STUDIES IN HAWAIIAN POLLEN STATISTICS

Part III

ON THE LATE QUATERNARY HISTORY OF THE HAWAIIAN VEGETATION

BY

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THE SUMMIT REGION OF WEST MAUI
(aerial photograph from the north)

The windward sides of the islands are deeply eroded. Montane mires form light-coloured patches in the dark green of the rain forests on many of the ridges and gentle slopes between the steep valleys. Their peat deposits are unique sources of information on the history of late Quaternary vegetation in the islands. By the aid of their fossil pollen contents great changes in the forest cover of the mountains can be traced. They reflect changes of climate such as have not hitherto been recorded from the tropics.

Several pollen diagrams refer to this mountain. They comprise an altitudinal belt of about 400 m (from the summit down to the lowest bog seen to the right) and indicate vegetational changes since the end of the Glacial Period. — Photo: 18th Wing Photo Lab., U. S. Army.

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Studies in Hawaiian Pollen Statistics

Part III

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By OLOF H. SELLING

PREFACE.

This volume concludes my studies in Hawaiian pollen statistics. My thoughts therefore revert with gratitude to all who have assisted me in various ways.

Firstly, my thanks are due to Professor C. Skottsberg, who was the first to conceive the idea of these investigations and has since promoted them in many ways, not only during the three months of field work in 1938 with his »Hawaiian Bog Survey», but also during the subsequent laboratory work. He introduced me to the problems of the Pacific plant world. For all this I shall always remain in gratitude to him. The third member of the Hawaiian Bog Survey, Miss L. M. Cranwell (now Mrs. Smith), also took great interest in my work and assisted with the rod in the levellings.

The field work has left me with pleasant memories of many other persons, only a few of whom can be mentioned here. The hospitality extended to the HBS during its sojourn in the islands has been described by Skottsberg in the »Ymer» 1940, and I on my part shall never forget it. Particularly I wish to thank Sir Peter Buck, Director of the Bishop Museum in Honolulu, and the botanists of the Museum with whom I came in close contact: Dr. and Mrs. F. B. H. Brown, Mr. E. H. Bryan, Jr., Mr. E. Y. Hosaka, and Miss M. C. Neal. Their unfailing kindness is a stimulating memory. I had the pleasure of accompanying several of them on excursions in Oahu; excursions were also made with the Hon. A. F. Judd, Messrs. C. S. and L. Judd, and Major General H. B. Wells. I am also greatly indebted to Mr. Otto Degener, the author of »Flora Hawaiiensis», for many similar trips. His home at Waialua was the starting point of a series of most interesting mountain excursions yielding rich botanical results. These are among my brightest recollections from the islands. The great hospitality shown to the members of the HBS in Kauai by Judge and Mrs. Ph. Rice, Senator and Mrs. Ch. Rice, Mr.

and Mrs. J. Plews, and Mrs. J. Wichman, will always be a cherished memory, as will the occasions when the two latter directed our rides in the montane forests around Kokee. Mr. D. T. Fleming was our kind host in W. Maui, and in the island of Hawaii Dr. T. A. Jaggar arranged, among other things, a profitable excursion to the subalpine forests of Mauna Loa. Professor H. St. John of Honolulu, who only returned to the islands shortly before I left, has since sent me important information. His contributions are quoted below; he drew the distribution map reproduced in Fig. 27. Dr. H. L. Lyon of Honolulu put the picture reproduced in Pl. 11 A at my disposal. My heartfelt thanks to them all.

The laboratory work was not commenced until the end of 1940. Most of the preparations and some preliminary analyses were completed between December 1940 and March 1941 at the Geological Institute of the Stockholm University, where Professor L. von Post kindly made room for me. I am very much obliged to him, not only for the working place during this period, but also for my previous initiation into and much valuable guidance on the problems of pollen statistics. Miss B. Björkman assisted in making part of the slides at this preliminary stage of the investigations.

The principles of the Hawaiian diagrams, and most of the analyses, were worked out later, partly at home and partly at the Botanical Institute of the Stockholm University. I wish to tender my cordial thanks to the head of that Institute, Professor M. G. Stålfelt, for his encouraging support in various ways. These have meant more to me than he may realize.

Military service has on several occasions caused interruptions in the investigations, and since, in 1944, I joined the staff of the Paleobotanical Department, Swedish Museum of Natural History, other lines of research have come into the foreground. The credit for the present work being finished at this time belongs to the Head of the Department, Professor T. G. Halle. His support has been invaluable, and I thank him cordially.

I had the privilege of discussing the climatological aspects of the present work with Professor T. Bergeron and Dr. C. Chr. Wallén, and was fortunate in getting the latter as author of the general climatological account dealing with subjects on which he has himself carried out unpublished researches; he has also read the manuscript of my notes on the local climatological data. Towards the end of my work I had the pleasure of discussing the symbols of the colour diagrams with Professors C. Malmström and L. von Post, Dr. and Mrs. S. Florin, Mr. M. Lundqvist, Head of the Stockholm Cartographical Institute, Ltd, and Messrs. H. Clair and O. Hedbom of the same Institute. Library staffs, especially that of the Royal Swedish Academy of

Sciences, have taken much trouble with the literature. The manuscript has been revised or — when not written in English — translated by Lt. Col. A. Poignant, O. B. E., M. C. Mrs. V. Eriksson assisted with the proof reading. To all of them my cordial thanks are due.

Several institutions have afforded my work financial support and a highly appreciated contribution was also received from Consul General S. A. Lovén of Djursholm. Funds were provided by the Foundation »Lars Hiertas Minne» in Stockholm on two occasions (1941, 1943), and the »Längmanska Kulturfonden» at Uppsala (1948). The greatest help was, however, given in the form of institutional assistance. I have mentioned above the institutions in which I have been working, and of them the Paleobotanical Department of the Swedish Museum of Natural History did by far the most for my work. To all these Institutions and persons I beg to tender my sincere thanks for the confidence shown to me. I also wish to express my gratitude to the Trustees of the Bishop Museum, who, at the request of Professor Skottsberg, have defrayed the costs of printing, except for the black and white plates which were paid for by funds obtained in Sweden.

It remains for me to mention three persons, whose personal attitude to my work has been of particularly deep significance, namely my parents, who from the first have given me their full support, and Professor W. A. Setchell of Berkeley, who followed my progress with indefatigable interest like a near relative. Unfortunately, he and my father are no longer in the land of the living.

Paleobotanical Department, Swedish Museum of
Natural History (Riksmuseets Paleobotaniska
Avdelning), Stockholm 50, May 28, 1948.

I. INTRODUCTION.

A. THE ORIGIN, OBJECT, AND SCOPE OF THE INVESTIGATION.

The botanical exploration of the Hawaiian Islands, initiated in 1778 when the islands were discovered, was at first exclusively directed to the study of their peculiar flora. With the increasing knowledge of the fundamental units, interest began to turn to the phytogeographical position of this flora, its age and origin. The literature on that subject is now large. A scientific study of the Hawaiian vegetation has lately also been attracting more and more interest. The Late Quaternary history of Hawaiian vegetation, however, is so far unexplored territory. In the most accessible parts of the islands the climate will effectively break up any plant remains, and the supply of deposits that might invite such investigations is accordingly very limited, nor are there any features in the present vegetation that have called for a study of these questions. More than 30 years ago, Daly (1916, p. 184) certainly stressed the necessity of »palaeontological work, such as that indicating a decidedly cooler climate for Java in the Glacial period», and of other possible criteria for the former chilling being worked out and applied to research in the Islands — traces of glacial activity had then recently been shown to occur on the upper parts of Mauna Kea in the island of Hawaii (Daly 1910; see further p. 116 below). But this proposal, which mainly referred to the Glacial period, did not give rise to investigations along this line. Professor C. Skottsberg, who had visited the montane mires in Kauai and Maui in 1922, was the first to suggest that pollen statistics, used with good results in Europe and elsewhere, should be applied to the peat deposits with a view to studying the history of vegetation, and also made a realization of that project possible by the Hawaiian Bog Survey 1938 (Skottsberg 1940 a).

The Survey visited the montane areas of the five big islands (Kauai, Oahu, Molokai, Maui, and Hawaii). Investigations were carried on along two lines: recent vegetation (Dr. Skottsberg and Miss Cranwell) and Late Quaternary plant-bearing deposits (the author). Materials for the latter investigations were collected in Kauai, Molokai and W. Maui (see map, Fig. 1, and Chapter III: C: 4).

A brief itinerary comprising the field work of the Survey and my own excursions (in brackets) is as follows:

[27/6: arrival in Honolulu, 28/6—1/7: Honolulu region, 2/7: do., Keanamano Valley (excurs. with A. and L. Judd and B. H. Wells), 3/7: head of Kipapa Gulch (with E. Y. Hosaka et al.)], 5/7: departure for Molokai, 6/7: arrival at Upper Maunahui Camp, from there visits to Pepeopae bog 6/7—13/7, 13/7: return to Kaunakakai, 14/7: W. Molokai and arrival in Honolulu, 19/7: departure for Maui, arrival at Wailuku, 20/7: arrival at Lahaina, 21/7: ascent of Puu Kukui from the W. side via Haelaau, night at Nakalalua, 22—25/7: summit mires of Puu Kukui, 26/7: return to Nakalalua, 27/7: »lowest bog» just above Nakalalua, 28/7: lowest bog and bog at 1575 m elev., 29/7—2/8: Haelaau region and NW—N coast, 3/8: departure (from Haelaau) for Wailuku, 4—5/8: crater of Haleakala, 6/8: Iao Valley, 7/8: arrival in Honolulu, 11/8: departure for Kauai, 12/8: arrival at Kokee, brief visit to Lehua maka noe, [13/8: Kilohana], 14/8: Milolii Valley (with Mrs. E. Plews and J. Wichman), 15—16/8: Kilohana, 17/8—21/8: Kokee region, 22/8: Waimea-Waialae Camp, 23/8: summit of Waialeale, 24/8: Waialae-Waimea-Kokee, [25/8: Nualolo trail], 26/8: Lihue, Koloa, 27/8: Hanalei coast, Haena Bay, 28/8: arrival in Honololu, [2/9: Pupukea-Kahuku trail (with O. Degener), 3/9: Puu Hapapa (do.)], 4/9: Honolulu, 5/9: departure for Hawaii, 6/9: arrival at Kawaihae, excurs. to Kona coast, arrival at Waimea, 7—10/9: Kohala along Upper Hamakua ditch trail, 11/9: Puu Waawaa region, 12/9: Waimea-Kilauea, 13/9: Kilauea »13 miles», 14/9: Kilauea, and Mauna Loa up to 2100 m elev., [15/9: arrival in Honolulu, 18/9: Kealia trail, Waialua region (partly with O. Degener), 25/9: ascent of Puu Kaala (with Degener), 27/9: Punaluu (with E. H. Bryan, Jr., and E. Y. Hosaka)], 28/9: round E. Oahu (with C. S. Judd), 29/9: [Salt Lake Crater and Pearl Harbour, (with E. H. Bryan, Jr.)], Manoa Valley, [30/9: departure for Sweden].

My main task was to plan and to fit into the itinerary the field work — sampling and levelling — of pollen-statistical investigations, with a view to obtaining material for diagrams giving an outline of the history of the vegetation, and primarily of the forest vegetation. Next in importance was to learn as many details as possible of that history. The series of samples were selected so as to illustrate the history not only of the forests, but also — supplementary to this — of the peat deposits as far as this could be done. My work was concentrated to the botanical, micro-paleontological aspects of the subject, however. In the field work I therefore also collected pollen and spores of several recent species for comparison; these collections were later supplemented by herbarium material.

In working up the material brought home my primary objects have been:

1) to ascertain whether usable pollen diagrams could be constructed;
2) if so, to work out in greater detail the principles of construction;
3) if this could be done, to determine the silvi-historical progression, not only in outline but also in greater detail, during the period covered by the diagrams;
4) to note, for purposes of comparison, also changes in the shrub and herbaceous vegetation;
5) to ascertain how far the intensity of peat humification at different times may help to elucidate vegetation-historical progress;

6) to try by comparison with other phenomena — also outside these islands — to achieve an absolute chronology covering at least the main phases of the development covered by the diagrams;
7) to note the occurrence of any species that are not met with in the present flora of the islands, or that may conceivably have immigrated to the islands;
8) to try to ascertain whether the pollens of species assumed to have been introduced by Polynesian settlers occur in circumstances that can throw some light on the date of immigration of these species.

In 1942 I published a very brief preliminary report on this investigation. A few results were incorporated in my 1944 paper. Brief reports have also been published in the Reports (for 1938 onwards) by the Director of the Bishop Museum (in the Bishop Museum Bulletin), and further by Skottsberg (1940 a, d) and von Post (1944, 1946).

