by examining Fig. 17. These dense isolated populations are found at the base of boulders rafted on the red lava flow from Puu-o-Maui. Ideal two-layer slopes are created in miniature by these boulders that supply fragments which are removed

in low spots by wind and water (compare Figs. 7 and 18). The best groups on the red flow are at its terminus, the Silversword Loop. Here, as at terminal moraines of glaciers, many large boulders are deposited to produce the best slope conditions found anywhere except on cinder cones. Windward faces of two flows also have the "rafted boulder" conditions and support two pockets of high regeneration, populations 2 and 40. Presently these populations comprise about 5% of Haleakala's total, a surprisingly high number for a collection of small populations. According to Table 1, Powell also thought the red flow from Puu-o-Maui had a high number of plants.

3. Moderate-to-low regeneration. -- All cinder and spatter cones have some portion of their slopes covered with thick gray agglutinates weathering *in situ* creating a covering a large equiaxial fragments several centimeters thick. Where this condition predominates (Table 1: locations 8, 10, 11, 13, 15) few silverswords have survived since 1938 perhaps because the cover is thicker than the maximu 5 cm through which a seedling will grow.

One explanation for Powers' "relative abundant" estimate of Halalii may be found by examining population 39, the only cluster of 25 or more plants on this cinder cone: all plants except one are less than 10 cm in diameter, and all plants are found on a steep 40 degree slope. This suggests that landslides may have removed the "relatively abundant" plants of 1938, and the present population may be in the process of reestablishing itself.

4. Low-to-zero regeneration. -- Three locations (Table 1: 9, 12,

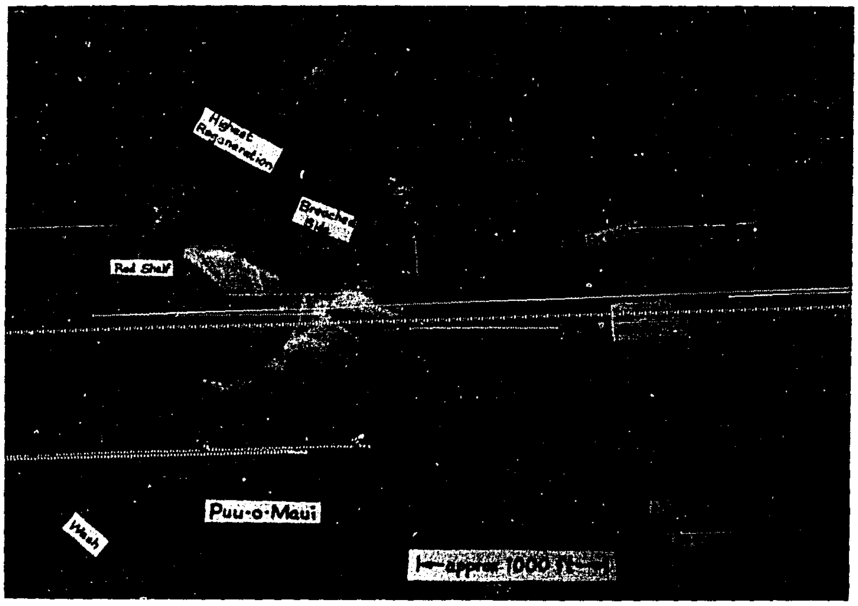


Fig. 16. -- Aerial plan view of Puu-o-Maui. Compare breach and red shelf with similar features on Ka-Moa-o-Pele Fig. 5. USDA ASCS photo EKN 4CC-20D 1/7/66.

