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PHYTOSOCIOLOGY AND ECOLOGY OF THE NATURAL DRY-GRASS COMMUNITIES ON OAHU, HAWAII

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CONTENT

ABSTRACT

Using the Braun-Blanquet and ordination techniques, nine dry-grass community types were recognized on Oahu, seven of which were dominated by exotic grasses and two by native grasses, *Heteropogoji* ***contortus*** and *Eragrostis variabilis.* These community types occured in summer-drought, **summer-dry** and humid climates. The distribution of certain community types could be correlated directly with rainfall and soil pH. In the summer-drought climate the occurrence of the community types was related to topography, wind exposure, rockiness of the land surface and stoniness of the soil. The nine community types were not related to the established soil series, organic matter content and water retaining capacity of the surface soils.

Three distinct soil-water regimes were recognized in five community types: drought, dry and wet types. Seasonal variations in soil-water content were correlated closely with the rainfall pattern.

The introduction and spread of exotic species resulted in a gradual disappearance of the native grass communities in the summer-drought zone. In the summer-dry zone, *Grevillea robusta* trees and *Melinis minutiflorw* grass mats were invading the *Rhynchelytrum repens* community. *Andropogon virginicus,* introduced in 1932, formed a wide spread herbaceous community in the humid zone. In some places, this community was invaded by *Dicranopteris linearis* fern mats and trees of *Acacia koa* or *Metrosideros collina.* Fire in both the summer-dry and humid zones maintained and extended the grass communities.

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1. INTRODUCTION

1.1. Purpose and scope of study

The current natural vegetation of Oahu consists structurally of grass, scrub and forest communities. For the purpose of this study, a dry-grass community is defined as any grass-dominated natural vegetation, in which the dry shoot mass of the grasses is dominant throughout the year. This distinguishes the dry-grass community from the predominantly green *Brachiaria mutica* grass community that occupies certain moist areas in the lowlands of Oahu, and from the introduced *Melinis minutiflora* grass community which currently occurs mostly only in small patch communities. Lawn grass and introduced pasture covers are excluded because they are considered cultivated and not natural communities.

Almost all dry-grass communities contain some woody plants, usually shrubs up to 2 m tall. A community is accepted as a dry-grass community for this study, if the scattered woody plant cover is less than 40 percent in an area of 100 square meters.

Dry-grass communities occur throughout Oahu, from sea level to the highest mountain crest. The extent varies considerably from a few square meters to larger tracts of several hectares.

However, within the dry-grass community covered by this definition, there are considerable floristic and dynamic variations.

No comprehensive study of the grass communities on Oahu has been made so far. The native grass communities are disappearing due to invasion by exotic species and human disturbance. At the same time, new grass communities dominated by *Andropogon virginicus* have developed within the last 40 years. It appeared, therefore, of value to study the dry-grass community in detail. The objectives of this investigation are to study the dry-grass communities on Oahu throughout their range to:

1. determine their structure and floristic composition, which will be the basis of the subsequent objective,
2. develop a community classification which will be useful for mapping and subsequent bio-environmental studies, and
3. explain the community pattern in terms of environmental parameters and dynamic relationships for gaining an understanding of the relative stability and permanency of the dry-grass communities on Oahu.

1.2. Review of literature

Most of the native vegetation of Oahu has been altered by man (Fosberg, 1961), except above an elevation of 500 m and on very steep slopes. Fosberg stated that in the humid zone the original vegetation types that remain were the cloud forests on the top of the mountain ranges, *Metrosideros collina* rain forests, some *Acacia koa* forests and vegetation on the steep slopes composed mainly of *Dicranopteris linearis.* In the dry lowland zone, Egler (1947) noted that relicts of the native grass communities formed by *Heteropogon contortus* and *Eragrostis variabilis* were still found. Many exotic plants, which were introduced mainly after the arrival of the Europeans in 1778, have become naturalized (Egler, 1947) and now form several distinct plant communities. For example, Egler noted that *Leucaena leucocephala* scrub and *Prosopis pallida* forest were the most wide-spread exotic woody plant communities in the arid parts of the island. The coastal lowlands, plains and hillsides in the arid areas were once occupied by native grass communities dominated by *Heteropogon contortus* (Egler, 1947; Hatheway, 1952; Rock, 1913; Vogl, 1969).

Egler (1939, 1947) noted that the relicts of the *Heteropogon contortus* communities were still present in the *Leucaena leucocephala* scrub, but *Rhynchelytrum repens,* an introduced grass, was found associated with it in the more moist part of the arid areas.

Egler (1939) and Hosaka (1937) stated that the common exotic plant communities in the wetter regions were the *Psidium cattleianum* and *Psidium guajava* scrubs. On the other hand, they did not record the occurrence of the *Andropogon virginicus* grass community, although Rotar (1968) and Whitney *et al.* (1939) pointed out that this grass was introduced in 1932.

: . The classifications of the Hawaiian vegetation by Hillebrand (1887, 1888) and Rock (1913) were based mainly on physiognomy, altitude and climate. Hosaka (1937) segregated the native and exotic plant communities on Oahu into six vegetation zones. This zonation constituted the basis for the later and more refined classifications (Ripperton & Hosaka, 1942; Hosaka & Ripperton, 1955) of the Hawaiian vegetation, in which five vegetation zones were recognized, though certain zones were further subdivided. The mean annual rainfall and altitude were the main criteria used. Egler (1939, 1947) recognized two major zones, the pluviotropical and xerotropical zones, with further subdivisions in each zone that essentially followed Hosaka's (1937) scheme. Krajina (1963) retained the five major vegetation zones of Ripperton and Hosaka (1942), but segregated the Hawaiian vegetation into fourteen biogeoclimatic zones, of which only nine occur on Oahu. Each zone has several distinct habitats which are under the control of either topographic, geologic or biotic factor. He stated that climate was the most important controlling factor of the zonation. Krajina's zonation is more useful than Egler's (1939, 1947), because his zones are floristically and edaphically more closely defined. Knapp (1965) briefly described the Hawaiian vegetation and divided it into four zones. In his scheme the vegetation of Oahu consists of two zones only, the rainforest and dry zones. He also recognized and briefly described a number of communities, including grass communities.

Other works on the vegetation of Oahu are local studies in physiographically restricted areas. McCaughey (1917) made a descriptive account of the vegetation of Manoa valley, in which he recognized eight vegetation types. His study was based on nine years' field observation. Hosaka (1937) studied the phytosociology, ecology, distribution and successional relations of various plant communities along the Kipapa Gulch. Grasses that were noted by Hosaka to be abundant in the dry and humid zones were *Heteropogon contortus, Rhynchelytrum, repens, Paspahim conjugatum* and *Paspalum orbicidare. Andropogon virginicus* was not recorded in his study. Egler (1947) recognized seven major communities in the non-maritime vegetation of the xerotropical zone. *Heteropogon contortus* communities were reported by Egler to occur in his makai, middle and mauka koa haole zones, *Rhynchelytrum repens* communities in the moist part of his mauka koa haole zone, and *Chloris barbata* communities in his makai koa haole zone. Egler stated that these grass communities were rather unstable, as there was an indication of invasion by woody species. *Paspalum orbiculare* communities, on the other hand, were found outside the arid area at higher elevations. Egler (1942) also pointed out that in successional changes the exotic species were pioneers, while the natives were aggressive arrivals in the later stages. He predicted that the native species would eventually push the exotics out. Hatheway (1952), who described some rare native dry forests in northwest Oahu, supported Egler's prediction. He reported that certain native woody species were invading the *Rhynchelytrum repens* and *Leucaena leucocephala* communities in that area.

De Ausen (1966), in a study of the coastal ecosystems, recognized thirteen ecosystem classes, of which two were dominated by *Chloris barbata*. Her ecosystem classes were related to rainfall, drought patterns, wind, surf and exposure. A recent study, made by Vogl (1969), dealt with the role of fire in the evolution of the Hawaiian flora and vegetation. Vogl stated that *Heteropogon contortus, Eragrostis variabilis* and other native species occurring in dry areas were resistant to fire, and that fire was the factor responsible for maintaining native grass communities.

The above account indicates that the previous ecological works have concentrated on classifying the Hawaiian vegetation or have been detailed studies in restricted geographic areas. This study took a somewhat different approach by being island wide, but restricted in detail to a particular structural community, namely the dry-grass community as defined earlier.

2. GEOGRAPHY AND GENERAL ENVIRONMENT OP OAHU

2.1. Geography

The six main Hawaiian Islands, whose landmass covers 6349 square miles, are located between the longitudes from 160° to 154° W, and the latitudes from 22° to 19° N, in which they occupy a narrow zone extending from NE to SW, 430 miles long. Oahu is the third largest (640 square miles) of the six main islands.

2.2. Geology and soils

The island of Oahu is composed of the remnants of volcanic domes that were formed during the Pliocene (Stearns, 1966). These have been much faulted and eroded, resulting in the present two, strongly dissected, roughly parallel, mountain ranges. These are the Koolau Range on the east side of the island and the Waianae Range on the west side. The highest elevation, Mt. Kaala in the Waianae Range, is 1227 m above sea level. The Punchbowl, Diamond Head, Koko Head and the Koko Craters were ash cones formed during the late Pleistocene (Stearns, 1966). The dominant geomorphological features of Oahu today are the steep cliffs facing the ocean, and the gentler slopes descending to the interior plain, the Schofield plateau. The interior plain separates the two mountain ranges. A dominant feature is also the coastal plains that extend to the north and south of the Schofield plateau.

Stearns (1940, 1966) stated that the mountain ranges were composed of basaltic pahoehoe and aa lavas with deposits of pyroclastic materials, such as cinder, pumices, spatter, tuff and breccia. These were formed primarily during the major and secondary eruptions in the Tertiary and Pleistocene periods respectively. The lava flows which were issued from the Koolau mountain range extended into the Schofield plateau. Reef limestone alternating with beds of clay, tuff and alluvium, is found along the coastal margin of the island. This limestone formation varies in width from a few feet to as much as five miles at Ewa. Unconsolidated recent marine sediments, mainly sand, occur near the beach. Unconsolidated recent calcareous dunes of sand blown inland and unconsolidated recent non-calcareous deposits, mainly younger alluvium, may also be found on the coastal area.

A variety of soils has developed from the surface geological deposits. Cline *et al.* (1955) reported fourteen Great Soil Groups on Oahu. Azonal soils, mainly Lithosols (rocky soils), cover about three quarters of the land surface primarily in mountainous areas. Latosols are the dominant zonal soils on Oahu. These soils have low silica and base contents, low silica-sesquioxide ratios and weak profiles.

2.3. Climate

The following account is based largely on the articles by Blumenstock & Price (1967) and Price (1966).

Oahu has an oceanic climate, but rugged topography causes unequal distribution of rainfall and temperature gradients, resulting in a great diversity of climatic conditions.

The northeast trade-winds that blow from the region of high pressure (the Pacific High) are a major climatic control over the island. During the period of May through September the trade-wind influence dominates. From October through April the trade-winds blow less regularly. During this period southerly winds (Kona winds) may prevail especially in January.

The mean annual rainfall on Oahu varies from 580 mm on the coast of the Waianae plain (leeward side of the Waianae Range) to 6138 mm on the mountain crest at Kahana (Koolau Range). This great variation of rainfall is due to the topography of the island. The orientation of the Waianae and Koolau Ranges is roughly parallel in a northwest to southeast direction. The ranges are almost at right angles to the direction of the trade-winds, thus the Waianae Range, sheltered by the Koolau Range, receives much less rainfall. The trade-winds bring only a moderate rainfall during summer, but from October through March, the average rainfall is higher because of the storms. The contrast between the rainy season and dry summer is very pronounced in low rainfall areas at low elevations, but less so in high rainfall areas at high elevations.

The difference between the mean summer and winter temperatures is very small in Hawaii. Below 1650 m the temperature range does not exceed 5° C. The small temperature ranges throughout the year are the result of slight variations in monthly solar radiation and because of the oceanic influence. The mean annual temperature in the coastal area on the windward and leeward sides is 24° C. The temperature lapse rate on the leeward side is 0.7° C per 100 m, and on the windward side is 0.8° C per 100 meters.

3. FLORISTIC RELATIONSHIPS

This section is concerned with the variations in species composition, structural characteristics and classification of the dry-grass communities.

3.1. METHODS

3.1.1. Vegetation sampling

The field work began with a thorough reconnaissance, which included the use of air photos. It was found that the dry-grass communities are structurally one of the major vegetation types. The dry-grass communities occur throughout the island of Oahu from sea level to about 1000 m elevation, thereby cutting through all recognized vegetation zones.

Sample plots were established wherever accessible dry-grass communities occurred. The sampling purpose was to include as many community variations as possible and to distribute the vegetation samples so that there was a geographic balance in sampling locations. In all, 106 plots were established (Fig. 1) and used in this study.

The size of each sample plot was arbitrarily chosen as 100 sq. meters. The minimal area was established by the nested plot technique (Cain & Castro, 1959; Ellenberg, 1956) to insure that the sample plot size was adequate. A minimal area is defined as the smallest area that contains a near-complete representation of the species of the community. By using Cain's (1938) criteria of near-complete species representation, it was found that the minimal area of the dry-grass communities was only 15 — 20 sq. meters. Cain's criterion designates as minimal area the point on the species-area curve, where an increase of 10% in the sample area yields only 10% more species. The 100 sq. m quadrat used for all sample plots was, therefore, much greater than the minimal area required.

The vegetation samples or relevés were analyzed by the Zürich-Montpellier method (Braun-Blanquet, 1964; Becking, 1957; Ellenberg, 1956; Poore, 1955). This was essentially a species list method, where the main emphasis was placed on a complete species record. Emphasis was also placed on the quantity of each species present, but not through counting of individuals or direct measurement of cover. Instead the quantity of each species was estimated by a cover-abundance rating scale. The scale used was that of Braun-Blanquet (1964).

Notes on the clumping tendency and vigor of each species were also made qualitatively, if these were unusual. The. average height of each species, excluding the seedlings, was measured. In addition, the percentage of cover of all trees and shrubs, herbs and bare ground was estimated separately. Each relevé analysis was supplemented with notes on location, altitude, topographic position, slope, wind exposure and landform.

Vegetation sampling was carried out in the summers (dry seasons) of 1965, 1966 and 1968. The plots were checked for seasonal floristic changes during the following winters (rainy seasons).

3.1.2. Analysis of data

3.1.2.1. Construction of the synthesis tables

The plots were divided in two groups according to their occurrences in the dry or subhumid to humid regions. The two regions are separated by the 1000 mm isohyet of mean annual rainfall. Since the dry region

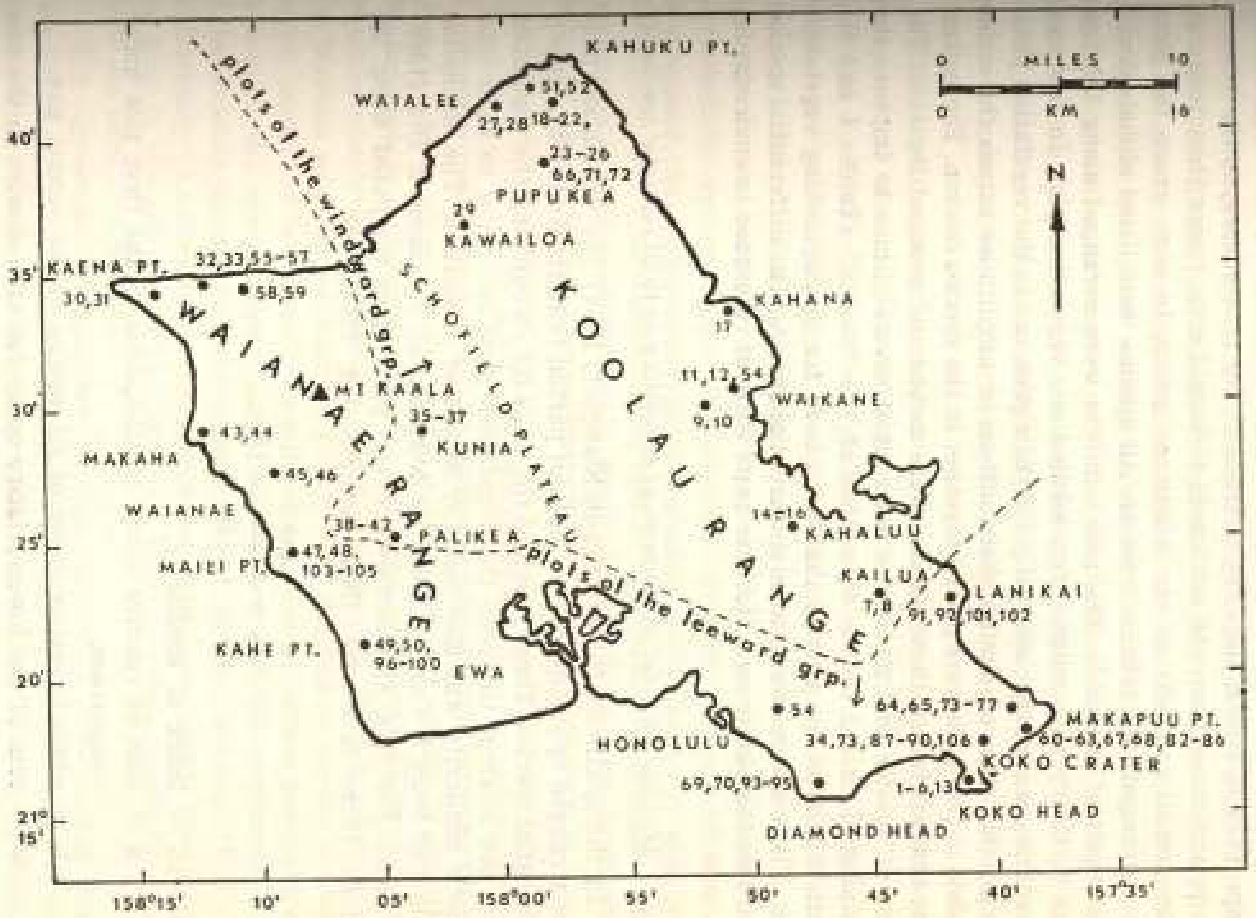

Fig. 1. Map of Oahu showing the geographical distribution of the study plots. Figures refer to the plot numbers.

(less than 1000 mm mean annual rainfall) corresponds roughly with the leeward side of the Waianae Range and partly with the leeward Koolau Range, the dry region plots are referred to, for convenience, as the leeward group, and those from the subhumid to humid area (more than 1000 mm mean annual rainfall) as the windward group. In each group the plots were arranged in a tabular manner. All species were listed alphabetically on the left of the table. The plot numbers were arranged along the top. Thus vertically each column represented one vegetation plot. In this way the species can be checked easily for their presence in the vegetation plots. Species that showed similar distributions or amplitudes across the series of plots in the table were placed together in the species column. Thereafter, plots that contained these species were moved and grouped together. The order of species and plots was rearranged several times to improve the grouping. This led to the formation of the "blocks" (Tables I and II) which displayed the species that were used for distinguishing vegetation units. These species were called differential species. The differential species were selected purely on a floristic basis without reference to environment.

3.1.2.2. Ordination: plot arrangement according to total floristic similarity

In the synthesis tables (Braun-Blanquet, 1964) the vegetation plots were arranged in groups on the basis of partial floristic similarity, namely differential species. These provided the basis for recognizing the vegetation types. An attempt to group the vegetation plots according to their total floristic similarity was also made by means of ordination. The ordination method of Bray & Curtis (1957) as described by Newsome & Dix (1968) was used. For this, similarities between plots were computed using the formula (Bray & Curtis, 1957; Greig-Smith, 1964) :

$$IS = \frac{2w}{(a+b)} \times 100\%$$

where IS = index of similarity,

a = sum of relative cover of all species in the first plot under comparison,

b = sum of relative cover of all species in the second plot,

w = sum of the lower relative cover for each species in the two plots; if a species occurs in only one of the plots, its lower relative cover is 0.

Relative cover is defined as the cover of one species expressed as a percentage of the total cover of all species in one plot. Relative cover is used in the formula for ease of computation, since in this case (a + b) is always 200. Therefore, the index reduces to IS = w. The values of w for all the plots were compiled in a matrix. Since the measure of quantity of a species in the plots was estimated by the Braun-Blanquet cover-abundance scale, each scale was first transformed into percentages as follows: + = 0.1%; 1 = 5%; 2 = 17.5%; 3 = 37.5%; 4 = 62.5% and 5 = 87.5% (Braun-Blanquet, 1964; Etter, 1948). The cover value for each species in each plot was further converted into relative cover, as mentioned above.

The two-dimensional ordination diagrams for the plots of the leeward group and the windward group were constructed following the procedure described by Newsome & Dix (1968). This procedure is a modification of Bray & Curtis' (1957) and Beals' (1960) methods. The modification relates to the selection of the reference plots for the ordination axes. As in the earlier methods, the objective is to obtain an unbiased selection of floristically extreme plots for each axis. However, a new criterion is incorporated that safeguards against selecting reference plots that are floristically totally unrelated to the rest of the vegetation samples. The criterion is that any reference plot must share at least three similarity indices of 50% or greater with all other plots under comparison.

3.2. RESULTS AND DISCUSSION

The dry grass communities on Oahu are here divided into two major groups: a leeward group (Table I) and a windward group (Table II). The leeward group occurred on the hillsides and flatlands of the dry lowlands, mostly on the leeward side or in the rain shadow portions of the Waianae and Koolau Ranges. This area is defined as having a mean annual rainfall of less than 1000 millimeters. The dry-grass communities in this rainfall zone occurred along the leeward and the northwest side of the Waianae Range and the southeast side of the Koolau Range (Fig. 1). Altitudinally the dry-area communities occurred from about 2 m above sea level to the position of the 1000 mm isohyet which ranges upwards from sea level to 790 meters.

The dry-grass communities in the subhumid and humid area (windward group) occurred on the slopes of both the Koolau and Waianae Ranges, where the annual rainfall exceeds 1000 millimeters. The dry-grass communities were found on abandoned fields, steep slopes, in openings among woody vegetation or in burned-over forest land.

In all 181 species were recorded. Of these. 35 were grass species (5 native, 30 exotic), 89 other herbaceous species including ferns (34 native, 55 exotic) and 57 woody species (22 native, 35 exotic). Among the native grasses, only *Heteropogon contortus* (Egler, 1947) and *Eragrostis variabilis* (Rotar, 1968) are currently dominant.

The leeward and windward community groups are divided into units, based on the species composition. These are abstract units, which are here referred to as community types.

In the synthesis tables (Tables I and II) a community type is defined by a single species or a combination of species that have a restricted range of distribution over the entire dry-grass plots.

Table I shows the completed synthesis table of the dry area community complex (leeward group). The species distributed throughout the dry-area grass community are listed under the species group 2. Six community types are recognized by hierarchical subdivisions. The species group 3 contains differential species of the *Heteropogon contortus-Rhynchelytrum repens* community type. In many plots *Rhynchelytrum repens* is an important associate, where it occurs with a cover value of 2 (i.e., 5 — 25% cover) or more. The distributional range of the species group 3 extends into the *Eragrostis variabilis* community type, which is separated from the *Heteropogon contortus-Rhynchelytrum repens* community type by the species group 4. The species group 5 separates four other community types from the *Heteropogon contortus-Rhynchelytrum repens* and *Eragrostis variabilis* community types. These are the *Chloris barbata* community type, the *Dichanthium aristatum* community type, the *Trichachne insularis* community type and the *Panicum maximum* community type. These four community types are separated from one another on the basis of a single dominant species only, in each case. These are the species shown by single species blocks on the right side of Table I. The species group 1 are ubiquitous species, present in both the dry and humid climates (see also species group 1 in Table II).

The two community types identified by the species group 3 and 4 occurred on the hillsides, whereas the four community types identified by the species group 5 were found on the flatland or on gentle slopes a the foot of the hills.

Table II shows the completed synthesis table of the windward group community complex. The species group 2 occurs throughout this area. Three community types have been identified, the *Rhynchelytrum repens* com. munity type by the species group 6, the *Andropogon virginicus* community type by the species group 3, and the *Melinis minutiflora* community type by one dominant cover of *Melinis minutiflora* in only one plot (No. 36). This type of community was not sampled by more plots, because the *Melinis minutiflora* cover is only marginal to the definition of the dry-grass community as given earlier. The species group 4 and 5 represent further subdivisions of the *Andropogon virginicus* community type. The species of group 4 were found in the plots located at altitudes above 400 m in the *Metrosideros* zone of Krajina (1963), and those in the species group 5 occurred in very wet almost boggy habitats, also in the rainforest zone. Except for plot no. 66, the plots containing the species of group 5 have poorly drained soils. Therefore, these two subdivisions reflect important habitat differences.

The results of relevé arrangement on the basis of the total floristic similarity are plotted in the form of two-dimensional ordination on Figs. 2 & 4. The grouping of the plots can be considered as indicating community types. It is similar to the grouping in the synthesis tables. Figure 2 shows the plots from the dry area (leeward group). They are segregated into seven groups recognized by seven dominant species, i.e., *Heteropogon contortus, Rhynchelytmm repens, Eragrostis variabilis, Chloris barbata, Dichanthium aristatum.*

The ordination diagram (Fig. 2) correlates with topographic gradient, in that the plots from the flatlands are located to the left of the diagram, those from the hillsides to the right and the ones occurring on gentle slopes in the center. The boundaries between them are indicated by solid lines. The diagram also separates plots dominated by exotic and native species. The separating line is indicated by a dashed line. To the left of the line are plots which are dominated by exotic grasses and to the right are plots dominated by native grasses.

Fig. 4 shows the clustering of the plots from the windward group. Two clusters are evident, one with *Rhynchelytrum repens* dominance and the other with *Andropogon virginicus.* One plot (No. 36) is dominated by *Melinis minutiflora.* These two clusters and one isolated plot constitute the three community types prevalent in the subhumid and humid areas. Three plots (No. 17, 35 and 42 in Table II) under *Rhynchelytrum repens* contain *Andropogon virginicus,* and one (No. 22 in Table II) contains *Heteropogon contortus.* These plots are treated as parts of the *Rhynchelytrum. repens* cluster because they have greater affinity to the plots of this cluster than those of the *Andropogon virginicus* cluster. One plot (No. 14) at the top center, has a high proportion of *Setaria geniculaia* and *Paspaium orbiculare.* This plot is included in the *Andropogon virginicus* cluster because *Setaria geniculaia* and *Paspaium orbiculare* rarely form

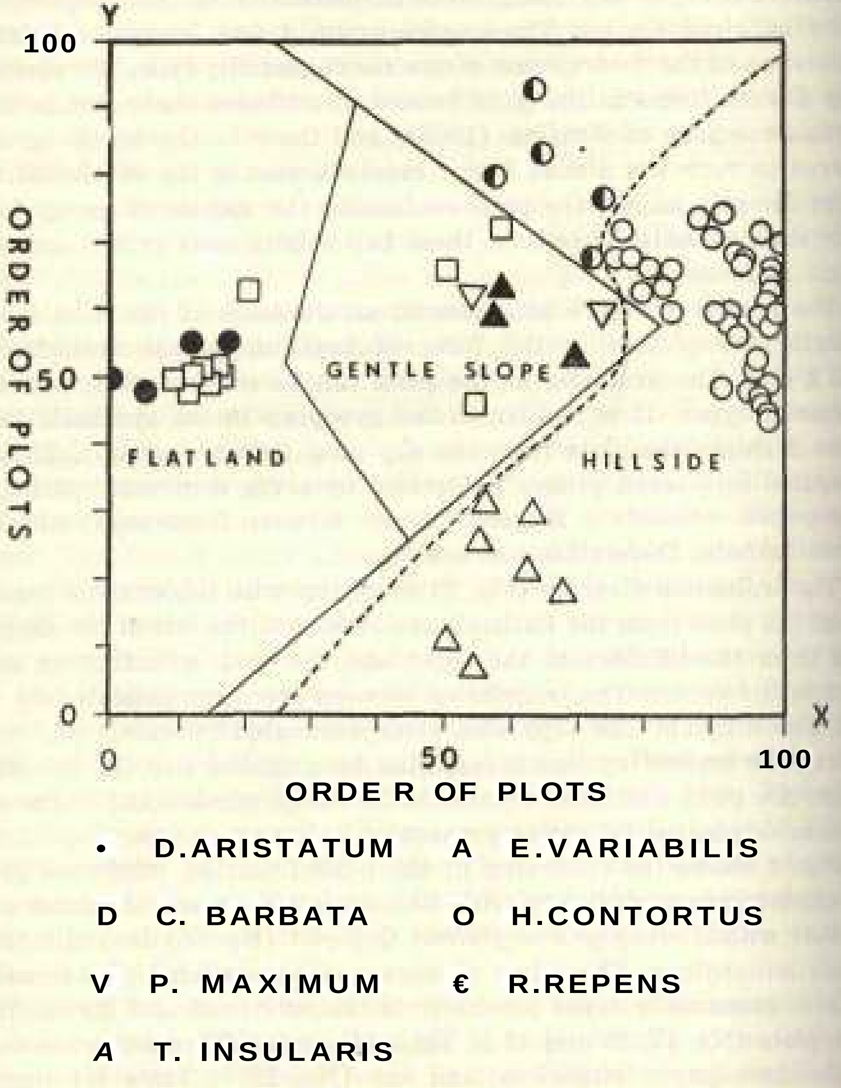

Fig. 2 Distribution of plots of the leeward group in a two-dimensional ordination diagram. The dominant species in each plot is indicated by a symbol. The clustering of plots is related to the topographic positions in the field, whose boundaries are indicated by solid lines. The dashed line separates plots dominated by native (to the right) and exotic (to the left) species. Order of plots refers to the positions of plots along the X- and Y- ordination axes.

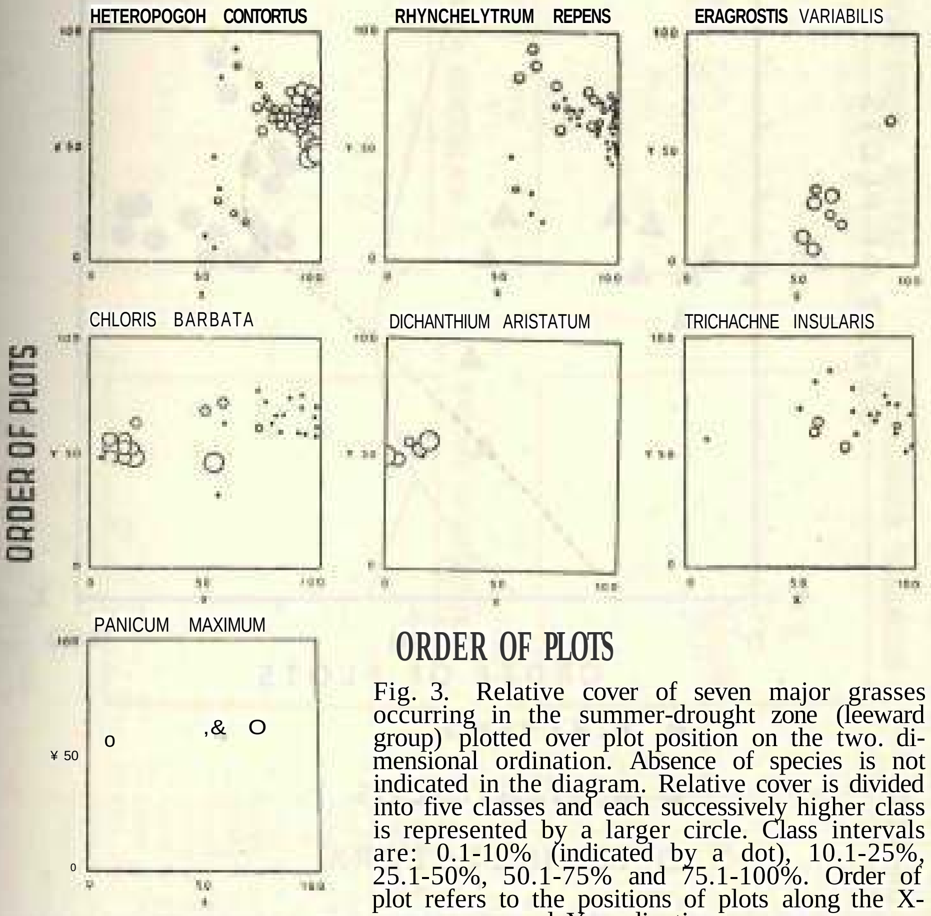

Fig. 3. Relative cover of seven major grasses occurring in the summer-drought zone (leeward group) plotted over plot position on the two-dimensional ordination. Absence of species is not indicated in the diagram. Relative cover is divided into five classes and each successively higher class is represented by a larger circle. Class intervals are: 0.1-10% (indicated by a dot), 10.1-25%, 25.1-50%, 50.1-75% and 75.1-100%. Order of plot refers to the positions of plots along the X- and Y- ordination axes.