B. SUITABILITY OF THE HAWAIIAN ISLANDS FOR POLLEN-STATISTICAL RESEARCH.

No group of islands in the wide expanse of the Central Pacific offers better opportunities for pollen-statistical research than the Hawaiian Islands. Nowhere else between Alaska and New Zealand are, as a matter of fact, the facilities equally great (cf. below). There alone are the islands sufficiently high and the precipitation sufficiently large for large scale peat formation, and there alone do these peat-forming plant communities occur at different altitudes. These islands are moreover situated at the northern limit of the trade wind belt (Fig. 1). The fossil contents of the peat deposits may accordingly a priori be expected to provide a particularly sensitive record of any changes in the vegetation conditioned by this principal link in the chain of atmospheric circulation, and to make these islands an important point in the network of observations which is so badly needed for Quaternary paleo-climatical research (von Post 1939, 1944, 1946). When, finally, it comes to deducing from these changes the generally applicable course of development — a matter of exceedingly great importance to teleconnexions, and accordingly also to the establishment of an absolute Late Quaternary island chronology —, the Hawaiian Islands are favourably situated. Thanks to the small depth and width of the Bering Strait, the North Pacific is a fairly stable area of atmospheric circulation. Quantitative variations in solar energy can here be supposed to be transmuted with a minimum of disturbing

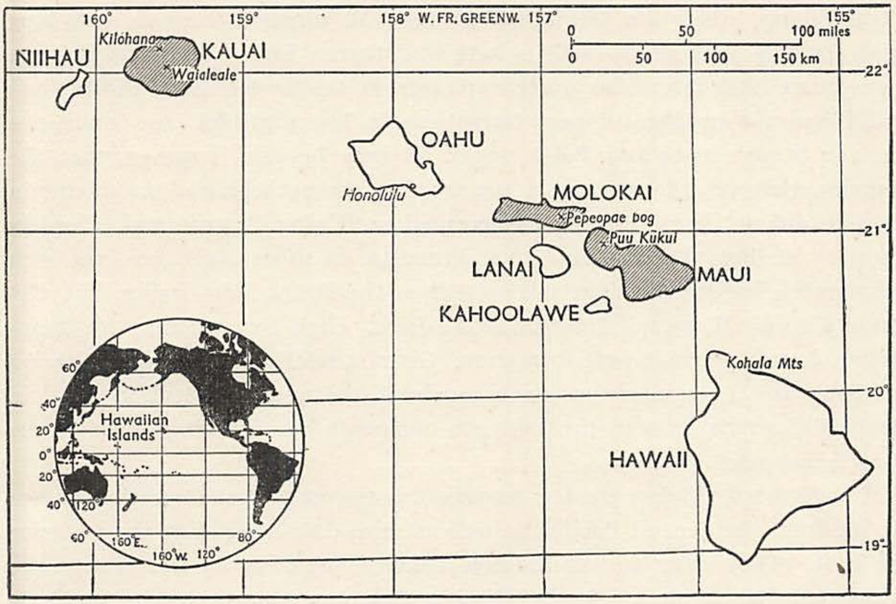

Fig. 1. Map of the Hawaiian Islands (windward section). Ruled areas: islands represented by pollen diagrams in the present paper. The localities in these islands are boring stations. Inset: Map showing the general position of the Hawaiian Islands.

factors in that circulation which puts its stamp on the vegetation. These variations may thus be expected to be well expressed by the fossil contents of the peat deposits.

The importance of the island peat deposits is inestimable. They are unique in many respects. The viewpoints brought forward above add much weight to the plea for their being declared National Monuments (see also p. 47).

C. THE POSSIBILITY OF SIMILAR STUDIES ELSEWHERE IN THE CENTRAL PACIFIC.

As mentioned above, the majority of the thousands of islands in these parts are low, and any plant remains on their surfaces are effectively broken down. The sludge deposits at the bottoms of pools, rivulets, and lagoons will hardly be of much help in elucidating any Late Quaternary vegetational changes. Whatever peat deposits can be found in these parts — especially in the tropical zone — will accordingly be of interest in this connexion. Schimper's opinion, expressed as late as in 1908, that in the tropics »zur

Torfbildung ausser im Gebirge über 1200 M. nirgends kommt» was long prevalent — and maybe still is here and there. But as early as in 1854 Junghuhn, and later also other explorers in the Dutch East Indies, had published information of peat formations in low altitudes (see summaries in van Steenis 1932 and Polak 1933). It may be said, however, that the opinion that peat formation in the tropics was not confined to mountain regions did not become generally accepted until after Potonié and Koorders in 1909 (cf. Potonié 1907, etc.). The literature on this subject has since been augmented by contributions not only from the Dutch East Indies, but also from Ceylon, Malaysia, America, and Africa. High temperatures by themselves do not preclude peat formation. Given a relatively large precipitation without any long interruptions throughout the year, production may in tropical districts, also in the lowlands, outweigh the breaking down of the peat substance.

I shall discuss below the few records of noteworthy peat formation known to me from the Central Pacific, as well as some data suggesting the presence of peat. They refer to Washington Island, Nukuhiva in the Marquesas, Raiatea in the Society Islands, Mangaia, Rarotonga and Atui in the Cook Islands, and Taveuni and Moala in the Fijis. Crater lakes occur in Samoa (Savaii; Dana 1849, Jensen 1907, Friedländer 1910, Thomson 1921), Tonga (Tofua; Jensen 1907), and the Wallis Islands (Uvea; Stearns 1945 b), and in the crater of Niuafoo, halfway between Samoa and Fiji, there is a big lake, Vai Lahi, 275 ft deep (Jaggar 1931, 1935, map p. 95; Macdonald 1948, map p. 68). On Tahiti there is another big lake formed by landslides at the head of Vaihira Valley. Lake Vaihira (»Vairia» in Jouan 1873, p. 33) is situated about 325 m (1140 ft) above sea level, its diameter is about 800 m and its depth about 30 m (Cheesman 1927, p. 179—203, with pl.; Williams 1933, p. 20, 21, Pl. 3 B). It is not known whether these lakes have produced any deposits that can be used with good results for investigations into the vegetation history, but at least Lake Vaihira appears fairly promising.

Washington Island. On arriving at this low atoll, situated in about lat. N 5°, on Aug. 14, 1924, the Whippoorwill expedition found the island enveloped in a light morning fog. In the interior of the island »extensive peat bogs» and a fresh water lake — unique in coral islands — were found (Gregory 1925, p. 25, Wentworth 1925, 1931, Christophersen 1927). The swamps are described by Christophersen (l. c., p. 50—53, Pl. VI) and Wentworth (1925, 1931, p. 17). They cover an area of 80—100 hectares (= 200—250 acres) formerly occupied by a lagoon. The average depth of the peat, which is formed by *Scirpus riparius*, is 70 cm. The surface of the swamp is at a higher level than the surrounding areas, but the roots of *Scirpus* reach the general ground water level (20—25 cm below the surface). The swamp is thus topogeneous (see below, p. 46). Filling has now ceased, and erosion has set in.

In a low island like this the possibility of tracing the Late Quaternary vegetation history by pollen statistics seems less promising, but the peat should of course be examined for plant remains. The flora is exiguous, and it would not be difficult to use the entire spore and pollen contents for such a study.

The Marquesas. Jardin (1856, p. 52, 53, 1862, p. 4, 5) seems to be the first to mention that in Nukuhiva »Le point central de l'ile, Tovii, consiste en un surface de terrain marécageuse» and that »La première part du N. E. de ce plateau et sort d'un ravin profond, que l'on appele improprement lac; les kanacs le désignent sous le nom de *Vai-Hohonu*, eau profonde.» F. B. H. Brown (1931, p. 16, 21; cf. Pl. XXXV B) has subsequently pointed out that »a shallow deposit of peat is formed in the marshes and boggy areas of Tovii», but that »the surface is well drained by numerous streams, with the exception of a few small areas, which have evidently been crater lakes and are now covered with marsh». With reference to the occurence in Tovii of *Cladium nukuhivense* he says (l. c., p. 112): »Here it covers a shallow, flat bed, evidently the site of a former crater lake, now practically filled with plant remains. This is the only place in the Marquesas where a true bog and bog flora were found.» Adamson (1936, p. 15) thinks that the term swamp can hardly be used for these small areas; they are dry at times. He further states that it seems certain that none of the ponds or small lakes mentioned from Tovii, is permanent. He says (l. c. p.): »There are no lakes in the Marquesas and in the high interior of the islands no permanent ponds of stagnant water were observed in the field work. When the mountain streams begin to dry up, small pools are isolated but they are soon washed out when the streams are again flowing. The pool named Vaihakameama (Water-that-dances-by-moonlight) in Tovii, Nukuhiva, was the largest I saw in the interior or learned about from the residents in the islands. In November 1929 its diameter was about 150 feet, its depth less than 3 feet, and the grass still rotting at the bottom showed that it was probably subject to occasional desiccation.» Still, these bogs may well give information on long term changes in the vegetation.

The Society Islands. Moore (1933, p. 20) mentions from Raiatea a »swamp about 2 kilometers south of Ituroa» as the habitat of *Cyperus raiateensis*. It is uncertain whether this swamp has produced peat. No peat deposits are known from the islands, and as according to Williams (l. c., p. 47) no podzols of the type plentiful in Hawaii — and to a smaller extent also in the Marquesas — have been found anywhere, they can hardly be expected, at any rate not of any large-size.

The Cook Islands. From Mangaia as well as from Rarotonga and Atui, Marshall (1925, 1927, 1930) reports that »swamps» fill the comparatively narrow area between the central peak of the islands and the Makatea, i. e. the surrounding coral reef platform raised above the sea level. They are apparently usually cultivated, at least in Mangaia, where conditions are described as follows by Marshall (1927, p. 35; cf. p. 7 and 1925, p. 17):

> »The Taro Flats are about 40 feet above sea level, where the streams that supply the water to them issue from the valleys. They descend in a series of artificial terraces and end about twenty feet above sea level at the foot of the Makatea cliff. Here the water enters a sink, which may be as much as ten feet below the general surface, and passes in channels through the Makatea. . . . At Lake Tiriara the level of the flat approaches so closely to that of the sea that the water drains away and a permanent lake remains, 400 yards long and 150 yards wide. It is said that in heavy weather some sea water is driven into the lake through the outlet channel, the water becomes brackish, and marine fish, such as the mullet, come in from the reef. . . . The material of the Taro Flats consists of the detritus derived from the volcanic hills, together with a great deal of organic matter.»

In Atui, taro and bananas are cultivated only on part of these areas. Marshall (1930, p. 68) writes:

> »Some of the ground is used for that purpose, generally that on the inner side only, near the points where the streams enter the swamps. Otherwise the swampy ground is waste land, covered with a growth of rush and other water weeds. The surface of the swamp is 20 to 30 feet above sea level. In the wet season the swamp contains considerable water, but the small Lake Tiriroto is the only permanent sheet of water with a surface free from growth of weeds.»

Under such conditions it does not seem impossible to find at least some deposits from old times, but the prospect of finding good unbroken series of greater compass is nevertheless not great. Moreover, Atui is very low (270 ft). Mangaia is 550 ft high, Rarotonga 2100 ft. The islands are therefore unfortunately not very suitable for pollen-statistical studies aiming at a general knowledge of Late Quaternary vegetation displacements and their underlying causes. However, every means of ascertaining what has happened to their vegetation should be tried.

Fiji. In the island of Taveuni (off Vanua Levu), about 700 m above sea level, is a large body of water, the largest and highest in the Fijis. It covers an area of about 2×4 miles. Very little can now be seen of the lake. The deep water is covered by a quaking crust of decayed vegetation, probably not more than a metre thick. The predominant plant of this floating swamp is a sedge, *Lepironia mucronata*, which is mixed with *Sphagnum Seemanni* and a medley of gelatinous microscopic algae. In the humus grow several small shrubs of *Metrosideros polymorpha*, *Myrsine sp.*, and *Weinmannia affinis*. The locality was discovered in 1860 by Seemann (1862, p. 28—29). A good description of it is given by A. C. Smith (1934, p. 274—275). How far this crust can be used for tracing the vegetation-historical development by pollen statistics is hard to say. The bottom deposits of the lake, however, could presubably provide useful material.

Smith (l. c., p. 279, Fig. 6 on p. 276) also reports a swamp with small deep pools on the summit plateau of Moala (about 400 m above sea level) between Lau proper and Viti Levu. The chief plant seems to be a sedge, *Fimbristylis annua*. It is not known whether the swamp contains any peat, however.

Summarizing the above, this survey may be said to confirm what is said above regarding the Hawaiian Islands' offering unparalleled opportunities for pollen-statistical research in the Central Pacific.

D. OTHER POSSIBILITIES OF APPROACH IN THE HAWAIIAN ISLANDS.

As said above, no plant-bearing deposits have been found in the Hawaiian Islands that have yet led to any elucidation of the vegetation history of the Islands in either Late Quaternary or older times, and one reason for this was indicated: the rapid decomposition of organic substances in the warm and at least at times fairly dry climate of the lower and more accessible parts of the Islands. The plant remains found in these regions are mainly of two kinds, and the possibilities of using them for studying the history of vegetation will be discussed in this chapter. The parts of the coral reefs referable to the vegetable kingdom, however, will not be touched upon in this paper. The two categories of remains are:

1. Plant remains deposited under water (fossils in the sediments of rivers, lagoons, and the few small pools);
2. Impressions, casts, and carbonized remains in lavas and volcanic ash.

Although Hinds (1930, p. 58) states that calcite »is being deposited in vesicles and fissures along the sea coast» — he refers to Kauai, but similar evidence has also been obtained in Oahu (Wentworth 1926, p. 27) — no lime-tuffs containing plant impressions, such as have been used with great success in for inst. Scandinavia for studying the history of vegetation, have been found in these islands.