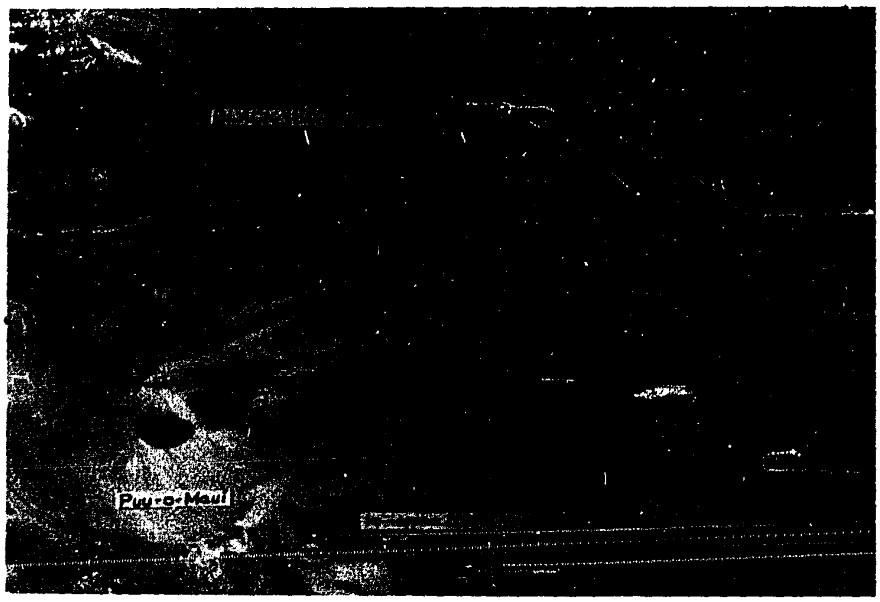


Fig. 17. -- Aerial plan view of red flow from Puu-o-Maui overlying black flows. Terminus is at the Silversword Loop. USDA ASCS Photo EKN 4CCD 1/7/66

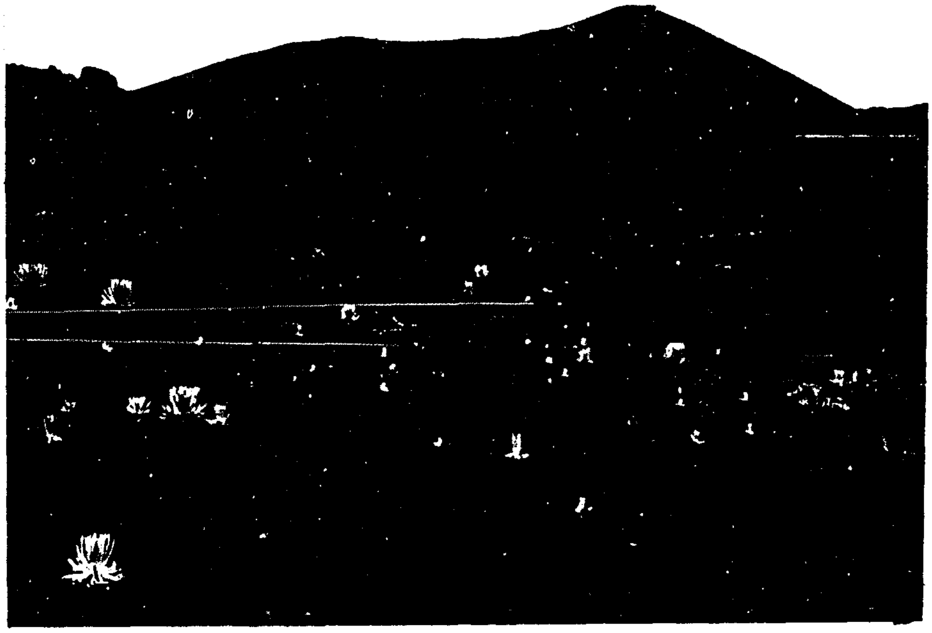


Fig. 18. -- High regeneration over a small area: pop. 41 on red flow near Silversword Loop. Trough of Puu-o-Maui in distant. Feb. 23, 1972

Fig. 19. -- Low regeneration on an area covered by wind-blown cinder: black aa flow near Silversword Loop elev. 2,200 m. Plant in left foreground is Dubautia menziesii Feb. 23, 1972

14) mostly covered by windblown cinder are poorest in silverswords. The crater rim and black aa flows consist of large rocks with interstices filled by windblown cinder (Fig. 19); plants are always found in rock crevices. Windblown cinder banked against the inner crater mixed with basaltic colluvium of the Kula Series are almost devoid of plant life (Figs. 20 and 21). For two of the three locations named by Powers (Table 1: 12 and 13) the number of plants have remained very low since 1938. However the third location, 9, Upper cliffs of palis on the western rim, was estimated to be "...third most abundant" by Powers. But according to interviews with men familiar with the Crater during the past 40 years and the recollections of this writer dating back 20 years, the western rim plants have not decreased substantially in number. Therefore the plants could not have been abundant in 1938 when they comprise less than 1% of the plants on Haleakala today.