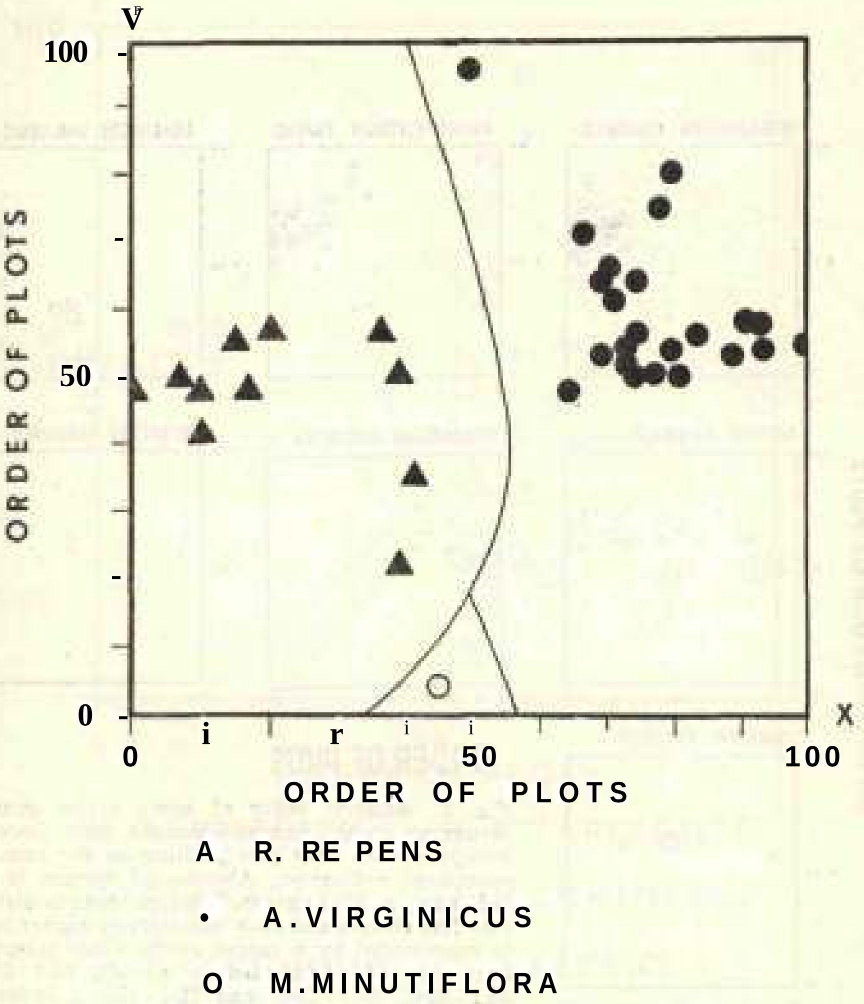

Fig. 4 Distribution of plots of the windward group in a two-dimensional ordination diagram. The clusters of the plots are separated by solid lines. The dominant species in each plot is indicated by a symbol. The order of the plots along the X axis is related to the rainfall and soil pH gradients. The amount of rainfall increases from left to right, and the soil pH decreases (see also Figs. 9 & 10).

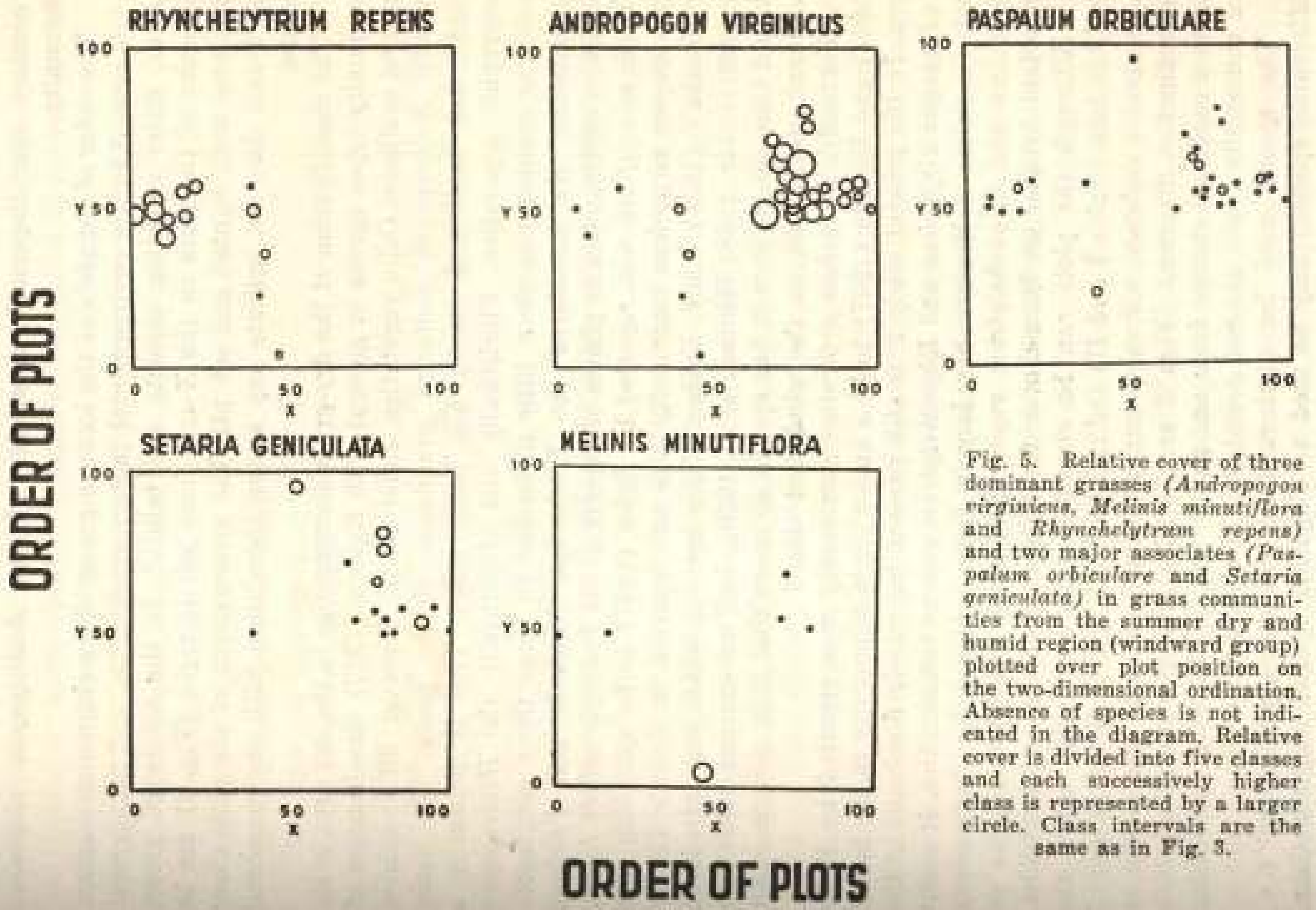

Fig. 5. Relative cover of three dominant grasses (*Andropogon virginicus*, *Melinis minutiflora* and *Rhynchelytrum repens*) and two major associates (*Paspalum orbiculare* and *Setaria geniculata*) in grass communities from the summer dry and humid region (windward group) plotted over plot position on the two-dimensional ordination. Absence of species is not indicated in the diagram. Relative cover is divided into five classes and each successively higher class is represented by a larger circle. Class intervals are the same as in Fig. 3.

a recurring community. Fig. 5 shows that *Setaria geniculata* and *Paspalum orbiculare* are important associates of the *Andropogon virginicus* community.

The order of the plots of the leeward group in the ordination diagram is not related to the environmental factors studied, i.e., soil pH, organic matter, water retention capacity and rainfall. In the windward group, the order of the plots on the X-axis from left to right (Fig. 4) can be correlated with rainfall and soil pH. The arrangement of the plots along the Y-axis does not indicate any known correlation with environmental factors.

The classification of the dry-grass communities in the dry area in six community types agrees in general with Egler's (1947) classification of the arid southeast Oahu vegetation. Egler (1947), however, differentiated between *Heteropogon contortus* grasslands of the makai koa haole, middle koa haole and mauka koa haole zones. This is primarily a geographic separation. Floristically and structurally the *Heteropogon contortus* communities show little difference in these three geographic subdivisions. He considered the *Trichachne insularis* and *Panicum maximum* communities as phases or aspects of the *Prosopis pallida* forest. *Melinis minutiflora* was reported by Egler (1947) to be spreading. The *Andropogon virginicus* community was not reported in Egler's (1947) or Hosaka's (1937) study. Evidently this species, which was introduced in 1932 (Rotar, 1968; Whitney *et al,* 1939), had not escaped cultivation at that time. Since then it has spread so much that it is now the most dominant grass cover on the windward side.

Formerly, *Paspalum orbiculare* community was reported by Egler (1947) and Hosaka (1937) to be a major grass community in the humid area. In the present study it is still present but rarely dominant in the *Andropogon virginicus* and *Rhynchelytrum repens* communities. It seems that *Paspalum orbiculare* has largely been replaced by *Andropogon virginicus* and *Rhynchelytrum repens. Paspalum orbiculare* is also an important invader on burned-over forest land, roadcuts and landslides.

Although the plots can be classified into community types, the floristic'data (Table I and II) indicate that the distributional ranges of most species embrace several community types. This is also shown in the ordination diagrams (Figs. 3 and 5). The total floristic composition shows a continual change from one plot to another, therefore, indicating the community types are not completely discontinuous.

The species used for distinguishing the community types (i.e., differential species) may be used as diagnostic species only for Oahu.

The classification may not be applicable to the other Hawaiian islands.

The following description relates to the general characteristics of the various dry-grass community types as segregated in the tw[7]o synthesis tables. The sequence of the description is as follows:

I. Leeward community types (Table I).
  1. *Heteropogon contortus-Rhynchelytrum repens.*
  2. *Eragrostis variabilis.*
  3. *Chloris barbata.*
  4. *Dichanthium aristatum.*
  5. *Panicum maximum.*
  6. *Trichachne insularis.*

II. Windward community types (Table II).
  7. *Andropogon virginicus* with its two variations in wetter and higher areas, *Andropogon virginicus-Metrosideros rugosa* and *Andropogon virginicus-Dissotis plumosa.*
  8. *Rhynchelytrum repens.*
  9. *Melinis minutiflora.*

3.2.1. *Heteropogon contortus-Rhynchelytrum repens* community type (Table I, 42 plots)

The *Heteropogon contortus-Rhynchelytrum repens* community type occurs on lands between outcropping bluffs on the slopes of the Koolau and Waianae ranges. The substrate may be basalt lava flows (Stearns, 1940) on Waianae, Koolau and Lanikai or cinder cone material (Stearns, 1966) on Koko Crater, Koko Head and Diamond Head. In most areas, the community type is represented only by patches of a few hundred square meters. On slopes with finely weathered substrates and fewer rock outcrops the community may cover a few thousand square meters. The communities form mosaics among the *Leucaena leucocephala* and *Acacia farnesiana* communities, or bands between lava outcrops.

Although in most plots *Heteropogon contortus* is dominant in cover, in some plots it becomes subdominant where *Rhynchelytrum repens* is dominant. Out of 42 *Heteropogon contortus* plots (Table I), 18 have values for *Rhynchelytrum repens,* of 2 or more (i.e., at least 5 — 25% cover). These plots occur in the higher rainfall areas such as Lanikai, the east facing slopes of the hill at Makapuu and Koko Head. Thus they form a variation of the *Heteropogon contortus-Rhynchelytrum repens* community type in more moist habitats.

The *Heteropogon contortus-Rhynchelytrum repens* community type shows a stratification in plant height. The first stratum with a height of over 50 cm, consists of scattered woody plants such as *Leucaena leucocephala* and *Acacia farnesiana.* In the second stratum which ranges between 15 and 50 cm, in addition to *Heteropogon coniortus* and *Rhynchelytrum repens, Sida fallax, Waltheria indica, Cassia leschenaultiana* and *Bidens pilosa* are the most common species. Plants less than 15 cm tall that constitute the third stratum are *Emilia sonchifolia, Euphorbia hirta, Ageratum conyzoides, Desmodium triflorum,* etc. In many plots during the wet season, *Emilia sonchifolia* may become dominant in the third stratum.

Fifty nine percent of the species in this community type are perennials and the rest are annuals. Although the community type as a whole is dominated by perennials, annuals may become dominant in the third stratum during the rainy season.

Soils under this community type are shallow (5 — 60 cm deep) and rocky. Dark Magnesium Clays are prevalent in the communities at Kaena Point, Kahe Point and Makapuu, Red Desert Soils at Koko Head and on the outer slopes of Koko Crater and Diamond Head, and Low Humic Latosols the rest of the dry area. In many plots, soils have a thick layer (about 10 cm) of grass litter. In some plots a powdery ash-like dry humus layer is present, especially where *Leucaena leucocephala* is high in cover value. The average depth of the main rhizosphere is 14 cm, ranging from 10 to 40 centimeters.

3.2.2. *Eragrostis variabilis* community type (Table I, 8 plots)

The *Eragrostis variabilis* community type occurs in the same climatic and geographic area as the *Heteropogon contortus-Rhynchelytrum repens.* community type. The individual communities of these community types often occur adjacent to or may intergrade with one another, but the *Eragrostis variabilis* communities are on the steeper slopes. On southeast Oahu the *Eragrostis variabilis* communities are always found on the east to northeast facing slopes that are exposed to strong winds. In addition to *Eragrostis variabilis, Fimbrystylis pycnocephala* and *Lipochaeta integrifolia* are particularly characteristic for this community.

In most cases this community type consists of three strata. *Eragrostis variabilis, Lantana camara, Cassia leshenaultiana, Waltheria indica* and *Leucaena leucocephala* are the species of the first stratum. The average height of the stratum is 40 cm. The second stratum ranges in height from 10 to 30 cm, consisting of *Sida fallax, Emilia sonchifolia, Bidens pilosa, Rhynchelytrum repens* and *Heteropogon contortus.* In the third stratum which is less than 10 cm height, the most common species are

Euphorbia hirta, creeping *Lipochaeta integrifolia, Desmodmm triflorum, Fimbrystylis pycnocephala* and *Ageratum conyzoides.* These species are growing between *Eragrostis variabilis* bunches on very shallow soils that are a few cm deep or directly on exposed soft weathering rocks. *Sida fallax,* found in all eight *Eragrostis variabilis* plots, assumes a creeping habit on rocky habitats.

Certain other woody species are found occasionally in this community type. These include low-branched shrubs, such as *Indigofera suffruticosa, Stachytarpheta jamaicensis, Phaseolus lathyroides, Pluchea odorata, Tephrosia purpurea,* a vine *Passiflora foetida* and a stunted native tree *Santalum ellipticum* which is found, however, only in one plot (No. 95) at Diamond Head. In addition, other grasses and forbs are found occasionally such as *Trichachne insularis, Panicum torndum, Doryopteris decipiens* and *Oxalis corniculata.*

Soils under this community type are usually shallow (10 — 30 cm deep), rocky and mainly confined to pockets between rocks. On steep cliffs, *Eragrostis variabilis* grows on terraces that are filled with finely weathered rocks. Soil material is similar to that of the Dark Magnesium Clay at Makapuu and the Red Desert Soil on the slopes of the Koko Crater. The soil is often covered with thick undecomposed grass litter (average thickness of 17 cm), and a very dark-grey brown humus layer (about 5 cm) may be present. The average depth of the main rhizosphere is 15 cm, ranging from 10 to 25 m.

3.2.3. *Chloris barbata* community type (Table I, 11 plots)

The *Chloris barbata* community type is usually found on the flatlands in small areas in disturbed habitats. The largest community is found on Makapuu Flat, between Wawamalu Beach Park and Makapuu Point, where it covers an area of about 18 hectares, gradually merging with the *Dichanthium aristatum* community type.

In the western part of the island, between Camp Kaena and Kaena Point, the *Chloris barbata* community type occurs on soil pockets between boulders with *Myoporum sandwicensis,* a native shrubby tree, covering about 15% of the total vegetation cover.

Only 28 percent of the species present in this community type are woody. *Lipochaeta lobata* and *Gossypium tomentosum* are the most important native shrubs, scattered throughout most plots, while *Myoporum sandwicensis* is found only at Kaena. All three species have a higher degree of frequency and cover than most woody species in this community type. *Phaseolus lathyroides,* a semi-woody species, tends to become dominant in some areas. Outside the grass community this species may form pure stands. It may also occur sparingly in the *Heteropogon contortus-Rhynchelytrum repens* community type. *Sida fallax, Leucaena leucocephala, Acacia farnesiana, Prosopis pallida* are additional woody species found in the *Chloris barbata* community type. *Desmanthus virgatus* is very common and often forms pure stands or mixed stands with *Leucaena leucocephala* outside the grass community. *Desmanthus virgatus* may occur also in the *Heteropogon contortus-Rhynchelytrum, repens* community type, but only sparingly. There are no obvious habitat differences between communities dominated by *Chloris barbata, Desmanthus virgatus* and *Phaseolus lathyroides.* The formation of the pure communities is apparently attributable to the seed availability in order to regenerate after a disturbance. It was observed in the field that *Chloris barbata* seed did not germinate in the shade and thick litter of the parent plants. Seedlings of *Phaseolus lathyroides* and *Desmanthus virgatus,* however, were common underneath parent plants. After fire the seeds of *Chloris barbata, Desmanthus virgatus* and *Phaseolus lathyroides* germinated readily wherever adequate soil moisture was available. Fire evidently helped in removing dead grass litter and in clearing the sites for *Chloris barbata* seeds to germinate.

Most of the associated species in this community type are scattered. *Ageratum conyzoides* and *Phyllanthus niruri* tend to aggregate in the openings between grass clumps. The other herbaceous species, which occur only during the wet season, are only minor components of the communities.

The *Chloris barbata* community type, occurring on level ground or occasionally on gentle slopes, is found on sandy loam to silty loam soils of the Red Desert Soils at Koko Head, on dark brown sandy loam soils at Diamond Head crater, and on alluvial clay soils and shallow stony clay soils at Kaena. The largest community occurs on Lualualei clay soil at Makapuu Flat. However, it is restricted to the stony phase and shallow portion of the flatland (average depth is 40 cm). The extensive occurrence of the *Chloris barbata* community here does not indicate any preference of this community to this particular soil, it may occur on any soil on level ground. Its occurrence is related to disturbance rather than soil type. The average depth of the main rhizosphere is 14 cm, ranging from 10 to 25 centimeter.

3.2.4. *Dichanthium aristatum* community type (Table I, 4 plots)

The largest community is found on the flatland at Makapuu. It occurrs in the same area adjacent to the *Chloris barbata* community. At the foot of the hill it merges with the *Panicum maximum* community. *Dichanthium aristatum* patches may also be found on wet ditches along the road side in the dry zone, but otherwise *Dichanthium* is only locally important here.

Dichanthium aristatum is a bunch grass whose thick dead shoots remain on the plants. Thick litter covers the ground between bunches. Very few species are associated with this community. *Lipochaeta lobata* and *Desmanthus virgatus* are the most common associates. *Gossypium tomentosum, Phaseolus lathyroides, Ipomoea cairica* and *Sonchus oleraceus* may also be present.

The *Dichanthium aristatum* community occupies the non-stony phase of the Lualualei clay soil, adjacent to the stony phase covered by *Chloris barbata* community. The depth of the soil extends to over 100 centimeters. The internal drainage of this soil is poor compared to the stony phase. This appears to cause the longer seasonal flooding after heavy rain, which seems to limit the extent of the *Chloris barbata* community on this area. *Dichanthium aristatum* may be better adapted to this condition than *Chloris barbata.* The average depth of the main rhizosphere is 24 cm, ranging from 15 to 35 centimeters.

3.2.5. *Panicum maximum* community type (Table I, plots no. 63 and 85)

This community type was sampled only on the gentle slope at Makapuu where it was well developed. However, it occurred throughout the island in occasional patches here and there. *Panicum maximum* was introduced to the island in 1880 (Rotar, 1968; Whitney *et al,* 1939) as one of the important forage grasses. This grass escaped from cultivation and established itself in several places. Apparently jt has spread to this area only in recent years, since Egler (1947) did not report its presence in the Makapuu area. *Panicum maximum* locally forms large bunches with very stout root stocks resulting in locally dense cover. It is usually associated with *Leucaena leucocephala.* Very few species, except *Sida fallax,* occur in the shade of this species. The community merges with *Chloris barbata* and *Dichanthium aristatum* communities on the flatland.

The *Panicum maximum* community type occupies similar soil material as found under the *Chloris barbata* and *Dichanthium aristatum* communities. At Makapuu the stony soils supporting the *Panicum maximum* community are found in narrow and deep crevices between boulders not affected by the seasonal flooding. The depth *of the main* rhfzosphere in *the* two plots is 20 centimeters.

3.2.6. *Trichachne insularis* community type (Table I, plots no. 31, 57 and 59)

Although *Trichachne insularis* is dominant only in three plots, it occurs also in many *Heteropogon contortus* communities, but with low cover. Whether *Trichachne insularis* occurs in single isolated bunches or as a closed and wide-spread cover, it is always associated with *Acacia farnesiana. Trichachne insularis* communities occur on gentle but rocky slopes where soils are found in the pockets between boulders. Therefore, the habitat is very similar to that occupied by *Panicum maximum* except for the difference in associated woody plants. *Trichachne insularis* was accidentally introduced in 1906 (Whitney *et al.,* 1939). It is unpalatable to cattle and considered a pest. Egler (1947) reported that *Trichachne insularis* was spreading very rapidly on grazed land because grazing animals were eliminating its competitors.

Soils are always confined to narrow and deep crevices (over 30 cm deep) between large boulders. The very dark grey to black soil material is similar to that of Dark Magnesium Clays, but the texture ranges from sandy loam to silty clay loam. It differs from the soil under *Panicum maximum* community by being darker in colour and more gravelly. The average depth of the main rhizosphere is 12 cm, ranging from 10 to 15 centimeters.

3.2.7. *Andropogon virginicus* community type (Table II, 23 plots)

The *Andropogon virginicus,* community type occurs both on slopes and on undulating terrain, particularly on the moist windward side. The community type extends from the guava into the ohia zones. Grass clumps even extend into the cloud zone on Mt. Kaala, about 1200 m above sea level. *Andropogon virginicus* communities occur on abandoned fields and in forest openings. *Andropogon virginicus* also forms patch-communities in *Psidium guajava* scrub, *Metrosideros-Acacia* and *Metrosideros* forests. In some places, *Andropogon virginicus* forms the grass matrix of a savanna formation with *Eugenia cumini* trees, for example at Kahaluu and Waikane. It forms extensive pure grass covers at Kahuku.

The species composition varies from one plot to another more than in the other large community, the *Heteropogon-Rhynchelytrum* type. Native species constitute only 36% None of them forms any significant cover. *Andropogon virginicus* was introduced in 1932 (Rotar, 1968; Whitney *et al.,* 1939), but now it dominates grass communities in the humid climate. It is a hardy perennial bunchgrass with thick leaves, the majority of which stand up as dry yellow shoots, giving this grass a dry-grass habit throughout the year. Spaces between bunches are usually covered with thick shoot litter. However, other species such as *Stachytarpheta jamaicensis* and *Cassia leschenaultiana* grow between the bunches and are able to reproduce by seedlings even under thick covers of *Andropogon virginicus* litter. *Andropogon virginicus* itself is unable to reproduce by seedlings under this situation. Seedlings, however, occur on open places underneath the parent plants where the ground is not completely covered by dead shoots.

Other grass species commonly found in the *Andropogon virginicus* community are *Paspalum orbiculare, Setaria geniculata* and *Chrysopogon aciculatus. Paspalum orbiculare* which was introduced in the pre-European times (Rotar, 1968; Whitney *et al.,* 1939) is a tufted perennial but not as hardy as *Andropogon virginicus.* Compared to *Andropogon virginicus, Paspalum orbiculare* is much less obvious in the community. *Setaria geniculata* is a rhizomatous perennial grass which is also an important associate in the community. In somewhat shaded places (under *Eugenia cumini), Setaria geniculata* may become dominant, for example in plot No. 14 (Table II). In such situations *Andropogon virginicus* grows with reduced vigour.

Andropogon virginicus grows best on deep soils in the windward zone, where the average height of the mature plants reaches 135 centimeters. However, on poorly drained soils in Pupukea (plots no. 23, 24, 71 and 72) it grows with lower vigour. Its average height is only 65 cm on such wet soils. In areas with low rainfall of about 1000 mm (subhumid) and on shallow soils in strongly wind-exposed positions, the maximum height does not exceed 30 cm and the cover is thin.

Floristic variation in some plots (see species group 4 in Table II) is related to altitude and soil condition. These plots no. 38 — 41, 23 — 25, 66, 71 72) occur at altitudes higher than 400 meters. They are located in areas surrounded by forest. Forest species, such as *Metrosideros rugosa, Cibotium chamissoi* and *Psychotria mariniana,* are present in these plots. *Grammitis tenella* and *Elaphoglossum crassifolium* are epiphytic ferns that occur usually in the forest. Although *Metrosideros collina* is present in other plots at lower elevation, it has higher cover-abundance values in these ten plots.

The species group 5 in Table II shows a still more restricted distribution associated with very wet soils. Plots 25 and 66 are on better drained but constantly moist soils. *Dissotis plumosa, Rhynchospora lavarum, Sacciolepis indica, Lycopodiiim cernuum* and *Machaerina angustifolia* are good indicators of such wet soils.

Andropogon virginicus constitutes the first stratum in pure grass communities. In communities containing trees and tall shrubs, *Andropogon virginicus* forms the second but still dominant stratum. The first stratum (150 cm or higher) is usually composed of such woody plants as *Scaevola gaudichaudiana, Wikstroemia oahuensis, Psidium cattleianum, Psidium guajava, Metrosideros collina, Metrosideros rugosa, Acacia koa* and *Eugenia cumini.* A third stratum (30 to 60 cm) consists of *Paspalum orbiculare, Setaria geniculata, Sphenomeris chusana, Nephrolepis hirsutula, Stachytarpheta jamaicensis, Cassia leschenaultiana* and occasionally, *Lantana camara.* The species common in the fourth stratum (less than 30 cm) are *Emilia sonchifolia, Centella asiatica* and *Chrysopogon aciculatus.'In* dry and extreme habitats and in purs grass communities the stratification may be reduced to three.

The *Andropogon virginicus* community type occurs on a variety of soils. They are Lithosols, Low Humic Latosols, Humic Latosols and podzolic soils. The Lithosols include the Nakalele silty clay complex (the rough broken land type) that occurs in the Kahuku area. The Lithosols here consist of deeply weatherd rocks with little soil material. The Low Humic Latosols occur in plots (26, 29) at the Kawailoa Forest Reserve and the northwest side of the Schofield plateau. The Humic Latosols are dominant on the slopes of the ridges at Kailua, Kahaluu and Waikane. The communities on the poorly drained soils occur on the flat portions of the ridge and on the slopes in high rainfall areas (with mean annual rainfall greater than 2500 mm) and at high elevation (greater than 400 m) in the Pupukea area. Soils under the *Andropogon virginicus* community type are usually very deep extending to over one meter. In Palikea, however, they are only 10 — 25 cm deep. The average depth of the main rhizosphere is 15 cm, ranging from 10 to 30 centimeters.

3.2.8. *Rhynchelytrum repens* community type (Table II, 12 plots)

The *Rhynchelytrum repens* community type occurs mainly on the slopes in the subhumid areas. They are found on abandoned fields or recently disturbed areas. However, the species may also be found in small colonies or growing on the roadsides in the subhumid climate.

The community type is composed mainly of exotic species. A native species, that constitutes an important component of this community type in some stands, is a creeping shrub, *Osteomeles anthyilidifolia.* Other natives such as *Bidens gracilloides, Bidens waianensis, Cocculus ferrandianus, Dodonaea viscosa, Eragrostis variabilis, Heteropogon contortus, Metrosideros collina, Plectranthus australis, Pteridium aquilinum* var. *decompositum, Rhynchospora scleroides, Schiedea kialeae, Sphenomeris chusana, Wikstroemia oahuensis* and *Wikstroemia vaccinifolia* may be present.

The community type shows a stratification. The first stratum consists mainly of tree saplings or shrubs with heights ranging from 60 to 200 cm, but they are scattered and do not form a closed canopy. The most common are *Lantana camara, Psidium guajava* and *Schinus terebinthifolius.* In some plots young trees of *Grevillea robusta* are present. Native trees and shrubs, such as *Metrosideros collina* and *Wikstroemia oahuensis,* and a woody herb, *Bidens waianensis,* may be encountered in the stands located in more moist areas. The second stratum is composed mainly of herbaceous species with heights ranging from 30 to 60 centimeters. These are *Rhynchelytrum repens* (the dominant), *Andropogon virginicus, Cassia leschenaultiana, Conyza parva, Osteomeles anthyllidifolia, Paspalum orbiadare, Stachytarpheta jamaicensis, Waltheria indica, Nephrolepis hirsutula, Heteropogon contortus, Pennisetum setosum, Pteridium aquilinum* var. *decompostitum, Spathoglottis plicata* and *Sphenomeris chusana.* In the third stratum are species that are less than 30 cm high including seedlings of plants of the upper strata such as *Cassia leschenaultiana, Conyza parva* and *Stachytarpheta jamaicensis.* The other common species are *Bidens pilosa, Chrysopogon aciadatus, Desmodium triflorum, Emilia sonchifolia* and *Vernonia cinerea. Centella asiatica, Phyllanthus niruri* and *Richardia scabra* are rare.

Rhynchelytrum repens is native to South Africa. It was first found growing in the Hawaiian Islands in 1894 (Rotar, 1968; Whitney *et al,* 1939) and is now growing throughout the islands from sea level to about 800 meters. It is a perennial usually with much branched stems that are often rooted at the basal nodes. Branch-rooting is the means of vegetative reproduction of this species. Reproduction, however, is more effective by seeds. Seedlings are common underneath the parent plants, but they thrive better in open places. Other seedlings that are commonly found are *Emilia sonchifolia, Conyza parva* and *Stachytarpheta jamai-*

censis. Seedlings of *Cassia leschenaidtiana, Bidens pilosa* and *Psidium guajava* may be present occasionally.

Grevillea robusta seedlings are also common near the parent trees in the stands where this species is present.

Rhynchelytrum repens can grow in the subhumid to dry climates. In the dry area *Rhynchelytrum repens* is an important associate of the *Heteropogon contortus-Rhynchelytrum repens* community type, in which it is present in the plots with varying proportions (Table I, Fig. 3), but it grows with reduced vigour, where generally the inflorescence height reaches only 40 centimeters. In the subhumid climate it grows with greater vigour to an average height of about 70 centimeters.

The *Rhynchelytrum repens* community type occurs on Humic Ferruginous Latosols (at Kunia) and the rough broken land types of the Lithosols. The latter include soils resembling the Humic Latosols (on a very steep slope at Waikane) and Dark Magnesium Clays (on a very steep slope above Kahana Bay) and the Nakalele silty clay complex (in the Kahuku area). In general, soils under the *Rhynchelytrum repens* community type are shallower than those under the *Andropogon virginicus* community type. The soil depth ranges from 15 to 100 cm with an average of 39 centimeters. The average depth of the main rhizosphere is 18 cm, ranging from 10 to 25 centimeters.

3.2.9. *Melinis minutiflora* community type (Plot no. 37, Table II)

This community type is represented by only one plot in this study. It is located adjacent to the *Rhynchelytrum repens* community at the edge of Schofield plateau. This community type is found mainly on slopes and develoos best in the dry to subhumid climates. One can find patches of this community at the edge of certain *Metrosideros-Acacia* forests in the humid climate or along road cuts.

Melinis minutiflora is an exotic species which was introduced in 1913 (Rotar, 1968; Whitney *et al.*, 1939). It is aggressive and can overgrow other communities or invades bare ground in the subhumid zone. It grows in thick mats and reproduces by rooting from the basal nodes of the branches. This growth habit contributes greatly to the aggressiveness of the species. The plants form a tight and thick cover that makes it impossible for other species to grow underneath. Certain herbaceous species such as *Pteridium aquilinum* var. *decomposition, Emilia sonchifolia* and *Conyza parva* may be present in the openings. Trees and shrubs, which are found in the community, apparently grew already on the site before *Melinis minutiflora* became established. Occasionally, *Andropogon virginicus* is present in the middle of the community, perhaps as a remnant of a previous *Rhynchelytrum repens-Andropogon virginicus* community. Since few species are associated with *Melinis minutiflora,* the community tends to be unistratal or bistratal if shrubs and trees are present.

The *Melinis minutiflora* relevé sampled (plot no. 37) occurs on Humic Ferruginous Latosol, although elsewhere it may be found on Humic Latosol and Low Humic Latosol soils. The depth of the main rhizosphere is 20 centimeters.

4. ENVIRONMENTAL RELATIONSHIPS

The nine community types described in the preceding section occur in different geographic areas, altitudes, habitats, topographic positions and climatic regimes. Certain but not all community patterns are related directly to the environmental factors. The major controlling factor complexes are climate and soil. Other factors, e.g., exotic species invasion, human activities and fire, play an important role in the development and maintenance of certain grass communities also. The latter factors will be discussed in the section dealing with dynamic, relationships. The following section deals with the climatic and edaphic factors that were found to show close relationships to the vegetation patterns as isolated in the synthesis tables and ordination diagrams.

4.1. CLIMATE

4.1.1. Methods

The climatic data of Oahu were analyzed using Gaussen's (1954) method (Walter, 1960; Walter & Lieth, 1960) that has been applied for evaluating the climate-vegetation relationships (Walter, 1964; Doty & Mueller-Dombois, 1966; Mueller-Dombois, 1969). The method involves construction of a climate diagram (Fig. 6). The abscissa of the diagram represents the months of the year from January to January with July in the center. The left hand ordinate refers to the temperature which is divided into units of 10° centigrade. The right hand ordinate refers to rainfall in unit intervals of 20 mm up to 100 millimeters. Above 100 mm, the intervals are reduced to 10 percent, thus each interval equals 200 millimeters. The curves represent mean monthly values.

Data for sixteen stations were selected from Blumenstock & Price (1967) and from a U. S. Weather Bureau report (1965) for constructing the climate diagrams. Eight stations had records of mean monthly temperature. For the other eight, the mean monthly temperature was calculated by extrapolation, using the lapse rate and altitudinal differences. The average lapse rate for the windward side is 0.8° C/100 m and for the *leeward side it is 0.7° C/100 meters. The calculation of the lapse rate was* based on the temperature data from 16 stations. Fourteen stations had rainfall records of 30 years or more and two, at Palehua and Mt. Kaala, had records of 10 and 15 years, respectively. The mean monthly rainfall for each station was plotted with reference to the right hand ordinate and the mean monthly temperature with reference to the left hand ordinate.

The annual median rainfall data from the rainfall stations nearest the plots were obtained also from Taliaferro (1959). To investigate the relationships between the rainfall and vegetation patterns, test of correlation between the rainfall values for the plots and the coordinates of the plots on the X- and Y- ordination axes were made.