1. Plant remains deposited under water. That such remains are found in the lowlands is by no means unknown. I saw many brought up during the excavations in the Nuuanu River in Honolulu in September 1938. Guppy (1906, p. 419) casually mentions that masses of fruits of *Aleurites moluccana*, etc., were dredged from the Honolulu harbour at the end of the 1890's. This does not prove that older, Late Quaternary vegetation has become similarly preserved; we do not know the age of these deposits. *Aleurites* has long been assumed to have been introduced into the Islands 1500 or 2000 years ago by the Polynesian colonists, but the uncertainty of this dating must be stressed (cf. p. 129). These finds indicate the possibility, however; nor are they the only ones. J. Moro found several logs embedded in gravel about 10 m below the present ground level when boring for water in the valley of the Hanapepe River on Kauai (Hinds 1930, p. 74), and some further particulars from Kauai are also given in the same work (p. 74): »Borings for the supports of the bridge which crosses the mouth of the Wailua River were sunk through at least 80 feet of alluvium without reaching the underlying lavas. No exact records were kept of any of these borings. .... masses of plant remains were encountered at some depth below the surface.» These remains do not seem to have been preserved (l. c., p. 65).

It is not astonishing, however, that material of this kind has not been used for studies of the history of vegetation. It is in the first place exceedingly difficult to decide whether a species found in alluvial deposits grew in the neighbourhood or had been transported there, and that alone greatly reduces the prospects of gaining useful results. Its state of preservation might of course give us some idea whether a specimen has been carried a long way or not, but rivers in spate may also rapidly transport much stuff from high levels down to the lowland, and at least part of this might under such circumstances arrive in more or less good condition. One such flood which filled the mountain water courses above the normal for a brief period, carrying leaves, branches and trunks in its imposing masses of water and sludge, is described by Coan (1902, p. 368):,

> »I have stood upon the bank of a deep canon in the Hilo district, while the heavy rainpour was deluging the slopes of Manua Kea. Far below, a pure mountain stream, easily fordable by leaping from one lava rock to another, was foaming seaward. Presently the noise of unloosed waters came from the mountain side, growing momentarily louder, and soon the torrent, yellow and turbid, came thundering down the rocky valley, with no less force and fury than if a great dam had broken in the mountains; suddenly the little stream was magnified into a roaring and impassable torrent, a hundred times the volume of a few moments before. For days afterwards, and for miles around, the sea would be discolored by the turbid discharge and the floating driftwood came ashore at distant points along the coast.»

It may further be difficult to decide whether the remains are primary or secondary, i. e. redeposited from older strata.

The fact that no accurate dating of these formations has so far been possible also limits their value.

This kind of material is thus definitely unsuitable for our present purposes, and it is but natural that it is not conductive to studies of the history of vegetation, at any rate until that subject has been attacked from another angle. The situation is slightly different, however, now that the post-Glacial developments in higher levels have become known. In spite of all difficulties, due attention should henceforth obviously be devoted to these fossils, too. For the lower levels they might supplement in several respects the picture of the development of vegetation provided by the pollen diagrams.

Plant remains should, of course, also be looked for in the sediments in some of the small crater lakes like the Green Lake (and its precursors) in the Kapoho Crater mentioned by H. Stearns in H. Stearns and Clark (1930, p. 146—148) in the Puna District of the Island of Hawaii. That lake is said always to contain water. Any megascopic plant remains discovered in such sediments must have come from the immediate neighbourhood, and should therefore be more easily interpreted than those from river and lagoon deposits.

An interesting opportunity to study the history of the vegetation in an alpine locality, which in several respects is reminiscent of the latter, also deserves to be mentioned in this connexion, viz. Lake Waiau on Mauna Kea, 3,950 m above sea level, i. e., far above the limits of the last glaciation (3,216 m).

This lake was discovered on December 17, 1832, by the Rev. Joseph Goodrich, who speaks of it as »a lake or pond of water — 75 rods in circumference, or 25 in diameter — half frozen over — — — very deep.» (1833, p. 199—201). It was mentioned and pictured by Brigham (1909, p. 5, and Figs. 5—6 on p. 7) and Hitchcock (1919, Pl. 24: 2) and has since been described in greater detail by Gregory and Wentworth (1937, p. 1726—1727), Neal (1939, p. 7, 32), and by Hartt and Neal (1940, p. 256), who also reproduced a good photo of it (Fig. 21, p. 257). Gregory and Wentworth say it is about 1½ acres (= 0.6 hectares) in area and 8—15 ft (= 2.5—5 m) deep. This was in August, when the water is low. In the spring it is probably 6 ft (= 1.8 m) deeper. Baldwin (1889) found its water »muddy». In a letter to Gregory, Harold L. Lyon calls it »a veritable infusion». The organic ooze deposited on the bottom of the lake contains amongst other things blue-green algae, desmids and diatoms, but no [megascopic] vascular plant remains whatever.

I do not know whether this apparently rather slow-growing ooze (cf. Hartt and Neal l. c. p.) is sufficiently thick to show much of the post-Glacial development by a detailed stratigraphic analysis of its microfossil contents, but an attempt would certainly be worth while. The analyses should comprise not only algae, but also pollens and spores. Some means might even be found to trace in this ooze the post-Glacial changes in the vegetation. The task is tempting, but necessitates — and this must be emphasized — the utmost care and the most modern methods, as at some future date, when the methods available and the problems to be investigated are more refined, the deposits of this small lake might be the objects of research for which much untouched material is essential.

2. Impressions and carbonized remains in volcanic ash and lavas. Impressions in volcanic ash have been described from numerous localities. Wentworth (1926, p. 27—28) thus mentions from Oahu »casts of stems and roots of small plants and trunks of trees», found »in both horizontal and vertical positions, many sufficiently branched to give an impression of the habit of the tree». Similar finds are reported from the neighbourhood of the Kilauea Volcano Observatory on the Island of Hawaii by H. Stearns and T. A. Jaggar (both in H. Stearns and Clark 1930, p. 151—152).

Specific identifications have also been possible from finds of this nature. Unfortunately, too little is known of the ages of the respective deposits, but most likely they are of an earlier period than that discussed in this paper. The occurrences deserve brief mention here, however.

A find from Moanaloa in SE. Oahu (Branner 1903, p. 315—316; Lyon 1930, p. 6—7), which inter alia has proved to contain *Pteralyxia* (see further Caum 1933), is of considerable age, roughly estimated by Lyon at 100,000 years, which is of course only an assessment on general grounds.

A locality adjoining Salt Lake on SE. Oahu, between Honolulu and Pearl Harbour, has been described by N. Stearns, from whose popular account (1935, p. 38—39) the following passage is reproduced:

> »When the Salt Lake drainage tunnel was being made, numerous fossil trees and leaves were encountered. They were found in an upright position of growth in the Salt Lake ash. Evidently a jungle forest was buried by the ash of the Salt Lake eruption. They include such trees as the koa [= *Acacia koa*], loulu palm [= *Pritchardia sp.*], and ohia [= *Metrosideros polymorpha*]. Some 15 species of plants closely related to or identical with species of the present day have been identified. These trees, especially the koa and the loulu palm, now grow only[!] in the rain belt, but at that time they were living close to sea level, at the site of the present Salt Lake. At the time of the eruption of the Salt Lake ash the climate at sea level must have been wetter than at present — and in all probability cooler also . . .
>
> Carbonised plants are found at Kapahulu quarry in Kaimuki [SE. of Honolulu], in the lower part of the Diamond Head ash. Blades of grass and sedge and leaves of a plant allied to the ohia have been found among the fossils. This vegetation was evidently growing at the site of the quarry when it was buried by the ash erupted from Diamond Head. Again, some of these plants now grow in the wetter, cooler parts of the island. . . .»

The superimposed bed of coral chalk, and the relations of the trunk impressions to the present sea level, prove that since that time the sea level has for a long period been higher in relation to the land than it is now, and that there has been a subsequent emergence. The buried forest is considered to have grown there at the time corresponding to the Waipio Sea; numerous submerged shore lines show that the sea level was then about 20 m below the present. H. Stearns (1935 a, b, etc.), considers the sea level to correspond to the last glaciation, but nothing is known of this with any certainty.

Impressions will be left in lavas when the oncoming lava stream, though still plastic, is not hot enough to effect the complete combustion of the embedded plant remains before congealing. There are numerous examples of this kind of fossil. Hillebrand describes (in Brigham 1909, p. 111) exceedingly well preserved impressions of tree ferns in lava from Kahuku on the south slope of Mauna Loa. Doerr (1938, p. 13—14) reports impressions of a fern — *Sadleria cyatheoides* — from the neighbourhood of the Kilauea Iki crater on the same island, and from the Makaopuhi crater on the east slope of Kilauea (cf. Krejci-Graf 1936, p. 385, Fig. 4). H. Stearns and Clark (1930, p. 77, Pl. 8 A) mention and figure impressions of grass in lava from the neighbourhood of the Great Crack, a 10 km long fissure on the SW. flank of Kilauea. The same authors also describe (l. c., p. 78, Pl. 10 A) some up to 2 m high impressions of upright tree trunks. Such impressions are, incidentally, not at all rare in the lava streams of the Island of Hawaii (cf. Westervelt 1907, p. 113—120; Krejci-Graf 1936, p. 385—387, Figs. 5—6), and have also been figured by N. Stearns (1935, p. 88—90), Skottsberg (1941, Pl. VIII: i), and others. Whether the »layers of earth, containing vegetable substances, from two feet to two feet seven inches in thickness», found by David Douglas in January 1834 to occur between lava beds on the slopes of Mauna Loa, were associated with any impressions is, however, not known (nor whether these layers of earth contained any identifiable plant remains). The locality — »the deep caves at Kapupala, two thousand feet above the level of the sea» — is described in his diary (1836, p. 176; 1914, p. 315).

It also happens that natural casts of trunks are formed by lava: a trunk is embedded in one lava stream, the organic remains gradually disappear, and the cavity thus formed is filled by another lava stream. Such a cast of a tree fern trunk from near Kilauea is figured by Krejci-Graf 1936, p. 388, Figs. 8 a and b (»*Cibotium Chamissoi*»).

In one important respect the plants preserved as impressions, casts, or carbonized remains in lava (and tuffs) are better than the remains deposited in rivers and lagoons: they may be assumed to be derived from the places where found. They are accordingly more readily utilized for appraising any changes that may have occurred, but unfortunately their value is limited by the difficulties of dating. Nothing but extremely rough datings, too approximate to serve our purposes, of the lava eruptions are as yet possible except in respect of those that have occurred in historical times, and historical time on these Islands begins in the latter half of the 18th century. The plant remains mentioned here were as a matter of fact all found in such recent lava beds: those found by Hillebrand were embedded in 1868, those mentioned by Doerr in 1832 and 1923, respectively. The finds of H. Stearns and Clark date from 1823, and N. Stearns' and Skottsberg's from 1923 and 1919, respectively, Krejci-Graf's from 1881. These examples are of interest to the student of the history of vegetation only in so far as they indicate certain possibilities.

To sum up, it must thus be stated that the material so far collected of the above groups is extremely meagre. It offers no starting point at all for the subject in hand, and it is but natural that the so far available data have not tempted anybody to make a systematic attack on the problem of the history of vegetation in these islands. There is, however, no reason why the possibility of their being utilized in future should be disregarded.

II. METHODS.

A. FIELD WORK.

A peat auger of Swedish type (Hiller model) with a 50 cm long chamber was used for the borings. A smaller borer (30 cm chamber) was used at first, but was discarded. Samples of each section were taken in glass tubes (7.5 cm long, internal diam. 1.3 cm), which were immediately stoppered at both ends with corks, on which the number of the sample was written in indelible pencil. The corks were dimensioned so that they would do also when shrunk. The distance between the samples as a rule varied from 2 to 5 cm. Subsequently, it was found that isolated pollen spectra could not be exactly put into large sections of the Hawaiian diagrams, and one series (10), which for lack of time had been taken with 25 cm between samples, proved of very slight value. In future investigations in these islands the average distance between them should therefore be 2 cm, often even less. The use of zinc linings would save much trouble, since in the field it is impossible to know the exact requirements.

Notes were taken during the sampling of the appearance of the deposit, the occurrence of megascopic plant remains, etc.

Levellings were done with a tube and a rod, but the incessant rains, coupled with strong winds, made readings very difficult. The sweeping rain frequently prevented the use of the tube at distances exceeding 8 m. A cup-shaped protection round the frontal lens would have been a great help on such occasions.

B. LABORATORY WORK.

1. PREPARATION OF SLIDES.

1. Preliminary examination of the peat samples indicated the necessity of getting their microfossil contents as concentrated and distinct as possible, and the acetolysis method (Erdtman and Erdtman 1933, etc.: Erdtman 1943; cf. Cain 1939) was therefore chosen although it is rather slow.