The importance of physical rather than chemical differences of the substrate in determining the distribution of plants was shown by laboratory work followed by observations in the field. The percent composition of selected major elements were about the same for red and black rock and sand analyzed by an atomic absorption spectrophotometer. Also, no statistical significance could be found between the mean percent germinants on red and black sand in the laboratory. In the field, several high-density populations, notably on Puu Naue and Puu Nole, are on variously colored mixtures of cinder; often a single cinder fragment has colors ranging from brick-red to grayish black. Apparently iron oxidation which takes place during the initial

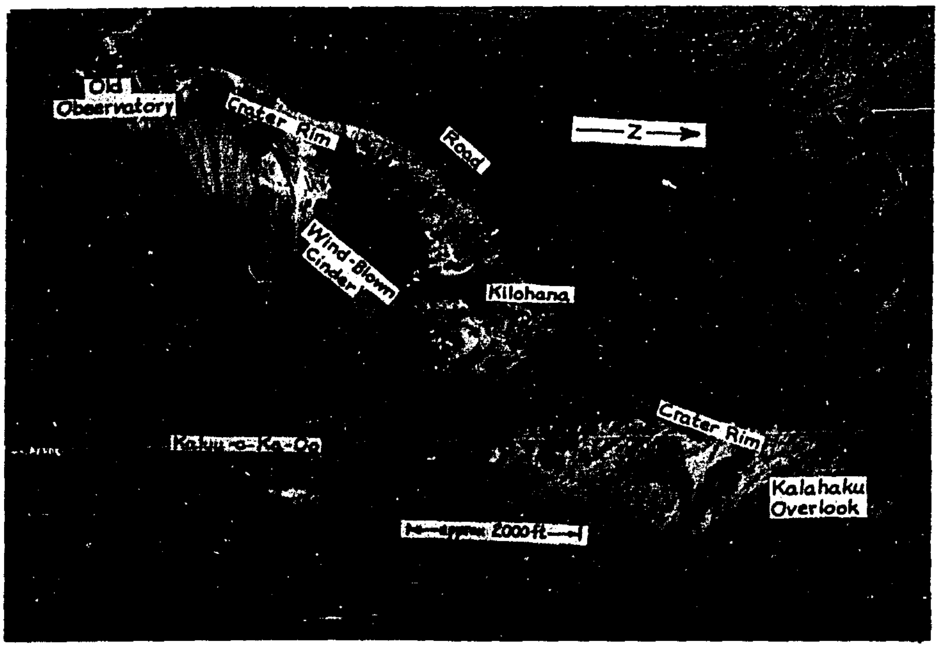


Fig. 20. -- Aerial view of the west crater rim windblown cinder banked against inner crater walls. USDA ASCS Photo EKN 3CC-20 3/31/65