4.1.2. Results and discussion

The important feature of the climate diagram is the 1: 2 relationship between temperature and rainfall. Gaussen (1954) suggested that the potential evapotranspiration in mm was equal to about twice the monthly temperature in degrees centigrade. Walter (1964) suggested that the temperature curve could be used as a measure of the yearly variation in evapotranspiration. A significant drought period may occur whenever the rainfall curve undercuts the temperature curve. A drought period is shown in Fig. 6 by the dotted field. The temperature-rainfall relationship agrees also with most rainfall efficiency formulae (Mueller-Dombois, 1969). A dry period is indicated by a mean monthly rainfall of less than 100 mm, when the rainfall curve remains above the temperature curve. A humid period is indicated by the dark field in the diagram which shows that the rainfall reached or exceeded 100 millimeters. For instance the climate diagram at the Waimanalo weather station (Fig. 6) has a winter humid period, fall and spring dry periods and a summer-drought period. It is also generally assumed (Major, 1963; 1967; Mueller-Dombois, 1969; Thornthwaite, 1948) that 100 mm rainfall is equal to the average storage capacity of the soil. Rainfall in excess of 100 mm, therefore, is expected to cause and disappear as run-off.

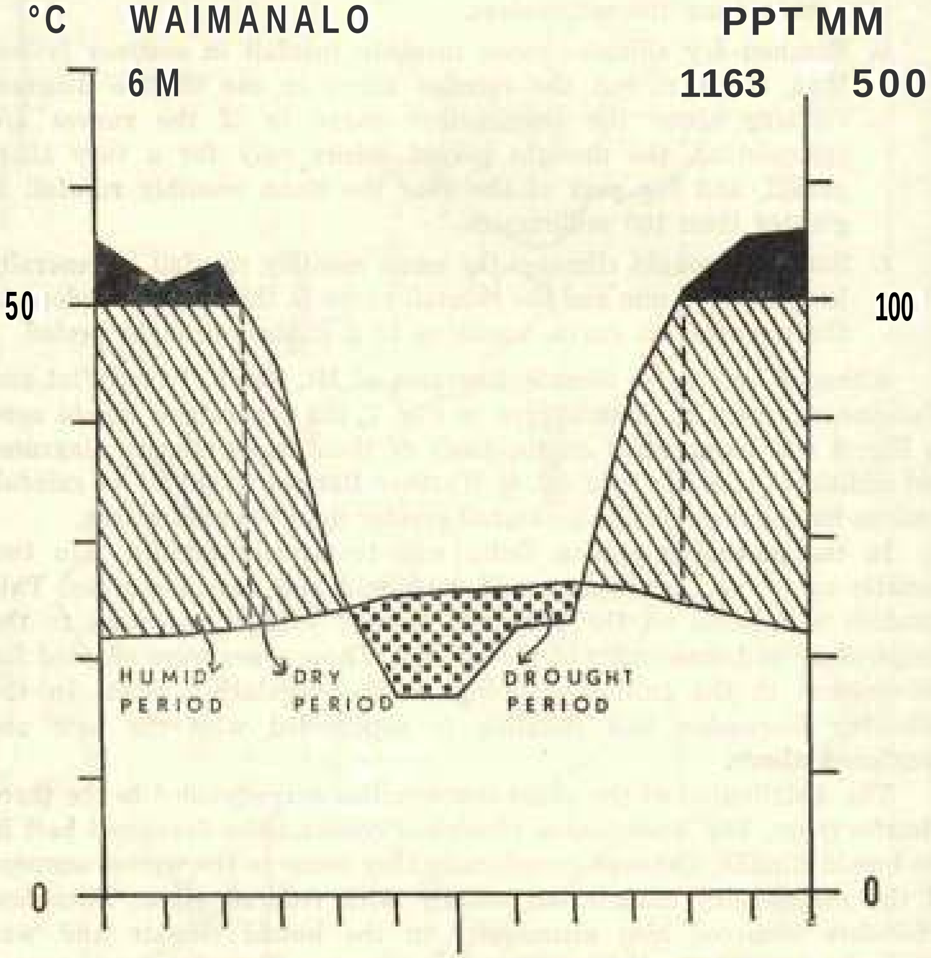

Fig. 6 The climate diagram of Waimanalo weather station, 6 m above sea level. The station has a mean annual rainfall of 1163 millimeters. The solid black field is the period of mean monthly rainfall greater than 100 mm, indicating a humid period. The stipled field indicates a drought period, that is when the rainfall curve undercuts the temperature curve. Dry periods occur when the mean monthly rainfall is less than 100 mm, but the rainfall curve lies above the temperature curve (part of the hatched field).

Three climatic zones can be recognized on Oahu from Fig. 7, derived on Fig. 8:

a. Humid climate: mean monthly rainfall throughout the year is greater than 100 millimeters.

b. Summer-dry climate: mean monthly rainfall in summer is less than 100 mm, but the rainfall curve in the climate diagram remains above the temperature curve or if the curves are intersecting, the drought period occurs, only for a very short period, and for part of the year the mean monthly rainfall is greater than 100 millimeters.

c. Summer-drought climate: the mean monthly rainfall is generally less than 100 mm and the rainfall curve in the summer undercuts the temperature curve, resulting in a distinct drought period.

Although only three climate diagrams of Mt. Kaala, Pauoa Flat and Waikane represent the humid type in Fig. 7, the generalized humid zone in Fig. 8 was constructed on the basis of these three climate diagrams and additional climatic data (U. S. Weather Bureau, 1965) of 14 rainfall stations having mean monthly rainfall greater than 100 millimeters.

In the preceding section Oahu was tentatively divided into two climatic zones, i.e., dry region and subhumid and humid regions. This zonation was based on the 1000 mm isohyet without reference to the temperature and seasonally of the rainfall. These zones were adopted for convenience in the initial grouping of the vegetation plots. In the following discussion this zonation is superseded with the new one mentioned above.

The distribution of the grass communities corresponded to the three climatic types. The *Andropogon virginicus* communities developed best in the humid climate, although occasionally they occur in the wetter segment of the summer-dry climate but usually with reduced vigor. *Paspalum orbiculare* occurred also abundantly in the humid climate and was sparingly present in the summer-dry climate. *Rhynchelytrum re-pens* communities and *Melinis minutiflora* patches were common in the summer-dry climate, although the *Melinis minutiflora* patches might be found in the drier part of the humid climate also. The area with summer drought climate on Oahu covered mostly the hillsides of the leeward Waianae and Koolau ranges, in which *Heteropogon contortus* formed the dominant grass cover. The *Eragrostis variabilis, Chloris barbata, Dichanthium aristatum, Trichachne insularis* and *Panicum maximum* communities were also found in the summer-drought climate. The *Heteropogon contortus*

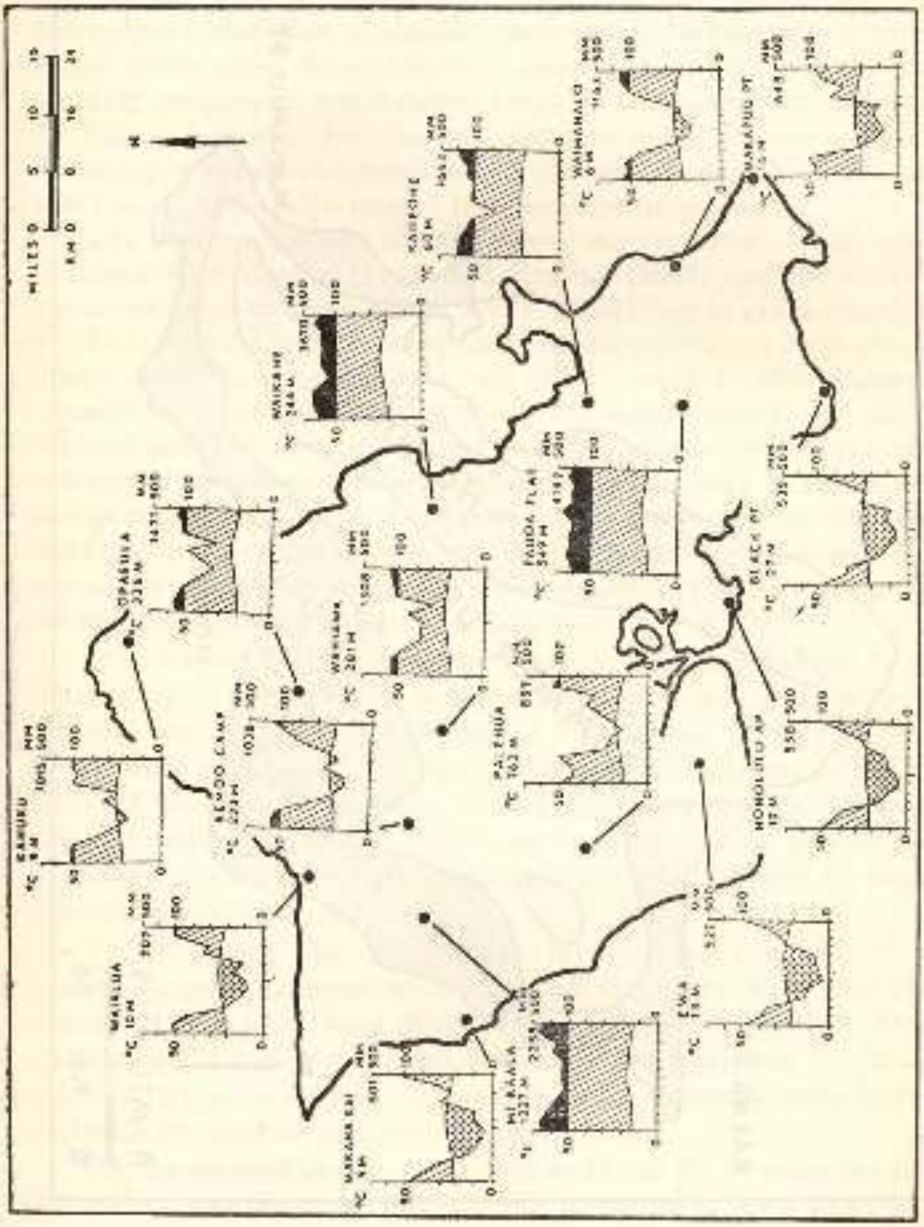

Fig. 7. Climate diagrams of 16 weather stations illustrating the climatic types of Oahu.

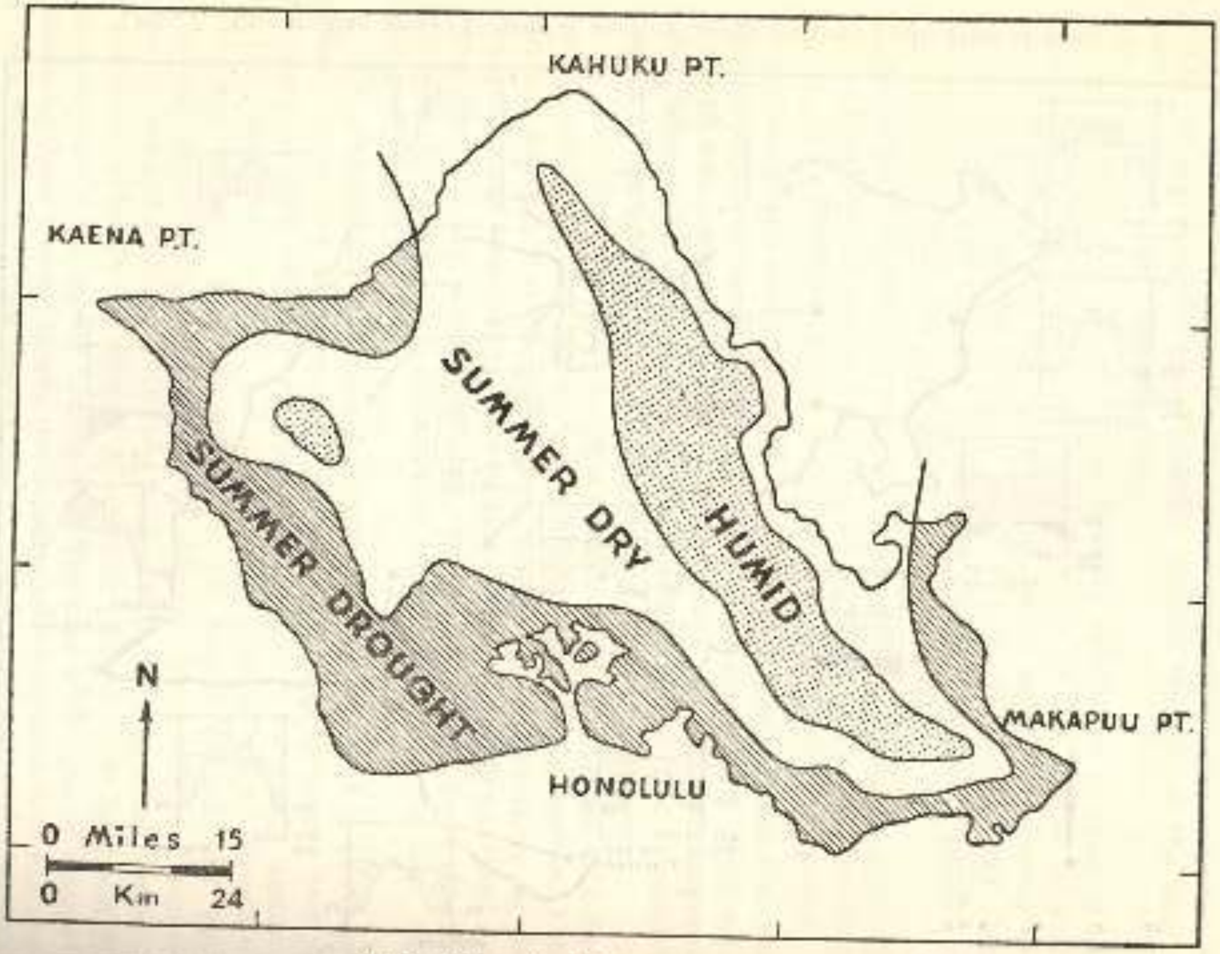

Fig. 8. Generalized climatic zones of Oahu.

community might be found occasionally in the summer-dry climate (i.e., plot no. 22, Fig. 1, at Kahuku). This was the wettest end of the *Heteropogon contortus* community distribution. Before the introduction of the exotic grass *Rhynchelytrum repens, Heteropogon contortus* was probably common in non-forested areas in the summer-dry climate. On the island of Hawaii, *Heteropogon contortus* and *Andropogon virginicus* communities had similar distributional patterns (Doty & Mueller-Dombois, 1966) as on Oahu with respect to these climatic zones.

The summer-drought climate covers the vegetation zones A and B of Ripperton & Hosaka (1942) and Krajina (1963) and the xerotropical vegetation zones of Egler (1939, 1947). In addition to grass communities, *Acacia farnesiana* and *Leucaena leucocephala* scrubs and *Prosopis pallida* forests were the most common vegetation covers in this climate. The summer-dry climate coincides with the vegetation zone C and the lower phase of zone D. Here *Psidium guajava* and *Schinus terebinthifolms* were widespread. *Leucaena leucocephala* may also be found in the drier part of this climate and *Acacia koa* forest in the wetter portion. The medium and high phases of the vegetation zone D coincide with the humid climate, where the vegetation consisted predominantly of *Metrosideros collina* forests and *Dicranopteris linearis* fern cover.

It is evident that on Oahu the grass communities occured in all the climatic types, from summer drought to humid. It was observed that this was also true for the island of Hawaii. This agrees with Egler's (1947) observation. Although the climate is the controlling factor in the distribution of the grass communities, other factors such as human disturbance, fire and ability of species to fill up available niches are important. Disturbance is particularly important in the establishment of the grass communities in the humid areas.

To investigate the relationships between the rainfall and grass community pattern, annual median rainfall data from the nearest rainfall stations to the plots were obtained from Taliaferro (1959). Tests of correlation between the rainfall values for the plots and the X and Y values of the plots relating to the ordination diagrams were performed following the method of Bray & Curtis (1957).

For the leeward group, no correlation (Table V) between the rainfall and the order of the plots on the X- and Y- ordination axes was observed. This was expected since the grass communities on the leeward side frequently occured side by side without any indication that their differences were related to a rainfall gradient.

For the windward group, there was a significant correlation (Table V) only between the amount of rainfall and the order of the plots on the X-axis. It has been shown in the ordination diagram (Fig. 4) that three community types can be recognized, the *Rhynchelytrum repens, Melinis minutiflora* and *Andropogon virginicus* community types. The relationship between the change of the grass dominance and the rainfall gradient along the X- axis is shown in Fig. 9. In this diagram the X-axis was divided into ten segments: 0.0 — 9.9; 10.0 — 19.9; 20.0 — 29.9; 30.0 — 39.9; 40.0 — 49.9; 50.0 — 59.9; 60.0 — 69.9; 70.0 — 79.9; 80.0 — 89.9 and 90.0 — 100.0. The intervals 20.0 — 39.9 and 50.0 — 69.9 were considered as individual units because there was only one plot in the intervals 20.0 — 29.9 and 50.0 — 59.9, respectively. Therefore, the number of segments on the X-axis reduced to eight. The relative cover of the species, the rainfall values nearest the plots and the order of the plots on the X-axis were averaged separately for each segment. The average rainfall values and the average relative cover of species in the segments were plotted against the average order of the plots in each segment along the X-axis (Fig. 9). In relation to the rainfall, it is clear that *Rhynchelytrum repens* thrived best in areas with an annual median rainfall between 1000 and 1500 mm, and *Andropogon virginicus* in areas with a rainfall greater than 1500 millimeters. The two species, however, overlapped in their distribution in the area where the rainfall is between 1100 and 2000 millimeters. *Andropogon virginicus* decreased in cover values in areas with very high rainfall exceeding 2500 millimeters. In these high rainfall areas soils tended to be boggy, where slopes were not too steep. The *Andropogon virginicus* communities on these boggy soils were characterized by the additional appearance of *Dissotis plumosa* and *Rhynchospora lavarum* (Table II, plots no. 23, 24, 71 and 72) mixed with the stunted *Andropogon virginicus.*

4.2. SOILS

4.2.1. **Methods**

In each vegetation plot a soil pit was dug in a portion of the plot that was well covered by grass. In the rocky land surface, where vegetation cover was not uniformly dense, this portion usually had the deepest soil. In the case of the uniformly vegetated plots, a pit was dug in the center of the plot. A soil profile description was made for each pit following the format of the Soil Survey Manual (Soil Survey Staff, 1951). Notes on variation of the soil depth, stoniness, rooting depth and microtopography within and outside the plots were also made. This was

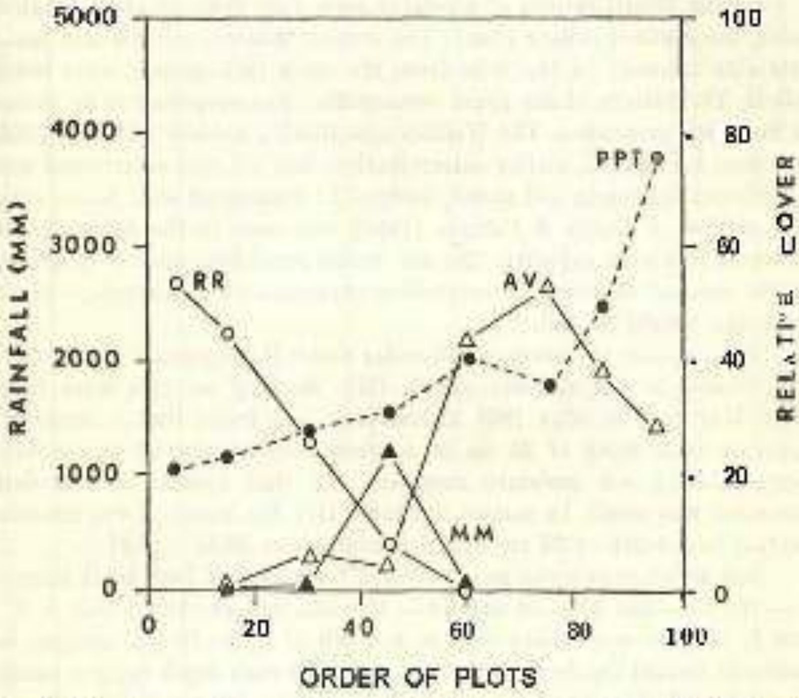

Fig. 9. The change of grass dominance from *Rhynchelytrum repens* (RR) to *Andropogon virginicus* (AV) with increase of median annual rainfall (PPT) along the order of plots on X-ordination axis. The X-axis is divided into ten segments: 0-9.9; 10-19.9.........and 90-100. The intervals 20-39.9 and 50-69.9, each one is considered one unit because there is only one plot in the intervals 20 - 29.9 and 50 - 59.9, respectively. The number of segments reduces to eight. The relative cover of species, the rainfall values in the plots and the order of the plots on the X-axis within each segment are averaged. MM refers to *Melinis minutiflora*.

particularly important in the plots located on rocky surfaces, as soils were usually restricted to pockets or depressions between rocks or boulders Soil samples were collected from each horizon and from the main rhizosphere. The main rhizosphere was defined as the upper portion of the soil profile that contained the greatest proportion of the grass root system

Colour identifications of air-dried soils were made in the laboratory using the Munsell collour chart. The organic matter, soil pH and water retaining capacity of the soils from the main rhizospheres were determined. The pattern of the grass communities was suspected to be related to these soil properties. The Walkley and Black's method (Allison, 1965) was used for organic matter determination. Soil pH was determined with a Beckman Zeromatic pH meter, using a 1: 1 air-dried soil: water ratio. The method of Curtis & Cottam (1962) was used in the determination of water retaining capacity. The soil water retaining capacity is defined as the amount of water at saturation expressed as a percentage of the oven dry weight of soil.

The seasonal variation of soil-water under the dry-grass communities was studied at ten stations (Table III). Monthly samples were taken from May 1967 to May 1968 inclusive. It was found that a single soil moisture to a depth of 25 cm of a given month could be considered a representative soil moisture condition for that month, as the daily variation was small. In station 2 (Table III) for instance, the moisture content to a depth of 25 cm in a dry month was 49.69 ± 3.67%.

Soil moisture samples were collected from each of four depth ranges: 0 — 10; 10 — 25; 25 — 70 and 70 — 100 centimeters. At stations 4, 7, 8 and 9, samples were taken only to a depth of 50 to 70 cm, because the bedrocks limited the depth of the fine soils. For each depth range a sample was collected. Three replicates were taken from separate borings at each monthly sampling. In addition to the moisture samples, rock samples were collected separately to deduct the amount of moisture bound within the rocks (Waring & Major, 1964) as this is unavailable to plants. This correction is necessary since stones may hold substantial amounts of water (Coile, 1953; Reinhart, 1961). The soil and rock samples were collected in friction-top cans. Upon arrival at the laboratory the samples ware weighed, oven-dried at 110° C for 48 hours and reweighed. The stones were removed from the soil samples by screening the fine fraction through a 2 mm sieve and then weighed. The amount of moisture in the stone fraction was calculated by multiplying the weight of the stone fraction with the moisture factor for the stones. The moisture factor for the stones, i.e., the weight of water in the stones divided by the oven-dry weight

Table III. Plots used for monthly soil water sampling, May 1967 — May 1968

	Station	Altitude (m)	Average slope (degree)	Mean annual rainfall (mm)	Cover	Soil
1.	Kailua (Plot no. 8)	240	45	1481	*Andropogon virginicus* community	Silty clay to clay loam soil, resembles the Humic Latosol, overlying soft weathering parent material.
2.	Kahaluu (Plot no. 16)	135	45	2576	*Andropogon virginicus* community	Silty clay to clay loam soil, resembles the Humic Latosol, overlying soft weathering parent material.
3.	Pupukea (Plot no. 23)	525	15	3187	*Andropogon virginicus* community	Dark grey clay, podzolized soil with perched water table, overlying yellowish red clay.
4.	Palikea (Plot no. 41)	870	40	1040	*Andropogon virginicus* community	Pockets of shallow sandy loam to silty loam soil, resembles the Humic Latosol with soft weathering an lava.
5.	Kunia (Plot no. 37)	300	14	1040	*Rhynchelytrum repens* community	Mahana silt loam soil of the Humic Ferruginous Latosol.
6.	Kahuku (Plot no. 22)	70	35	1015	*Rhynchelytrum repens*-*Heteropogon contortus* community	Nakalele silty clay complex of the Rough Broken Land type, Lithosol.

Table III. (Continued) Plots used for monthly soil water sampling, May 1967 — May 1968

	Station	Altitude (m)	Average slope (degree)	Mean annual rainfall (mm)	Cover	Soil
7.	Makaha (Plot no. 43)	60	40	501	*Heteropogon contortus* community	Pockets of shallow rocky silty loam soil with highly weathered material from basic igneous rocks; soil material resembles that of the Low Humic Latosol.
8.	Koko Head (Plot no. 3)	105	25	869	*Heteropogon contortus* community	Pockets of very shallow (10 cm) loamy sand, resembling the material of the Red Desert Soils overlying cemented tuff.
9.	Makapuu Flat (Plot no. 67)	3	0	648	*Chloris barbata* community	Lualualei Clay, stony phase, Dark Magnesium Clay.
10.	Makapuu Flat (Plot no. 68)	3	0	648	*Dichanthium aristatum* community	Lualualei Clay, non-stony phase, Dark Magnesium Clay.

of the stones, was determined separately by weighing and oven-drying separate stone samples. The amount of moisture in the soil fraction was calculated by subtracting the amount of moisture in the stones from the amount of moisture in the combined stone-soil sample.

For each depth range bulk density was determined by the excavation method (Blake, 1966). The method was slightly modified by using thin plastic bags and water instead of dried sand to fill up the holes in determining soil volume, because water was easier to measure than sand.

The soil moisture content was expressed in terms of mm rainfall equivalent (Walter, 1960). For example, for a soil that has a moisture content of 60% (on oven-dry weight basis) and a bulk density of 0.8, the volume of water in a 1 sq. m by 10 cm deep soil block is 0.6 x 0.8 x 100 = 48 liters or 48 mm rainfall equivalent.

For each depth range, the soil-water (moisture) contents of the soil fraction at 1/3 and 15 atmosphere were determined using the pressure membrane apparatus. The water contents of soil at 1/3 and 15 atmospheres were considered as the estimate of water contents at field capacity and permanent wilting respectively (Buchman & Brady, 1964). Thorne (1949) showed that for three Hawaiian soils, the Low Humic Latosol, Humic Ferruginous Latosol and Brown Forest soil, the correlation between permanent wilting and moisture at 15 atmospheres were highly significant.

In each of the ten stations, a rain gauge was installed and checked monthly at the time of soil sampling. Daily rainfall records were also obtained from the rainfall stations nearest each plot station, as reported by the U. S. Weather Bureau (1967, 1968) and in the unpublished files of the Hawaiian Sugar Planters Association.

4.2.2. Results and Discussion

4.2.2.1. Soil type

None of the nine community types recognized in this study was restricted to a particular soil type. Each community type may occur on a variety of soils. However, soil features such as stoniness, depth, drainage and topography, in some cases, were important local habitat factors that segregated the grass communities. They were related to the water regime in the soils. Egler (1939, 1947), Hosaka & Ripperton (1955) and Krajina (1963) observed only correlations between vegetation zones and major soil groups, where rainfall had a dominant effect on these correlations. They noted also that within each vegetation zone, topography, geology and biotic factors might be responsible for the vegetation differences. Hosaka & Ripperton (1955) stated that the absence of correlation between soil groups of lower category and vegetation was due to the replacement of native species by exotics in many areas, except in forest reserves at higher elevations.

The soils of the study plots occurred in six Great Soil Groups: Humic Latosols, Low Humic Latosols, Humic Ferruginous Latosols, Red Desert Soils, Dark Magnesium Clay and Lithosols. Most of the plots occurred on Lithosols which include the following types: stony land, rockland, eroded land and rough broken land. In many cases the A horizons of the soils were eroded away. The boundaries between horizons were usually very weak. The depth varied from 10 cm, especially on the hillsides, to over 100 centimeters.

Shallow stony soils occurred in depressions and crevices between rocks on the hillsides in the summer-drought climate. Cline *et al.* (1955) classified them as rocklands and stony land types (Lithosols). These land types supported the *Heteropogon contortus-Rhynchelytrum repens* and *Eragrostis variabilis* community types as well as the shrub communities of *Leucaena leucocephala* and *Acacia farnesiana* or *Prosopis pallida* forest.

The *Heteropogon contortus-Rhynchelytrum repens* and *Eragrostis variabilis* community types occurred on soils classified as the Low Humic Latosols, Dark Magnesium Clay and Red Desert Soils. Soils under *Eragrostis variabilis* were shallower than those under *Heteropogon contortus* and generally occurred on steep slopes and in positions exposed to strong winds.

Soils under the *Trichachne insularis* and *Panicum maximum* community types differed little. Under *Trichachne insularis*, soils tended to be darker and more gravelly. They were stony Lualualei clay soils that occurred on gentle slopes. The surface showed many large outcropping boulders and fine soil was confined to pockets between them.

On the flatland, the Lualualei clay stony phase supported the *Chloris barbata* community type and the non-stony phase the *Dichanthium aristatum* community type. *Chloris barbata* communities occurred also on Red Desert Soils and alluvial soils.

In the summer-dry and humid climates, the soils varied in depth from 1 to 100 cm and were variably stony. They merged with highly weathered parent material on hillsides and in most cases formed a continuous mantle over the parent rocks. The *Andropogon virginicus* community type occurred mainly on deep soils of the Humic Latosols, Low Humic Latosols and Nakalele silty clay complex (Lithosols). In high rainfall areas it occurred on boggy soils that resembled podzolic soil. On steep slopes soils under this community type were shallow and stony.

The *Rhynchelytrum repens* community type occurred on shallow and stony Lithosols and Red Desert soils as well as on deep Humic Ferruginous Latosols. Although this community type was prevalent in the summer-dry climate, it occured occasionally in the humid climate on steep slopes where soils were stony. In this case the high rainfall was less effective because the steep slope and stony soil produced a drier than normal habitat. The *Melinis minutiflora* community type in the plot studied occurred on the Humic Ferruginous Latosols, but elsewhere this community may be found on the Humic Latosols also.

4.2.2.2. Soil pH

The average values of soil pH (Table IV) from the main rhizospheres formed a gradient in relation to the grass community types.

In the summer-drought zone, there was no indication that soil pH differences were related to rainfall. The community types showed a small scale mosaic pattern unrelated to the rainfall distribution. There was also no correlation between the change of the pH values among individual plots and their arrangements along the phytosociological gradients (X- and Y-ordination axes) (Table V). The mean pH values of the soils ranged from 6.2 to 7.5. There was not clear cut difference in soil pH among community types, instead changes were gradual. The soils under the *Panicum maximum, Dichanthium aristatum* and *Chloris barbata* community types had mean pH values above 7.0. These community types were located mainly on the coastal flatland or on gentle slopes. The flatland habitats of these community types appeared to be influenced by the seepage of sea water and perhaps by the underlying coral rocks. Two plots (No. 69 and 70, Table I) of the *Chloris barbata* community types were located inside the Diamond Head Crater, where calcium carbonate concretions were common. The *Heteropogon contortus-Rhynchelytntm repens, Eragrostis variabilis* and *Trichachne insularis* community types had mean pH values below 7.0. They occurred on the hillsides or on gentle slopes at the foot of the hills *(Trichachne insularis),* where there was no direct influence of sea water except from the salt spray. Lower pH values were perhaps related to the effect of leaching in the *Heteropogon contortus-Rhynchelytrum repens* and *Ergarostis variabilis* community types, and

Table IV. Mean values and standard deviations of pH, percent organic matter (O.M.) and water retaining capacity (W.R.C.) of the soils from the main rhizospheres in the nine community types

Community type	pH	O.M.	W.R.C.
Summer-drought zone:			
Panicum maximum	7.5 ± 0.4	1.6 ± 0.4	68.0 ± 1.8
Dichanthium aristatum	7.3 ± 0.3	2.2 ± 1.7	69.6 ± 6.7
Chloris barbata	7.2 ± 0.3	2.4 ± 1.0	73.8 ± 14.1
Eragrostis variabilis	6.9 ± 0.1	2.8 ± 0.9	79.5 ± 5.5
Heteropogon contortus-Rhynchelytrum repens	6.7 ± 0.5	2.8 ± 1.7	68.0 ± 18.2
Trichachne insularis	6.2 ± 0.3	9.6 ± 2.8	69.7 ± 3.4
Summer-dry zone:			
Rhynchelytrum repens	5.7 ± 0.2	3.2 ± 1.1	64.8 ± 8.3
Melinis minutiflora	4.8	4.9	85.5
Humid zone:			
Andropogon virginicus	4.7 ± 0.1	8.2 ± 1.0	66.0 ± 15.7

Table V. Correlations between phytosociological gradients (ordination axes) and soil pH, percent organic matter (O.M.), annual median rainfall and water retaining capacity (W.R.C.). Values in the body of the table are correlation coefficients, r. Double asterisks indicate a significant correlation at the 1% level of probability

Ordination axes	pH	O.M.	Rainfall	W.R.C.	Degrees of freedom
Summer-drought zone (leeward group):					
X	0.011	0.029	0.036	0.216	68
Y	0.013	0.058	0.158	0.184	
Summer-dry and humid zones (windward group):					
X	0.730 **	0.209	0.546 **	0.000	34
Y	0.074	0.154	0.036	0.031	

due to high organic matter content in the *Trichachne insularis* community type.

In the summer-dry and humid zones the soil pH under the *Rhynchelytrum repens* and *Andropogon virginicus* community types differed significantly; the pH values did not overlap. In general soils under these community types were more acid than those in the summer-drought zone. There was also a significant correlation (Table V) between the pH values of the individual plots and the arrangements of the plots along the horizontal phytosociological gradient (X-ordination axis), but not with the vertical gradient (Y-axis). Fig. 10 shows that the change of the soil pH along the horizontal gradient was accompanied by a change in species dominance from *Rhynchelytrum repens* to *Andropogon virginicus,* which was also related to the increasing annual median rainfall (Fig. 9). The change of soil pH was largely the result of change in rainfall (r = 0.415, significant at the *2%* probability level).