The result of boiling in KOH was not satisfactory. The procedure was as follows:

a. Chlorination. 4 ½ cm^3 of concentrated acetic acid (for the sake of economy, more might well be used) and 1/2 cm^3 of concentrated hydrochloric acid were poured on to the sample in a (strong) centrifuge tube. Two or four samples were prepared at the same time, according to the number of holders in the available centrifuge. The tube contents were stirred with a glass rod, and 3—4 drops of 33 % sodium chlorate solution were added: strong development of chlorine and chlorine dioxide, bleaching and breaking down of lignin and humic acids. Stirring was continued for a short while, and the contents were then centrifuged, washed by being shaken with distilled water (any foam was removed by acetone), and again centrifuged. Further washing and centrifuging were usually not required.

b. Acetolysis. 18 cm^3 of anhydrous acetic acid and 2 cm^3 of concentrated sulphuric acid (or double the quantity of each) were mixed in a cup and — when the mixture had ± cooled down — divided equally between the two (or four) tubes. The consequent heating was continued in a water bath from about 60—75° Celsius to boiling point. Some plant remains would then still be left, but the polysaccharides of the peat were effectively broken down, and the pollen became dark and distinct. (If the pollen is corroded or delicate, the process should be discontinued just before the boiling point is reached). The tubes were taken up and immediately centrifuged for 1/2—3/4 minute, after which the contents were carefully decanted, leaving all the sediment. This was followed by another rinsing as above, centrifuging (for about 1 minute), and a second rinsing. The tubes were for a moment tipped upside down on a filter paper to allow some of the water on the walls to drain off. The samples were then stirred and rinsed in 50—65 % glycerine, centrifuged for about two minutes, carefully decanted (sometimes also tipped upside down on a filter paper for a moment) and were then ready for mounting. In order to make the pollens and spores mobile in the microscopic analysis, the samples were immersed in concentrated glycerine and the glasses glued with Lagerheim's preparation glue (1902 a). This delayed access of the air and prevented the too rapid bleaching and swelling of the pollen, which otherwise would proceed fairly rapidly from the edges inwards and quite naturally hamper the comparison with the recent material described in Selling 1946 and 1947.

Only the following need be added regarding this: To obtain an even effect of the chemicals the sample must be powdered, which — as the soil is easily broken up — generally causes no damage to speak of to the pollen. But several of the Hawaiian samples consist largely of humus, and become horny when dry, and in them the pollen will be more easily crushed than in others; they accordingly require more careful treatment. As a rule, the result will be acceptable if instead of being powdered they are first softened by immersion in acetic acid and then broken up with a glass rod.

2. Clay samples were treated by the hydrofluoric acid method worked out by Assarsson and Granlund (1924):

The sample is powdered, mixed with HF, and boiled in a small platinum crucible until most of the liquid is evaporated. Water is then added, the sample centrifuged, boiled with potassium hydroxide in a test tube, centrifuged, and carefully washed several times.

While pollens and spores treated on the acetolysis method are as a rule more or less brown, and need no colouring, it is generally better to dye samples treated with hydrofluoric acid.

All peat samples were prepared under as nearly the same conditions as possible: ± equal quantities were taken of the dried samples (which were not weighed, however), the treatment was exactly the same every time, and as many drops of glycerine were always carefully stirred into the residues of each prepared sample before the cover glass was put on, all in order that the absolute number of pollen grains in each preparation should as closely as possible reflect the variations in the number of pollen grains per unit weight of peat. These variations might conceivably be used for deciding questions relating to the history of vegetation, e. g. the conditions governing the humification of the peat. Such changes of pollen frequencies in European peat strata have — particularly in recent years — been studied with good results, and methods of obtaining particularly accurate values are found in Ording 1934 and Overbeck 1947. For the present investigation the procedure outlined above proved sufficient, however. The »F» diagrams are based on the values obtained, which will be discussed in greater detail below (Chap. IV: B).

2. RECORDING OF MICROFOSSILS.

The microfossils in the slides were counted in each row with the aid of a cross-rule table, taking care, when it was not necessary to search the whole of a slide, to distribute the rows as equally as possible over its whole surface (as, moreover, great care was from the first taken to obtain homogeneous preparations). The absolute pollen numbers could then be determined by simple arithmetic. The magnification was about 300. The whole microfossil contents were recorded, definitely identified types by their names, while the others were sketched pending identification. The positions of fossils that might require subsequent control were marked [the number of the row from the upper edge of the slide with the addition L(eft), C(entre), or R(ight)]. The counted numbers of pollens and spores of the kinds on which the main diagrams were to be based were kept around 200. This proved a fair average (for comparison with extra-Hawaiian conditions, see Barkley 1934 and the literature cited there, also Ording 1934, p. 161 ff., and Westenberg 1947; a paper by Woodhead and Hodgson 1935, mentioned by Westenberg, has not been available). In certain cases the numbers amount to over 750 per slide. In an analysis of unknown material like this, which necessarily includes not only these main constituents but every other regonizable spore and pollen grain, each analysis may take a very long time — one extreme case took me 12 hour's work a day for one week to get the requisite numbers of the principal tree pollens in a single sample. This accounts for part of the numbers below 150 found in the last columns of the diagrams. These values can, however, be checked by comparison with diagrams from not far distant localities.

III. DATA FOR COMPARISON.

A. THE CLIMATE OF THE HAWAIIAN ISLANDS.

1. CLIMATIC CONDITIONS IN RELATION TO THE GENERAL CIRCULATION (BY C. C. WALLÉN).

The climate of the Hawaiian Islands is conditioned primarily by the general circulation of the atmosphere on the latitudes in question, which is dominated by the prevailing North Pacific high pressure, and partly by the cooling influence of the sea. The high pressure area, caused by the subsidence generally ruling at the tropical circle, is developed during the whole year but varies in position and intensity at different times. It is best developed during July—September. Then its centre is situated immediately N of lat. 40 and at about 150° W (Daingerfield 1921). Fig. 2 shows an example of the distribution of the atmospheric pressure over the North Pacific area in a typical summer situation.

During the winter (November—March), the high pressure is less developed and shifted considerably to the S or SE: its centre lies on an average between lats. 30 and 40 and substantially 10° more east than in the summer (l. c.). Fig. 3 shows its appearance in a typical winter situation.

The gradient between the North Pacific high pressure and the permanent low pressure at or N of the equator gives rise to the NE trade wind. The greater intensity of the high pressure during the summer renders the trade wind more persistent during this part of the year than during the winter, when the high pressure area is less developed and under certain conditions divided into two cells.

A recent investigation of the precipitation conditions on Oahu and their relation to the general circulation (Yeh and Wallén ms.), elicits a number of facts regarding the circulation above the Hawaiian Islands. Statistical frequency calculations of various daily meteorological situations thus show that during July—August up to 96 % of these are of pronounced trade wind character. This also includes such situations as when the high pressure area at times is shifted to the W so that the trade wind acquires a more E—SE direction above the islands.

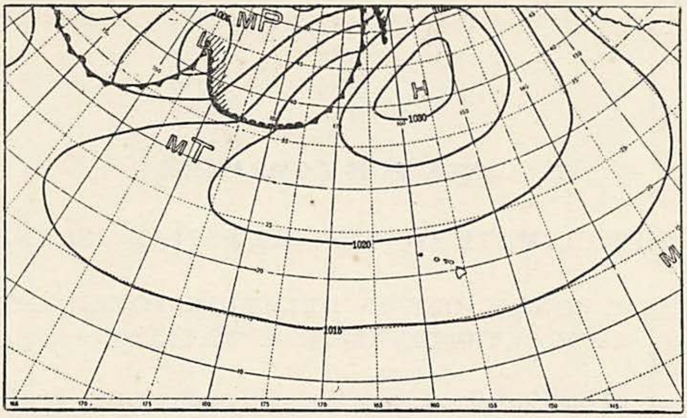

Fig. 2. Synoptic weather map of the North Pacific, July 7, 1938 (sea level, 1300 GMT); typical summer situation. — Simplified from »Historical Weather Maps», Weather Bureau, Washington, D. C.

In the winter the subtropical high pressure area is at times shifted to the S under the influence of fairly regularly recurring outbreaks of polar air which make their way from the powerfully chilled Eurasian continent, mostly in a NW current, towards southern latitudes. Thereby shifting storm centres are formed so far south that the relevant frontal system touches the Hawaiian Islands (Henry 1925). Under such conditions and especially in connexion with a very strong frontal disturbance the high pressure area is divided into two cells. When this occurs, or else in connexion with a low pressure trough within the high pressure area W of the Hawaiian Islands, raging S—SW storms arise, which have of old been known as »Kona storms» (Daingerfield 1921, Henry 1925). During November—February daily weather conditions of cyclonic type occur in more than 50 % of all the cases (Yeh and Wallén ms.). In February, trade wind situations occur only in about 40 % of the daily weather conditions.

The Hawaiian climate is characterized by a reciprocal action between anti-cyclonic (trade wind) and cyclonic weather conditions.

2. PRECIPITATION (BY C. C. WALLÉN).

The climate of the islands is oceanic and subtropical, and the majority of the climatic elements accordingly show a marked uniformity over the year. We find one element, however, which is intimately related to the general

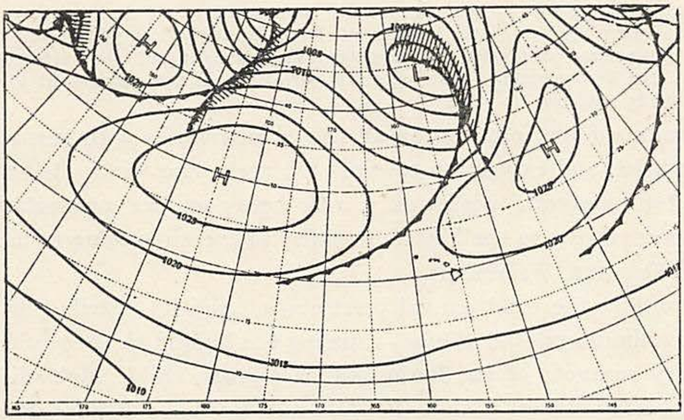

Fig. 3. Synoptic weather map of the North Pacific, Feb. 25, 1937 (sea level, 1300 GMT); typical winter situation. — Simplified from »Historical Weather Maps», Weather Bureau, Washington, D. C.

circulation discussed above and which is very variable: the precipitation. As out of the various climatic elements on the islands this is of the greatest importance for the vegetation conditions, it will be dealt with first.

It has long been known (e. g. Henry 1925, Tüllmann 1936) that the precipitation of the Hawaiian Islands is linked up with both (1) anti-cyclonic and (2) cyclonic situations. They include:

1 a) Trade wind precipitation, which occurs in connexion with orographical lifting of the air by the trade wind impinging on the steep and high windward sides (Fig. 4). Turbulence and convection in connexion with the rough topography of the islands cause very great local variations.

1 b) Precipitation, often of local character, due to sea breeze effects during the evening on the larger islands or else to radiation chilling at high levels during the night, principally over the smaller islands (Loveridge 1924).

2 a) Precipitation in connexion with more or less clearly defined cyclonic situations, where extra-tropical low pressure troughs or frontal systems pass over the islands from W to E.

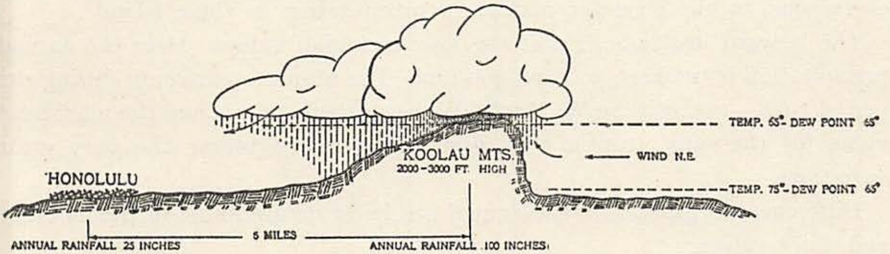

Fig. 4. Cumulus clouds. Cross section of the cloud-cap over Koolau Mountains, East Oahu. — After Hamrick 1918, p. 416, Fig. 1.

2 b) Precipitation connected with the occurrence of low pressure troughs with movement from E to W, should, from the point of view of the general circulation, be mentioned as a special type. They are probably connected with the displacements and intensity variations in the permanent low pressure area around the equator.

The amount of precipitation on all the islands varies with seasons, height above sea level, and exposition towards the prevailing wind. As regards the latter factor, southern winds as a rule bring greater precipitation than northern ones, owing to the higher humidity of the air coming from southern latitudes (Yeh and Wallén ms.).

If we consider the total annual precipitation and its distribution, we find that the maximum rainfall values — among the highest in the world — occur on the very summits of the lower islands (Kauai, Oahu, Molokai, and W. Maui) but on the highest islands (E. Maui and Hawaii) fairly far down on the windward side. More detailed data and rainfall maps are found in Chap. III: C: 4 (data) and III: C: 2 [maps simplified from Hinds (1931) and H. Stearns and Macdonald (1942, 1947)]. The said difference has previously been discussed (e. g. Henry 1919), but no conclusive explanation has yet been presented. A decisive cause of the intensity of the precipitation and its vertical distribution is probably the height of the inversion, which in the subtropical high pressure area is mostly well developed (Jones 1939). The average height of the inversion lies at about 2000 m (aeroplane soundings over Honolulu; Yeh and Wallén ms.). The mountain peaks of E. Maui and Hawaii rise considerably above this limit, while on the other islands they lie below it. As release of precipitation above the inversion occurs only in exceptional cases such as for example in the form of isolated snowfalls during the winter — and then at a very great height — the highest parts of E. Maui and Hawaii are very dry. That the zone of maximum rainfall on the higher islands lies considerably below the level on the lower northern ones is probably due to the fact that the air current which catches these high islands has to find its way round them. The level for maximum convergence might well correspond to the level for maximum precipitation in these islands.