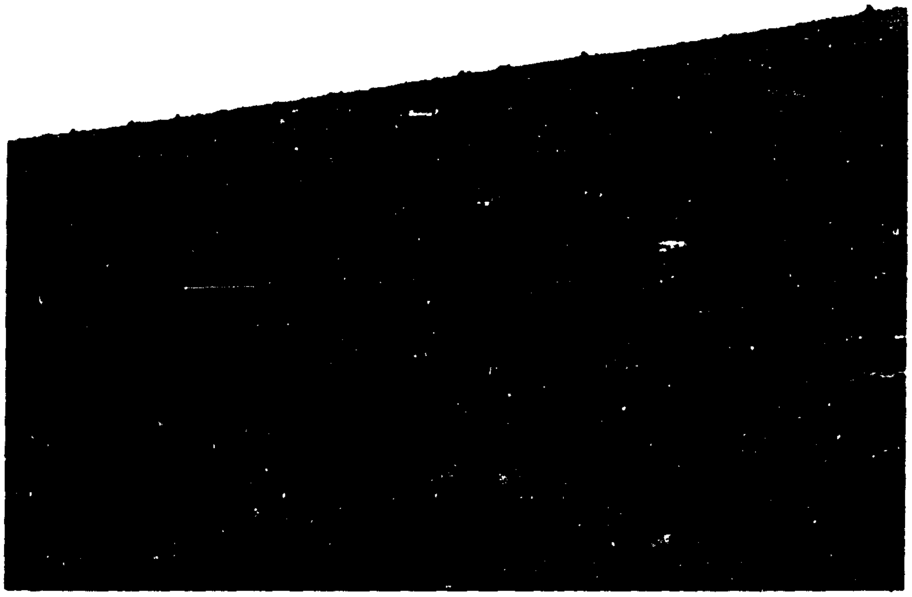


Fig. 21. -- Zero regeneration on windblown cinder banked against the inner crater wall. Sliding Sands Trail elevation 2,960 m. 1969

eruption, and subsequent chemical weathering of the parent material are relatively unimportant in the present range of the silversword.

Major Non-edaphic Factors Affecting the Silversword

Vandalism, browsing, and insect damage to seeds are the three factors always mentioned in any general description of the Haleakala silversword. But this writer's research based on three years of field observations and field data indicated that these factors may not be important under the management policies of the National Park Service and the present range of the silversword.

Vandalism and browsing were not factors prior to the arrival of western man and his herbivores. However, before the establishment of a permanent National Park Ranger position in the late 1920's, many thousands of plants were "...uprooted and shipped away as ornaments..." and "...hundreds of flower buds were eaten by wild goats" (Bryan 1948). But for the past 40 years, no one including Lamb (1935a) has reported any loss of plants rivaling Bryan's figures probably because of intensive patrolling and hunting by Park personnel. Presently vandalism and browsing may not be important because:

1. affected plants are found only near and along the crater rim where man and goats are most prevalent (only 1% of total),

2. the incidence of vandalism and browsing has been extremely low in the area of the affected plants where damage or removal of large individuals are noted quickly, and

3. browsing itself may increase the seedcrop by the induction of lateral flowering branches (tillering) even when the single floral meristem is eaten.

Insect damage to seeds, unlike vandalism and browsing, is a natural ecologic factor because the species involved (Rhynchephestia rhabdotis and Tephritis cratericola) are specific to the silversword. Since the capitula in all populations are infested, and the infestations are difficult to prevent (Lamb 1936), insects are probably more important than vandalism and browsing. However, no capitulum had seeds completely destroyed by insects and large dense populations were found to have the highest infestations in 1971. Therefore, the importance of this factor is yet unresolved and await further studies.

Trampling and soil erosion by man and goats may be more important than vandalism or browsing on this loose, non-cohesive easily compressed cinder substrate. Thirty-two plants of population 58, Kalahaku Overlook tagged with date and crown size during 1968-69 were relocated and remeasured in 1962. Most of the plants of less than 10 cm size were missing or had little growth and with roots exposed. Therefore, it appears that young plants are especially sensitive to disturbance of the cinder substrate causing root breakage in this species which has evolved in the absence of mammals. Kalahaku Overlook on the crater rim is one of the most disturbed areas on Haleakala compared to adjacent slopes having the same exposure, vegetation, and parent material.

Factors That Await Further Research

The flowering stimulus is still unknown, although during the past four years heavy flowering was preceded by a higher-than-average winter rainfall. A reliable count of flowering plants must be kept for several consecutive years before rainfall can be definitely correlated with flowering.

A large number of empty achenes in every mature capitulum examined suggests that there is high self-incompatibility within a population and a dependence on pollen from external sources. Since only one plant flowered last season (1972), research could not be carried out, and the nature of the genetic and pollination mechanism remains uncertain.

SUMMARY

Argyroxiphium sandwicense DC. on Haleakala Crater, Maui is well-adapted to the Hawaiian alpine milieu, not only because of xerophytic features such as tomentose succulent leaves, but also because of its ability to sustain high regeneration under dynamic substrate conditions that eliminate all but a few exotic and endemic species. Within Haleakala Crater, away from man and herbivores against which it has evolved little protection, the silversword is able to germinate and emerge at the surface at optimum temperature and moisture conditions determined by the characteristics of an overlying layer of cinder fragments. In turn, these characteristics are best met on the slopes of large breached cinder cones.