It is evident that the distribution of the community types was related to soil pH, especially in the summer-dry and humid zones. Similar correlations between plant communities and soil pH were reported by Koslowska (1934), Salisbury (1921), Wherry (1927) and Mueller-Dombois (1959). According to Pearsal (1952) soil acidity was stable in undisturbed native vegetation, as the vegetation and soil were in a steady state, which may be interpreted that the supply and depletion of the hydrogen ions in the soils were in balance. In serai communities, like most grass communities in this study, soil acidity may be unstable. Godwin and Turner (1933), Ovington (1953) and Pearsal (1952) observed that succession resulted in a change of soil acidity. This is perhaps partly due to the change of rate of the organic matter supply, which is one of the sources of the hydrogen ions in the soils. Pearsal (1952) and Whittaker (1970) stated that the rate of litter production differed in different plant communities and the type of litter had an influence on the rate of decomposition.

h.2.2.3. Soil organic matter

Table IV shows the mean values of the organic matter content of the soils from the main rhizospheres in nine community types. There was no relationship between the organic matter content and the community types. However, the mean values for the community types, except for the *Trichachne insularis* community type, in the summer-drought zone were

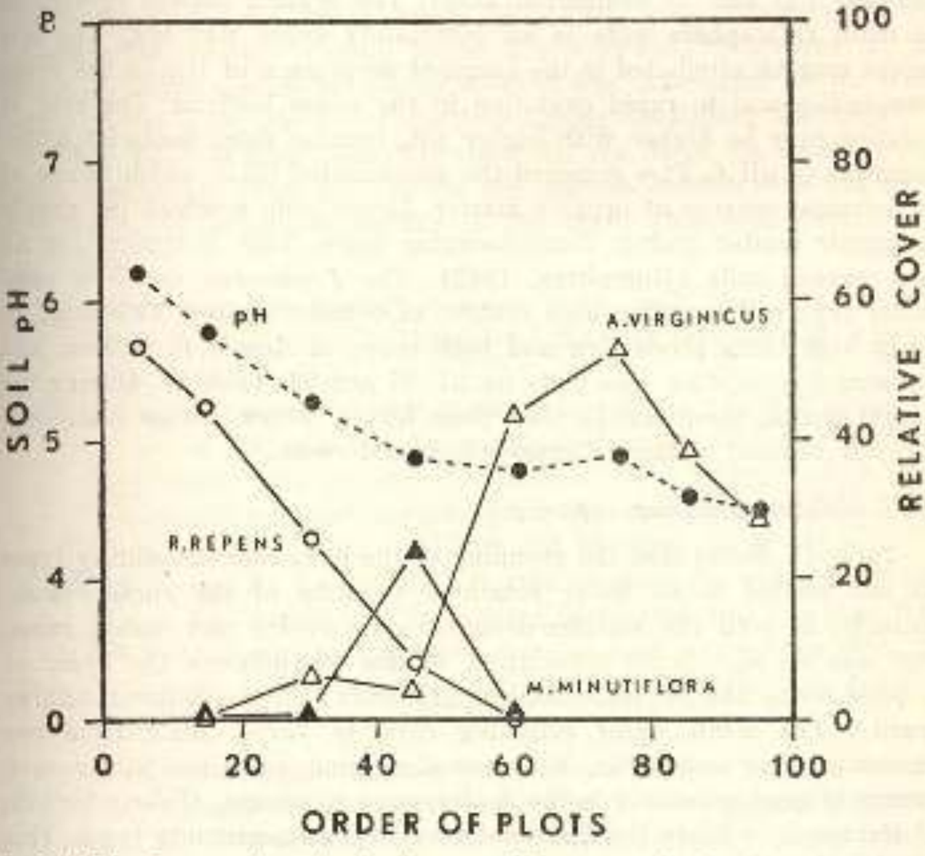

Fig. 10. The change of species dominance and decrease of soil pH along the order of plots on the X-ordination axis. The construction of the diagram is the same as in Fig. 9. The dominant grasses are *Rhynchelytrum repens, Melinis minutiflora* and *Andropogon virginicus.*

less than 3%, whereas for those in the summer-dry and humid zones were greater than 3%. This agrees with Dean (1937), who reported that the organic matter content in the surface Hawaiian soils in the dry areas was less than 3% and in the humid areas greater than 3%. There was no significant correlation (Table V) between the organic matter content in the plots and the arrangements of the plots along the phytosociological gradients (X- and Y- ordination axes). The organic matter content in the main rhizosphere soils in all community types was low. The low content may be attributed to the frequent occurrence of fire in the grass communities and to rapid oxidation in the warm lowland. The rate of oxidation may be higher with higher pH, because more bacterial action occurs above pH 6. Fire removed the accumulated litter which is one of the potential sources of organic matter. Hence soils received the supply of organic matter mainly from decaying roots. This is typical for all grass-covered soils (Humphrey, 1962). The *Trichachne insularis* community type had a rather High content of organic matter. This migt be due to high litter production and high cover of *Acacia farnesiana* and *Leucaena leucocepkala* (see plots no. 31, 57 and 59, Table I). During the drought period these shrubs shed their leaves, which are an additional source or organic matter to grass leaves and roots.

4.2.2.4. Water retaining capacity

Table IV shows that the grouping of the plots into community types was not related to he water retaining capacity of the surface soils. Similarly, in both the summer-drought, summer-dry and humid zones, there was no significant correlation (Table V) between the order of the plots along the phytosociological gradients and the water retaining capacity. The mean water retaining capacity varied little from one community type to another, but showed a great variation within each community type, especially in the *Andropogon virginicus, Chloris barbata* and *Heteropogon contortus-Rhynchelytrum repens* community types. This indicates that the water retaining capacity was not a determining factor in the distribution and development of the grass communities. Also since the water retaining capacity gives an indication of the soil texture (Wilcox, 1951), it can be implied that the grass community development and distribution was not dependent on the soil texture.

The water retaining capacity is not a measure of soil-water storage capacity, because it does not include depth to bedrock or volume of soil and slope which are important factors in the water relations of a given location.

4.2.2.5. Soil-water regimes

The study indicates that the present distribution of the grass communities was primarily conditioned by the duration and amount of water available. The soil-water regime was related to the amount and distribution of the rainfall, but was modified by topographic position, i.e., slope, aspect, stoniness and soil depth. It will be shown under the section of dynamic relationships that the establishment of various grass communities was related to the invasion of exotic species following disturbance such as fire. However, which species became established was determined by the water regime in the soils, also by competition among developing seedlings.

Figs. 11 —14 and Table VII show the results of the monthly soil-water samplings. These are for the ten stations described in Table III. Three type of soil-water regime in the main rhizosphere have been recognized:

1 Wet type: The amount of water in the soils was always higher than the field capacity throughout the year (station 1, 2, 3 and 4; Fig. 11).
2 Drought type: In at least three months of the year the amount of water in the soils was below the permanent wilting percentage. Therefore, long soil-drought periods were evident which were interupted by short periods when the water content was above field capacity (stations 7, 8, 9 and 10; Figs. 13 & 14).
3 Dry type: An intermediate regime between the wet and drought types. The duration of the wilting percentage was less than three continuous months and there were at least six months when the soil water content was above the field capacity (stations 5 and 6; Fig. 12).

The wet soil-water regimes were found under the *Andropogon virginicus* communities (stations 1—4). The drought soil-water regimes were under the *Heteropogon contortus* (stations 7 and 8) *Chloris barbata* (station 9) and *Dichanthium aristatum* (station 10). The dry or intermediate soil-water regimes were associated with the *Rhynchelytrum repens* communities (stations 5 and 6).

U.2.2.5.a. Wet type

In the wet soil-water regime under the *Andropogon virginicus* cover (Fig. 11), soil moisture was in excess of the field capacity not only in the-main rhizosphere (0 — 25 cm) but also throughout the profile to a depth of 100 cm (Table VII). A study of the daily rainfall patterns of

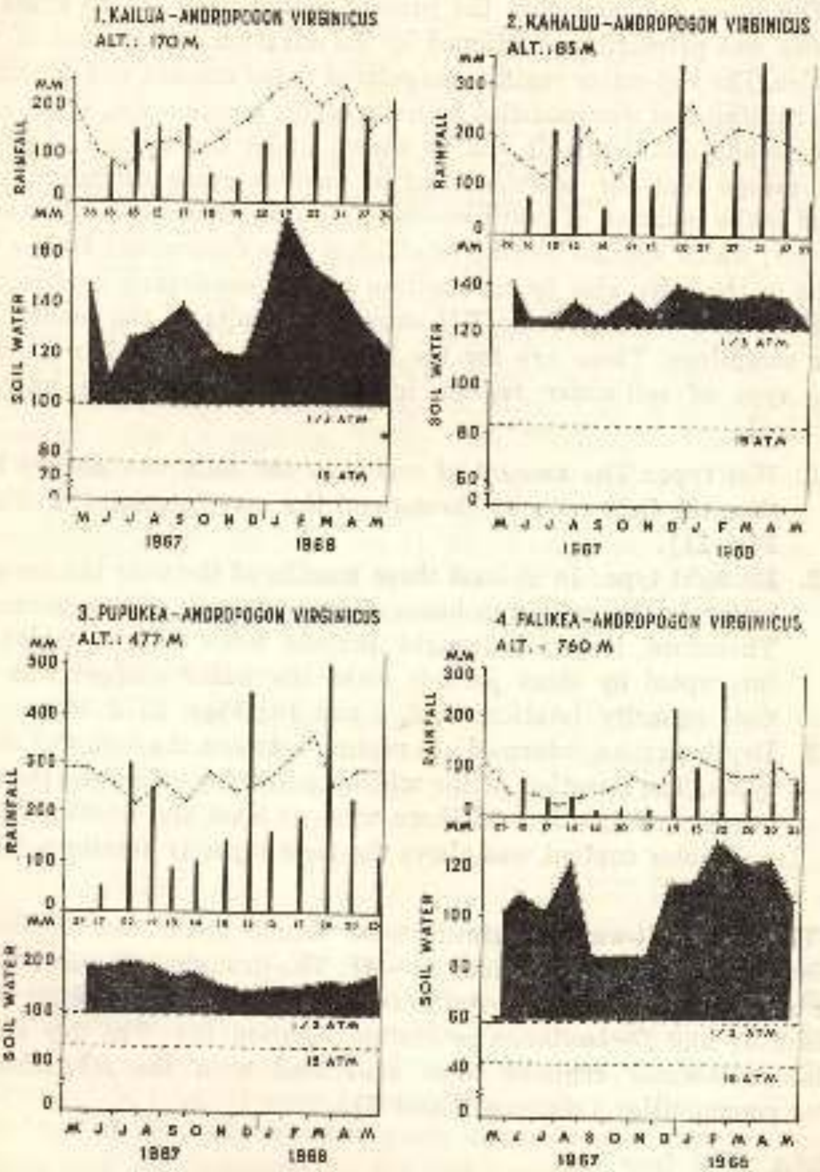

Fig. 11. Fluctuation of soil-water to a depth of 25 cm in Andropogon virginicus communities, from May 1967 through May 1968. The vertical bars indicate the amount of rainfall between sampling dates, the dashed curves the mean monthly rainfall at the nearest rainfall stations. The figures along the X-axis of the rainfall curves are the dates of sampling.

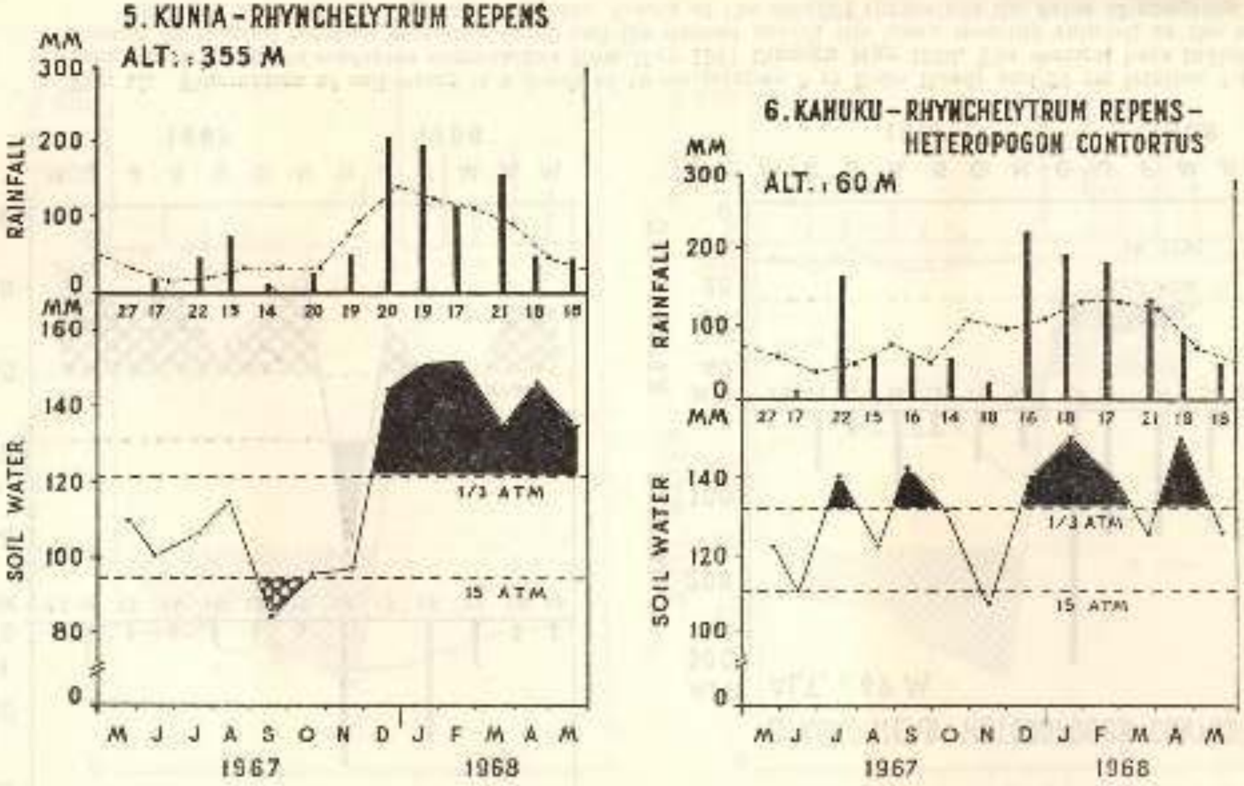

Fig. 12. Fluctuation of soil-water to a depth of 25 cm in a *Rhynchelytrum repens* community (station 5) and *Rhynchelytrum repens-Heteropogon contortus* community (station 6) from May 1967 through May 1968. The vertical bars indicate the amount of rainfall between sampling dates and the dashed curves the mean monthly rainfall at the nearest rainfall stations. The figures along the X-axis of the rainfall curves are the dates of sampling.

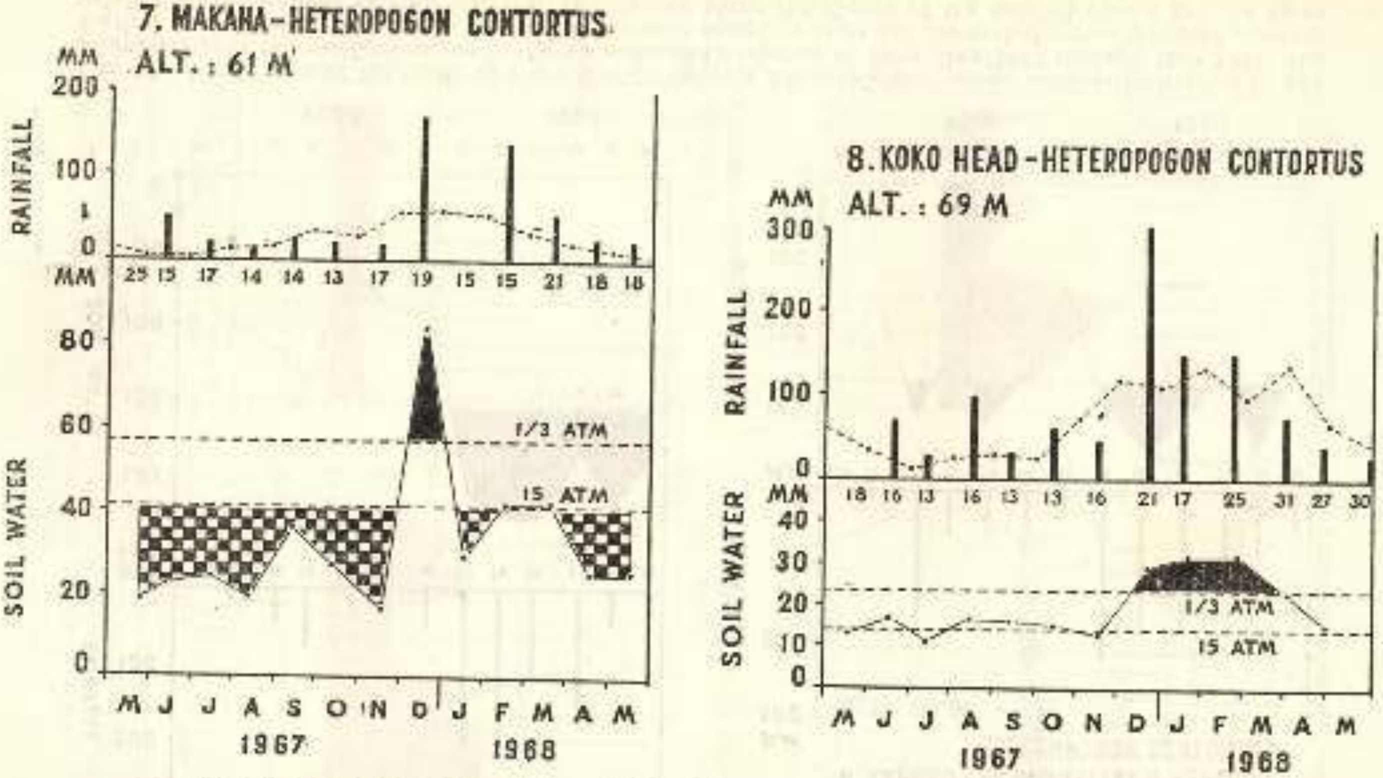

Fig. 13. Fluctuation of soil-water to a depth of 10 cm (station 8 at Koko Head) and 25 cm (station 7 at Makaha) in *Heteropogon contortus* communities from May 1967 through May 1968. The vertical bars indicate the amount of rainfall between sampling dates and the dashed curves the mean monthly rainfall at the nearest rainfall station. The figures along the X-axis of the rainfall curves are the dates of sampling.

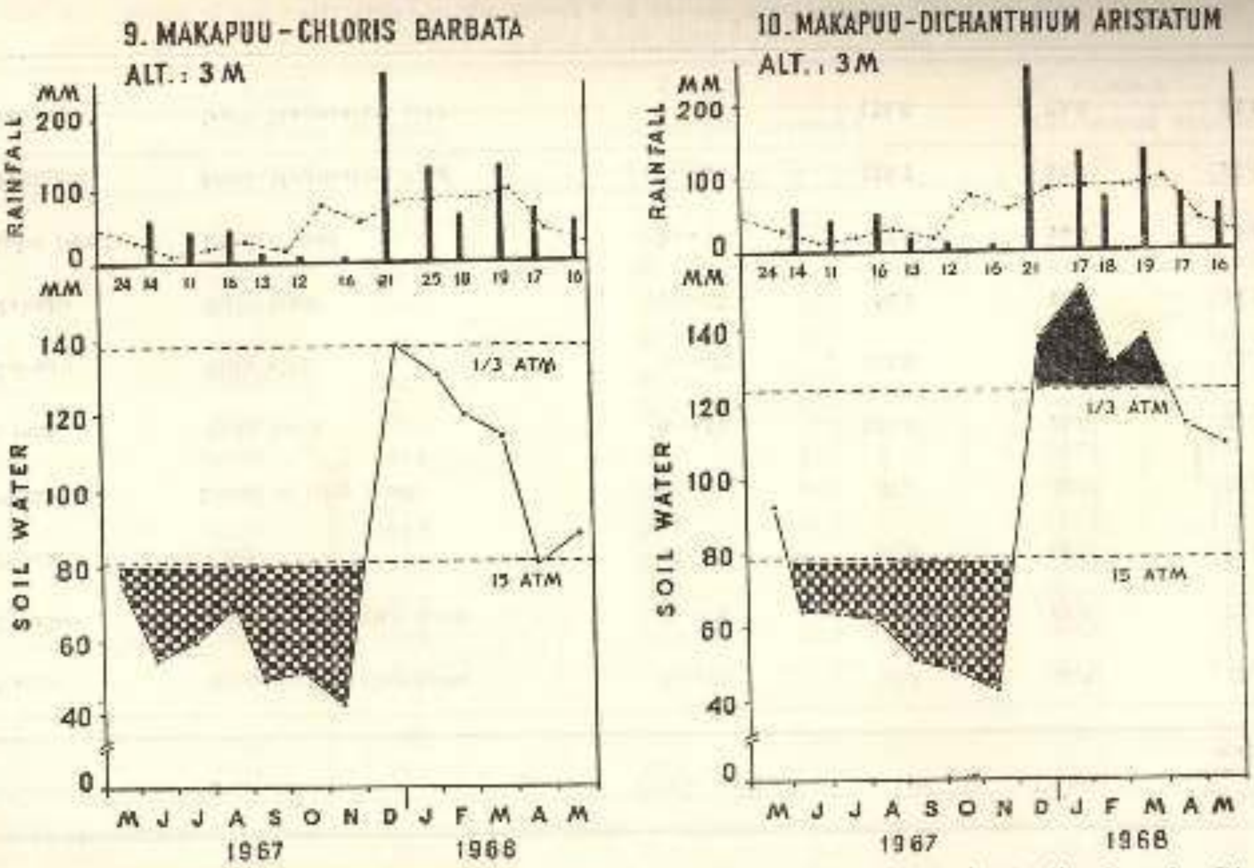

Fig. 14. Fluctuation of soil-water to a depth of 25 cm in a *Chloris barbata* community (station 9) and a *Dichanthium aristatum* community (station 10) from May 1967 through May 1968. The vertical bars indicate the amount of rainfall between sampling dates and the dashed curves the mean monthly rainfall at the nearest rainfall station. The figures along the X-axis of the rainfall curves are the dates of sampling.

Table VI. Soil-water (mm) at ½ Atm. and 15 Atm., and potentially available water in the soils from the main rhizosphere in various stations. Available water is defined as the difference between the amount of water held at ½ Atm. and 15 Atm.

	Station	Soil texture	Depth (cm)	½ atm.	15 atm.	Potentially available water
1.	Kailua	Silty clay to clay loam	0 — 25	99.1	75.7	23.4
2.	Kahaluu	Silty clay to clay loam	0 — 25	123.1	83.9	39.2
3.	Pupukea	Clay	0 — 25	98.8	86.0	12.8
4.	Palikea	Loam to silty loam	0 — 25	57.7	41.6	16.1
5.	Kunia	Silty loam	0 — 25	122.0	94.6	27.4
6.	Kahuku	Silty clay	0 — 25	132.3	109.9	22.4
7.	Makaha	Silty loam	0 — 25	56.7	41.9	14.8
8.	Koko Head	Loamy sand	0 — 10	23.9	14.6	9.3
9.	Makapuu	Dark Magnesium clay	0 — 25	135.7	80.7	56.0
10.	Makapuu	Dark Magnesium clay	0 — 25	121.8	79.0	42.8

Table VII. Fluctuation of soil-water (mm) in the subsoil * of various grass communities from May 1967 through May 1968. Figures in blocks indicate water content lower than permanent wilting percentage

Station	1. Kailua		2. Kahaluu		3. Pupukea	
Community	*Andropogon virginicus*		*Andropogon virginicus*		*Andropogon virginicus*	
Depth (cm)	25 — 70	70 — 100	25 — 70	70 — 100	25 — 70	70 — 100
May	235.1	161.9	95.6	92.1	303.0	211.9
June	243.7	169.4	87.7	80.3	268.2	199.5
July	245.2	168.4	91.7	60.9	269.1	171.2
August	261.6	163.8	89.1	84.3	289.8	197.4
September	239.9	182.1	97.1	93.0	261.5	208.3
October	251.4	167.8	88.5	87.7	269.6	189.4
November	221.0	161.0	85.2	81.7	256.1	193.4
December	233.6	164.3	95.2	96.8	248.4	174.0
January	242.7	182.2	98.8	84.8	252.0	169.1
February	252.2	171.2	91.1	86.3	238.1	190.3
March	292.6	182.2	95.3	89.5	243.0	176.4
April	241.6	174.3	93.8	83.2	266.9	177.3
May	234.6	172.8	93.6	87.5	211.8	165.1
⅓ Atm.	194.0	130.7	91.2	75.5	155.1	154.5
15 Atm.	156.6	98.1	69.6	67.1	138.8	127.4
Potentially available water **	37.4	32.6	21.6	8.4	16.3	27.1

* Surface soil moisture values were used for Fig. 16 and are not shown here.

** The difference of the amount of soil-water held at ⅓ and 15 atmospheres.

Table VII. (Continued) Fluctuation of soil-water (mm) in the subsoil of various grass communities from May 1967 through May 1968. Figures in bold face indicate water content lower than permanent wilting percentage.

Station	4. Palikea		5. Kunia		6. Kahuku	
Community	*Andropogon virginicus*		*Rhynchelytrum repens*		*Rhynchelytrum repens*	
Depth (cm)	25 — 70	70 — 100	25 — 70	70 — 100	25 — 70	70 — 100
May	190.9	—	296.2	151.5	257.6	114.9
June	199.9	—	224.6	151.6	236.2	166.0
July	280.3	—	211.2	144.0	267.4	139.1
August	203.6	—	229.0	155.0	249.5	158.2
September	179.7	—	**198.6**	142.6	247.5	173.6
October	212.9	—	**197.1**	**128.6**	220.2	153.4
November	144.6	—	**206.9**	**131.0**	233.3	158.0
December	210.2	—	254.7	161.9	263.4	156.5
January	274.0	—	261.0	162.2	254.7	169.4
February	236.6	—	267.6	163.7	265.0	182.0
March	261.5	—	287.5	152.0	266.8	176.3
April	248.9	—	248.3	165.3	257.8	184.3
May	257.4	—	280.6	153.6	244.8	175.9
⅓ Atm.	110.6	—	233.5	156.5	246.5	164.3
15 Atm.	87.8	—	209.0	134.0	183.8	102.7
Potentially available water	22.8	—	24.5	22.6	48.0	61.6

Table VII. (Continued) Fluctuation of soil-water (mm) in the subsoil of various grass communities from May 1967 through May 1968. Figures in bold face indicate water content lower than permanent wilting percentage.

Station	7. Makaha		8. Koko Head		9. Makapuu		10. Makapuu	
Community	*Heteropogon contortus*		*Heteropogon contortus*		*Chloris barbata*		*Dichanthium aristatum*	
Depth (cm)	25 — 70	70 — 100	10 — 25	25 — 50	25 — 70	70 — 100	25 — 70	70 — 100
May	**53.2**	—	**48.1**	90.2	82.9	—	178.7	153.5
June	**54.0**	—	57.7	104.3	**75.4**	—	167.6	159.7
July	**45.0**	—	**45.5**	**86.8**	**71.6**	—	173.7	154.9
August	**40.5**	—	61.1	**33.1**	**58.6**	—	**145.0**	**143.7**
September	**40.5**	—	**47.3**	**69.4**	**59.1**	—	**138.1**	**144.0**
October	**36.0**	—	**44.1**	**79.1**	**75.0**	—	164.8	**144.4**
November	**41.1**	—	**47.0**	**77.6**	**74.4**	—	**132.9**	**125.5**
December	134.0	—	77.3	141.9	105.3	—	224.8	**135.7**
January	**59.8**	—	82.9	157.3	117.6	—	227.8	**139.8**
February	69.5	—	83.0	153.7	111.7	—	248.2	151.6
March	**59.6**	—	69.3	147.8	97.5	—	233.2	150.2
April	**42.9**	—	57.5	112.3	91.9	—	237.7	151.0
May	**44.3**	—	57.3	98.4	85.7	—	212.6	154.9
⅓ Atm.	91.9	—	58.7	102.2	140.4	—	257.4	213.6
15 Atm.	67.0	—	48.2	88.3	78.6	—	164.7	149.1
Potentially available water	24.9	—	10.5	13.9	60.8	—	92.7	74.5

the nearest rainfall stations (U. S. Weather Bureau, 1967, 1968) at Kailua and Kahaluu during the period of investigation showed that the average numbers of rainless days per month was 10, ranging between 2 and 16. The longest period continuously without rain was only 9 days, recorded in February at Kahaluu, while in other months rain fell almost daily. No daily rainfall records were available for stations 3 (Pupukea) and 4 (Palikea). However, these stations are located at higher elevations, therefore, rain would be expected to fall more frequently. Because of the higher frequency of rainfall in stations of the wet type, soils were recharged before the water was depleted between showers. This resulted in soils that were always wet throughout the year. In station 3 (Pupukea) the absolute amount of water, especially in the upper 25 cm was much higher than in stations 1, 2 and 4. This was because of a perched water table. The upper 25 cm were always water-soaked throughout tha year resulting in a bog-like situation.

Despite water being available throughout the year to a depth of 75 to 100 cm in all four stations, *Andropogon virginicus* showed seasonal drying of the shoots. The shoots began to dry up in November after the fruiting season was over, and by the end of February most of the shoots were dead. The new green shoots began to appear in March and reached maximum vegetative growth in September, while dead shoots of the previous growth remain on the plants. At this time flowers were produced and in October they reached the fruiting stage. This indicates that seasonal drying in this species was certainly not a response to a drought condition. The shoot-drying is part of the life cycle, and since it always occurs after seed production each shoot is probably monocarpic. *Andropogon virginicus* is a native of the eastern United States (Keever, 1950; Oosting, 1942), where it undergoes a rest-period during the winter months in this temperate climate.

It is evident that *Andropogon virginicus* grew best in places where water was always available throughout the year. In moderately low rainfall areas it showed reduced growth and gave way to *Rhyncheiytrum repens*. In the eastern United States it occurs in uniformly and moderately low rainfall areas (Oosting, 1942) and is reported to be more drought resistant than forbs such as *Aster pilosus* (Keever, 1950).

The excess of water beyond the field capacity may be attributed not only to the continuously humid climate, but it may also be a reflection of the poor water consumption by *Andropogon virginicus*. Veihmeyer (1953) showed that grasses extracted l-ess water from soil than woody plants. Mueller-Dombois (unpublished data) reported also that water loss from woody plants per unit land area was several times greater than from *Andropogon virginicus,* although according to Keever (1950) *Andropogon virginicus* could extract more water compared to forbs such as *Aster pilosus.*

Residual excess water as found under the *Andropogon virginicus* communities may cause undesirable effects. Run-off and erosion may increase and the occurrence of puddling in the subsoils may result in landslides. This may explain why landslides are rather common on the grassy hills in the humid areas of Kahaluu and Waikane.

Because trees and shrubs can extract more water than grass in the humid climate, it would seem more beneficial to replace the grass cover on the wet hilly areas by trees and shrubs. It will undoubtedly reduce the frequency of landslides and fire. Scott (1969) reported that soil avalanching (landslide) was more frequent under false staghorn fern thicket than under forest.

4,2.2.5. b. Drought type

The drought soil-water regimes (Figs. 13 & 14) stations 7, 8, 9 and 10) occurred in the summer-drought climate, where the mean annual rainfall ranges from 500 to 860 millimeters. The duration of the availability of soil-water was related to topography and local variation of the rainfall distribution. The shoot drying was correlated with the soil drought. The soil drought ranged from 3 to 11 months.

In station 7 (Makaha, Fig. 13), which was in a *Heteropogon contortus* community, the period of available water lasted only for one month, while in station 8 (Koko Head, Fig. 13), also under *Heteropogon contortus* cover, water was available in the main rhizosphere for five months. The daily rainfall data from the nearest rainfall stations indicated that the average number of rainless days per month at Makaha was 24 with a range of 18 — 29, while at Koko Head it was 18 days ranging from 11 — 25. At Makaha the soil-water in September increased, but remained below the permanent wilting percentage. The increase to about 36 mm was due to the rain of about 36 mm that fell early in the morning on the day of sampling. During the rainy period from December through March, rain occurred more frequently. The highest rainfall was recorded in December which was reflected in the soil water content. The decrease of soil water to the permanent wilting level in mid-January was because no rain fell between the sampling dates in December and January. In February and March the soil was wetted, but the soil-water barely reached the permanent wilting level. In February heavy rain occurred about 3 to 4 weeks before the sampling date. Except for December the amount of water was below permanent wilting level at depths between 25 and 70 cm (Table VII).

In response to the seasonal changes in soil-water, the aerial parts of *Heteropogon contortus* and other herbaceous species were dry between March and December. Woody species such as *Acacia farnesiana* and *Leucaena leucocephala* shed their leaves gradually. Between August and December they were completely barren. New shoots of *Heteropogon contortus* appeared from old bunches immediately after heavy rain in December, but the old dry shoots remained on the plants. At this time *Heteropogon contortus* and forb seedlings were rather uncommon. However, seedlings of woody species such as *Acacia farnesiana, Leucaena leucocephala, Abutilon incanum* and *Waltheria indica* were very common.

Mature *Leucaena leucocephala* and *Acacia farnesiana* were resprouting and *Heteropogon contortus* produced flowers in January. *Heteropogon contortus* maintained good vegetative and reproductive growth until the end of March when the aerial parts began to dry up again. At that time the fruiting stage was already over. *Rhynchelytrum repens,* in the *Heteropogon contortus* community, followed the same pattern of drying.

In station 8 at Koko Head (Fig. 13) under a *Heteropogon contortus* community, soil-water in the upper 10 cm fluctuated around the permanent wilting level from April through November. The fluctuations of soil-water during this period were minor due to rather uniform rain distribution from month to month. During the rainy season from December to March, soil-water was at or above field capacity. Daily rainfall data from the nearest rain gauge at Portlock Road showed that very heavy rainfall was recorded in December and January and light showers occurred frequently. In February no heavy shower was recorded, but rain was rather evenly distributed throughout the month. It rained about every three days. The high frequency of light showers and occasional heavy rainfall appeared to be sufficient to keep the soil moist throughout the rainy season which lasted for only four months. The soil in this station was only 10 cm deep. Below this layer was tuff which often cracked and formed blocks.