The leeward lowlands exhibit the lowest rainfall values. Here the annual precipitation is between 300 and 400 mm. The absolute minimum during the period 1916—1932 was on W. Maui (Tüllmann 1936) 51 mm and the maximum value for the same station 1856 mm. This clearly shows the very great variations.

Differences as great as in the annual precipitation are found in the monthly and daily values.

Acc. to Henry (1925), the value of 31.95 in. (812 mm) was recorded on one day and no less than 102.46 in. (2610 mm) in one month. These figures represent absolute maxima. Great changes from year to year occur, both in monthly and annual values. A variation by months can be clearly established, however. Tüllmann (1936) has investigated and proved this annual variation. Precipitation maxima occur on all the northern islands (Kauai to Molokai) during November—January and secondarily in April, on the southernmost (Hawaii and Maui) somewhat later, namely secondarily in November—February, the absolute maximum being in April—May. A weaker secondary maximum recurs everywhere within the islands during May—September.

So far as goes the variability of the monthly values, frequency studies of the annual variation in the monthly precipitation within different regions of Oahu (Yeh and Wallén ms.) have revealed the following main features: The frequencies of low monthly values increase from winter to summer, and the really high values are encountered practically only in winter. The variations in frequencies decrease with increasing height above sea level; this applies to Oahu which is only 1200 m high. It applies more clearly to the windward than to the leeward sides. Finally, the relative variations of the monthly precipitation values everywhere are greatest during the autumn and spring and least during the summer. The pronounced trade-wind rain months accordingly show the greatest uniformity from year to year.

The investigation previously quoted (Yeh and Wallén ms.) has afforded a number of results which contribute to an understanding of the connexion between the precipitation and the meteorological situation. It comprised a study of the frequency of 8 daily weather situations during 25 years. A brief account of the various types and their frequencies are given in Fig. 5.

As pointed out previously, the precipitation maximum occurs on all the islands during the winter, i. e. concurrently with the highest frequency of cyclonic situations. It has therefore often been concluded that the maximum during the winter is mainly caused by cyclonic rains.

The investigation of the connexion between daily meteorological conditions and precipitation for three stations on Oahu revealed, however, the following (see Fig. 6): At the leeward stations, in this case Honolulu, cyclonic rains prevail from October to April with the exception of December. During the remaining months trade wind rains dominate. At the highest station, Luakaha (c. 300 m elev.), only somewhat to leeward of the mountain crest (E. Oahu), the trade wind rains dominate during all the months of the year.

The precipitation probability shows a distinct maximum in the high regions of Oahu and a minimum at the leeward coast. Each of the stations shows a maximum during July, which means that, irrespective of the actual amount of rain, the trade wind brings rain nearly every day during this period of the year. Since the precipitation maximum occurs during the winter but the probability shows

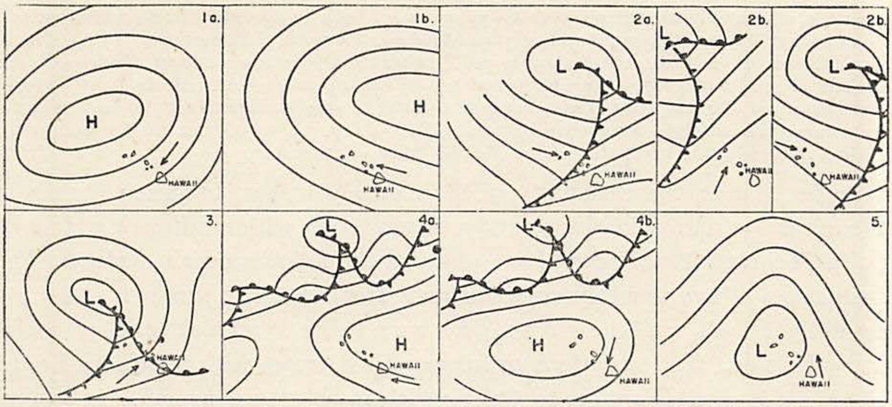

Fig. 5. The eight main types of synoptic situations around the Hawaiian Islands. 1 a and b are trade wind (anti-cyclonic) situations, 2—5 are cyclonic types. 1 a, causing NE trade, is more frequent throughout than 1 b, which gives rise to SE or E winds. Among the cyclonic types, 2 b (low pressure trough near the islands that moves eastwards) is the commonest with a frequency of 20—30 % during November—March. Type 3 is rare (average frequency once a year). Type 5 comprises types with low pressure troughs moving westwards. Its frequency shows little variation, the maximum being reached in winter with about 3—5 %. — After Yeh and Wallén ms.

maximum during the summer, the rain intensity must be greater during the winter than during the summer. Further, the difference in intensity from summer to winter is greater in the mountains than in the lower regions, since the probability varies most within the former districts.

The probability of precipitation in a trade wind situation is greatest at the mountain stations on the windward sides and least on the leeward (Fig. 7). The diagram in Fig. 7 also shows that the greatest probability occurs at Luakaha during the summer, but in Honolulu during the winter. This proves that during the winter the trade wind rains must be of importance also at the leeward stations, from which it further follows that the mechanism in the atmosphere which regulates the trade wind, must be subject to variations from summer to winter. Probably the trade wind inversion becomes weaker. The possibility of trade wind precipitation, if only in comparatively small quantities, also on the leeward sides thereby increases from summer to winter.

The cyclonic situations show values for precipitation probability which vary at the different stations by surprisingly small amounts. Even here Luakaha has a maximum (due to the orographical effect), which however is considerably less than in cases of anti-cyclonic precipitation. Neither can any variation in the probability worth mentioning be traced during the months

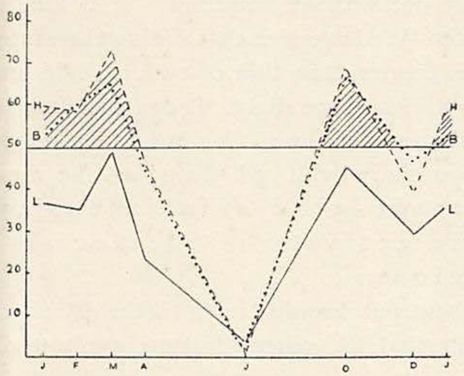

Fig. 6. Annual variation of percentage of precipitation due to cyclonic situations at three stations in Oahu. (L = Luakaha, B = Schofield Barracks, H = Honolulu). Values for May, June, August, September, and November excluded. The ruled areas mark the periods of dominating cyclonic precipitation. See further the text. — After Yeh and Wallén ms.

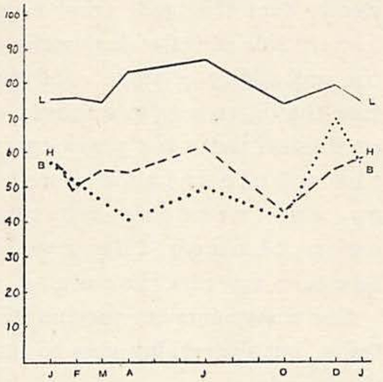

Fig. 7. Annual variation of probability of rainfall conditioned by anti-cyclonic situations at the same stations as in Fig. 6. Values for May, June, August, September, and November excluded. — After Yeh and Wallén ms.

when cyclonic rains occur. This in its turn shows that variations which occur in the total rain probability during the winter must be due to variations of the trade wind frequency.

Finally, it is of interest to study the amount of precipitation which is normally to be anticipated during the various weather types. The period 1930—1940, which had to be used in the investigation referred to, is too short to give reliable mean values. However, the variations during the year can be studied and some comparisons be made. At all the stations the daily precipitation is greater during the winter than during the summer, both for cyclonic and anti-cyclonic rainfall. This indicates clearly that the rain invoked by the trade wind is much more intensive in the winter than during the summer in all regions of Oahu. For mountain stations such as Luakaha the trade wind precipitation is in addition more intensive than the cyclonic precipitation throughout the year (primarily for orographical reasons). At the leeward station Honolulu and even at the plateau station Schofield Barracks in the central part of Oahu, the cyclonic rains produce greater daily amounts than the anti-cyclonic, but the difference is surprisingly small. In January a typical cyclonic situation at Honolulu shows on an average 8.6 mm per day, while the trade wind rain gives 5.8 mm. At Schofield Barracks the corresponding figures are 9.9 and 6.4 mm. This illustrates even more clearly that the trade wind rains are not without significance even for the leeward side of Oahu during the winter. We have seen that during the winter the probability of trade wind rain is greater than that of cyclonic rain and that the differences in intensity of both kinds are slight. It can therefore be established that the precipitation during the winter over the whole island must to a fairly high degree be due to an increase of the trade-wind rain intensity, even though the cyclonic activity is the decisive factor in the leeward regions.

The viewpoints on precipitation here put forward refer to the Island of Oahu, but everything goes to indicate that the general features apply to all the islands.

3. WINDS.

The most important characteristics of the direction of the winds are presented in Wallén's account of the general circulation conditions (Chap. III: A: 1), to which reference is made (see also p. 90, note 1). The wind velocity will on the other hand to some extent be dealt with here.

Acc. to Pilot Charts, the average velocity of the trade wind out at open sea is about 4 Beaufort = 6—8 m/sec. Beals (1927 b, p. 221) considers 15—20 miles/h = c. 8 m/sec. to be an acceptable average.

Those surveys which have been carried out for example in Honolulu naturally show lower values. Acc. to Beals (l. c., p. 221, Tab. 14; cf. Daingerfield 1926, p. 6) the mean velocity of the trade wind there during the period 1905—1925 was 3.9 m/sec. At a windward station, Haiku on E. Maui, the velocity of the trade wind is again considerably greater and attains in July about 7 m/sec. (Daingerfield 1926, p. 6). In the mountain passes it can rise to far above normal values. 27 m/sec. has thus been recorded in the upper part of the Nuuanu Valley (Hamrick 1918, pl. facing p. 416). Hillebrand states (1888 a, p. 305) that the trade wind in exceptional cases can blow up to »Stürmen von eben so grosser Intensität als die Südwinde» (see p. 100 below, however).

The annual average velocity of the trade wind varies but little. During the period 1905—1925 in Honolulu it was as a rule between 8.1 and 9.0 miles/h (= 3.6—4.0 m/sec.), 1917 however 7.5 and 1918 9.2 miles/h (= 3.4 and 4.1 m/sec.) (Beals 1927 b, p. 221). Lindgren (1903, p. 16) states that the trade wind is strong especially in the winter. The situation most often is the contrary, however. Beals (l. c., p. 220) has thus shown that if the value 10 represents the force of the trade wind during the summer, then the value for the autumn is 9, the winter 7 and the spring 9. The daily variation has been dealt with by Beals (l. c., p. 221); we can here pass over these data.

The velocity of the Kona storms varies considerably. Jarves (1847, p. 13) points out that »No hurricanes have been known». Hillebrand (1888 a, p. 306) mentions that »die um die Regenzeit vorkommenden Stürme, obgleich heftig genug, um alte Bäume zu entwurzeln, doch kaum je den Character der Cyklonen tragen; eine Ausnahme jedoch macht vielleicht der im September 1871 vorgefallene Sturm, welcher viele Verwüstungen angerichtet hat; an ihm hat man in seinem Fortschreiten deutlich die Drehungen der Windrose beobachten können.» A similar case is reported by H. Stearns (in H. Stearns and Macdonald 1942, p. 27): »A tornado accompanied by heavy rain swept inland from Kihei [E. Maui] on January 30th, 1937, damaging buildings and trees along its path . . . Fallen trees indicated a counter-clockwise rotation of the wind. It is the only tornado recorded in the Territory.» Acc. to a table for the period March 1914 — February 1921 (Daingerfield 1921, p. 329) a wind velocity of 51 miles/h (= 22.8 m/sec.) was attained at Honolulu on January 18, 1916.

4. TEMPERATURE.

The mean temperatures for the various parts of the year show slight variation, especially in the lowlands (cf. Loveridge 1926, p. 370—372). Thus the annual average for Honolulu during the period 1890—1925 only varies between + 23° and + 24°.5 C (l. c., p. 372, Fig. 1). The average is + 23°.3. The monthly temperature at the same station varies between + 21°.3 (Jan.) and + 25°.3 (Aug.), the extreme day temperatures between + 11°.1 (Feb. 1902) and + 32°.2 (Oct. 1891), all acc. to Schott (1938, p. 27). The 24 hour variation in Honolulu is 5°.7 (5°.6—6°.2) C (l. c. p.).