A. sandwicense is presently not endangered on Haleakala. Fully half of the 43,000 plants counted are on Puu-o-Maui cinder cone, the most isolated and least disturbed area where the optimum regeneration conditions are found. If large animals, including man, are kept away from the highest regenerating areas where surface layers are at a delicate steady-state equilibrium, the silversword should be able to maintain itself indefinitely within the Crater.

Contrary to popular belief, vandalism and browsing are probably not important under the present management of the National Park Service. But with further increase in visitors, root breakage by trampling (now found only near and on the crater rim) may become a factor within the Crater. The impact of seed damage by insects is unresolved and awaits further investigation.

APPENDIX I

MAXIMUM AND MINIMUM AIR TEMPERATURES AT TWO CLIMATOLOGICAL STATIONS AND FOUR WEATHER SHELTERS °C DEC. 1970-FEB. 1972

	Elev. m	From: To:	12/20 2/20	2/21 4/15	4/16 6/1	6/2 7/18	7/19 10/9	10/10 11/25	11/26 12/30	12/31 2/22
Ranger Station U.S.W.B. 338 (a)	2130	max	18	24	19	23	23	20	20	17
		min	-1	2	2	5	3	2	2	-1
Haleakala Summit U.S.W.B. 338.4 (a)	3040	max	16	14	14	18	18	17	13	12
		min	-2	-2	0	2	2	1	-2	-1
Sliding Sands Tr. Shelter no. 1 (b)	2860	max	20	17	18	23	26	17	16	17
		min	3	4	3	6	3	2	-2	-2
Puu-o-Maui cone Shelter no. 2 (b)	2280	max	22	20	20	24	24	21	20	19
		min	2	2	3	6	4	3	0	0
Ka-Moa-o-Pele cone Shelter no. 3 (b)	2210	max	19	20	20	23	25	21	19	18
		min	-3	-3	-2	-1	-2	-1	-2	-2
Silversword Loop Shelter no. 4 (b)	2190	max	20	20	20	24	24	21	18	18
		min	12	-1	0	9	1	1	0	-2

a. Climatological stations are located at rain gages in Fig. 2 and described in U.S.W.B. 1962.

b. Shelters are located in APPENDIX IV, and described on page 23.

APPENDIX II

PRECIPITATION, AND FOG-INTERCEPTION PLUS PRECIPITATION
DEC. 1970 - FEB. 1972 AT EIGHT LOCATIONS - mm

	Elev-m	From: / To:	12/20 2/20	2/21 4/15	4/16 6/1	6/2 7/18	7/19 10/9	10/10 11/25	11/26 12/30	12/31 2/22
Central Crater 8-inch gage (a)	2230	open	1470	640	220	5	90	140	150	450
Sliding Sands Tr.	2860	open	*	*	50	0	60	60	120	*
Rain gages no. 1		fog	*	*	120	0	*	*	140	*
Sliding Sands Tr.	2500	open	*	*	50	0	40	80	130	*
Rain gages no. 2		fog	*	*	90	0	*	*	160	*
Puu-o-Maui cone	2280	open	*	*	130	0	10	60	90	*
Rain gages no. 3		fog	*	*	140	0	120	*	*	*
Ka-Moa-o-Pele	2210	open	*	*	0	0	70	M	140	*
Rain gages no. 4		fog	*	*	60	0	150	M	*	*
Puu Kauaua cone	2210	open	*	*	0	0	30	80	70	*
Rain gages no. 5		fog	*	*	20	0	80	90	80	*
Silversword Loop	2190	open	*	*	150	0	90	90	110	*
Rain gages no. 6		fog	*	*	170	0	100	100	120	*
Kalahaku Overlook	2840	open	*	*	120	0	50	70	80	*
Rain gages no. 7		fog	*	*	140	0	*	*	150	*

Rain gages 1 through 7 are indicated as triangles on the map in APPENDIX IV.

a. Official U.S.W.B. non-recording gage indicated as circle on map in Fig. 2.

* Gage overflowed, maximum capacity is 180 mm.

M Missing data, gages damaged by vandals.