During the dry season, where the soil moisture was fluctuating about permanent wilting percentage, *Heteropogon contortus* did not dry up as severely at Koko Head as at Makaha. *Heteropogon contortus* at Koko Head was able to produce new shoots and flowers whenever there was a high rainfall, such as in August, September and October (Fig. 13, station 8). However, the main growth and flowering period from December through

April was related to the greater availability of the soil-water. A similar observation was reported by Tothill (1966) who found in north-eastern Australia that the flowering of *Heteropogon contortus* occurred in the wet season, although he considered short day-length more important than soil moisture. Other herbaceous species, such as *Emilia sonchifolia, Stachys arvensis* and *Hyptis pectinata,* were dead between June and November. New seedlings of these species appeared immediately after heavy rainfall in December. Small woody and semi-woody species, such as *Sida fallax, Cassia leschenaultiana* and *Passiflora foetida* (a vine) remained green throughout the year, but new leaves were produced during the rainy season. The taller shrub, *Acacia farnesiana,* on the other hand, was leafless at the end of the dry season. It produced new leaves in December and began to flower in March.

Although *Heteropogon contortus* rooted mainly in soil layer, its roots formed dense mats in the cracks between blocks of tuff. The tuff could hold substantial amounts of water, as evident from a relatively high content of potentially available water from 10 to 14 mm (Table VII, station 8) in the subsoil at depth of 10 — 50 centimeters. Water collected in the cracks and retained in the tuff may serve as an additional water supply to that retained in the fine upper soil. This may explain why growth continued during the dry season.

The *Eragrostis variabilis, Trichachne insularis* and *Panicum maximum* communities are expected to have soil-water conditions of the drought type, since they occurred in the same rainfall regime and on similar topographic positions as the *Heteropogon contortus* community. Under the *Eragrostis variabilis* community, however, the month to month soil-water content may be less than under *Heteropogon contortus* because **the** *Eragrostis variabilis* community occurs in the areas exposed to the strong trade-winds.

Soils under *Chloris barbata* and *Dichanthium aristatum* (Fig. 14, stations 9 and 10) had greater water reserves than under *Heteropogon contortus* in spite of similar rainfall regimes. This may be attributed to their location on the flatland which received additional water from seepage and run-off from the neighboring hills. The soil under these communities was montmorillonite clay with high magnesium which had a high value of potentially available water (Table VI and **VII,** stations 9 and 10). Fig. 14 indicates that soil-water under *Chloris barbata* cover was much less than under *Dichanthium aristatum* cover during the rainy season, although the soil material and rain fall were the same. This **may** be **the** result of the undulating land surface, allowing more surficial seepage to accumulate in the *Dichanthium aristatum* community.

Chloris barbata began to dry up in May 1967. At this time, soil water was already below the permanent wilting percentage (Fig. 14, station 9). Drying up of the shoots continued following the gradual decrease of soil-water until the end of the dry season in November. The shoots were dead but the rhizomes were still alive. In August 1967 there was a brief period of growth when *Chloris barbata* produced new shoots and even flowers, but rather sparingly. This was related to a shower that fall in the middle of the month for three consecutive days totalling about 50 millimeters.

The growth period started in December immediately after the soil was fully recharged. Flowers began to appear in January. *Chloris barbata* reached its maximum vegetative growth in March. In May 1968 the shoots were still about 70% green. The soil-water was still above permanent wilting percentage in contrast to May 1967 when the soil-water had just dropped below the permanent wilting percentage (see Fig. 14, station 9). Woody species, such as *Gossypium tomentosum, Lipochaeta lobata, Phaseolus lathyroides* and *Desmanthus virgatus* started to resprout in December. In May 1968 they were still green. The flowering period of *Gossypium tomentosum* started in May 1968, that of *Lipochaeta lobata, Phaseolus lathyroides* and *Desmanthus virgatus* in January 1968. At the beginning of the wet period, annuals started to germinate. These included *Ageratum conyzoides, Vernonia cinerea, Sonchus oleraceus, Commelina benghalensis, Boerhavia diffusa* var. *tetrandra Portulacca oleracea*, *Emilia sonchifolia*, *Phyllanthus niruri* and *Echinochloa colonum.*

Resprouting of *Dichanthium aristatum* from the old bunches started immediately after the soil in the upper 25 cm was fully recharged in December. In January *Dichanthium aristatum* reached its full vegetative production and began to form flowers. At the end of the study period in May 1968, about 30% of the shoots turned yellow and the fruiting period was just over, but the soil-water was still far above the permanent wilting level (Fig. 14, station 10). It become dry in June 1968.

Although the *Heteropogon contortus, Chloris barbata* and *Dichanthium aristatum* communities were found in the same climatic zone and in the same geographic area, their soil-water relations were different. *Heteropogon contortus* could utilize water available for a short period more efficiently. Resprouting and flowering occurred after short summer showers during the drought period. *Chloris barbata* and *Dichanthium aristatum* were correlated to soils in which water was available for a longer period. Although their water regime was studied only for a special soil, the Dark Magnesium Clay, it is possible that the predominant occurrence of *Chloris barbata* on flatland habitats is related to periodic seasonal inundations. Under such conditions *Heteropogon contortus* may be less competitive. The periodic seasonal inundations may explain why *Chloris barbata* and *Dichanthium aristatum* were dominant on the flatland and never on the hillsides, where *Heteropogon contortus* was dominant instead with occasional plants of *Chloris barbata.*

Considering that *Heteropogon contortus* is a bunch grass, which was able to use water very efficiently and capable of surviving prolonged periods of soil drought, it is ideally suited to these habitats and should be maintained on the hillsides to prevent erosion.

h.2.2.5.c. Dry type

In the dry soil-water regime (Fig. 13) water content was lower than the permanent wilting percentage only once for a short period throughout the investigation. For the rest of the year, water was always available in the main rhizosphere. Excessive water was present for six months. In station 5 (Kunia) there were two distinct seasons, one of low and one of high soil-water condition. In station 6 (Kahuku) soil-water fluctuated from month to month. A somewhat longer period of excess water occurred from December through February. In both stations the soil-water quantities were directly related to the monthly rainfall.

In station 6, where the proportion of *Heteropogon contortus* was high in the *Rhynchelytrum repens* community, *Heteropogon contortus* and *Rhynchelytrum repens* were completely dry in May, June and November 1967J, coinciding with the low soil-water level. Growth occurred between **July** and October 1967 and between January and April 1968.

The soil-water measurements were taken for one year only. Therefore, the results only approximate the normal trend of soil-water changes. However, comparison between the rainfall pattern during the study period (vertical bars, Figs. 11 — 14) and the long terms (10 — 30 years) monthly mean rainfall pattern (dashed curves) does not show too great a deviation.

5. DYNAMIC **RELATIONSHIPS**

In the summer-drought zones, two native and four exotic grass community types have been recognized on the basis of their dominant grass species. However, exotic species were present in varying proportions in these community types. It appeared that the two native **community** types were invaded by exotic species. On the other hand, where seed sources are available, Egler (1947) contended that native species may also replace exotics. This has been shown by Hatheway (1952) who noted that the *Leucaena leucocephala* and *Rhynchelytrum repens* communities were invaded by native woody species, such as *Canthium odoratum, Erythrina sandwicensis, Reynoldsia sandwicensis* and *Sapindus oahuensis.* The arid lowland vegetation of Oahu at one time consisted of savannahs (Hillebrand, 1888) and grasslands (Egler, 1947; Hatheway, 1952; Rock, 1913; Vogl, 1969) which were dominated by *Heteropogon contortus* associated with other native species.

In the summer-dry and humid zones, the grass community types were dominated exclusively by exotic species, i.e., *Melinis minutiflora, Rhynchelytrum repens* and *Andropogon virginicus.* The grassy hills in the humid zone, now dominated by *Andropogon virginicus,* were formerly covered by *Paspalum orbiculare* and *Setaria geniculata* and in the wetter area by *Pospalum conjugatum* (Egler, 1947; Hosaka, 1937). In some areas there were indications that native as well as exotic species were invading the grass communities. It was reported by Hosaka (1937) that *Dicranopteris linearis* fern-mats were invading the *Paspalum orbiculare* communities with a rate of advancement of 0.9 m per year. Scott (1969) reported the invasion of *Dicranopteris linearis* on avalanche scars. The established *Dicranopteris linearis* fern-mats were thought to be serai communities (Fosberg, 1961). Fosberg stated that these communities would be eventually invaded by native woody species, thus leading towards the establishment of forest communities. Among native woody trees **that** are commonly found in the *Dicranopteris linearis* fern-mats, as well as in the grass communities, are *Metrosideros collina* and *Acacia koa.*

Acacia koa regenerates profusely after fire (Judd, 1935) or on cleared forests, which seems to agree with Whitesell's (1964) finding that *Acacia koa* seeds can germinate only on moist bare grounds exposed to sunlight. However, Mueller-Dombois (1967) noted that the only **form** of regeneration of *Acacia koa* in grass-covered areas above 1200 m elevation on Mauna Loa, Hawaii, was from sucker growth. This is a second successful reproductive mechanism of *Acacia koa* in the grass communities. **The** saplings of *Acacia koa* grow rapidly. Judd (1920) observed that the saplings became 9 m tall in 5 years, and Whitesell (1964) reported **that,** in a 12-year old plantation, *Acacia koa* had an average height of 7.6 **m** and a diameter at breast height of 10.9 centimeters. Whitesell stated **also that *Acacia koa* saplings** were **killed by fire.**

Grevillea robusta of different size classes occurred in local clumps of a few trees each in the *Rkynchelytrum repens* and *Melinis minutiflora* communities at Kunia, suggesting that *Grevillea robusta* was invading the two grass communities. Webb *et al.* 1967) reported that, in the subtropical forests in Australia, *Grevillea robusta* was a heavy seed producer and had a high rate of seed germination (80%). Thus it can be implied that *Grevillea robusta* has a potentially strong regenerating power and is a potential invader. However, Webb *et al* (1967) found that, in a pure *Grevillea robusta* plantation, the regeneration and seedling development were extremely poor. They attributed these situations to unknown toxic substances exuded by the adult *Grevillea robusta* trees occurring in the immediate neighborhood of the seedlings, thus indicating an allelopathy phenomenon (Tukey, 1969).

Fire occurred in the grass communities and in the forest zone, and is thought to be an important factor in establishing and maintaining the community types. According to Vogl (1969), 198 fires, ranging from 0 to 41 per year, were recorded on Oahu between 1943 and 1967. Many native Hawaiian species, such as *Eragrostis variabilis, Gossypium tomentosum, Heteropogon contortus* and *Sida fallax* were reported by Vogl (1969) to be fire resistant. Egler (1947), Fosberg (1961) and Vogl (1969) stated that fire maintained and extended the grass communities on Oahu. It was reported also that fire played an important role in maintaining the *Heteropogon contortus* grasslands in the Pacific Islands (Porteres, 1962), Africa (Stapples, 1926) and Australia (Moore, 1966; Shaw, 1957; Tothill, 1969).

The objective of this part of the study was to investigate the vegetation changes and the effects of fire associated with the grass communities. An understanding of these relationships may help to explain the origin and relative stability of the current grass communities on Oahu.

5.1. METHODS

5.1.1. Vegetation change **in the** grass **communities of the summer-drought zone**

The percent cover of exotic species (invaders) was used to indicate the degree of foreign invasion into the native communities. The vegetation data were examined using the method of Christensen (1963), who studied the invasion of exotics into the bunchgrass vegetation of Utah. The native and exotic species composition in seventy plots from the summer-drought zone was reanalyzed. The percent cover of exotic and native species relative to the total percent cover of all species in each plot was calculated. The plots were then grouped into the following five classes according to the percent cover of the exotic species: 0 —19.9% ; 20 — 39.9%; 40 —59.9% ; 60 — 79.9%.; 80 — 100%. For each resulting plot group the mean percent cover was then calculated for each species and compiled in a table (Table VIII).

Leucaena leucocephala is an aggressive exotic shrub (Egler, 1947) that appears to invade the native grass communities. The trend of a species to invade and establish itself in a community can be shown by the numbers of individuals in various size classes. Counts of *Leucaena leucocephala* were made in samples of three stands of *Heteropogon contortus* (on the outer slope of Koko Crater, Makapuu and Makaha) and two stands of *Eragrostis variabilis* (on the outer slope of Koko Crater) with 0.25 sq. m quadrats. The quadrats, 390 in total, were placed systematically after each five steps. The plants were tallied in three height classes: 0 — 25; 25 — 100; 100 + centimeters. Two stands of *Leucaena leucocephala* at Makapuu and Makaha were also sampled in the same manner with 40 quadrats per stand to study the regeneration under its own shade.

5.1.2. **Vegetation change in the summer-dry and humid** zones

5.1.2.1. Invasion by herbaceous species

In the humid zone some *Andropogon virginicus* communities (plots no. 10, 15, 23, 25 and 38) bordered the *Dicranopteris linearis* fern-mats and in the summer-dry zone the *Rhynchelytrum repens* (plots no. 35 and 37) bordered a *Menilis mimttiflora* community. From casual observations these borders were continuously changing. The *Dicranopteris linearis* fern-mats tended to advance into the *Andropogon virginicus* communities in the absence of disturbance, and the *Melinis minutiflora* community tended to advance into the *Rhynchelytrum repens* community.

The encroachment of these two species was studied in permanent 1 sq. m quadrats. Eleven quadrats (in plots no. 10, 15, 23, 25 and 38) were established on *Dicranopteris-Andropogon* boundaries, and four quadrats (in plots no. 35 and 37) on *Melinis-Rhynchelytrum* boundaries. Each square meter was divided into one hundred 10 x 10 cm subquadrats. Within each quadrat the vegetation cover was mapped on cross-section paper. Mapping was repeated every six months for two years. A quadrat that became completely covered by *Dicranopteris* or *Melinis* was extended in the direction of the *Dicranopteris* or *Melinis* movement. Fig. 15

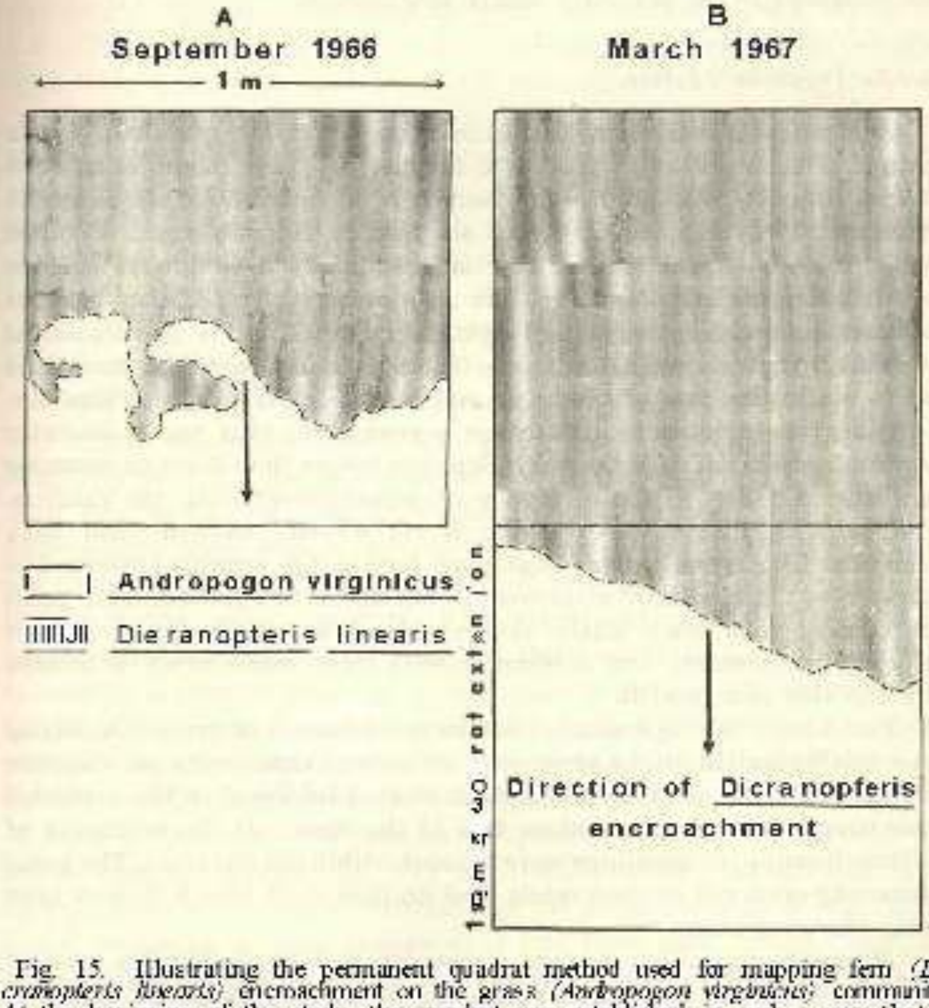

Fig. 15. Illustrating the permanent quadrat method used for mapping fern (*Dicranopteris linearis*) encroachment on the grass (*Andropogon virginicus*) community. At the beginning of the study, the quadrat was established in such a way that it included part of the invading fern and part of the grass cover. When the quadrat was completely covered by the invading fern-mat, it was extended in the direction of the invader's movement. The illustration above illustrates a *Dicranopteris linearis* fern-mat invading an *Andropogon virginicus* community (plot no. 25).

illustrates the technique used in recording invasion. The increase of area occupied by *Dicranopteris* or *Melinis* for every six month period was calculated from the map and expressed in square centimeters. The area was measured to the nearest 5 square centimeters.

5.1.2.2. Invasion by tree

In some plots there were indications that *Metrosideros collina, Acacia koa* and *Grevillea robusta* tended to invade the grass communities. The rate of invasion was studied by counting the number of seedlings in permanent 1 sq. m quadrats every six months for two years. Counted seedlings were tagged so that new arrivals and old seedlings could be recorded. Heights and diameters were also measured. In addition, periodic measurements of diameters and heights of saplings occurring outside the permanent quadrats were also made. The purpose of these measurements was to study the rate of diameter and height increase of the saplings. A sapling was arbitrarily defined as a young tree that had a diameter between 1 and 5 cm near the base. Saplings larger than 5 cm in diameter were excluded due to the difficulty of measurement with the calipers. Saplings with diameters exceeding 5 cm already showed dead bark formation. The measured saplings were tagged for remeasurement. The diameter was periodically measured 15 cm above the ground. This point was marked with black plastic cement. Measurements began in August 1966. Remeasurement and seedling counts were made every 6 months over the two year period.

For *Acacia koa,* 30 saplings were measured and 3 permanent quadrats were established in the *Andropogon virginicus* community at Pupukea (plot no. 25). The permanent quadrats were established in the unshaded grass cover near the only mature tree in the stand. At the beginning of the investigation, no seedlings were present within the quadrats. The grass community occurred on moderately well drained, dark brown to dark grey loamy clay.

Metrosideros collina seedlings were studied at three sites, two at Pupukea (plots no. 23 and 66) and one at Palikea (plot no. 39). The three sites were also in the *Andropogon virginicus* communities.
At Pupukea, Site I was located on a steep slope with exposed, well-drained, reddish brown sandy loam soil,, which appeared to have been deposited from road construction. The grass cover of this site was sparse and *Metrosideros* saplings were abundant and rather evenly distributed. Mature *Metrosideros* tree were present in the surrounding forest. Two

permanent quadrats for seedling counts were established in the center of the grass community about 5 m apart. Twenty one saplings that occurred outside the permanent quadrats were also measured for their diameter and height. The tree density in different size classes (< 0.5; 0.5 —1.0; 1.0 — 2.5; 2.5 — 5.0; > 5.0 cm) was determined by systematic sampling with forty 0.25 sq. m quadrats which were placed at five step intervals.

Site II was located on a poorly drained, podzolized, dark grey clay soil with very dense cover of *Andropogon virginicus* (plot no. 23). The size of the grass community was about 500 square meters. Mature *Metrosideros* trees were present in the surrounding forest and a few stunted ones within the community. Three permanent quadrats were established within the grass cover about 5 m apart. In addition to the seedling count within the quadrats, 11 saplings and young trees occurring outside the quadrats were also measured for diameter and height.

At Palikea (Site III), the *Andropogon virginicus* cover (plot no. 39) was sparse and wind-trained. The grass community was located on a steep and convex slope. The substrate consisted of soft weathered rocks with fine weathered rock fragments or soils in the pockets. Mature *Metrosideros* trees were present in the surrounding vegetation and a few low creeping clumps of *Metrosideros* were present in the grass community mainly at the upper boundary. Five permanent quadrats for seedling counts were established, two near and three about 10 m away from the *Metrosideros* clumps occurring at the upper boundary. The diameter and height of the saplings and young trees outside the permanent quadrats were not measured, because the creeping habit of the stem and the wind-trained upright shoots made the measurement problematic.

The *Grevillea robusta* invasion was studied in a dense *Rhynchelytrum repens* community (plot no. 37) on a well-drained, red silt-loam soil. The *Grevillea robusta* tree population in the grass community was rather dense, occurring in local clumps of a few trees each. Sixteen saplings were measured for diameter and height. Four permanent quadrats (Group I) were established at the beginning of the study (August 1966) in the unshaded part of the grass cover between mature trees. Five additional quadrats (Group II) was established in August 1967, because most of the seedlings recorded in the previous four quadrats had died at that time. Density of trees in different size classes (1 — 5; 5 — 25; 25 — 50; > 50 cm) was determined by absolute count.

5.1.3. Effect of fire

5.1.3.1. Summer-drought zone

The *Chloris barbata* and *Dichanthium aristatum* communities occurred over a large area (about 29 hectares) on Makapuu Flat between Wawamalu Beach Park and Makapuu Point. The *Chloris barbata* community has been accidentally burned-over three times since 1965. The change from the *Chloris barbata* community to the *Dichanthium aristatum* community appeared to be related to the rockiness of the soil, resulting in different water regimes under these two communities.

To investigate the effect of fire and the relationship between the distribution of the two communities and the rockiness of the soil, the area was sampled in spring 1968. Fig. 16 shows a sketch of the vegetation cover and the lay out of the sampling. Sampling was carried out as follows:

1 A base line was set up along the telephone line which runs lengthwise across the area.

2 Thirteen transects were established along this base line at intervals of 50 paces. Except for transect 13, all the transects were perpendicular to the base line. The first transect was subjectively selected in such a way that it did not run over the edge of the community.

3 Along each transect the vegetation was sampled by the step point method (Costello & Schwan, 1946) for cover, by quadrats for frequency of all species, and by the quarter method (Curtis & Cottam, 1962) for the density of *Gossypium tomentosum.* With the step point method the vegetation was recorded by walking along the transect and a sampling point was established at every second step. At each point, a 110 cm long thin steel rod, with a cross bar on one end, was pushed into the ground. Then a long fine wire was gradually lowered to the ground from one side of the cross bar, and every species that was hit by the tip of the wire was recorded. A given species was recorded only once at each point regardless of the number of the hits the wire made on the plants of this species. The records were made from 200 points in each transect. The relative cover of a given species was estimated by:

the number of hits for a given species the
total number of hits for all species

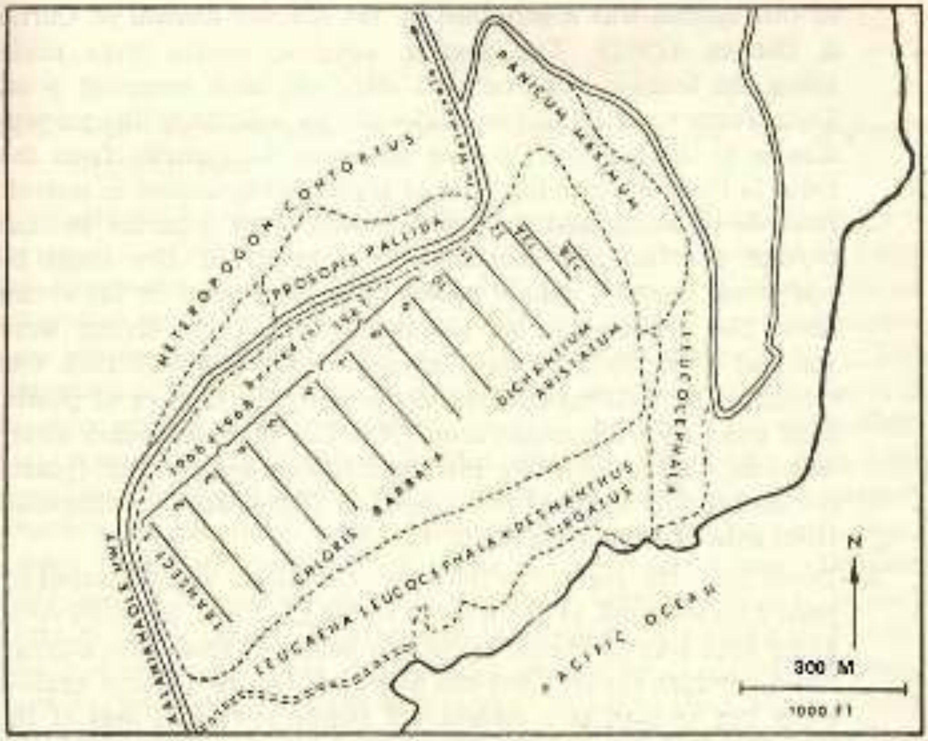

Fig. 16. Sketch of vegetation cover and sampling layout at Makapuu Flat.

and the percent surface cover of the total vegetation was calculated by:

the total number of points with vegetation

the total number of points (= 200)

To record the frequency, a 0.25 sq. m quadrat was placed after every 15 points along the transects. The total number of quadrats in 13 transects was 170.

1 Preliminary observation showed that *Gossypium tomentosum* occurred randomly in the grass community. Therefore, the density of this species was determined by the quarter method of Curtis & Cottam (1962). The quarter sampling points were made along the transects at every 60 steps. At each sampling point 4 quadrants were defined by projecting an imaginary line perpendicular to the transect. In each quadrant the distance from the point to the nearest living or dead plant was measured in meters. Records of living and dead plants were kept separate so that percent survival and mortality as a result of fire could be compared. Seventy sample points were established in the entire area. The distances of all plants, both dead and living, were summed to obtain the total distance. The average distance was calculated by dividing the total distance by the number of plants, dead and living. The mean area (M.A.) of plant in square meter was computed by squaring the average distance. Density (plants per hectare) is assumed to be equal to 10,000/M.A. as computed from data of Curtis & Cottam (1962).

2 Depth from the surface to the rock or hardpan was measured by pushing a steel rod (110 cm long) to the ground at every 30 steps along each transect resulting in 170 points in total. The average depth to which the steel rod can be pushed before it lodges against rocks can be used as a measure of comparative rockiness of the soil (Daubenmire, 1964).

5.1.3.2. Humid zone

A fire occurred also in the humid zone at Kahaluu in August 1968. It burned an area of about 8 hectares that was covered in parts by a *Wikstroemia-Psidium* scrub stand, *Dicranopteris-Metrosideros* woodland and *Andropogon virginicus* grass cover. At the same time, about 20 hectares of *Dicranopteris-Metrosideros* woodland at Kawailoa Forest Reserve, Pupukea, were also burned. To investigate the effect of fire on these communities, the unburned and burned *Andropogon virginicus* grass cover, the burned *Wikstroemia-Psidium* scrub stand and *Dicranopteris-Metrosideros* woodland were sampled one year after the fire. For frequency of the species the quadrat method was used. Forty 0.25 sq. m quadrats were systematically placed in each community at intervals of 10 paces along the east-west compass line. The cover was estimated by the step point method, and the total number of points sampled was 400 in each community. In Pupukea, only about one quarter of a hectare of the burned-over *Dicranopteris-Metrosideros* woodland was sampled.

5.2. RESULTS AND DISCUSSION

5.2.1. Vegetation changes in grass **communities** in the **summer-drought zone**

Table VIII presents the results of grouping the plots according to the percent cover of the exotic invaders. The native *Heteropogon contortus* and *Eragrostis variabilis* decreased with an increase of exotic species. *Gossypium tomentosum, Lipochaeta lobata* and *Myoporum sandwicensis* were native shrubs that occurred in grass communities with a high proportion of exotic herbaceous species. The absence of these species in the plots with fewer exotics, i.e., the plots in the first 3 classes in Table VIII, was due to their special habitat relations. Plots with high cover of exotics (the last 2 classes in Table VIII) were located on the flatland, primarily coastal flats, where these three native species were found. Coastal flats were the typical habitats of *Lipochaeta lobata* (Degener, **1957)** and *Gossypium tomentosum* (Stephen, 1964). *Myoporum sandwicensis*, however, was not restricted to the flatland. According to Webster (1951) it occurred on the lowland hills as well as at higher elevations. However, on Oahu it occurred only in one location at the northwest coast. The three species retained a high cover value in communities with a high cover of exotic herbs which are now dominated by *Chloris barbata* or *Dichanthium aristatum.* The three native species did not compete for space, at least above ground, with the exotic herbaceous plants. The increase in cover by the exotic species and the corresponding decrease in cover by native species applied only to the life forms of the closed stratum; which was the dominant stratum in this community. Other native species showed a sudden decrease where exotic species were numerous but did not completely disappear in communities with a high proportion of exotic

Table VIII. Relative cover of species in grass communities from the summer-drought zone along the gradient of the exotic invasion, as defined by the percent cover classes of the exotic invaders

Percent cover classes of exotic invaders	0 — 19.9	20.0 — 39.9	40.0 — 59.9	60.0 — 79.9	80.0 — 100.0
Number of plots (relevés)	8	15	17	18	17
Heteropogon contortus	57.2	58.9	42.4	14.9	1.5
Eragrostis variabilis	24.6	12.5	2.2	—	0.2
Sida fallax	4.8	1.7	6.8	8.3	2.5
Myoporum sandwicensis	—	—	—	4.5	—
Gossypium tomentosum	—	—	—	0.8	3.8
Lipochaeta lobata	—	—	—	2.1	2.8
Others	4.9	1.3	1.2	1.6	1.9
Exotic species:					
Emilia sonchifolia	1.2	1.7	7.8	9.7	2.1
Leucaena leucocephala	tr (trace)	8.8	7.1	7.7	3.3
Acacia farnesiana	tr	4.1	2.5	3.2	2.0
Rhynchelytrum repens	tr	0.5	9.7	10.8	6.3
Waltheria indica	3.4	2.6	2.7	1.4	0.6
Chloris barbata	—	tr	2.2	9.7	30.0
Phaseolus lathyroides	tr	tr	0.6	0.2	3.0
Dichanthium aristatum	—	—	—	0.8	15.5
Desmanthus virgatus	tr	0.8	0.7	1.9	3.9
Trichachne insularis	—	—	tr	5.8	—
Cassia leschenaultiana	tr	3.7	2.9	2.0	0.7
Panicum maximum	—	—	—	0.2	9.5
Others	4.3	8.8	11.8	14.6	11.9

Rhynchelytrum repens, Chloris barbata and *Dichanthium aristatum* were the most important invading grasses. The invasion of *Rhynchelytrum repens,* in association with other exotics into areas covered by *Heteropogon contortus* and *Eragrostis variabilis,* was prevalent on the slopes. On the flatland, however, *Chloris barbata* and *Dichanthium aristatum* were the most prevalent invaders. Other grass invaders were *Panicum maximum* and *Trichachne insularis,* but they seemed to spread more slowly.

Table VIII shows that the woody *Leticaena leucocephala* had low cover values in all five classes of percent cover of exotic invaders. This was because all the plots, except three plots (no. 45, 48 and 57, Table I), were selected in dry-grass covers that showed less than 40% cover of woody plants. For the same reason, *Prosopis pallida,* an exotic woody invader (Egler, 1947), was recorded only rarely in the grass plots. This is in part the result of the poor dispersal mechanism of the seeds which are spread by cattle (Egler, 1947) seemingly after passing through their digestive tracts.

Invasion of the native grass communities by exotic grasses seemed more successful on the flatlands than on the hillsides. The possibility of the disappearance of the native grass communities on the hillsides is more likely attributable to the invasion by exotic shrubs and trees, such as *Acacia farnesiana, Prosopis pallida* and especially *Leucaena leucocephala* was aggressively invading the native *Heteropogon contortus* and *Eragrostis variabilis* communities. Table IX shows that plants of different size classes were well represented in these native grass communities in the areas where the count was made. Pure or mixed (with *Acacia farnesiana* and *Prosopis pallida)* stands of *Leucaena leucocephala* were abundant in the summer-drought zone. Within the *Leucaena leucocephala* communities, *Heteropogon contortus* and *Eragrostis variabilis* are likely to disappear because they are not shade-tolerant species.

Although the exotic species may be able to fill up empty niches in the native vegetation, the rapid invasion of the latter by exotics is enhanced by man's activities. Man's activities that affect native vegetation and result in disturbance include partial or complete clearing of vegetation, burning, selective removal of certain species, introduction of exotic plants and animals (Fosberg, 1960) and in recent years bulldozing. Thus degree of invasion, as indicated by the percent cover of exotic invaders in a given community, may indicate the degree of disturbance. However, the degree of invasion can be used as a measure of disturbance effects only when dealing with the same vegetation stratum, successional stage and. habitat type. The invasion of the native grass communities by woody

Table IX. Density (plants per hectare) of *Leucaena leucocephala* in different size classes under its own canopy and in the *Heteropogon contortus* and *Eragrostis variabilis* communities

Community	*Heteropogon contortus*		*Eragrostis variabilis*		*Leucaena leucocephala*	
Locality	Makaha	Koko Crater	Makapuu	Koko Crater	Makaha	Makapuu
Number of quadrats	40	80	80	110	40	40
Height classes (cm)						
0 — 25	1,250	2,000	6,625	5,091	61,000	17,125
25 — 100	750	7,000	750	5,455	2,813	49,500
100 +	2,125	1,000	750	0	8,250	53,000

species such as *Leucaena leucocephala* may not be the result of disturbance but simply normal successional change.