The values quoted for Honolulu can in the main be considered to be representative of the lower parts of the islands, although the temperature, which varies principally with the height above sea level, to a certain extent is also influenced by the exposition. Districts with high precipitation and cloudiness, as is often the case to windward of the islands, have lower temperatures than those situated as Honolulu on the leeward sides of the mountains. At Hilo the annual average is thus 1° C lower than in Honolulu. The warmest month is August, except on Maui (September). The coldest month on the most northerly islands, Kauai and Oahu, is January, otherwise February. The variation in monthly averages is slight. If the values given by Daingerfield (1926, p. 5) are arranged in a N—S series, we find the following gradual decline:

Kauai	7°.9 F	= 4°.4 C
Oahu	7°.4 »	= 4°.1 »
Molokai	7°.2 »	= 4°.0 »
Lanai	6°.4 »	= 3°.6 »
Maui	6°.1 »	= 3°.4 »
Hawaii	5°.2 »	= 2°.9 »

The highest temperature that has been observed in the islands is stated by Clark (in H. Stearns and Clark 1930, p. 165) to be 97° F = + 36° C, noted at Aiea and Wailua Mill, Oahu. A higher value was reported on 27/6, 25/7, and 21/8 1915 in Mahukona, at the ocean to leeward of the Kohala Mts (Hawaii): 98° F = + 36°.5 C. This is the highest officially recorded air temperature known from the islands. The lowest temperature that has been recorded in the lowlands below 300 m alt., is + 5° C (Daingerfield 1926, p. 5; Oahu: Schofield Barracks). During the winter the temperature falls regularly to below freezing-point within the upper parts of the highest islands: Haleakala on E. Maui and the three highest mountains on the island of Hawaii (see map, Text-fig. 27). The snow on these peaks disappears in the summer; an isolated patch in sheltered spots in the highest elevations can remain, however, as already noted by Jarves (1847). Frost is probably experienced in these areas practically every night throughout the year (see Guppy 1906, Jones and Bellaire 1937, p. 119). In exceptional cases frost is experienced in the belt where the montane mires occur, right down to the 1200 m level. On lower levels temperatures below freezing-point are extremely rare. Daingerfield (1926, p. 6) states that it seems doubtful if frost ever occurs below the 2,500 ft (= 760 m) level. He remarks, however, that on January 7, 1911 in Glenwood (Hawaii, 2300 ft = 700 m alt.) only + 3° C was recorded — the lowest temperature known from so low a level in the islands — and that the Volcano Observatory at Kilauea (3884 ft = 1184 m) had frost on the same morning. It may be added that the lowest temperature which Wilkes (1845) recorded, — 11° C, is considerably below the lowest officially recorded temperature which Daingerfield (1926, p. 6) reports from the islands. This was — 4° C (March 6, 1912, at Humuula, 2025 m elev., Hawaii). As regards the belt where the mires are situated, 1200—1800 m elev., reference is made to Chap. III: C.

Compared with the other districts on the same latitude, Honolulu's annual average is fairly low and below the general average by about 6° C. This is probably due primarily to the influence of the surrounding ocean currents and also to the persistent trade wind (Bishop 1904, p. 74), the retarding effect of which on the summer maximum is especially distinct. This occurs, as we have seen, in August or September.

As the vertical temperature gradient is steepest in the warm regions, a rise here as a rule involves a greater temperature fall than does a similar rise on higher latitudes. A formula for calculating the temperature at a certain spot, knowing its height above sea level, has been worked out by J. F. Vorhees (see Jones and Bellaire 1937, p. 112, note 2). Schott (1938, p. 27) gives the temperature fall for 100 m rise as: 0—400 m: 0°.85 C; 400—1000 m: 0°.60 C; 1000—2000 m: 0°.55 C. Radio soundings from Honolulu in 1947 gave the following mean values (Celsius degrees) of the temperature gradient per 100 m during summer and winter months (Mr T. C. Yeh, Chicago, in letter to Dr C. C. Wallén, Stockholm):

	Dec.	Jan.	Febr.	June	July	Aug.
0—1000 m	0°.89	0°.87	0°.77	0°.94	0°.95	0°.91
1000—2000 m	0°.43	0°.32	0°.41	0°.35	0°.48	0°.57

It is a well-known fact, recently emphasized not least by Troll (1941), that in the tropics also on higher levels the greatest temperature variation is not between the seasons but is conditioned by the difference in radiation between day and night: a pronounced 24-hour variation thus prevails and increases with altitude. For example, Lyons (1902, p. 364) states that the 24-hour variation at a lowland station, Pepeekeo (Hilo, Hawaii), attains 4° C, in Honolulu 6° C, and on somewhat higher levels 8°—9° C. On the summit of Mauna Loa both Wilkes (1845) and Guppy (1906, p. 210—211) found a 24-hour variation of about 17° C; Hillebrand (1888 a, p. 306) in August 1862 found on the high plateau of the Island of Hawaii a variation reaching up to about 19° C. A Table in Guppy 1906 shows the slight difference between the seasons. This type of variation is not, as Guppy believed, unknown in continental types of climate but is due to the latitude of the locality, and its strong accentuation, as stated, to the altitude.

B. GENERAL SURVEY OF THE HAWAIIAN VEGETATION.

None of the islands of Oceania present a wider range of habitats than the Hawaiian Islands. They extend from the tropical littoral to the alpine desert at 4210 m above sea level, their windward sides are thickly forest-clad and have local mires, due to heavy precipitation — among the heaviest in the world — while their leeward sides are barren or covered by scrubs and dry forests[1]). There is hardly any place in the world where the climate and vegetation vary so much within so small an area. The islands comprise only 16,784 km², of which 10,398 km² is accounted for by the highest island, Hawaii.

Schemes of major divisions of the Hawaiian vegetation have been proposed on many occasions. Hardly any of them are quite consistent, however, as they coordinate leading altitudinal belts with regional facies. Hartt and Neal (1940) took a step in the right direction when — although without discussing the systems of Hillebrand (1888 a, b) and Rock (1913, 1915) in their entirety — they pointed out that the three first of Schimper's (1903, etc., see also for inst. Krašan 1883, p. 291, and above all van Steenis' valuable account of 1935 with numerous references to previous literature) world-wide altitudinal belts of vegetation, basal, montane, subalpine, and alpine, correspond to the lower, middle, and upper forest zones, respectively, of the said authors. Hartt and Neal are largely correct in adding that »no region corresponding to the alpine zone of Schimper was described by either Hillebrand or Rock»

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[1]) The term forest, as used in this paper, comprises all formations in which trees are predominant and characteristic, whether in closed or open formation. A more restricted use of the term would perhaps be better (see further Burtt Davy 1938).

(l. c., p. 241). Both Hillebrand and Rock recognize the existence of an upper limit of tree growth, however, but evidently hesitated to apply the word »alpine» to the belt above this. Rock (1913, p. 23) mentions »alpine zones» in the Island of Hawaii, but only in passing. This hesitation has a long previous history and is apparently largely due to a misconception that an alpine belt must be characterized by a set of species confined to it, which the Hawaiian is not.

In using the term alpine, Skottsberg (1930 b, 1931 a, b), Robyns (1938), Robyns and Lamb (1939), and Hartt and Neal (1940) have had predecessors among the early explorers. Thus, Chamisso (1821, p. 144; 1830, p. 315; 1836, p. 298), Gaudichaud (1827, p. 89), and Douglas (in Hooker 1836, p. 164) speak correctly of an alpine flora. (Wawra's use of the term will be dealt with below). The abovementioned misconception can be traced to members of the U. S. Exploring Expedition in 1838—42. Wilkes summarized their experience (1845, p. 283):

> »The botanical regions may be divided into that of the seacoast, the wooded district below the altitude of six thousand feet, and a third division at a still higher level. Alpine plants do not occur here.»

Pickering's version is (1876, p. 478):

> »The Hawaiian Islands, as will be perceived, contain only two botanical regions. And notwithstanding the great height of the mountains, the congested alpine phase of vegetable growth does not occur upon them.»

Still, Pickering and Brackenridge on their ascent of Manua Kea in January, 1841, speak of »an Arctic flora» (Wilkes 1845, p. 202) — a designation which, however, should be restricted to plants of Arctic latitudes.

Remy (1862, p. XX, XXIII) correctly tried to re-introduce an alpine belt, but this was again dismissed by Brigham on floristic grounds (1868 b, and note in Mann 1869 a, b), and indirectly by Mann (l. c.), who does not mention it in his survey. Their opinions are repeated by several authors (Jouan 1873, Meinicke 1876, Wallace 1880, Hemsley 1885, etc.) and are also probably the ultimate reason why Hillebrand (1888 a, b), Guppy (1906), Rock (1913, 1915), Bryan (1915), Mac Caughey (1916 a, 1917 a, b), Forbes (1921), and others, are silent on this point.

The following table gives an idea of the various interpretations in the course of time. Since the term »basal» appears inappropriate for areas where there are no other belts on top, I have proposed the name of »inferial» for the lowest belt; this designation appears more neutral. van Steenis (1935, p. 329) calls this belt — the »lowland zone» of authors — the »tropical zone», but it can be objected that, strictly speaking, all altitudinal belts in the tropics are tropical. I shall discuss below the views on the so-called bog zone. It may be added that the table is in general restricted to papers that are intended to give a generally applicable scheme for the vegetation zones on the windward sides of the islands and the classifications of which are based on the pre-European vegetation. The most recent system (Ripperton and Hosaka 1942) is primarily intended for agricultural purposes and not for a survey of the said vegetation; its relation to this is moreover partly not quite clear.

A generally applicable scheme for the vegetational zoning of the leeward sides, and its parallelization with the zoning of the windward sides, meet with considerable difficulties on account of the even more diffuse character of their boundaries and of the local differences in climate to the leeward of mountain massifs of varying sizes. Rain forests conditioned by essentially different wind systems may therefore be intercalated in considerably varying altitudes. I shall revert below to the vegetation on the leeward sides.

As will be seen from the Table, the montane mires have erroneously been considered to represent a belt of their own, equal in rank to the leading belts. The most peculiar of these interpretations is Mann's (1869 a, p. 539). In his scheme they constitute the »Dry Mountain Region» (l. c., p. 541) — which is expressly stated to refer to »A small region on the summits of West Maui and Kauai, which lies above 6000 [!] feet and which is not wooded» — two of the very wettest places of the world! Mann and Brigham must have been there in a period when the moisture-laden trade wind did not blow and the ground had temporarily dried up.¹) Pickering's (1876) classification is no better: it includes the mires in the Mountain region above 6700 ft (= the subalpine and alpine belts). Wawra (1873, p. 62) even considered them alpine, and as late as in 1934 (p. 33) Yuncker speaks of »the so-called alpine bogs» of the islands. Hillebrand does not discuss the general relations of his bog zone. He merely states that »a place apart» must be assigned to it, and deals with it as zone No. 5 in his series of leading zones (see Table). Subsequent authors have followed him when considering this zone. These mires are clearly a facies of the montane vegetation, however, and their leading rank in the zonation system must therefore be withdrawn.

The vegetation in different altitudes, primarily divided into windward and leeward sides, is briefly surveyed below. This classification seems to be most appropriate when one has to trace changes in the vegetation due to the altered balance of the two competing wind systems, the anti-cyclonic trade winds and the cyclonic kona storms. These have the paramount influence on the precipitation in the islands, and are thus the leading factors determining the

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¹) See further Mann 1866, p. 233, where the summit of W. Maui is stated to rise »to a height of about one thousand feet above the general level of the clouds»(!).

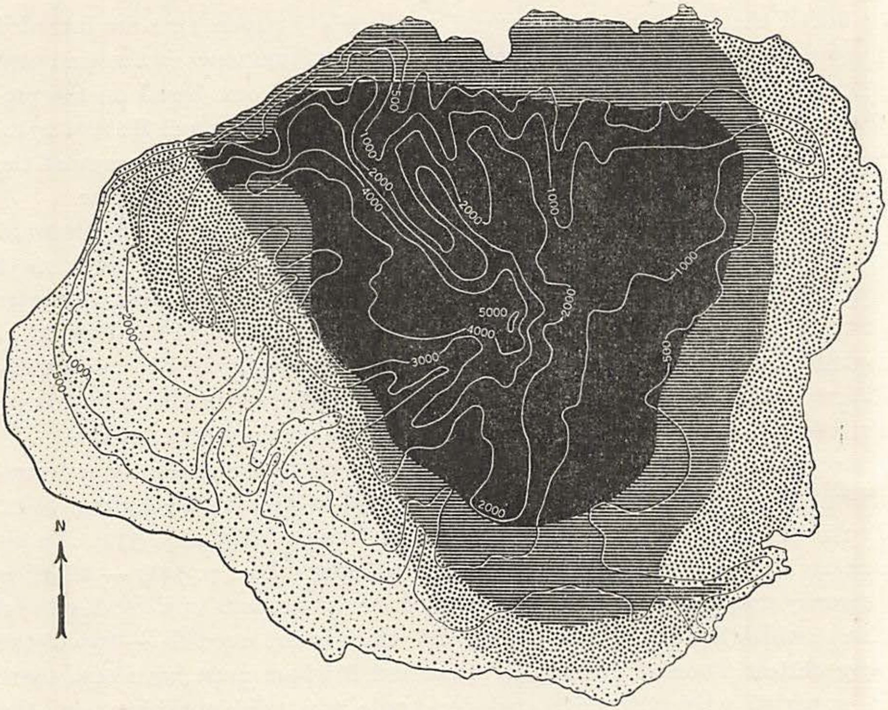

Fig. 8. Vegetation map of Kauai. Black: wettest type of rain forest (= Zone D$_2$ of Ripperton and Hosaka 1942), ruled: less humid rain forest (= Zone D$_1$), dotted: intermediate and dry zones (crowded dots of larger size: Zone C$_1$, dots of two sizes: Zone B, small dots: Zone A). — Simplified from colour map in Ripperton and Hosaka 1942. Scale: see Fig. 9.

major features of their vegetation below the inversion limit (see p. 28). Obviously, nobody adopting this basis of classification would take into account the direction of the wind as such (cf. Egler 1939, p. 47), any more than he would, when studying the altitude values, try to establish any interdependance of plants and barometric pressure. Attention must also obviously be given to the relative as well as the absolute altitudinal changes in the vegetation, as the atmosphere is stratified, and an elucidation of the interrelations of the several strata is as important in an analysis of the whole question as the study of conditions in each. The simplest way seems to be that adopted in the above Table, viz. to attempt to determine in the first place the leading climatic altitude belts, and to distinguish between these and the facies within the belts. Little weight will here be attached to the less readily circumscribed and often ± local subordinate zones that may be distinguished in present-day vegetation.