APPENDIX III

CENSUS OF SILVERSWORD POPULATIONS
WITH MORE THAN 25 PLANTS, TAKEN 1969-72 (a)

Population designation	Location	No. crown diam. <20 cm	No. crown diam. >20 cm	No. flowered(c) 1969	No. flowered(c) 1971
1	Upper Sliding Sands Trail	20	6	0	0
2	"	290	24	5	0
3	"	27	8	0	0
4	"	425	28	3	0
5	"	42	1	0	0
6	"	197	45	12	2
7	"	27	11	1	0
8	Puu-o-Pele cinder cone	29	6	1	0
9	"	35	8	2	0
10	"	790	98	13	11
11	"	2100	89	9	8
12	"	210	53	8	6
13	Lower Sliding Sands Trail	23	6	0	0
14	Kamaolii cinder cone	230	64	4	2
15	"	900	230	2	0
16	"	60	35	3	0
17	Puu-o-Maui cinder cone	700	300	2	0
18	"	3500	250	4	0
19	"	6000	500	2	0
20	"	7000	600	4	1
21	"	400	80	3	2
22	"	30	12	3	0
23	"	420	85	2	2
24	"	280	48	5	0
25	"	950	72	0	0
26	Un-named cones	75	14	2	0
27	"	320	38	5	4
28	"	120	54	6	7
29	"	1500	250	5	23
30	"	360	8	1	1
31	Ka-Moa-o-Pele, Upper Area V	264	27	2	0
32	" Lower Area V	71	10	2	1
32	" Area VI	230	60	1	1
33	" Upper Area V	250	23	1	2
34	" Upper Area V	78	34	2	1
35	" Area IV	470	30	7	11
36	" Area I	1020	180	3	7
37	" Area II	1100	130	16	29

APPENDIX III CONTINUED

CENSUS OF SILVERSWORD POPULATIONS
WITH MORE THAN 25 PLANTS, TAKEN 1969-72 (a)

Population designation	Location	No. crown diam. <20 cm	No. crown diam. >20 cm	No. flowered(c) 1969	No. flowered(c) 1971
38	Ka-Moa-o-Pele outlier	49	2	0	1
39	Halalii cinder cone	43	1	0	0
40	Near official rain gage	271	93	4	3
41	Puu Naue cinder cone	800	150	6	16
42	"	2000	300	9	16
43	"	150	8	0	0
44	Puu Nole cinder cone	1200	520	6	8
45	"	1100	120	2	5
46	"	89	10	0	2
47	Red flow from Puu-o-Maui	150	40	2	0
48	"	200	98	1	0
49	"	30	4	0	0
50	"	31	3	0	0
51	"	125	4	3	0
52	"	30	4	1	2
53	"	19	7	0	0
54	"	120	15	1	0
55	"	32	3	0	1
56	"	560	52	6	2
57	Silversword Loop (red flow)	300	130	20	25
58	West rim, Kalahaku Overlook	59	98	13	3
59(b)	" group not browsed	11	1	0	0
60(b)	" grp heavily browsed	0	13	0	0
	TOTALS:	37,863	5,193	195	206