As a result of the invasion by exotic species, the native *Heteropogon contortus* and *Eragrostis variabilis* communities in the summer-drought zone have changed and are still changing in their species composition. In many places this change has led to the formation of various exotic communities. Fig. 17 shows a diagram illustrating the possible changes of the native grass communities into various exotic communities. Fat arrows and thin arrows indicate changes as a result of disturbance and normal succession, respectively. Double arrows indicate reversible changes. The *Chloris barbata* and *Dichanthium aristatum* communities, for instance, may be invaded by *Prosopis pallida* if left undisturbed, and conversely the *Prosopis pallida* community may be replaced by *Chloris barbata* and *Dichanthium aristatum* after disturbance.

A change of the native grass communities into the *Rhynchelytrum repens* community occurs in more moist part of the drought zone.

It appears that the changes are leading directly or indirectly towards the formation of the *Leucaena leucocephala* or *Prosopis pallida* communities, which seem to be the end points of the vegetational changes. However, *Leucaena leucocephala* is an aggressive pioneer too (Egler, 1947). Therefore, pure stands of this species may be considered serai communities. The replacement of the *Leucana leucocephala* community by others will depend on the availability of species that can survive arid conditions and can germinate and develop under the shade of *Leucaena leucocephala.* However, *Leucaena leucocephala* is also able to reproduce from seeds under its own canopy as is evident from Table IX. Therefore, the *Leucaena leucocephala* community may remain stable in the absence of invading species.

Field observations indicate that the *Leucaena leucocephala* community helps in retaining and improving soils. Soils are usually dark because of higher organic matter content than under grass covers. Surface soils under *Leucaena leucocephala* seem also more moist than under grass covers in the same area. These soils may provide better seedbeds for the germination of woody species than those under grass covers. On the other hand, survival conditions may be poor due to root competition and shade. Where seed sources are available, native species may replace exotics. Therefore, there is a possibility that the *Leucaena leucocephala* community may be replaced by native woody plants provided there is a seed source. In the absence of native species in the area studied, the *Leucaena leucocephala* community will probably remain in the summer-drought zone

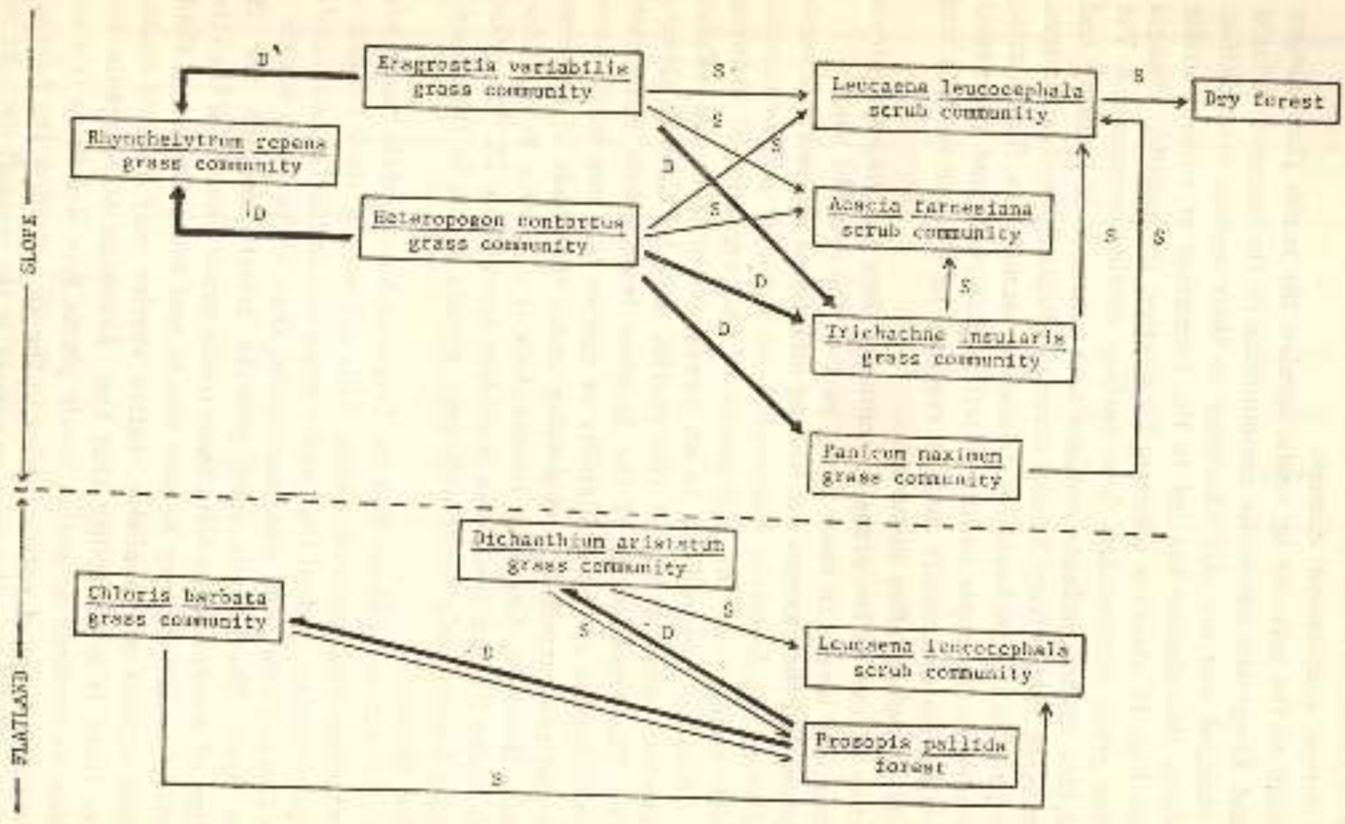

Fig. 17. Possible trends of the vegetational changes in grass communities in the summer-drought zone. D and S indicate the changes as the results of disturbance and normal succession, respectively.

for a long period of time because it can regenerate under its own canopy. The *Leucaena leucocephala* community can develop in a grass community only if there is no grazing and also a grass fire must be absent for some time. In the present investigation, where grazing was absent in the study areas, there were indications that *Leucaena leucocephala* was aggi"essively invading (Table IX) the *Heteropogon contortus* and *Eragrostis variabilis* grass communities. The rate of invasion is yet to be determined.

The remants of native grass communities, composed of *Heteropogon contortus* or *Eragrostis variabilis,* still exist in the summer-drought zone on Oahu today. They occur only in patches of smaller areas in contrast to the exotic woody communities. Photographic records of late 1800's and early 1900's compiled by Scott (1968, note espically p. 583, 675, 692, 700, 719, 791 and 843) indicate that many areas now covered by *Leucaena leucocephala* and *Prosopis pallida* and urban areas were grass communities with scattered trees, apparently spreading *Prosopis pallida.* Therefore, there are reasons to believe that at one time the arid vegetation of Oahu was grassland dominated by *Heteropogon contortus* or *Eragrostis variabilis.* Native trees and shrubs, such as *Canthium odoratum, Gossypium tomentosum, Lipochaeta lobata, Myoporum sandwicensis, Erythrina sandwicensis, Osmanthus sandtuicensis, Reynoldsia sandivicensis, Sapindus oahuensis* and *Santalum ellipticum,* were probably scattered throughout. Most of these species are still found in the dry area and many of them are also components of the semideciduous seasonal forest (Hatheway,

1952).

5.2.2. Vegetation changes in grass communities in the summer-dry and humid zones

5.2.2.1. Invasion by herbaceous plants

(i) *Dicranopteris linearis*

The *Dicranopteris linearis* fern-mats were encroaching into the *Andropogon virginicus* communities at a steady rate. Fig. 18 shows the regression of the area gained by *Dicranopteris linearis* on time, which was significant at the 0.1 percent level. The rate of encroachment per square meter was 0.05 sq. m/month (0.6 sq. m/year) or a linear distance of 0.6 m per year.

In most cases *Dicranopteris linearis* was advancing actively, but in two quadrats (in plot no. 23 at Pupukea) *Dicranopteris linearis* growth

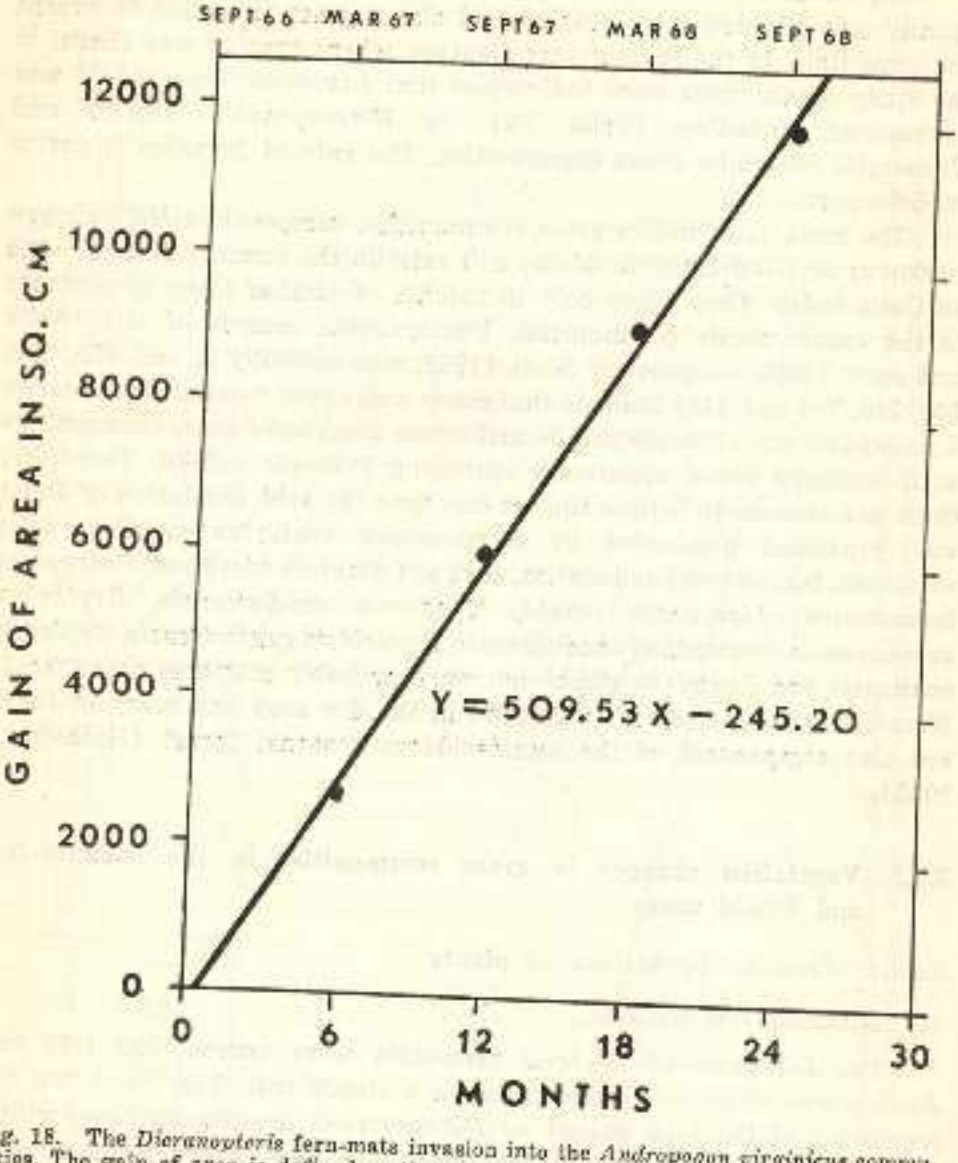

Fig. 18. The *Dicranopteris* fern-mats invasion into the *Andropogon virginicus* communities. The gain of area is defined as the total area of the ground cover by *Dicranopteris linearis* within the plot or extended plot at a certain period of measurement minus the area at the beginning of the study. The regression is highly significant ($t = 43.364 > t_{05}$).

was poor, it often died back. The poor growth was probably due to the poorly drained soil.

The rhizomes of *Dicranopteris linearis* send up erect stipes of the fronds. The fronds branch repeatedly forming thickets that overtop the grass bunches shading out the grass. Once the fern-mats are established, it is almost impossible for other autotrophic species to grow. The invasion of the *Dicranopteris linearis* fern-mats by native woody species seems possible only if the fern-mat breaks apart. Openings will permit seeds to germinate and seedlings to develop. The frequent occurrence in the *Dicranopteris linearis* fern-mats of woody species, commonly *Acacia koa* and *Metrosideros collina,* may be explained as tree establishment before the advent of *Dicranopteris linearis* or concurrently with it. *Acacia koa* and *Metrosideros collina* can germinate best on bare moist ground when exposed to direct sunlight.

The rapid encroachment of *Dicranopteris linearis* thickets into the *Andropogon virginicus* communities will eventually eliminate the latter in areas where both are found together. However, the total disappearance of the *Andropogon virginicus* cover is prevented by fire. Available evidence (see the section dealing with the effect of fire) indicates that burned *Dicranopteris linearis* does not resprout, but fire favours the regrowth of *Andropogon virginicus.* A burned-over *Dicranopteris linearis* thicket was invaded by grasses, such as *Paspalum orbiculare, Setaria geniculata* and *Meiinis minutiflora* in the first year after the fire, and later it appeared to be followed by *Andropogon virginicus.* Fire, therefore, not only perpetuates the grass cover but may extend it also.

(ii) *Melinis minutiflora*

The *Melinis minutiflora* grass-mats were encroaching into the *Rhynchelytrum repens* communities. The rate of encroachment varied from time to time following the fluctuation of rainfall. Fig. 19 shows the regression of the area gained by *Melinis minutiflora* on time. Although the regression was significant, the growth of *Melinis* was rather erratic. In some quadrats the area gained in 12 months was less than in the previous 6 months record, and in one quadrat it even showed a slight retreat. At another time (after 20 months), the area gained was 3 to 12 times the area gained in the first six months. The erratic growth of *Melinis* was related to the fluctuation of the rainfall. The highest rate of growth occurred in the second year of observations from September **1967** through April 1968, where the rainfall recorded was the highest.

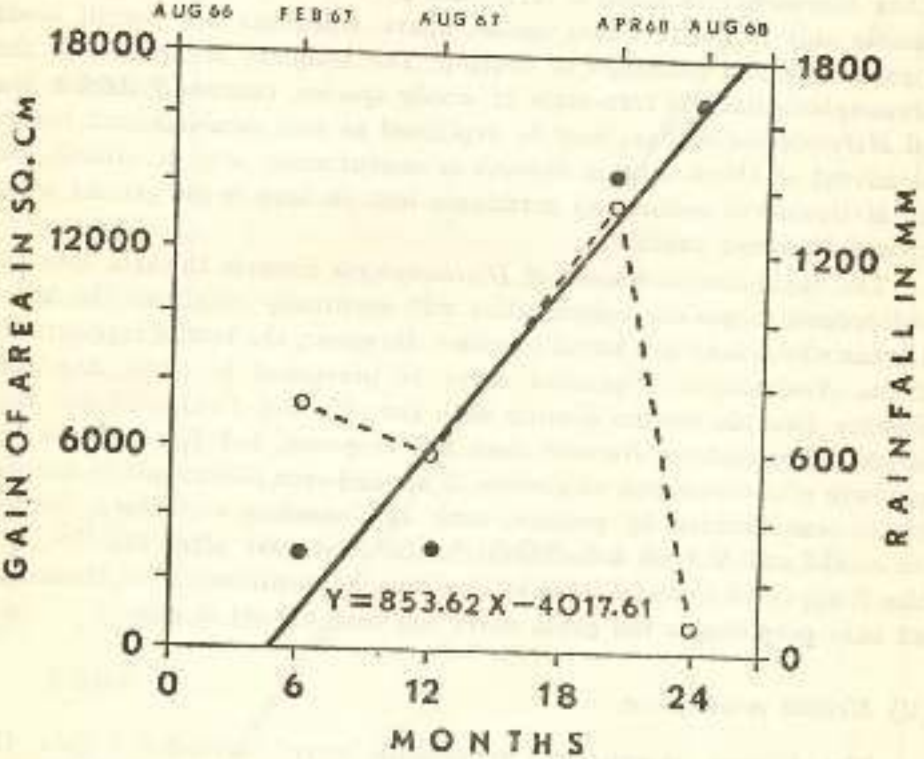

Fig. 19. The *Melinis minutiflora* encroachment into the *Rhynchelytrum repens* community. The regression is significant at $t = 4.486 > t_{.05}$. The dashed curve indicates the rainfall during the observation period as recorded at the nearest rainfall station (Kunia Camp).

Although the rainfall dropped to less than 100 mm between April 1968 and August 1968, *Melinis* still increased in area. Soil might be wet enough to maintain the *Melinis* growth. Soil moisture data from the neighboring *Rhynchelytrum repens* community (Fig. 12, station 5 and Table VII) showed that at least untill the end of May 1968 the soil moisture was available.

Although the increase of area varied from quadrat to quadrat and from time to time, the average values showed a definite increase of the *Melinis minutiflora* cover with time. The average rate of increase per square meter was 0.09 sq. m/month (1.08 sq. m/year). This implies that out of a square meter of the *Rhynchelytrum repens* cover that borders the *Melinis minutiflora* community, *Melinis minutiflora* gains the whole square meter plus 0.08 sq. m each year. Thus with the annual encroachment rate of *Melinis minutiflora* of 1.08 m/year in linear distance, it would take 9.25 years to overgrow the 10 m distance in a 10 x 10 sq. m of a *Rhynchelytrum repens* community that is bordered by the *Melinis minutiflora* cover. It was observed also that the *Melinis minutiflora* invaded bare ground either by vegetative reproduction or by colonizing it with seeds.

The established *Melinis minutiflora* community forms a thick mat consisting of interwoven branches that make it almost impossible for other autotrophic plants to grow. The presence of woody plants within the community may not be due to recent invasion but rather to their establishment before the advent of *Meiinis minutiflora.* Its ecologial effects are, therefore, quite analogous to those of *Dicranopteris linearis.*

5.2.2.2. Invasion by trees

(i) *Acacia koa* invasion

Acacia koa was unable to invade the dense *Andropogon virginicus* community. *Acacia koa* seed germinated only on moist ground that was exposed to sunlight. The presence of *Acacia koa* saplings within the *Andropogon virginicus* communities was not due to the recent invasion but rather to their establishment before the arrival of *Andropogon virginicus* or concurrently developed with it after fire. The rate of diameter and height growth of *Acacia koa* saplings was linear with time. Because of the shading effect of *Acacia koa* and the *Dicranopteris linearis* encroachment, it can be predicted that the *Andropogon virginicus* community in plot no. 25 will disappear in less than 12 years.

During the two years of study, no seedlings of *Acacia koa* were recorded in the permanent quadrats or seen nearby, although seeds were abundant from the parent trees surrounding the grass plot. Evidently these seeds were unable to germinate under the thick cover of *Andropogon virginicus.* Field observations elsewhere showed that seeds readily germinated in either cleared forest (for planting) or burned-over forest. In Kahaluu and Pupukea, in the burned-over forests (burned in August 1968), seeds germinated readily and seedlings reached an average height of 5 cm one month after the fire. In one year the average seedling height was 101.2 cm and the average diameter at 15 cm above the ground was 0.95 cm as calculated from 25 seedlings. In a two acre burned-over *Pandanus* forest at Kahaluu, where two mature *Acacia koa* trees were present, systematic sampling with forty 0.25 sq. m quadrats resulted in an estimate of seedling density of 41,214 per hectare (16,486 per acre).

The diameter and height measurements of 30 *Acacia koa* saplings were taken in an area of about 300 sq. m, which was covered by an *Andropogon virginicus* community (plot no. 25) located in a *Metrosideros Acacia* forest opening. The results are shown in Figs. 20 *&* 21. It is evident that the relationships between the diameter and height were linear with time. The rate of the diameter increment was 0.65 mm per month (7.8 mm per year), and that of the height was 3.99 cm per month (48 cm per year). The increment of height and diameter was closely correlated as shown by the high correlation coefficient (r = 0.962). The average height increment per 1 mm diameter was 5.97 centimeters. This indicates that *Acacia koa* grows rapidly and steadily, at least in the early stage of growth.

By extrapolation from the regression equations, the values of 10.9 cm for diameter and 7.3 m for height were obtained for the age of 12 years. These values are extremely close to the values obtained by Whitesell (1964) from direct measurements of diameter and height in a 12-year old plantation. This shows that the rate of the diameter and height growth until this age can be assumed linear with time. Therefore, one may predict the size increase of *Acacia koa* saplings from the regression equations up to 12 years. The current mean diameter and height of *Acacia koa* saplings, occurring in the 300 sq. m *Andropogon virginicus* plot, are 2.3 cm and 2 m respectively. In 12 years these saplings will reach the young tree stage with a diameter of 10.9 cm and a height of 7.3 meters. The crown spread of a tree of this size was estimated to be about 10 sq. meters.

(There was a close correlation between the crown diameter and stem diameter of the saplings with r = 0.892). The 30 saplings will have a

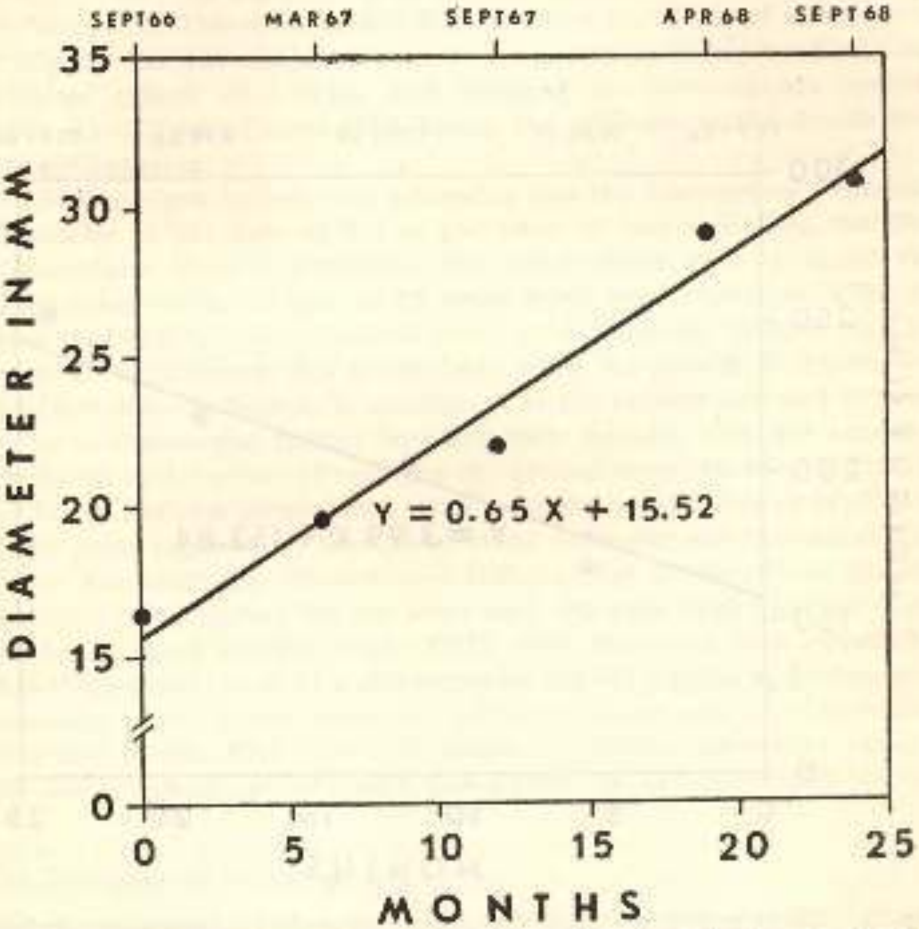

Fig. 20. Diameter growth rate of 30 *Acacia koa* saplings in an *Andropogon virginicus* community at Papukea. The regression is significant at $t = 11.54 > t_{.01}$

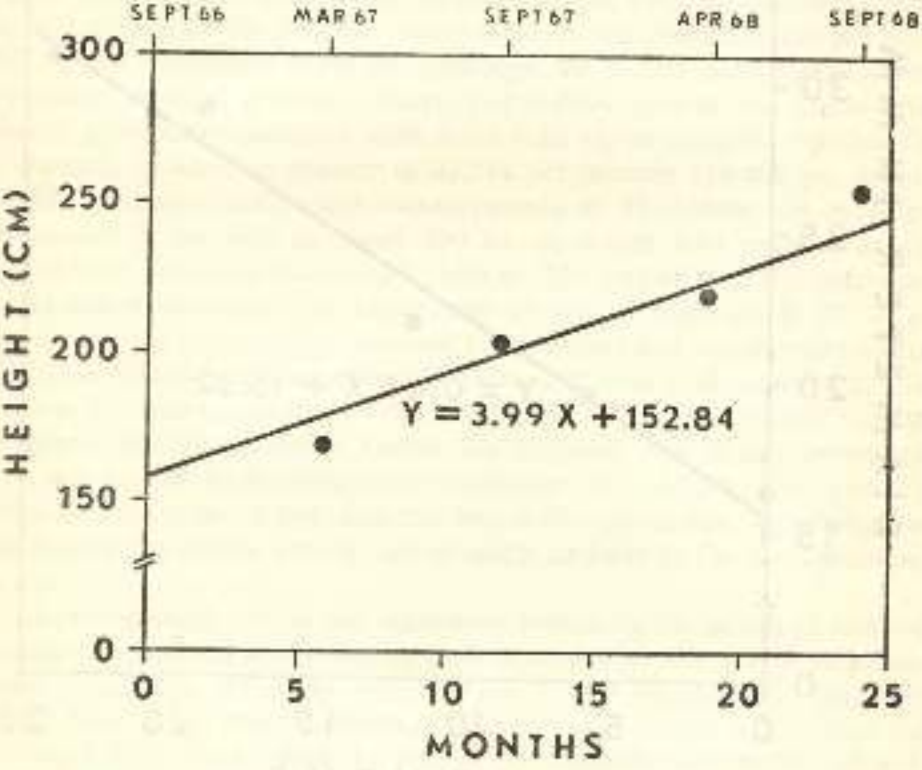

Fig. 21. Height growth rate of 30 *Acacia koa* saplings in an *Andropogon virginicus* community at Pupukea. The regression is significant at $t = 5.890 > t_{05}$.

total crown cover of 300 sq. m in 12 years. However, these saplings occur on one side of the grass community and the crown cover will shade out approximately one half (150 sq. m) of the grass cover only. *Andropogon virginicus*, a major species of serai communities on abandoned fields (Bazzaz, 1968; Harlan, 1956; Keever, 1950; Oosting, 1942), is not a shade tolerant grass. Therefore, it will die out under the shade of *Acacia koa.* In this plot the *Andropogon virginicus* community was almost rectangular in shape (about 20 x 15 m) and bordered by *Dicranopteris linearis* fern-mats on two adjacent sides facing the sides where the *Acacia koa* saplings occurred.

Dicranopteris linearis was advancing into the *Andropogon virginicus* community at the rate of 0.6 m per year. It was estimated that the *Dicranopteris linearis* fern-mats will cover about 250 sq. m of the *Andropogon virginicus* plot in 12 years from now. Therefore, after 12 years the *Andropogon virginicus* cover on the 300 sq. m area may no longer exist. However, this is true only when the growth of *Acacia koa* and *Dicranopteris linearis* is maintained at the present rate and if there are no environmental factors impeding their growth. Fire, for example, despite its initial effect of reducing the ground cover, thereby favouring the *Acacia koa* seed germination, will favour the maintenance or expansion of the grass community, because it would reduce or kill the established *Acacia koa* seedlings. Observations indicate that *Dicranopteris linearis* fern-mats when burned did not come back one year after fire, but were invaded by grass species (Table XXI). Fire, therefore, may extend the area of the grass cover. Fire also increases the importance of *Andropogon virginicus* in this grass community as the frequency and cover increased after fire (Table XX). The *Andropogon virginicus* community plays a role also in promoting fire since it forms a continuous inflammable matrix.

(ii) *Metrosideros collina* invasion

Metrosideros collina was unable to invade the dense *Andropogon virginicus* communities. However, it invaded several sparse *Andropogon virginicus* communities occurring in moist and dry habitats with a rate of seedling establishment of 27.2% and 8.3%, respectively. In moist and dry habitats the diameter growth of the seedlings was slow and the height growth was erratic. On the other hand, the diameter growth of the saplings in the moist habitat was faster than that of the seedlings. Using the regression equations of the diameter growth of the saplings, it is predicted that in the moist habitat *Metrosideros collina* will replace the

Andropogon virginicus community in less than 50 years, while on the boggy habitat *Andropogon virginicus* will remain the main cover in the community. Because of the strong wind effect, *Andropogon virginicus* in the habitat will remain also the dominant cover.

Table X shows data on invasion of *Metrosideros collina* into three *Andropogon virginicus* communities. In site II (plot no. 23), where a poorly drained soil supported a dense *Andropogon virginicus* cover, no seedlings were recorded at the beginning and at the and of the observation period. In sites I and III, where *Andropogon virginicus* bunches were sparse, the number of seedlings was high. The seedlings grew exposed to sunlight. No seedlings were observed under the dense cover. Observations in the surrounding forests and elsewhere showed that seedlings were growing on dead tree trunks and even on living trees, if these were exposed to sunlight. The three sites were located in areas surrounded by *Metrosideros* forests.

The lower percent of mortality in site I compared with site III was probably attributable to better environmental conditions for seed germination and seedling development. The soil at site I was deep, well-drained and constantly moist. The site is located in the high rainfall area, where the annual median rainfall is 3302 millimeters. The higher mortality at site III may be attributed to the fact that the seedlings were growing on shallow soil pockets (10 — 30 cm deep) between rocks. This site is located in the lower rainfall area, where the annual median rainfall is only 785 millimeters. A dry period occurs in the summer (i.e., it is in a summer-dry climate). In addition, strong winds blow throughout the year at site III which might have a desiccating effect on both soil and vegetation. It is also likely that there was a competition for water between grass and *Metrosideros* seedlings. The vegetation cover of the site was thin, where the average height of the grass shoots and *Metrosideros collina* was only 30 centimeters.

Figs. 22 & 23 show the growth rate of the *Metrosideros collina* seedlings. There was a significant regression of the diameter increase on time in both sites I and III. The diameter growth rate of the seedlings in site I was 0.025 mm/month and in site III 0.024 mm/month. At both sites the growth rate was slow and showed the same pattern. Since site I was located in a better habitat than site III, factors controlling the growth rate may not be physical factors alone. Slow growth was perhaps due to an unknown inherent factor. Table XI shows that there was an insignificant height increase of the seedlings in site I, while in site III the height decreased. In site III it was observed that the shoot tips often died

Table X. *Metrosideros collina* seedlings in the *Andropogon virginicus* communities during two year observations. The figures are mean numbers of seedlings per square meter or percent values

	Pupukea		Palikea
	Site I	Site II	Site III
	Slope, deep well-drained soil, sparse grass cover	Gentle slope, deep boggy soil, closed grass cover	Slope, rocky shallow soil, sparse grass cover
Number of quadrats	2	3	5
Number of seedlings first recorded (Sept. 1966)	26.0	0	28.8
Number of later arrivals in two years	13.5	0	14.6
Total number of seedlings in two years	39.5	0	43.4
Number of seedlings dead after two years	18.0	0	36.2
Number of seedlings surviving after two years	21.5	0	7.2
Percent of seedlings establishment rate per year	27.2	0	8.3
Percent of mortality	46.6	0	83.4
Percent of survival	54.4	0	16.6

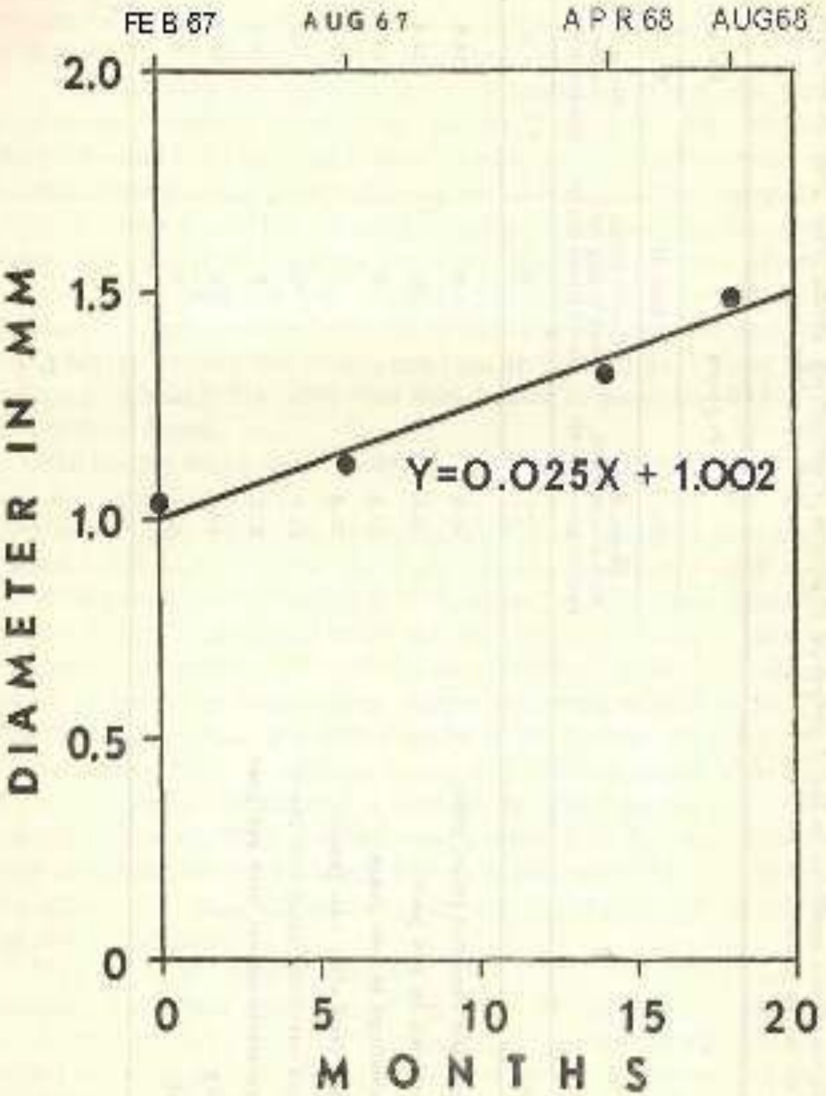

Fig. 22. Diameter growth rate of *Metrosideros collina* seedlings in an *Andropogon virginicus* community, occurring on a well-drained soil at Pupukea (Site I). The regression is significant at $t = 8.071 > t_{.05}$.