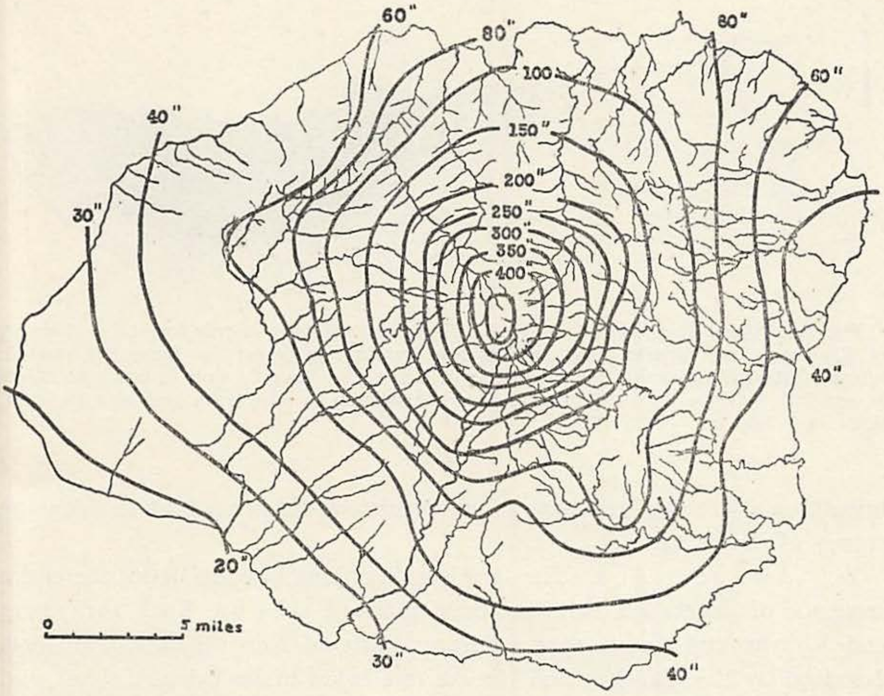

Fig. 9. Rainfall and drainage map of Kauai. — Simplified from Hinds 1931, Fig. 1.

With few exceptions, there is no modern special literature from which a survey on these principles can be made. Early explorers such as Cook, Vancouver, Menzies, Chamisso, Gaudichaud, Byron, Macrae, Bloxam, Meyen, Douglas, Brackenridge, Pickering, and Seemann, give too general descriptions. Several of them, as well as Wawra, Hillebrand, and Rock, largely adopt floristic points of view. Hall (1904; 1916 not seen) deals only with the ecology of the most important forest trees, and moreover very briefly and only from the practical points of view; his altitude figures are of little value, and he does not describe the forest communities. The first detailed investigations of regional forest ecology are those of Hosaka (1937), Egler (1939; cf. 1937 and 1942), Robyns and Lamb (1939), and Hartt and Neal (1940). [Forbes (1912, 1914), Mac Caughey (1917 c), Robyns and Lamb (l. c.), and Skottsberg (1941), have devoted special studies to the succession on the younger lava flows of the island of Hawaii]. The task of making a detailed survey of the Hawaiian vegetation usable for pollen-statistical purposes cannot be satisfactorily completed without further thorough studies in the field. I have had to confine

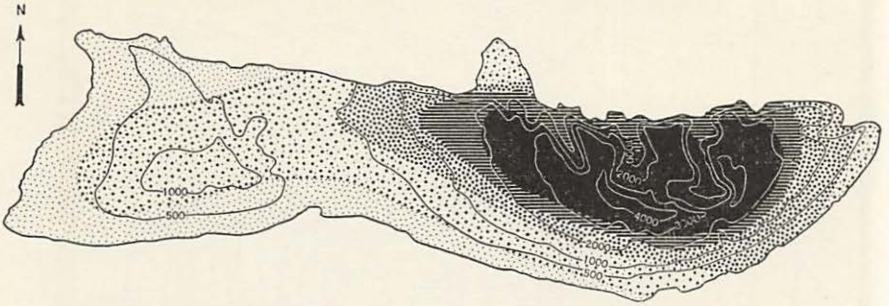

Fig. 10. Vegetation map of Molokai. Black: wettest type of rain forest (= Zone D_2 of Ripperton and Hosaka 1942), ruled: less humid rain forest (= Zone D_1), dotted: intermediate and dry zones (crowded dots of larger size: Zone C_1, dots of two sizes: Zone B, small dots: Zone A). — Redrawn after colour map in Ripperton and Hosaka 1942. Scale: see Fig. 11.

myself mainly to the literature, as my excursions did not permit an adequate survey of conditions.

Windward sides. The treatises describing in some detail the entire sequence of vegetation belts on the windward sides are Rock 1913, 1915 and Robyns and Lamb 1939. Certain parts of this vegetation are also described by Mac Caughey and Hosaka (see below under Leeward sides), and by Fosberg and Hosaka (see Montane Mires).

The low altitude vegetation, the beach plants (see Mac Caughey 1918 d, e) and forest communities of *Pandanus tectorius* var. *sandwicensis* and *Cocos nucifera* on the coast and *Aleurites moluccana* (Pl. 11 B) and *Pandanus* further inland (the Coastal-Lowland forest of Robyns and Lamb; cf. Mac Caughey 1912), does not appear in the pollen diagrams from the montane mires, and will therefore only be briefly mentioned. These forests are now largely replaced by plantations or else recently introduced competitive species (e. g. *Leucaena glauca*) have encroached upon their area. It is therefore difficult to get any idea of their original appearance and extent (cf. Egler 1942), especially if the conception original vegetation is limited to conditions before the introduction in the islands of *Aleurites*, which is generally assumed to have been one or two thousand years ago (as to the dating, see p. 129).

Montane rain forests, the dominant type of forest in the islands — in 1903 Hall (1904) estimated them at three fourths of the native forests — begin at the average lower limit of the cloud belt about 600 m above sea level (p. 27, Pls. 1 A and 2 B, and fig. on p. 364 in Brigham 1868 a: cloud cap of W. Maui), and cover the windward sides of all the large islands except E. Maui and Hawaii from that level upwards (cleared areas not considered). The leading

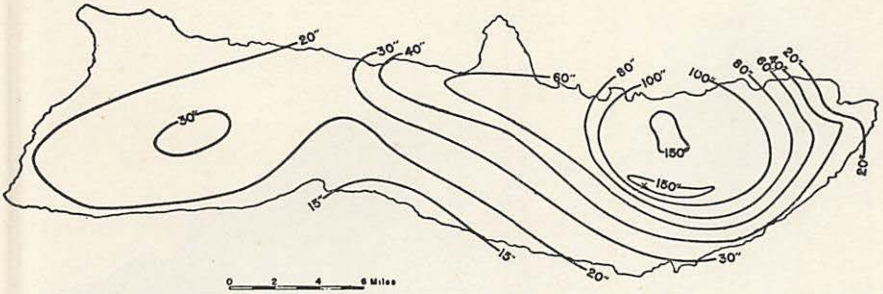

Fig. 11. Rainfall map of Molokai. — Simplified from H. Stearns and Macdonald 1947, p. 39, Fig. 6.

tree species is *Metrosideros polymorpha*. Other important species are *Myrsine Lessertiana* and *sandwicensis*, *Cheirodendron trigynum*, tree ferns of the genus *Cibotium*, species of *Pelea*, and others (Pls. 4—11). Herbs occur, but ligneous species dominate. Trunks, branches, and aerial roots are covered by mosses, liverworts, and other epiphytes. Robyns and Lamb (1939, p. 259) distinguish four layers in the lower parts of the rain forests in the island of Hawaii, the same number as that given by Hosaka (1937, p. 204—211) from the lower parts of the rain forests down the leeward side of the Koolau Range in Oahu. The more one approaches the wind-swept mountain tops and ridges, the lower and more scrubby are the trees, the poorer the under-vegetation in the dense thickets, and the deeper and wetter the mud on the ground. Often it is impossible to distinguish more than two layers of vegetation (see Hosaka l. c., p. 206; also Wawra 1872, p. 299; etc.). Pl. 8 gives an example, though not of the most extreme types, of which it is hardly possible to take clear photographs.

In the Island of Hawaii large areas are covered with fern forests [Pls. 10, 11 A (= Lyon 1919, Fig. 3, Campbell 1926, Pl. XXVII, Skottsberg 1940 a, Fig. 9), 20; see Part I, p. 43]. None of the other islands show similar developments; in them — as well as in other parts of the Island of Hawaii — the tree ferns generally form an under storey of the rain forest (Pl. 6, cf. Pl. 10 B). These differences will be discussed in Chapter V.

Mires — both swamps and raised bogs — are found in the upper parts of the rain forests from about 1200 m upwards (Frontispiece and Pls. 12—19). They are the source of the peat strata in the pollen diagrams. A separate chapter (III: C) will be devoted to them.

The rain forests cease towards the upper limit of the cloud belt at altitudes of from about (1800 to) 2000 m, where they ± gradually merge into the subalpine forests, to which Robyns and Lamb (1939, p. 263) applied the designation

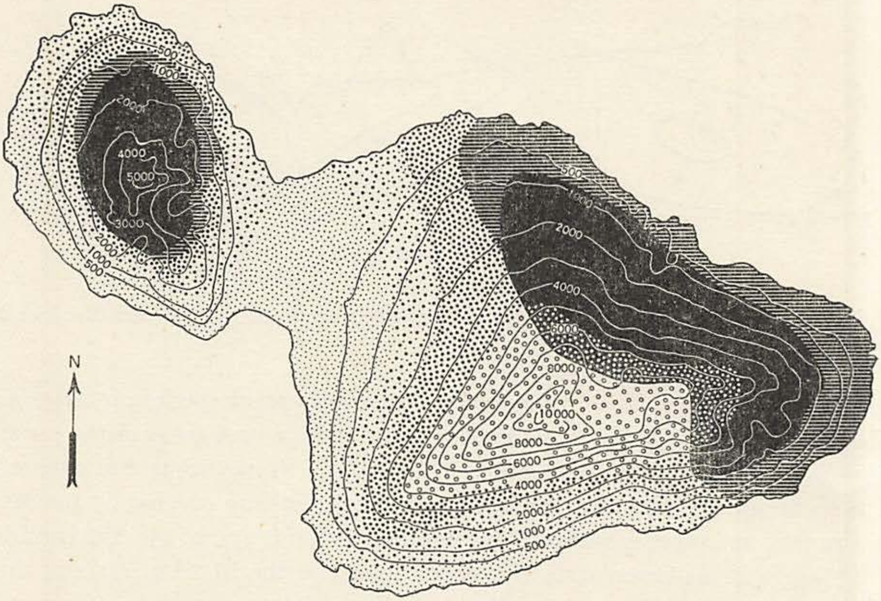

Fig. 12. Vegetation map of Maui. Black: wettest type of rain forest (= Zone D_2 of Ripperton and Hosaka 1942), ruled: less humid rain forest, low phase (= Zone D_1), black with white dots: do., high phase (= Zone D_3), circles: subalpine and alpine vegetation (= Zone E), dotted: dry and intermediate zones of lower elevations (crowded dots of larger size: Zone C, dots of two sizes: Zone B, small dots: Zone A). — Simplified from colour map in Ripperton and Hosaka 1942. Scale: see Fig. 13.