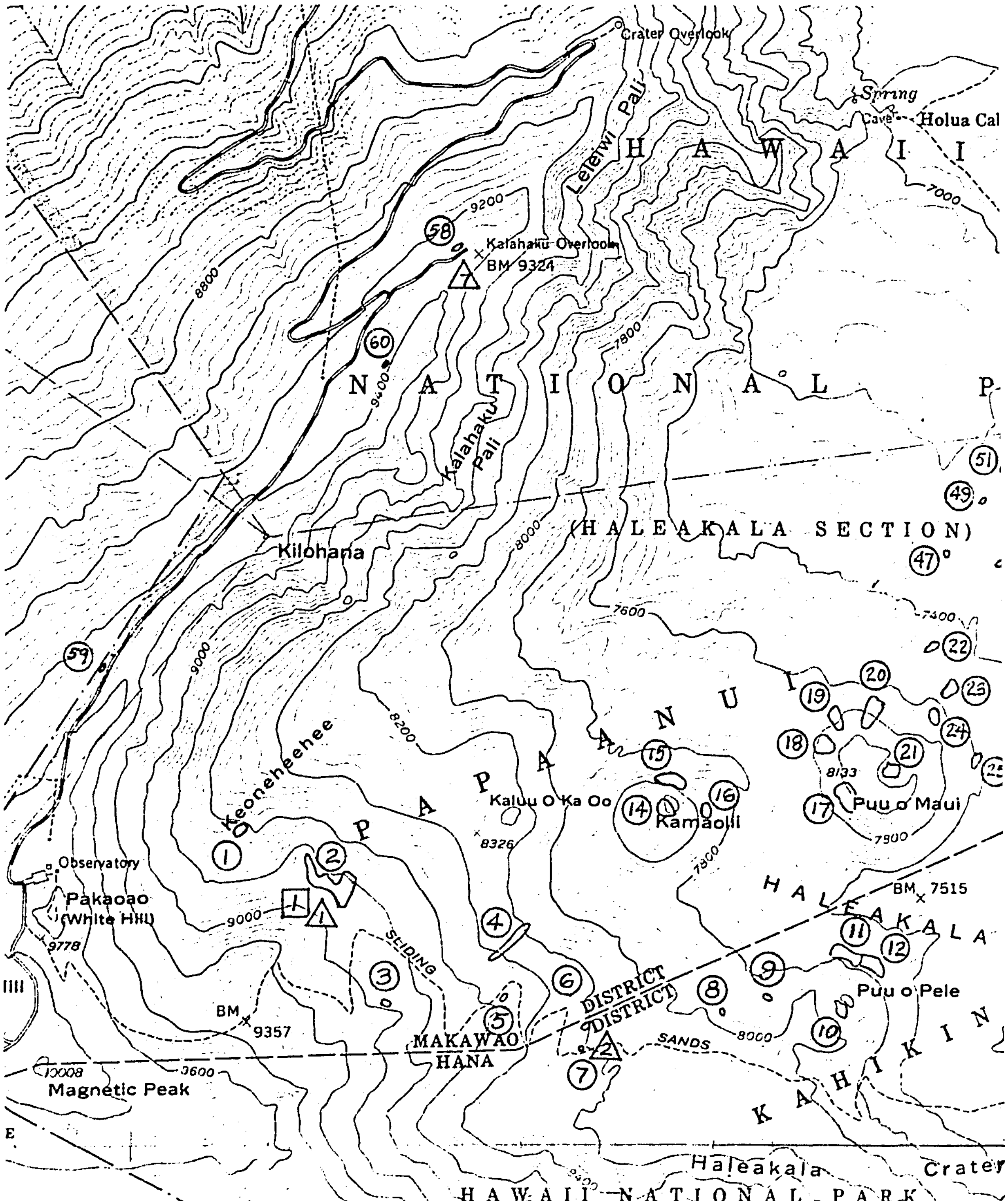
a, Numbers listed are actual counts, and not estimations. Larger plants and flowering individuals are more accurately tallied because of their smaller number and conspicuous appearance.