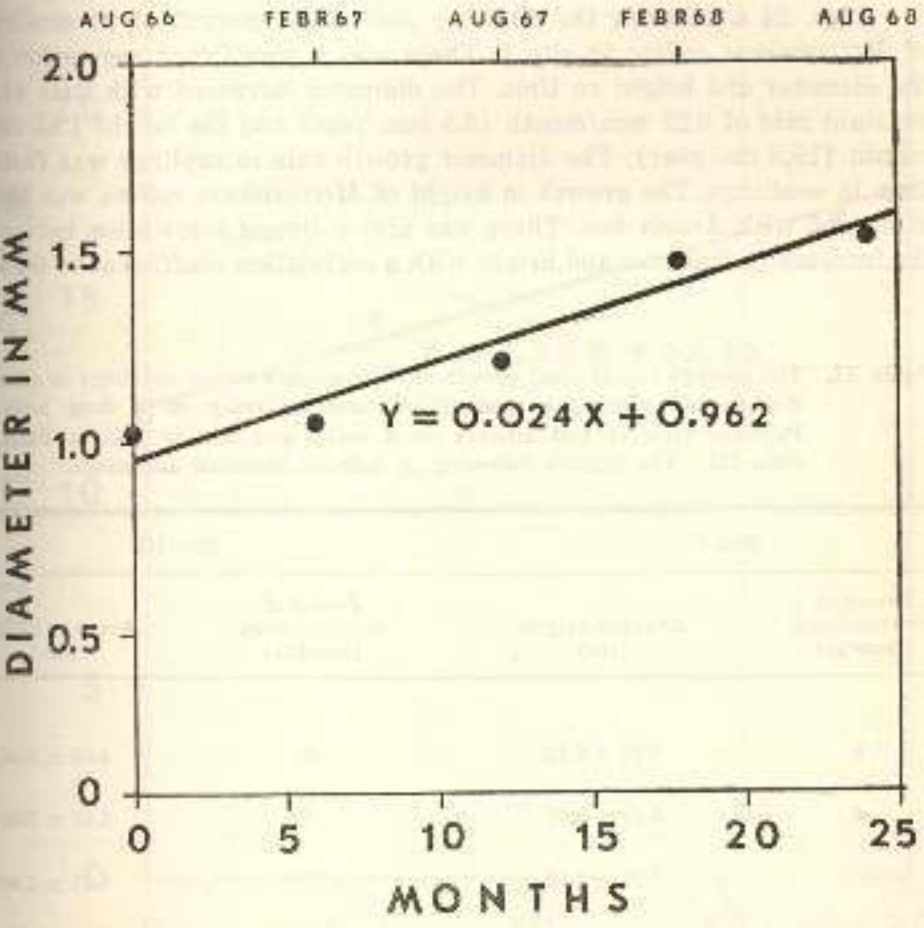

Fig. 23. Diameter growth rate of *Metrosideros collina* seedlings in an *Andropogon virginicus* community, occurring on a rocky, shallow soil at Palikea (Site III). The regression is significant at $t = 7.668 > t_{.05}$.

back, perhaps due to the desiccating effect of wind. The presence of galls at the tips of the seedlings would have also prevented the growth of the terminal shoots, but the seedlings did continue growing by producing lateral shoots. Some individuals, however, grew to 12 cm in 1.5 years, while others did not increase at all. It appeared that individuals were effected differently.

Figs. 24 & 25 show the diameter and height growth of 21 saplings of *Metrosideros collina* in site I. There was a significant regression of the diameter and height on time. The diameter increased with time at a constant rate of 0.29 mm/month (3.5 mm/year) and the height 1.65 cm/month (19.8 cm/year). The diameter growth rate in saplings was faster than in seedlings. The growth in height of *Metrosideros collina* was slow compared with *Acacia koa*. There was also a strong correlation between the increase of diameter and height with a correlation coefficient of 0.942.

Table XI. The average height (cm) growth of *Metrosideros collina* seedlings in sparse *Andropogon virginicus* communities, one occurring on a deep soil at Pupukea (site I) and another on a rocky and shallow soil at Palikea (site III). The figures following ± indicate standard deviations.

Site I		Site III	
Period of measurement (months)	Average height (cm)	Period of measurement (months)	Average height (cm)
0	4.56 ± 3.42	0	4.86 ± 3.56
6	6.19 ± 3.69	6	4.48 ± 3.60
14	7.38 ± 4.12	12	4.81 ± 2.90
18	7.86 ± 4.05	18	4.45 ± 2.29
		24	4.25 ± 2.69

There was no significant regression of the height increase on time, with $t = 1.414 < t_{[illegible]}$ for site I, and $t = 2.063 < t_{19}$ for site III. The number of seedlings measured was 25 in site I and 20 in site III.

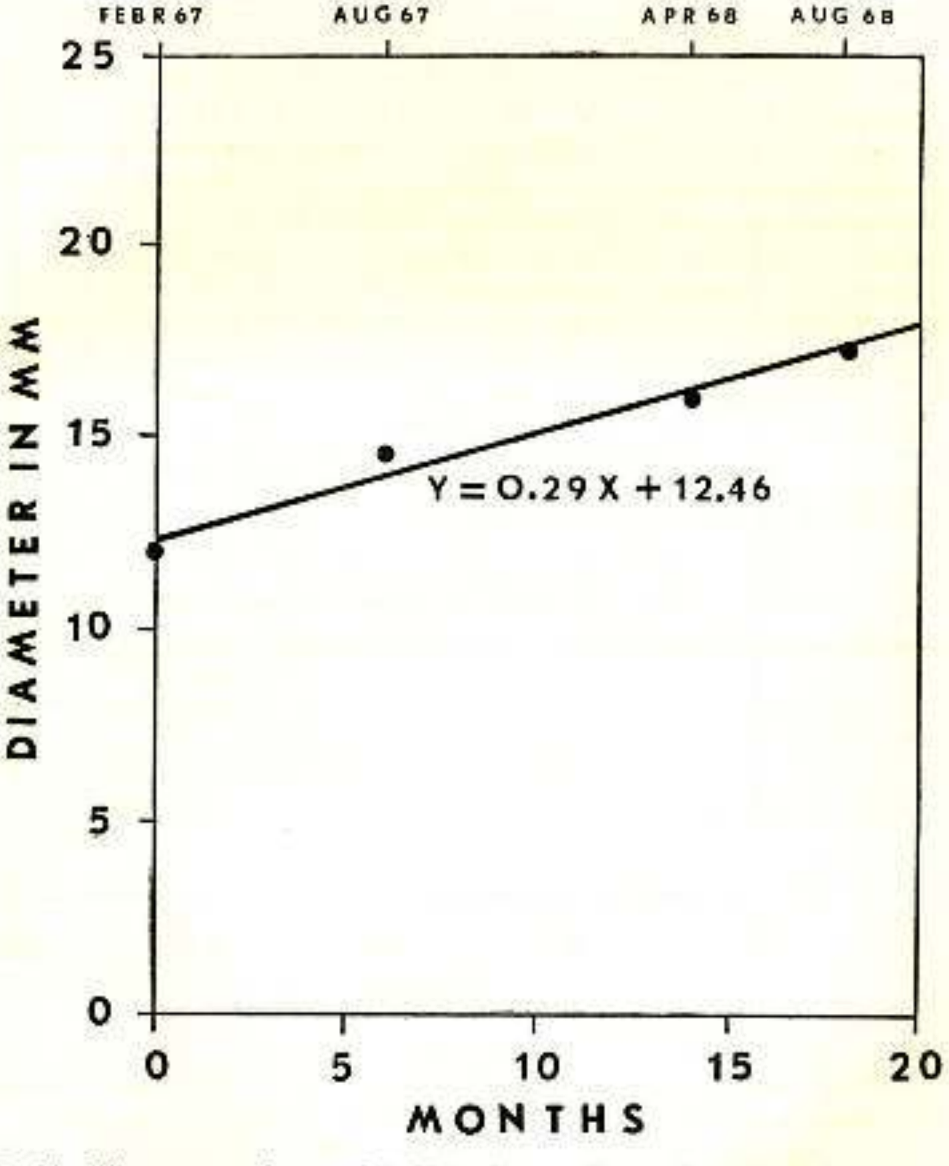

Fig. 24. Diameter growth rate of 21 *Metrosideros collina* saplings in an *Andropogon virginicus* community, occurring on a well-drained soil at Pupukea (site I). The reregression is significant at $t = 11.693 > t_{99}$.

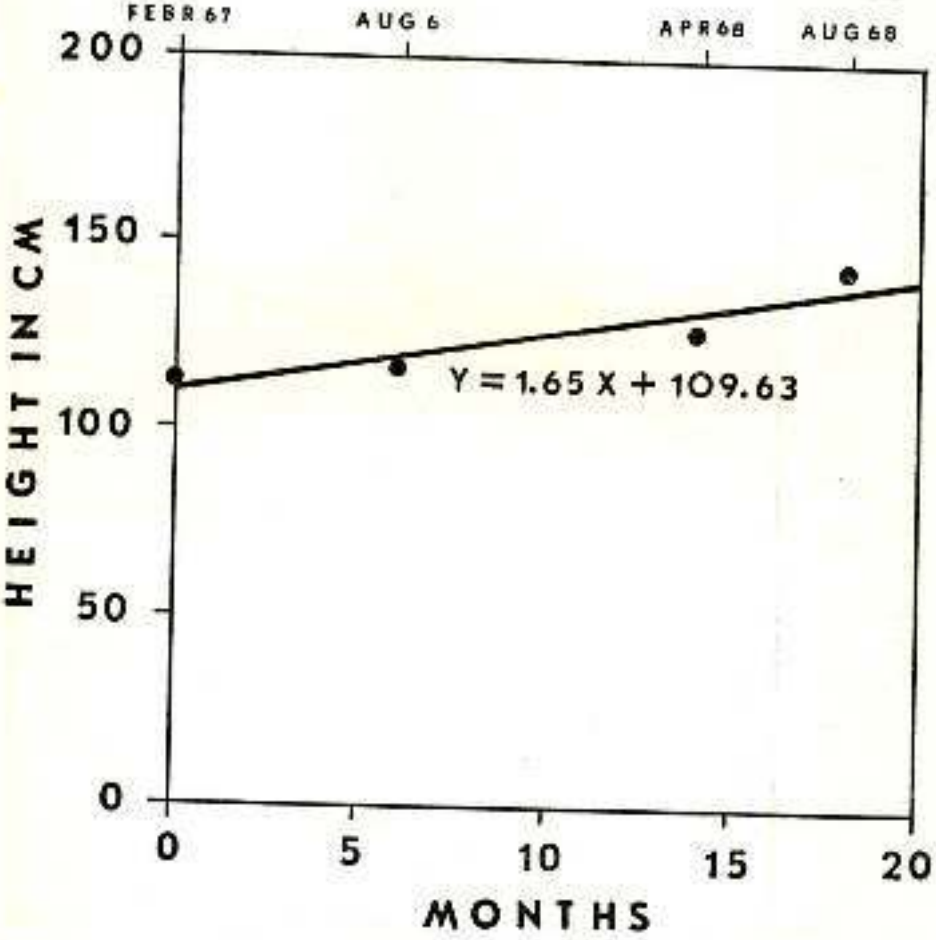

Fig. 25. Height growth rate of 21 *Metrosideros collina* saplings in an *Andropogon virginicus* community, occurring on a well-drained soil at Pupukea (site 1). The regression is significant at $t = 4.697 > t_{.05}$.

The average diameter of twenty measured old *Metrosideros collina* trees in the surrounding forest was 19 ± 5 centimeters. The time required to reach 19 cm diameter for saplings, now having an average diameter of 1.52 cm, can be estimated by extrapolating the average diameter of the mature trees into the regression equation Y = 0.29 X + 12.46, giving the value of time 610.7 ± 224.4 months (51 ± 19 years) at 5% probability level. This time calculation assumes that the rate of growth is constant at 0.3 mm per month. However, in reality the rate of diameter growth may not be constant, because diameter growth is strongly influenced by density. The estimated value obtained may not be accurate, but it may serve as a rough approximation. The relationship between the diameter growth and time is probably curvilinear, but with the short observation time, an estimation with curvilinear regression may be misleading. It is reasonable, therefore, to predict that site I will be forested in 30 to 70 years, provided the tree density remains high. At present, site I is densely populated (Table XII) by *Metrosideros collina* saplings of different size classes. The disappearance of the *Andropogon virginicus* cover on this site may occur in a shorter time.

In site II where the soil was boggy throughout the year because of a perched water table, the rate of diameter increase (Fig. 26) was only 0.14 mm/month. The height of the plants fluctuated from time to time (Table XIII) because the apical shoots died back frequently and regrowth was continued by lateral shoots. The average height of 11 trees was only 1.04 meters. These short plants were mature as they produced flowers and fruits every year. *Metrosideros collina* trees in the surrounding forest had an average diameter of 18.7 cm and an average height of 8.5 meters. Considering the slow growth rate of the trees on this site, namely only 3.5 mm diameter increment and no height growth in two years (Table XIII), and the absence of any new tree regeneration by seedlings in two years, the *Metrosideros* stand will probably stay open and stunted, while *Andropogon virginicus* will remain the main cover.

(iii) *Grevillea robusta* invasion

Grevillea robusta was invading a *Rhynchelytrum repens* community with a slow annual rate of seedling establishment, i.e., 26.5% in the first year and *4.6 fo* in the second year. The height and diameter growth of the seedlings was extremely slow. On the other hand, the diameter and height growth of the saplings was faster than that of the seedlings. Using the regression equation for the diameter growth, it was predicted that

Table XII. Relative density and relative frequency of *Metrosideros collina in various* size classes in an *Andropogon virginlcus* community on a well-drained soil at Pupukea (site I)

Diameter classes (cm)	Relative density (%)	Relative frequency (%)
< 0.5	63.5	
0.5 — 1.0	16.9	33.8
1.0 — 2.5	15.2	26.5
2.5 — 5.0	4.5	1.5
> 5.0	—	—

Table XIII. Average height growth of 11 *Metrosideros collina* trees in a dense *Andropogon virginicus* community, occurring on boggy soil at Pupukea (site II). Figures following ± indicate standard deviations

Period of Measurement (months)	Average height (cm)
0	101.8 ± 11.0
6	99.4 ± 16.4
12	102.9 ± 19.8
20	104.6 ± 25.1
24	103.8 ± 21.8

the *Rhynchelytrum repens* and *Melinis minutiflora* communities would be replaced by a *Grevillea rosbusta* community in less than 45 years, provided that the tree density increases or remains unchanged.

Observations on the *Grevillea robusta* invasion were carried out from August 1966 to August 1968 every 6 to 8 months. The results are summarized in Table XIV. In group I, where four one sq. m quadrats were established, 18 out of 33 total seedlings recorded were dead at the

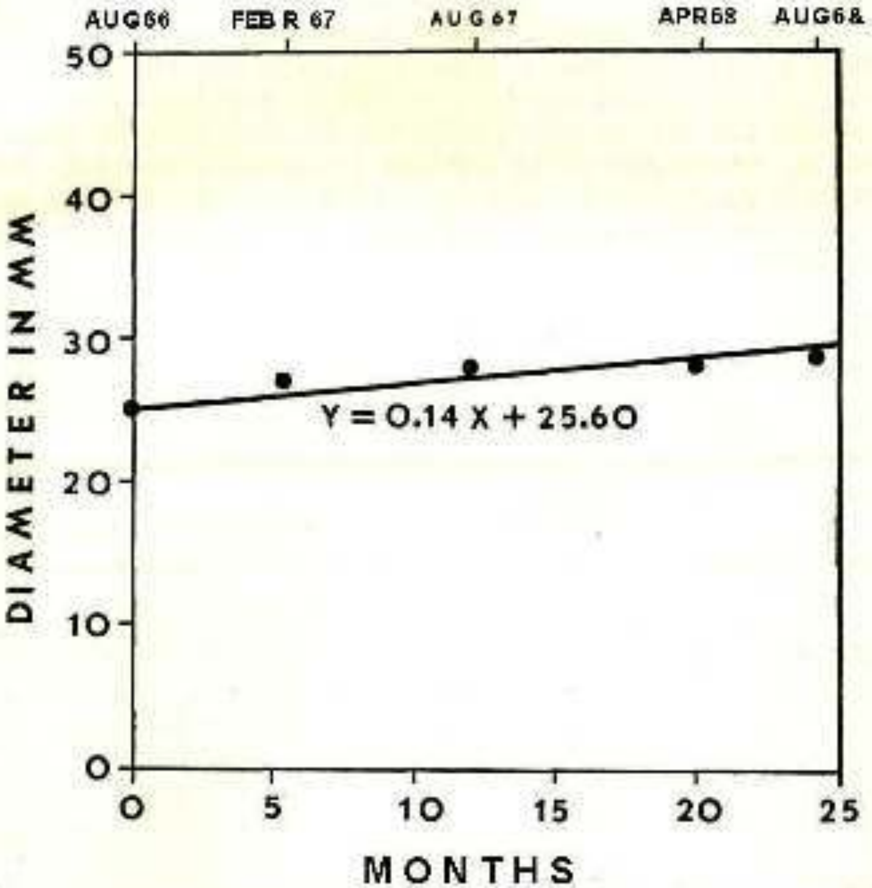

Fig. 26. Diameter growth rate of 11 *Metrosideros collina* trees in an *Andropogon virginicus* community, occurring on a boggy soil at Pupukea (site 11). The regression is significant at t = 7.45 > tn.

end of the first year of observation (August 1967) resulting in a mortality rate of 60.67c. At the conclusion of the study (August 1968) the rate *sf* mortality increased to 90.9% and the only survivors were the new seedlings recorded in April 1968. In group II (five additional quadrats established in August 1967) the seedling mortality one year later was 71.4%. This was higher than that recorded in the first year in group I.

The average diameter of 6 months old seedlings was 1.3 mm and the height was 8.7 cm (average of groups I and II). It was difficult to follow the growth of the seedlings for more than one year, sines most of the seedlings died one year after germination. However, Table XV indicates that the growth rate of the surviving ssedlings was extremely slow. The slow growth rate and high mortality of seedlings may be due to a toxic substance exuded by the neighbouring adult *Grevillea robusta* trees (allelopathy).

i. Table XVI shows that the *Rhynchelytrum repens* community and the adjoining *Melinis minutiflora* community were populated by *Grevillea robusta.* The distribution of the size classes suggests that the entry of *Grevillea robusta* into the grass communities took place at different times. Saplings and young trees were found within the grass communities away from the adult trees. This supports the allelopathy theory (Tukey, 1969) concerning seedling survival.

Considering that *Grevillea robusta* has a high mortality and slow growth rate of the seedlings, it may be inferred that this species is not an aggressive invader.

Figs. 27 & 28 show that the diameter and height of saplings increased steadily with time. The average growth rate for 16 saplings was 0.72 mm/ month (8.6 mm/year) in diameter and 4.98 cm/month (60.0 cm/year) in height. The average diameter at breast height of 10 mature trees growing at the edge of the grass community was 40.4 centimeters. Extrapolation of this value into the sapling regression equation for diameter gave the estimate of time of 533.53 ± 43.12 months (44.5 ± 3.5 years). From this, one may imply that *Grevillea robusta,* whose current average diameter was 2.9 cm, will reach the mature tree stage (defined as 40 cm diameter at breast height) in about 44 years. In reality, however, it may take less time.

Provided that the tree density (240/hectare, see Table XVI) remains unchanged or increases, one may predict that the grass community will be mostly shaded by *Grevillea robusta* in less than 45 years. Since the currently present grasses are not shade-tolerant, most of the grass cover will probably disappear from the area. The time to reach this stage is

Table XIV. *Grevillea robusta* seedlings in a *Rhynchelytrum repens* community during two years of observation. The figures are mean numbers of seedlings per square meter or percent values

	Group	
	I (Aug. '66 — Aug. '68)	II (Aug. '67 — Aug. '68)
Number of quadrats	4	5
Number of seedlings first recorded	2.75	7.00
Number of later arrivals	8.25	2.80
Total number of seedlings	11.00	9.80
Number of seedlings died	10.00	7.20
Number of seedlings survived	1.00	2.60
Percent of seedling establishment rate per year	4.60	26.50
Percent of mortality	90.90	73.5
Percent of survival	9.10	26.5

Tables XV. Average diameter and height of *Grevillea robusta* seedlings in a *Rhynchelytrum repens* community during two years of observation. The data were based on 8 seedlings in group I and 11 in group II. The measured seedlings that died during the observation were excluded

		Date of measurement				
		Aug. '66	Febr. '67	Aug. '67	Apr. '68	Aug. '68
Group I	Diameter (mm)	1.1	1.3	—	—	—
	Height (cm)	6.1	6.3	—	—	—
Group II	Diameter (mm)	—	—	1.1	1.2	1.2
	Height (cm)	—	—	11.2	11.2	11.2

Table XVI. Size class distribution of *Grevillect robusta* in 0.5 hectare *Rhynchelytrum repens* and *Melin'is minutiflora* communities at Kunia. The number of plants was obtained by counting all the trees within this 0.5 hectare area

Diameter classes (cm)	Number of plants per hectare	Percent density
1-5	72	30.0
5 — 25	136	56.7
25 — 50	32	13.3
>60 N*		

Total number of trees: 240

perhaps shorter since the majority of the saplings and young trees have larger diameters (5 — 50 cm, Table XVI), than the saplings (1 — 5 cm in diameter) used for the camputation of the regression curves.

5.2.2.3. Conclusions

Andropogon virginicus is an exotic species of recent introduction. The development of all *Andropogon virginicus* communities has taken place within the last 40 years. The area now occupied by this community type was probably covered by *Paspalum orbiculare* and *Setaria geniculata.* These two grasses were present in the *Andropogon virginicus* communities but occupied less than 10 percent of the vegetation cover. The *Andropogon virginicus* communities were invaded by *Dicranopteris linearis* fern-mats, wherever the two communities had a common boundary.

There was also an indication that *Acacia koa* was invading the *Andropogon virginicus* communities in the koa zone which was possible with the help of fire that cleared the grass cover and exposed the ground to light, thus facilitating seed germination; Likewise,Me*trosideros collina* seemed to require exposure to light for seed germination. It entered the *Andropogon virginicus* communities when the grass cover was sparse. Therefore, in this respect it behaves like *Acacia koa.* Under favourable environmental conditions, the *Andropogon virginicus* that were invaded

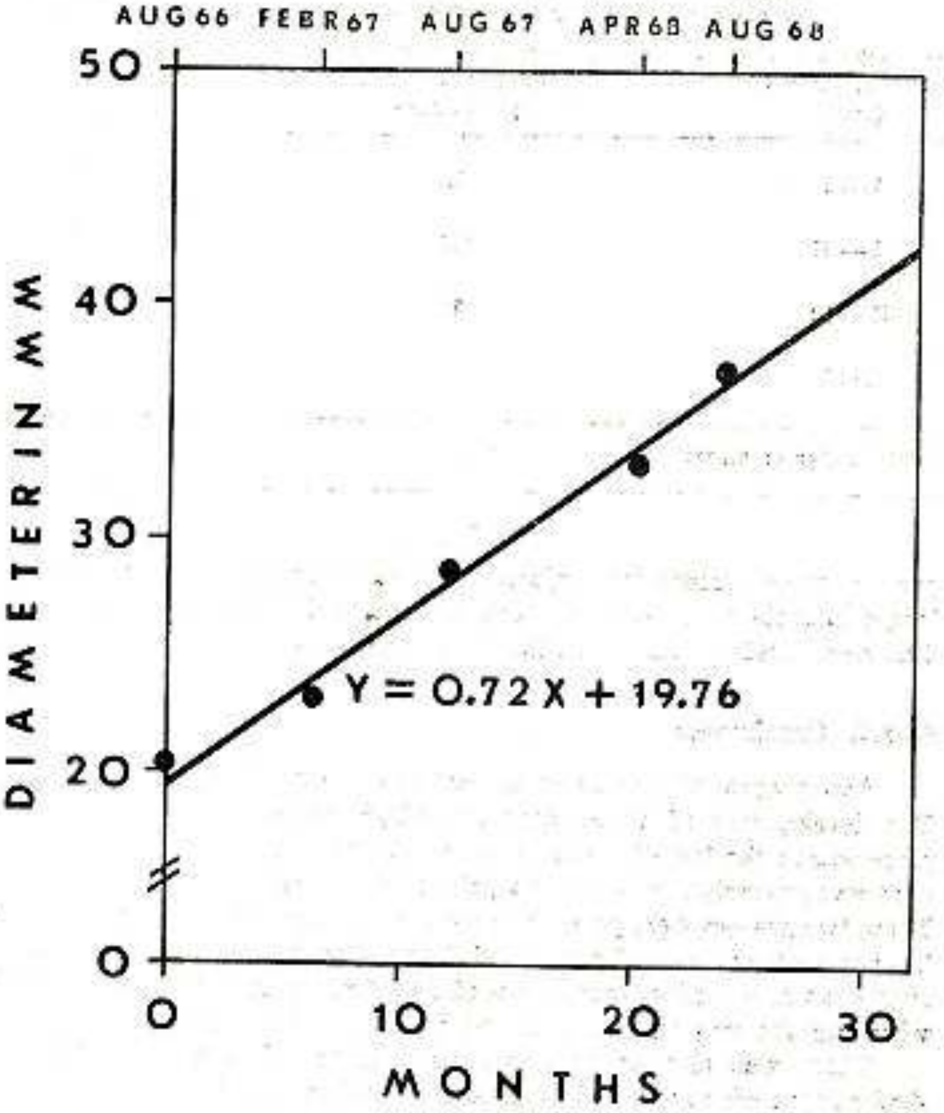

Fig. 27. Diameter growth rate of 16 *Grevillea robusta* saplings in a *Rhynchelytrum repens* community. The regression is significant at $t = 27.69 > t_{.01}$

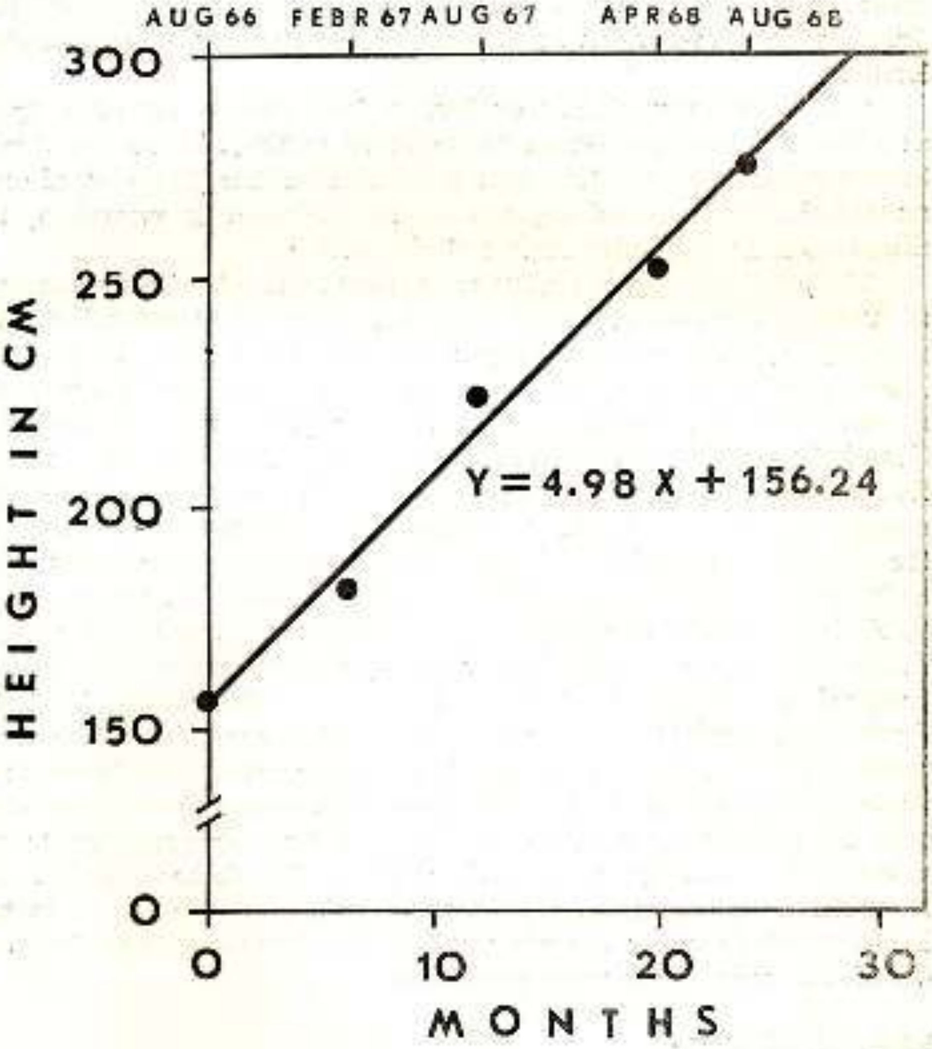

Fig. 28. Height growth rate of 16 *Grevillea robusta* saplings in a *Rhynchelytrum repens* community. The regression is significant at $t = 24.90 > t_{.01}$

by *Acacia koa* and *Metrosideros collina* seedlings may change into forests in less than 50 years. However, the two native tree species usually do not occur in the same habitats, and their invasion is locally restricted to areas with neighbouring native tree stands. There was evidence that *Grevillea robusta* was invading certain *Rhynchelytrum repens* communities locally.

The grass communities may develop from various vegetation types as a result of fire (see section on the effect of fire). Thereafter it may become replaced by specific woody plant communities. The kind of community that will succeed depends on the surrounding vegetation, the climate and the soil-water regime of the habitat.

The possible trends of vegetation changes that lead to the development of various grass communities and the kinds of communities that may replace them may be diagrammatically summarized in Fig. 29. The vegetation changes after fire (described in the next section) are also included in this diagram. These are the changes from the *Dicranopteris linearis* fern-mats to the *Melinis minutiflora* grass communities and to **the** *Paspalum orbiculare-Setaria geniculata* grass communities. Fire is also responsible for the change from the *Psidium-Wikstroemia* scrub to **the** *Paspalum orbiculare-Setaria geniculata* grass communities. The replacement of *Paspalum orbiculare-Setaria geniculata* grass communities by *Andropogon virginicus* is based on a historical record cited earlier. Today the *Paspalum orbiculare-Setaria geniculata* community type is marginal in size and localized in distribution. The change from the *Andropogon virginicus* communities to the *Dicranopteris linearis* fern-mats occurs in the koa zone, and the replacement of the *Andropogon virginicus* communities by *Metrosideros collina* forests occurs in the ohia zone. The replacement of the *Rhynchelytrum repens* community by *Melinis minutiflora* community occurs locally at Kunia. The dashed lines indicate hypothetical changes from the *Paspalum orbiculare* community to the *Dicranopteris linearis* fern-mats and from the *Grevilea robusta* forest to **the** *Melinis minutiflora* grass community.

5.2.3. Effect of fire

5.2.3.1. Chloris barbata and Dichanthium aristatum communities

In spring 1969, the vegetation on Makapuu Flat covered 82 — 99% of the surface area. Exotic species constituted 90% of the vegetation cover. The distribution of the *Chloris barbata* and *Dichanthium aristatum* communities was related to the rockiness of the soil. The frequency and

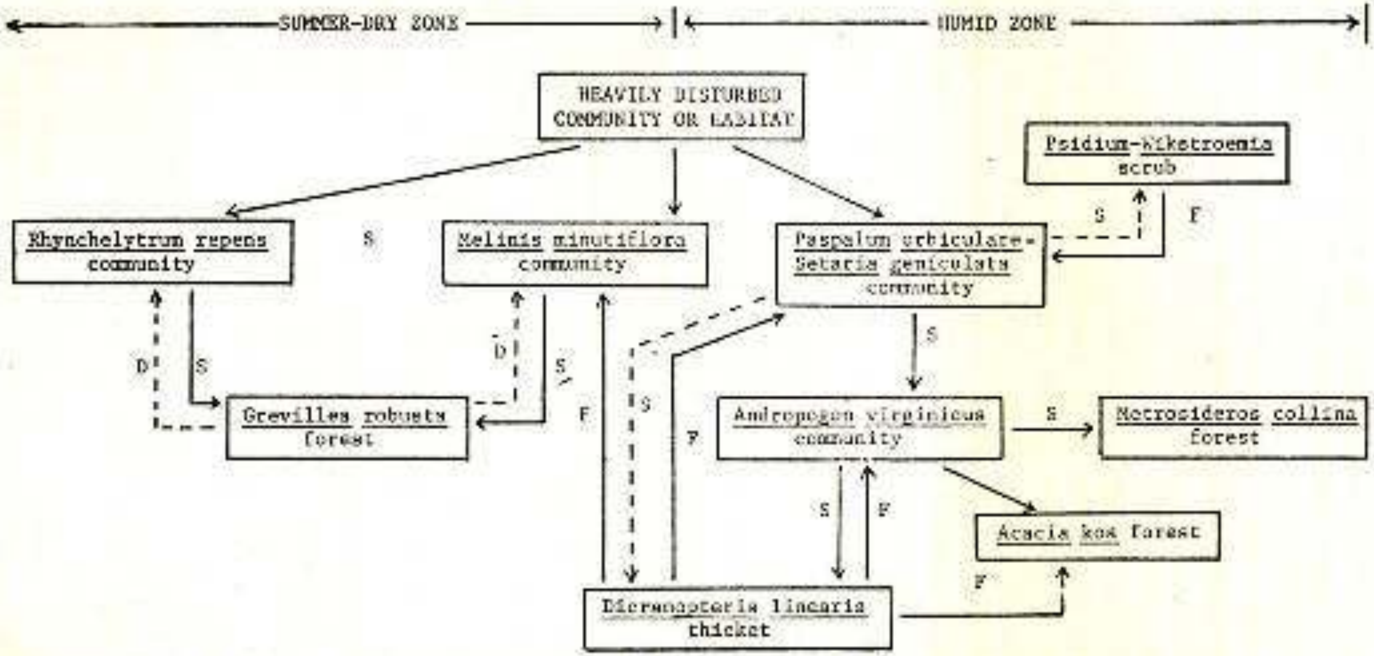

Fig. 29. The development of, and the possible trends of vegetation changes in grass communities in the summer-dry and humid regions. The causes of changes are indicated by: D - disturbance, F - fire and S - normal succession. The dashed line indicates a hypothetical change.

cover of *Chloris barbata* was greater in the twice burned community than in the community that was burned but once. The increase was accomplished by prolific seed germination after fire. Native woody species, *Gossypium tomentosum*, *Lipochaeta lobata* and *Sida fallax* responded favourably to fire by resprouting. *Gossypium tomentosum* had a high rate of survival which was maintained not only by resprouting from the old burned stems but from seeds.