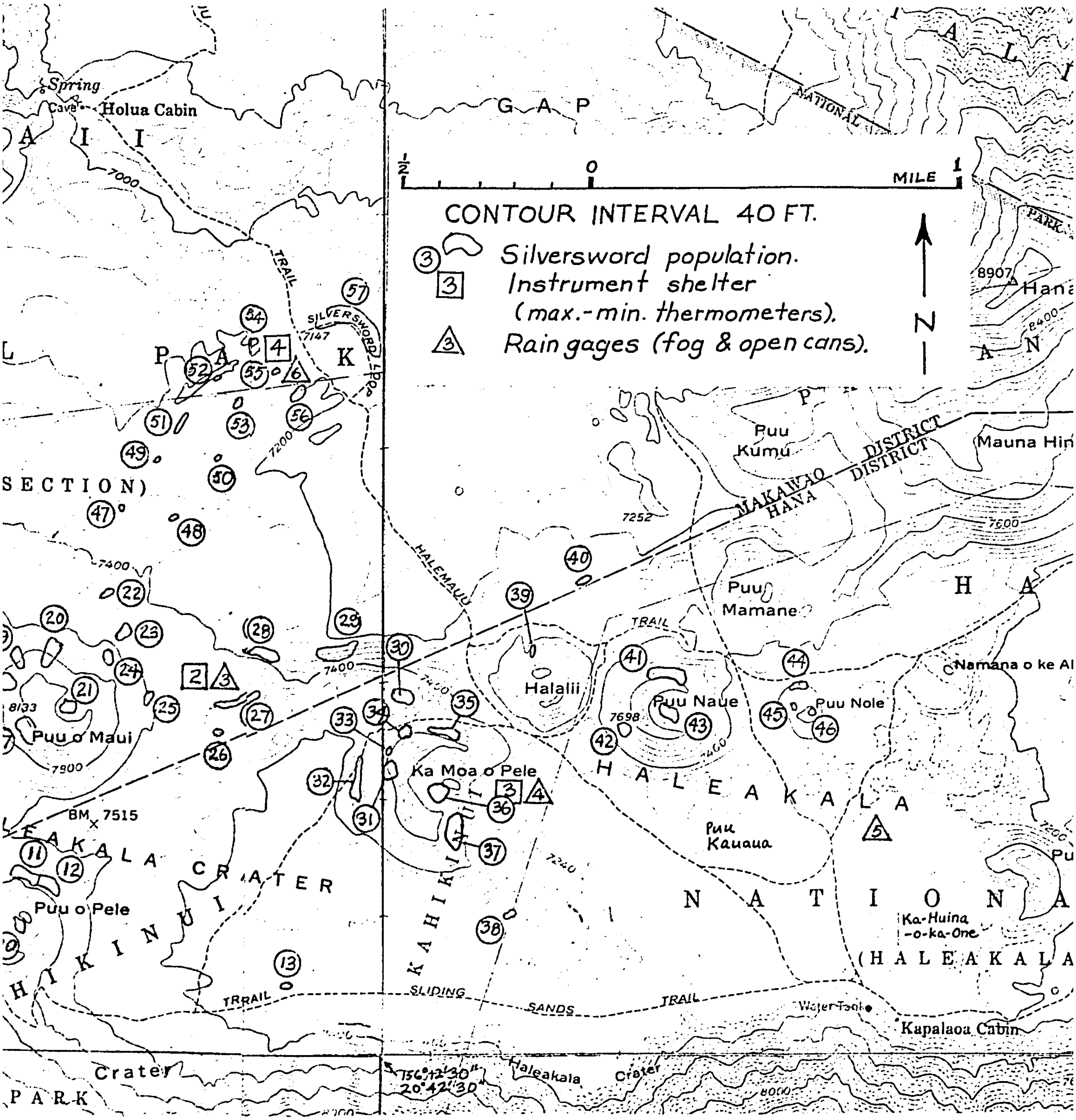
b. Populations 59 and 60 included because of their easy accessibility.

c. None flowered in 1970. Only one flowered in 1972, on Puu Naue (personal communication, Laurence Guth, Park Ranger, Haleakala N.P.).

APPENDIX IV

LOCATION OF SILVERSWORD POPULATIONS, INSTRUMENT SHELTERS, AND RAIN GAGES




CONTOUR INTERVAL 40 FT.
½ 0 MILE 1
Silversword population.
Instrument shelter
(max.-min. thermometers).
Raingages (fog & open cans).
N
Spring
Cave
Holua Cabin
GAP
NATIONAL
PARK
8907
Hana
Mauna Hina
SECTION)
TRAIL
SILVERSWORD LOOP
7147
7000
7200
7400
7252
7600
Puu Kumu
MAKAWAO DISTRICT
HANA DISTRICT
HALEMAUU
TRAIL
Puu Mamane
Namana o ke Akua
Halalii
Puu Naue
Puu Nole
7698
8133
Puu o Maui
7900
BM 7515
Ka Moa o Pele
HALEAKALA
Puu Kauaua
KAHIKINUI
CRATER
Puu o Pele
NATIONAL
Ka-Huina-o-ka-One
(HALEAKALA
SLIDING SANDS TRAIL
Water Tank
Kapalaoa Cabin
Crater
PARK
156°12'30"
20°42'30"
Haleakala Crater
8000

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