Table XVII shows the species composition of the grass community in terms of the importance value. The importance value of each species was derived by summing the relative cover and frequency. The two major component species were *Chloris barbata* and *Dichanthium aristatum.* Fig. 30 shows that these species formed a gradient in their importance values along the series of transects. To the left of the gradient, *Chloris barbata* dominated and to the right *Dichanthium aristatum.* Two other important species, *Echinochloa colonum* and *Phaseolus lathyroides* (Table XVII), tended to develop best to the left of the gradient, but were sparingly present or completely absent to the right. Two native shrub, *Gossypium tomentosum* and *Lipochaeta lobata* were common in the area. *Gossypium tomentosum* was more frequent in the *Chloris barbata* community, whereas *Lipochaeta lobata* had a significantly higher importance value in the *Dichanthium aristatum* community.

Two community types were identified along the gradient, i.e., the *Chloris barbata* and *Dichanthium aristatum* community types. These community types were identified earlier in the synthesis table (Table I) and ordination (Fig. 2) of the grass communities from the summer-drought zone. In most cases the inter-transect similarity indices within each community type were greater than 40%, but between the two community types they were less than 40%. The pattern of vegetation was related to the rockiness of the soil. The decrease of importance values of *Chloris barbata* was proportional to the increase of rockiness, as indicated by a highly significant correlation between the importance values and the soil depth ($r = 0.695 > 0.684$, correlation coefficient at the 1% level). *Chloris barbata* developed best on shallow and rocky soils, *Dichanthium aristatum* better on deeper and non-rocky soils. The soil in all parts of the study area was of the same type, i. e., the Lualualei clay soil series which belongs to the Dark Magnesium Clay great soil group. The better establishment of *Chloris barbata* in the more stony soil was probably due to a better drainage. During the rainy season the non-rocky soil was always flooded longer than the rocky soil. This was perhaps partly due to the undulating land surface and greater seepage from hillsides at the

Table XVII. The importance values of species in the grass community at Makapuu Flat

	Burned in									Unburned			
	1966 and 1968						1967						
Transect number	1	2	3	4	5	6	7	8	9	10	11	12	13
Chloris barbata	81.8	59.5	56.1	48.0	53.4	58.3	58.2	29.2	23.2	7.9	40.3	2.5	8.5
Desmanthus virgatus	10.7	10.6	9.4	19.7	20.0	22.5	25.0	7.3	7.8	4.5	4.8	0.6	—
Ageratum conyzoides	21.5	11.8	13.4	7.1	10.2	8.4	—	15.1	11.4	17.8	28.1	0.6	10.9
Echinochloa colonum	12.0	81.4	43.7	35.9	33.2	11.8	21.7	46.2	46.6	16.7	6.6	5.2	1.3
Phaseolus lathyroides	39.5	49.3	26.5	12.0	24.4	6.2	13.8	26.8	30.9	6.9	—	—	—
Gossypium tomentosum	4.1	11.0	3.3	5.5	8.2	3.5	2.7	14.0	5.7	5.4	4.4	—	—
Emilia sonchifolia	21.0	13.4	25.9	13.2	24.9	19.0	1.5	11.4	15.1	4.5	—	1.7	—
Solanum nigrum	2.1	2.2	—	2.5	1.3	3.9	0.5	37.1	12.3	6.2	4.4	—	—
Chloris virgata	—	—	4.7	10.2	—	1.8	34.8	37.1	12.3	6.2	—	—	—
Vernonia cinerea	—	—	8.6	15.4	3.8	8.5	—	—	2.8	—	—	—	—
Sonchus oleraceus	7.4	—	1.2	2.2	—	10.1	0.5	2.7	—	—	0.4	—	—
Malvastrum coromandelianum	—	—	—	8.0	—	4.4	—	—	—	—	—	—	—
Setaria verticillata	—	—	5.7	1.8	2.5	14.7	11.5	—	—	—	—	—	—
Commelina benghalensis	—	2.2	—	6.5	—	4.2	—	—	—	—	—	—	—
Panicum maximum	—	—	2.5	1.0	—	1.8	—	—	—	—	—	—	—
Ipomoea cairica	—	—	—	—	7.8	—	—	—	2.8	—	—	—	—
Portulaca oleracea	—	—	—	4.0	2.6	—	—	—	—	—	—	—	—
Abutilon incanum	—	2.2	0.3	—	—	—	—	—	—	—	—	—	—
Waltheria indica	—	—	0.3	—	—	1.8	—	—	—	—	—	—	—
Boerhavia diffusa var. *tetrandra*	—	—	—	1.0	—	—	—	—	—	—	—	—	—
Digitaria sanguinalis	—	—	—	1.0	—	—	—	—	—	—	—	—	—
Merremia aegyptia	—	—	—	—	—	1.8	—	—	—	—	—	—	—
Marsilea villosa	—	2.2	—	—	—	—	—	—	—	—	—	—	—
Euphorbia hirta	—	2.2	—	—	—	—	—	—	—	—	—	—	—
Atriplex semibaccata	—	—	1.0	—	—	—	—	—	—	—	—	—	—
Leucaena leucocephala	—	—	0.3	—	—	—	—	—	—	—	—	—	—

Table XVII. (Continued) The importance values of species in the grass community at Makapuu Flat

	Burned in									Unburned			
	1966 and 1968						1967						
Transect number	1	2	3	4	5	6	7	8	9	10	11	12	13
Xanthium strumarium	—	—	—	1.0	—	—	—	—	—	—	—	—	—
Phyllanthus niruri	—	—	1.8	—	—	—	—	—	—	—	—	—	—
Dichanthium aristatum	—	—	2.5	—	—	—	—	10.5	45.5	111.5	88.5	154.1	149.2
Lipochaeta lobata	—	—	1.8	2.8	0.4	1.8	0.5	1.0	5.7	25.6	22.8	32.6	21.6
Ocimum basilicum	—	—	—	—	—	—	—	—	—	—	—	—	—
Sida fallax	—	2.2	—	6.1	9.0	6.6	6.1	7.3	2.6	—	—	—	—

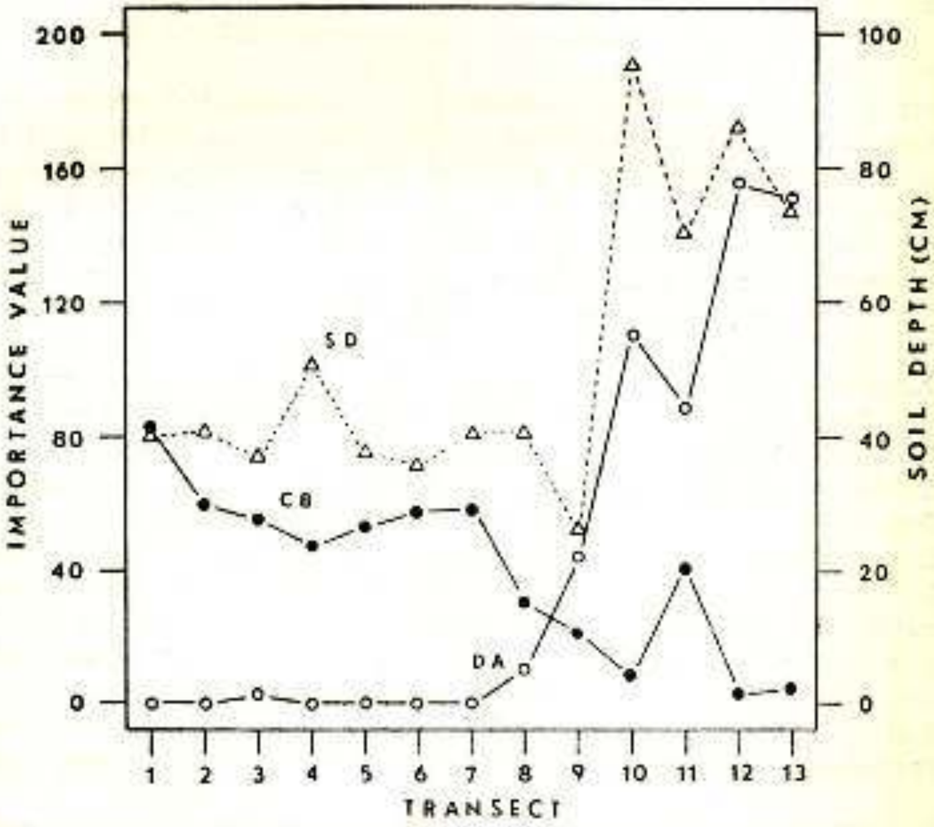

Fig. 30. The change of importance values of *Chloris barbata* (CB) and *Dichanthium aristatum* (DA) along the transects at Makapuu Flat. The change of importance values is related to rockiness of the soil as measured by the averaged soil depth (SD). The importance value is the sum of relative cover and relative frequency.

Dichanthium aristatum side of the grass flats. This condition did not favour the establishment of a *Chloris barbata* community. It was, however, favourable for the growth of *Dichanthium aristatum,* whose habitat normally is muddy places (Chippindall, 1959; Hitchcock, 1950). Soil moisture records also showed that the soil under the *Dichanthium aristatum* community was more moist during the rainy season that under the *Chloris barbata* (Fig. 14).

Transects 1 to 6 were burned in late summer 1966 and again in the same period in 1968, transects 7, 8 and 9 in late summer 1967, and transects 10 to 13 remained unburned at least since 1965. Valid comparison between the burned and unburned transects could not be made along this series since the burned and unburned transects belonged to different communities. Furthermore, the effect of fire was complicated by the effects of inundation and soil rockiness, which seemed to be the controlling factor in the distribution of the two grass communities on this grass flat. However, a comparison between the 1967 and 1966 — 1968 burns indicate that the three common species in the community, *Chloris barbata, Desmanthus virgatus* and *Phaseclus lathyroid.es* had higher average importance values in the 1968 burn. The higher number of species recorded in the 1968 burn (31) compared with the 1967 burn (17) was due to a higher number of casuals (Table XVII). The result of the sampling of *Gossypium tomentosum* is presented in Table XVIII." It is evident that the *Gossypium tomentosum* population was denser in the burned *Chloris barbata* community than in the unburned *Dichanthium aristatum* community. The importance values of *Gossypium tomentosum* (Table XVII) show the same pattern. Living plants in Table XVIII are defined as plants that were burned but were able to resprout during the growing period (rainy season) and as plants that developed from seedlings. *Gossypium tomentosum* had a high rate of survival after fire as is evident from

Table XVIII. Population of *Gossypium tomentosum* in burned and unburned grass communities at Makapuu Flat, sampled with quarter niethdd. Number of plants refers to the number recorded in 13 transects

Diameter classes (cm)	Number of plants per hectare	Percent density
1-5	72	30.0

a low percent of mortality (24.1%). Fire burned and killed branches, but in the rainy season new shoots developed from the base of the stem, and flowering took place 4 to 5 months later. Table XIX shows that *Gossypium tomentosum* seeds germinated after burning.

Fire was not detrimental to *Gossypium tomentosum.* This was clear from the high rate of survival (75.9%) and from the almost unchanged frequency and cover in the once and twice burned transects. Fire had even beneficial effects on *Gossypium tomentosum.* Plants regenerated by resprouting as well as by seed germination. They grew and developed vigorously and reached the mature stage in less than one year. The new plants were healthier than the old unburned ones. In the absence of fire, regrowth was little and reproduction seemed less vigorous.

Except for *Gossypium tomentosum* and *Lipochaeta lobata* which resprouted after fire, all other species reappeared through seed germination. Table XIX shows the seedling populations of seven species that appeared first in the burned-over *Chloris barbata* community following a heavy rainfall.

The increase of importance of the major species in the community was probably attributable to the prolific germination of the seeds after the fire. Seed germination took place immediately after moisture was available. In the established, not recently burned, community, *Chloris barbata* did not regenerate by seed germination but by resprouting from the old bunches. The absence of *Chloris* seedlings can be attributed to

Table XIX. Seedlings density in a burned *Chloris barbata* community at Makapuu Plat, sampled with ten 0.25 sq. m quadrats that were systematically placed at every ten paces, sampling was carried out one week after heavy rainfall in December 1967

Species Number of plantsper 100 sq. m

Diameter classes (cm)	Number of plants per hectare	Percent
1-5	72	30.0
5 — 25	136	56.7
[illegible]	[illegible]	13.3

shading and lack of space. *Chloris barbata* seed germination apparently requires light. *Phaseolus lathyroides* and *Desmanthus virgatus,* however, did germinate in their own shade, although less prolifically than in the open. Fire occurred in 1966 and 1968, killing *Chloris barbata, Phaseolus lathyroides, Desmanthus virgatus* and other herbaceous species. Fire also facilitated germination by removing the accumulated dry matter. Also the immediate fertilizing effect of the ash (Ehrenreich and Aikman, 1963) might have enhanced the growth of the seedlings. Prolific germination of *Chloris barbata, Desmanthus virgatus* and *Phaseolus lathyroides* might have been stimulated by heat generated by fire. Siegel and Smith (1969) reported that the germination rate of *Leucaena leucocephala, Desmanthus virgatus* and *Phaseolus lathyroides* were stimulated 3- to 5-fold by 10 minutes exposure to 150° centigrade. This short but high temperature exposure is the condition that one might expect in grassland fire.

Chloris barbata is a pioneer species on disturbed habitats. It appeared that the *Chloris barbata* communities were arrested by fire in the pioneer stage. There was no indication that the communities were being invaded by *Prosopis pollida,* although this species was present in the vicinity of and within the communities. Its invasion was probably prevented by recurrent fire. In a burned *Prosopis pallida* stand, it was observed that this plant failed to resprout and no seed germinated one year after the fire. Therefore, if *Prosopis pallida* was found in a *Chloris barbata* community the community was probably exposed only to light or spotty and quick burning fires or fire might have been absent for some time. However, with a low frequency of fire one would expect a shift in the community composition.

In the present investigation, no study on the effect of fire on the *Heteropogon contortus* and *Eragrostis variabilis* community types was made. However, traces of fire, in the form of charcoal in the soils and old burned grass bunches and stems of woody plants, were found in many grass-covered areas, suggesting that these community types are also maintained by fire.

5.2.3.1. Andropogon virginicus community, Dicranopteris-Metrosideros woodland and Psidium-Wikstroemia scrub

Andropogon virginicus remained the dominant species, whose frequency and cover increased after fire. Regeneration occurred by resprouting and seedlings. On the other hand, *Setaria geniculata* and

Table XX. Percent frequency and cover of species in the burned and unburned *Andropogon virginicus* communities at Kahaluu. The unburned stand adjacent to the burned one was used as a control for comparison. Sampling was carried out in August 1969, one year after fire

	Percent frequency		Percent cover	
	Burned (1968)	Unburned	Burned (1968)	Unburned
Andropogon virginicus	97.5	87.5	97.3	85.8
Emilia sonchifolia	55.0	2.5	0.5	0.5
Cassia leschenaultiana	52.5	12.5	5.5	0.5
Chrysopogon aciculatus	17.5	2.5	2.3	0.8
Eugenia cumini	2.5	—	0.5	—
Wikstroemia oahuensis	2.5	—	—	0.3
Lantana camara	2.5	—	—	—
Paspalum orbiculare	50.0	77.5	14.5	26.5
Stachytarpheta jamaicensis	30.0	45.0	2.3	4.3
Setaria geniculata	30.0	65.0	8.0	19.3
Psidium guajava	—	5.0	0.3	0.3
Sphenomeris chusana	—	15.0	—	7.8
Spathoglottis plicata	—	5.0	—	1.8
Centella asiatica	—	—	0.5	—
Metrosideros collina	—	—	—	0.3
Pteridium aquilinum var. *decompositum*	—	—	—	0.3

Paspalum orbiculare decreased in frequency and cover. Some woody species resprouted after fire and others died. Fire transformed the *Psidium-Wikstroemia* scrub and *Dicranopteris-Metrosideros* woodland into grass communities. It was speculated that the grassy hills in the humid zone were the results of and maintained by recurrent fires.

Table XX shows the species composition of the burned and unburned *Andropogon virginicus* communities occurring on the same habitat. A total of 16 species were recorded in the communities. Comparison of the burned and unburned stands shows that *Andropogon virginicus* remained the dominant species in the communities. The frequency and cover of *Andropogon virginicus* increased after fire, regenerating by resprouting and seedlings. *Emilia sonchifolia, Cassia leschenaultiana* and *Chrysopogon aciculatus,* which were present only occasionally in the unburned community, occurred more frequently after fire although their combined cover was less than 10 percent. *Emilia sonchifolia* and *Cassia leschenaultiana* occurred mainly as seedlings, and *Chrysopogon aciculatus* resprouted from the old rhizomes. *Paspalum orbiculare, Setaria geniculata* and *Stachytarpheta jamaicensis,* which were important species in the unburned community, decreased in frequency and cover in the burned community. *Spathoglottis plicata* and *Sphenomeris chusana,* common associated species in the *Andropogon virginicus* community, did not reappear one year after the fire. There was no indication that *Eugenia cumini* and *Metrosideros collina* tree seedlings were invading the burned area. Only one seedling of the shrub *Wikstroemia oahuensis* was encountered.

No quantitative assessment on the effect of fire on woody species, present within or outside the grass community, was made. Observations, however, showed that *Wikstroemia oahuensis, Scaevola gaudichaudiana* and *Pandanus odoratissimus* failed to resprout after fire. Most of the *Metrosideros collina* trees were dead. Those that resprouted were not completely burned. *Eugenia cumini, Psidium guajava, Lantana camara* and *Cibothtm chamissoi* resprouted after fire. *Acacia koa* seedlings were abundant around the burned parent trees that were also resprouting.

Tables XXI and XXII show that the burned *Dicranopteris-Metrosideros* woodlands and *Psidium-Wikstroemia* scrub were dominated by grasses and herbaceous species one year after the fire. The vegetation covered 85 —100% of the total ground area. Most of the species present were exotics. Seven species were common to both burned *Dicranopteris-Metrosideros* woodlands and *Psidium-Wikstroemia* scrub. These were *Setaria geniculata, Paspalum orbiculare*, *Centella asiatica, Stachytarpheta jamaicensis, Erechtites hierarchifolia, Emilia sonchifolia* and *Andropogon*

Table XXI. Percent frequency and cover of species in burned *Dicranopteris-Metrosideros* woodlands at Kahaluu and Pupukea

	Kahaluu		Pupukea	
	% Frequency	% Cover	% Frequency	% Cover
Centella asiatica	77.5	29.5	23.4	3.0
Setaria geniculata	52.5	41.5	23.4	9.3
Paspalum orbiculare	30.3	19.3	18.4	11.7
Stachytarpheta jamaicensis	25.0	1.5	11.7	6.3
Erechtites hieracifolia	15.0	—	21.7	3.0
Emilia sonchifolia	2.8	3.0	8.4	2.0
Scaevola gaudichaudiana	0.8	1.0	20.0	1.3
Melinis minutiflora	—	4.0	60.0	16.3
Cassia leschenaultiana	—	—	20.0	2.7
Pteridium aquilinum var. *decompositum*	—	—	18.4	20.0
Andropogon virginicus	7.5	0.8	—	1.0
Bidens pilosa	0.3	—	1.7	—
Paspalum conjugatum	0.5	—	—	—
Wikstroemia oahuensis	0.8	—	—	—
Conyza parva	0.3	—	—	—
Metrosideros collina	—	0.3	—	—
Acacia koa	—	—	—	—
Mimosa pudica	—	—	3.3	0.7
Digitaria violascens	—	—	1.7	—
Euphorbia geniculata	—	—	1.7	—
Passiflora edulis	—	—	—	1.3
Lantana camara	—	—	—	1.0
Psidium guajava	—	—	—	0.7
Cocculus ferrandianus	—	—	—	0.7
Passiflora suberosa	—	—	—	0.7
Phyllanthus niruri	—	—	—	0.8
Phytolacca octandra	—	—	—	0.3

Table XXII. Percent frequency and cover of species in a burned *Psidium-Wikstroemia* scrub community at Kahaluu

	% Frequency	% Cover
Setaria geniculata	97.5	88.8
Paspalum orbiculare	95.0	50.4
Centella as-iatica	70.0	3.3
Stachytarpheta jamaicenms	65.0	8.0
Erechtites hierarchifolia	10.0	1.5
Psidiiim guajava	10.0	3.0
Emilia sonehifotia	5.0	1.0
Andropogon virginicus	2.5	6.5
Paspalum conjuffatum	2.5	—
Cassia leschenaultiana	—	0.5
Lantana camara	—	0.5
Pandanus odoratissimus	—	0.3
Pteridium aquilinum var. *decomposition*	0.3	

virginicus. The most important grasses were *Setaria geniculata* and *Paspalum orbiculare* which were present with high frequency and cover. The decrease in frequency and cover of *Paspalum, orbiculare* and *Setaria geniculata* in the burned *Andropogon virginicus* community was probably due to a strong competition from resprouting bunches as well as seedlings of *Andropogon virginicus.* In the burned *Dicranopteris-Metrosideros* woodlands and *Psidium-Wikstroemia* scrub, on the other hand, *Paspalum orbiculare* and *Setaria geniculata* entered the burned sites without encountering competitors except for forbs such as *Erechtites hierarchifolia, Emilia sonchifolia* and *Centella asiatica.*

In the Pupukea burn, *Melinis minutiflora* was dominant (Table XXI) covering about one half of the sampled area. The invasion took place by seedlings. This species was able to invade this area in such a short period because the burn was located close to an established *Melinis minutiflora* community.

Andropogon virginicus was not an important species in the developing community, but its presence suggests that it may establish itself in the more advanced stage of succession as the dominant. *Andropogon virginicus* becomes important only in the third or fourth year of the secondary succession on abandoned fields in the temperate zones on the mainland United States (Bazzaz, 1968; Harlan, 1956; Keever, 1950; Oosting, 1942). In the presence of *Melinis minutiflora* such as at Pupukea, *Andropogon virginicus* may not be able to invade the area, because of strong competition from *Melinis minutiflora* which can spread rapidly by vegetative means. The chances of *Andropogon virginicus* to enter the community in the latter stage are small, because the thick mat-forming habit of *Melinis minutiflora.*

Paspalum orbiculare, Setaria geniculata and *Erechtites hierarchifolia* occurred not only in the open but they were also very common and grew more vigorously underneath *Pandanus odoratissimus* and *Acacia koa.* The native tree and shrub species that appeared to invade the burned community were *Acacia koa, Scaevola gaudichaudiana, Metrosideros collina* and *Wikstroemia oahuensis.*

It is evident that fire could transform various vegetation types into grass communities. Fire paved the way for the entry of aggressive exotic grasses, especially *Melinis minutiflora, Paspalum orbiculare* and *Setaria geniculata.* It is likely that many grassy hills in the humid area, now dominated by *Andropogon virginicus,* were the results of recurrent fires. The presence of charcoal in the soils in many study areas supports this speculation. Fires still occur frequently. Before the introduction of *Andropogon virginicus,* the grassy hills in the humid zone were dominated by *Paspalum orbiculare* and *Setaria geniculata.* Present observations indicate that the *Andropogon virginicus* communities are maintained and extended by fire. On the other hand, when native woody species, such as *Acacia koa* and *Scaevola gaudichaudiana,* are present in the vicinity of the grass community, fire aids these species to invade the community also, by clearing the ground and providing favourable conditions for seed germination. This is especially true for *Acacia koa* whose seeds germinated abundantly immediately after fire.

6. GENERAL CONCLUSIONS

The grass communities studied have been classified into nine community types, six occurred in the summer-drought zone, two in the summer-dry zone and one in the humid zone. The community types were identified by dominant and differential species and by similarity indices between plots. The grouping of plots in the synthesis tables (Tables I and II) and the clustering of plots in two-dimensional ordinations (Figs. 2 & 4) were similar. Each group of plots was designated as a community type. The community types were well separated when the interplot similariy indices within each group were greater than 40% and between groups less than 40%. Although the grass communities were classified into community types, the distributional range of many species embraced several community types, thus suggesting a partial continuity of the community types.

Certain community types were distributed along the climatic gradient. In the humid climate, the *Andropogon virginicus* community type was prevalent and in the summer-dry climate the *Melinis minutiflora* and *Rhynchelytrum repens* community types were present. The grass dominance changes from *Rhynchelytrum repens* to *Melinis minutiflora* to *Andropogon virginicus* with increasing rainfall and decreasing soil pH (Figs. 9 & 10). At present the *Melinis minutiflora* community is less prevalent than either of the two. In areas of joint occurrences with either the *Rhynchelytrum repens* and *Andropogon virginicus* communities, there is evidence of encroachment by *Melinis minutiflora.* This species is capable of replacing either of the two communities particularly in the subhumid climate. The replacement of the *Rhynchelytrum repens* community appears to be a normal successional event, that of the *Andropogon virginicus* community is related to renewed disturbance by fire. It is possible that the present existing distribution of the three community types will be considerably modified by an expansion in area of *Melinis minutiflora* grass cover on the expense of the *Rhynchelytrum repens* and *Andropogon virginicus* community types within the next decade. In the very high rainfall areas, *Andropogon virginicus* occurred with reduced growth, because soils tended to be boggy.

In the summer-drought zone, six community types occurred: *Heteropogon contortus-Rhynchelytrum repens, Eragrostis variabilis, Trichachne insularis, Panicum maximum, Dichanthium aristatum* and *Chloris barbata* community types. The occurrence of the six community types was related to the topographic position, wind exposure, the rockiness of the land surface and the stoniness of the soils.

The occurrence of the nine community types was not related to the soil series, although the great soil groups were correlated with the vegetation zones, and therefore with the climatically controlled community types. Rainfall rather than temperature was the more important factor affecting the distribution of the grass community types, both geographi cally and altitudinally. The grass community type distribution in the lowlands from the leeward to the windward sides (i.e., along the rainfall gradient) and the distribution from the sea level to the montain crests in the leeward side showed this pattern of relationship.

Soil acidity (pH) of the main rhizospheres under different community types formed a gradient. The acidity gradient corresponded with the rainfall gradient also. This was expected since the soil acidity was to a great extent affected by rainfall. In the summer-drought zone, the acidity gradient was related to topography and proximity to the sea.

No relationship between the community types and organic matter content and water retaining capacity of the soils from the main rhizospheres were observed. The organic matter content in all community types, except in the *Trichachne insularis* community type, was low (Table IV). This was perhaps due to the frequent occurrence of fire that removed the bulk of the organic matter supply (shoot and litter). The absence of correlation between the community types and water retaining capacity suggests that the establishment of various grass communities was not determined by the maximum amount of water the soil can hold. It is also an indication that soil texture was not a determining factor. Water retaining capacity of soils may be used as a measure of the textural properties of soils.

The occurrence of various community types was related to the soil-water regime. The seasonal behavior of soil-water was in a close agreement with the climatic pattern, in which rainfall was the governing element. However, the soil-water regime showed locally significant modifications that were not evident from the rainfall pattern. These were related to topographic position and soil depth. The modifications were closely reflected in some grass cover types. In the summer-drought climate, where *Heteropogon contortus* was dominant on the hillsides, and *Chloris barbata* and *Dichanthium aristatum* on the flatland, soils at the main rhizospheres experienced 3 to 9 months summer-drought (Figs. 11 —14). During this period, the soil-water content was lower than the permanent wilting percentage. The amount and period of water continuously available to plants were greater on the flatlands than on the hillsides, indicating the importance of topography as a factor affecting the soil-water regime. These conditions allow the establishment of the *Chloris barbata* and *Dichanthium aristatum* communities. It perhaps explains why *Chloris barbata* occurred only sparingly and never became dominant on the hillsides. On the flatlands, the occurrence of *Chloris barbata* and *Dichanthium aristatium* communities was determined by the duration of the availability of water. It was also related to the stoniness of the soils (Fig. 30).

In the summer-dry climate, under the *Rhynchelytrum repens* communities, water was available throughout the year except for one month of soil drought (Fig. 13). During the wet season water was in excess of field capacity. In the humid climate, under the *Andropogon virginicus* communities, soil-water was always higher than the field capacity throughout the year (Fig. 11).

The native grass communities once occurred over a large area on the lowlands in the dry area (summer-drought climate). Today *Heteropogon contortus* communities are still quite prevalent, but *Eragrostis variabilis* communities occur only as relicts in this area. The gradual decline of the native communities and the emergence of exotic communities were the results of introduction of exotic species that invaded after disturbances. Disturbance, primarily as the results of man's activities, includes fire, partial or complete destruction of the original vegetation and grazing. However, the invasion of exotic species did not always follow disturbance, because some species, for example *Leucaena leucocephala,* were able to fill empty niches within native *Heteropogon contortus* and *Eragrostis variabilis* communities.

Heteropogon contortus and *Eragrostis variabilis* decreased at the expense of exotic invaders. On the hillsides, the prevalent grass invader was *Rhynchelytrum repens,* whereas on the flatlands the prevalent invaders were *Chloris barbata* and *Dichanthium aristatum. Panicum maximum* and *Trichachne insularis* were the dominant grass invaders on the gentle slopes with rock outcrops. *Leucaena leucocephala* was an aggressive woody invader as was evident from its size class representation in the native grass communities. The absence of grazing and reduced burning periodicity in the study area aids in the rapid spread of this species.

The *Andropogon virginicus* community is a serai community prevalent in the humid zone. It developed only in the last 40 years. Under environmental conditions favourable for its growth, *Dicranopteris linearis* invaded the *Andropogon virginicus* community, whenever these two communities had a common boundary. The mean rate of invasion was 60 cm per year. *Acacia Jcoa* and *Metrosideros collina* were unable to invade dense *Andropogon virginicus* communities. In the study area, the entry of *Acacia Jcoa* was possible only after fire or some other mechanisms cleared up and exposed the ground. *Metrosideros collina* invaded only thinly covered *Andropogon virginicus* communities surrounded by mature trees with a rate of seedling establishment per square meter of 8.3 — 27.2 per year. The rate of mortality ranged from 45 to 84%, depending primarily on the soil-water regime. Under favourable conditions, the diameter growth rate of *Acacia koa* saplings was 7.8 mm/year and that of *Metrosideros collina*

3.5 mm/year. In the humid zone, the *Andropogon virginicus* communities contained a large number of *Acacia koa* or *Metrosideros collina* saplings. It was predicted that the grass community would disappear in less than 50 years because of the shading effect developing from the tree canopies. This was also true for the *Rhynchelytrum repens* community (at Kunia), which was invaded by *Grevillea robusta.* It may disappear in less than 45 years. The invasion rate of *Grevillea robusta* was slow (i.e., 0.5 — 2.6 seedlings/year/sq. m) with a high seedling mortality. The sapling growth of *Grevillea robusta* was 8.6 mm/year for diameter and 60 cm/year for height. The *Rhynchelytrum repens* community at Kunia was also invaded by *Meiinis minutiflora* at a rate of 1.1 m/year.

Fire, both in the summer-drought and humid climate, maintained and extended the grass communities. In the humid climate, fire could transform the *Dicranopteris-Metrosideros* woodland and *Psidium-Wikstroemia* scrub into grass communities. Fires paved the way for the entry of exotic grasses, especially *Meiinis minutiflora, Setaria geniculata* and *Paspalum orbiculare.* There was also an indication that *Andropogon virginicus* might enter the *Paspalum orbicular e-Setaria genicidata* community in subsequent years. It is likely that many grassy hills in the humid areas are the results of recurrent fires. Present observations indicate that the *Andropogon virginicus* community was maintained and extended by fire. However, when native woody species, such as *Acacia koa* and *Scaevola gaudichaudiana,* were present in the vicinity of the grass community, fire helped them to invade the community by providing a more favourable seedbed. This was particularly true for *Acacia koa* whose seeds germinated abundantly after fire.

In the summer-drought zone, the frequency and cover of *Chloris barbata* was greater in the twice burned community than in the community through prolific seed germination afer fire. Native woody species, *Gossypium tomentosum, Lipochaeta lobata* and *Sida fallax,* responded favourably to fire by resprouting. *Gossypium tomentosum* had a high rate of survival (76%), which was maintained not only by resprouting from the old burned stems but also by seedlings.

The development of and the possible vegetational changes in various grass communities in the summer-dry and humid zones are summarized in Fig. 29 and those in the summer-drought zone in Fig 17. At present, it seems that the vegetational changes in the summer-drought zone are leading directly or indirectly towards the formation of the *Leueaena leucocephala* or *Prosopis pallida* community, which appears to be the end point of the changes. The replacement of these communities will depend on the availability of species that can survive arid conditions and are able to germinate and develop under the shade of *Leueaena leucocephala* or *Prosopis pallida.* Considering that *Leueaena leucocephala* is able to reproduce under its own canopy, in the absence of invading species, the *Leueaena leucocephala* community will remain in the summer-drought zone for a long time. Although the exotic species invasion was the most important factor that brought about vegetational changes, the floristic pattern of a community and the direction of change were determined by climate (especially rainfall), soil-water regime, topography and the surrounding vegetation.

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