»Mountain Parkland». The transition between these belts in the island of Hawaii is described by Rock (1913, p. 35—36), and Wawra (1872, p. 365—366) has dealt with conditions in E. Maui (see map in the present paper, Fig. 12) Robyns and Lamb also note that *Acacia koa* may in some cases form a forest »as the uppermost association in the mountain forest, just below the mountain parkland» (1939, p. 264). The park land (see Pl. 21) consists of grasslands with scattered stands of *Acacia koa, Sophora chrysophylla,* and *Myoporum sandwicense,* and some arborescent species of *Railliardia.* Certain biotypes of the truly polymorphous *Metrosideros polymorpha* are also found there, but they only play a subordinate part. With these are associated shrubs of *Coprosma, Dodonaea, Geranium, Railliardia, Styphelia,* and *Vaccinium.* Robyns and Lamb quote a statement by Menzies in 1794, indicating that this parkland formation existed before grazing ever affected conditions. The forest limit is usually between 2100 and 2400 m above sea level, but the values may vary considerably. The tree limit is at an altitude of about 3000 m; the latter value is from Mauna Kea (Hartt and Neal 1940, p. 243). The regional variations

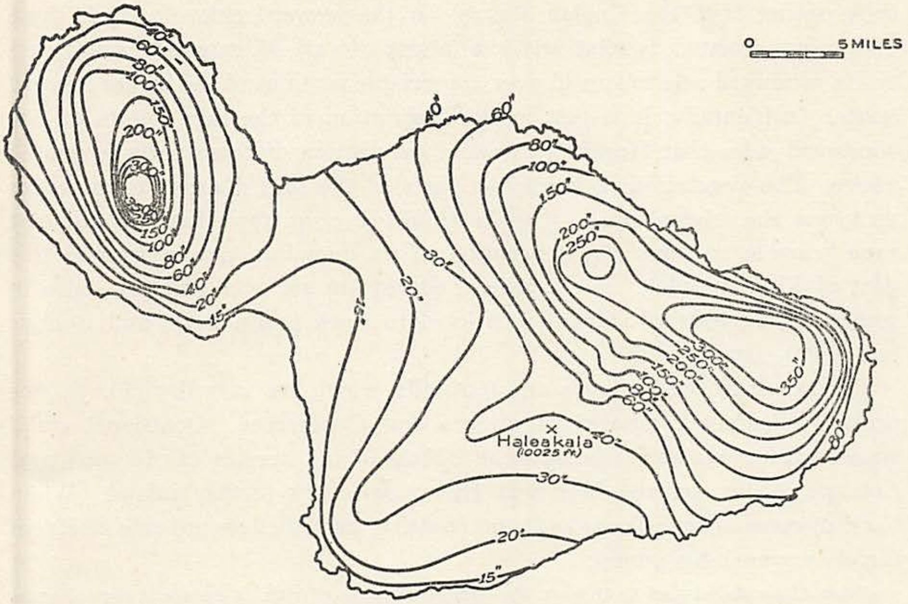

Fig. 13. Rainfall map of Maui. Simplified from H. Stearns and Macdonald 1942, p. 29, Fig. 5.

of the forest and tree limits, whether due to edaphic or climatic conditions, are inadequately known, and should be specially studied.

The alpine belt is in its lower parts characterized by shrub communities (cf. the foreground in Pl. 21 A) like those in the subalpine zone, and in its upper part by sparse occurrences of mosses and lichens, and scattered vascular plants (Pl. 22 B). On this subject see in particular Hartt and Neal (1940); Skottsberg (1930 b, 1931 a, b) has summarized the floral elements. The altitude limit of vascular plants is 4100 m above sea level (*Asplenium adiantum-nigrum;* Hartt and Neal 1940, p. 248). None of the mountains reach the snow limit, but the summit of Mauna Kea is probably close to it.

Leeward sides. The native vegetation and its distribution on a well developed leeward side have unfortunately never been thoroughly investigated, which is all the more regrettable as the original vegetation types of this category have now mostly disappeared. Mac Caughey (1917 a) and Hosaka (1937) examined parts of the leeward side of the Koolau Range in Oahu. Robyns and Lamb (1939, p. 244) call the Kipapa Gulch examined by Hosaka »a typical gulch on Oahu», but neither this nor the Manoa Valley near Honolulu examined by Mac Caughey are typical of the leeward sides as such, seeing that the Koolau Range, on the leeward side of which these valleys are situated, is relatively low (about 950 m), allowing the rain forest on its windward side to spread over appreciable portions of the higher leeward levels. Incidentally, it is just in the description of the rain forests on the windward sides that Hosaka's excellent description of these parts is quoted above. The vegetation in the lower parts of the said districts is moreover no longer the original one — Hosaka thinks (l. c., p. 179) that it is now not even possible to form any conception of its quondam composition in this part of Kipapa Gulch. For a general survey we are accordingly — also in respect of the leeward sides — restricted to Rock (1913, 1915) and Robyns and Lamb (1939).

Vegetation in the lowlands and foot-hills, which are very dry (Pl. 3), was probably mainly composed of grasses and Cyperaceae. Occasional small copses of for example *Chenopodium oahuense* and species of *Abutilon* and *Sida* probably occurred here and there, especially further inland. When Cook discovered the islands he found (1784, p. 225) the leeward side of Kauai largely covered by »grass»:

> »From the wooded part to the sea, the ground is covered with an excellent sort of grass about two feet high, which grows sometimes in tufts, and though not very thick at the place where we were, seemed capable of being converted into plentiful crops of fine hay. But not even a shrub grows naturally on this extensive space.»

When Vancouver visited Kauai about 13 years later, in March 1792, he gave a similar description (1798, p. 170):

> »The sides of the hills. . . . . to the commencement of the forest, a space comprehending at least one half of the island, appeared to produce nothing but a coarse spiry grass from an argillaceous soil which had the appearance of having undergone the action of fire, and much resembled that called red dirt in Jamaica and there considered little better than a *caput mortuum*».

These early observations almost preclude the idea of any great cultural effects having cooperated in originating this type of vegetation, subsequently described (e. g. by Chamisso 1821, p. 143—145; 1836, p. 293 and 298; Meyen 1835, p. 119 and 137; Wilkes 1845, p. 58, 60, 61, 78, etc.; Pickering 1876, p. 383: leeward side of Oahu). Several species were shortly introduced which have now fundamentally changed the landscape, among them *Acacia Farnesiana*, *Leucaena glauca*, *Prosopis juliflora*, *Opuntia megacantha*, and *Lantana camara*. Pl. 3 A and B show present-day vegetation in the dry and hot lowlands.

Higher up — in the island of Hawaii in recent times from the altitude of about 500 m, but formerly probably lower down — begins the type of forest with a multitude of different species which Rock (1913, p. 15 ff.) called »dry» or »mixed» forest; Robyns and Lamb (1939, p. 254—256) use the less expressive term »transition forest». It is a xerophytic evergreen forest (only a few species shed their leaves periodically; see Pl. 3 C), in which no species can be said to dominate. More than half of the many species of trees in these islands belong to this dry forest. Rock has given detailed floristic descriptions of it (incl. the under-vegetation). In Kauai, Oahu, Molokai, and W. Maui, they have nowadays mostly disappeared, or are strongly affected by cultivation (cf. Hall 1904, p. 16—17: Molokai), and only remains of what once existed are left elsewhere: Auahi (E. Maui), Kipuka Puaulu, Kapua, and Puu Waawaa (Hawaii), and Kanepuu (Lanai; Fosberg 1936 b). *Osmanthus* (l. c., Fig. on p. 123) is typical of these forests among the pollen diagram species, but some of the others are found there, too.

The upper limit of these forests varies with the height of the respective islands. Behind the largest mountain massifs local rain-carrying convection currents in the air strata (»kona winds», not to be confused with the cyclonic »kona storms») produce patches of rain forest above this dry forest (see the maps of the island of Hawaii in Robyns and Lamb 1939 and in Hosaka and Ripperton 1942). On slightly smaller mountains, where these wind conditions (although the mountains still extend considerably above the inversion limit) are not as pronounced, the dry forest changes into the subalpine forest known from the descriptions of the zones on the windward sides. In still lower islands it is replaced by rain forest in the higher levels — the majority of the larger islands are not too high for the rain-carrying trade winds to influence also their upper leeward portions. The rain forest vegetation conditioned by the trade wind may thus in varying degrees disturb what might be called the »undisturbed» zone divisions on the leeward sides, and this holds for all the islands investigated for this study. The maps of Ripperton and Hosaka (1942), partly reproduced in Figs. 8, 10, and 12, give some idea of the extension of the most extreme rain forests over the leeward side in each island. The original extension of the less humid rain forests is difficult to illustrate cartographically. The belts of the leeward side rain forest — they must be kept apart from the belts of the windward side rain forest, since the rainfall conditions are different — have been described in the first place by Hosaka (1937), and somewhat less exactly by Rock (1913, 1915), to some extent also by Mac Caughey (1917 a). Rock's account is of importance in this connexion as it describes conditions in Kauai, to which I will revert when discussing the diagrams (p. 95). No corresponding data are available from Molokai or W. Maui. Rock states (1921, p. 16) that the rain forests on the leeward side of Molokai begin 900 m above sea level.

In the higher levels, above the inversion limit, the differences between the windward and the leeward sides gradually disappear, though facies and altitude conditions may differ. Differences in the exposition towards the sun become more prominent here (Troll 1941).

As the climate varies greatly in different localities, there will obviously be many deviations from the schedule outlined above according to their respective positions. Due attention must of course be given to this when interpreting the pollen diagrams.

C. THE MONTANE MIRES OF THE HAWAIIAN ISLANDS.

1. GENERAL INTRODUCTION.

A few lines will first be devoted to the meaning of the terms I am using in this paper. The motley terminology of mires will not be discussed, however.

»Mire» is here used as a general designation of all types of peatlands and their vegetation. It is thus a geographical term (Högbom 1906: Swedish »myr»). Of the various proposed systems of mire classification the genetic division acc. to water supply has been adopted. von Post and Granlund (1926) propose three groups:

1) Topogeneous (mainly fed by water of the ground); this type thus includes »Lake swamps» and »Spring swamps» (see for inst. Nichols 1918, p. 354).
2) Ombrogeneous (fed exclusively by precipitation); corresponds to raised bogs.
3) Soligeneous (a mixed type, occurring in humid regions; fed by rain and surface water).

Much would be gained if the designation »swamp» could be entirely discarded for the ombrogeneous type, and »bog» for the others so as to avoid the considerable confusion hitherto prevailing in literature. I have adopted the terms as proposed here. The designation »mosses» used by for instance F. J. Lewis about 40 years ago, in a general sense, and recently used in Scandinavian literature for ombrogeneous mires, is less good. It should be avoided since it is likely to cause confusion in combinations like mossy forest, etc.; in this respect I agree with Skottsberg (1940 d).

Montane mires — raised bogs and soligeneous swamps — have been found in four of the islands: Kauai, Molokai, Maui, and Hawaii, besides a type of vegetation coming close to true bogs in Oahu. Particulars of the various localities will be given below. The mires occur in altitudes from about 1200 to 1765 m; the highest limit of conditions permitting peat growth is probably somewhat higher. High precipitation [about 5000 mm (200 inches) a year] is a sine qua non (periods that have been far from dry and would have been represented in for inst. Boreal bogs are therefore unrepresented in the Hawaiian bog strata). Temperature is not quite as important as shown by the exceptional Wahiawa bog (Kauai) 600 m above sea level. Bülow (1929) writes: »In dem Bereich mediterranen, semiariden oder subtropischen Klimas ist bislang noch keine oligotrophe Moorbildung beobachtet worden. Selbstverständlich in den Tropen noch weniger.» Still, it has been observed there (see van Steenis 1932, etc.). The Hawaiian mires to be dealt with below belong to a temperate climatic belt, however.

In some cases (see Fig. 19, p. 67) the bogs occur on cliffs directly exposed to the trade winds, which are often deflected in the valley systems. The local orientation of the bogs may thus vary. In other cases their relation to the trade winds is more obscure. At any rate, my material is not sufficient for an elucidation of the problem. Lehua maka noe (Kauai) is exposed towards the SE, the lowest bog in W. Maui towards the NW (see Figs. 15 and 20). The mires at Kilohana (Kauai) and Pepeopae (Molokai) are separated from the trade-bringing valley by a narrow strip of forest. The conditions may possibly be due to microclimatic conditions such as pictured by Geiger (1930). Variations in the direction of the rain-bringing winds during the periods concerned may also have influenced their orientation. The scope for future study along these lines is wide.

Before entering on the vegetation and stratigraphy of the mires, a remark on their general importance to Pacific research should be made. About 30 years ago — Rock reports this in 1919 a, p. 73 — part of the Puu Kukui bog (W. Maui) was drained by the Louisiana drain method, of course to no good purpose whatever. Cultivation of these regions is out of question. In pleading for the montane mires' of the islands being declared National Monuments, Skottsberg (1940 d, p. 528) mentioned the serious consequences of destroying mire vegetation, and to them can now be added the loss of a unique source of information on the Late Quaternary history of the Central Pacific, the use of which has now barely begun.

2. VEGETATION.

The literature contains no thorough study of Hawaiian mire vegetation. The most detailed — though far from satisfactory — account so far available has been published by Rock (1913, 1915; I have not seen Mac Caughey 1916 b)

Brief notes have been published on many occasions, from Wilkes (1845), Mann (1867), Wawra (1873), Pickering (1876), Alexander (1883), and Hillebrand (1888 b) onwards; some of them will be quoted below under each island. In 1922, Skottsberg began a study of the mire vegetation. His investigations were continued in 1938 with the assistance of Miss Cranwell, and will be published later. A brief report was presented to the Sixth Pacific Science Congress (Skottsberg 1940 d). Part of this is used in the following sketch. It is also based on my own observations, supplemented by Skottsberg's field notes from 1938, which were kindly placed at my disposal.

Much of the montane Hawaiian mire vegetation consists of soligeneous mires formed mainly by densely tufted species of *Rhynchospora*. Where the soligeneous character is very pronounced, the surface of the mires remains fairly even, plants like *Oreobolus furcatus* and species of *Aira* and *Panicum* — generally occurring in the shape of compact cushions — form carpets merging into what might be called a »wet grass heath». In this occur scattered low shrubs (*Metrosideros polymorpha, Styphelia, Vaccinium, Coprosma,* etc.), herbs (*Selaginella deflexa, Schizaea robusta, Acaena exigua, Drosera longifolia* — the latter in Kauai only — and species of *Lagenophora* and *Viola,* etc.), together with mosses, liverworts, and lichens. In other places the shrubs become more prominent and crowded. They are still mainly dwarf forms of *Metrosideros polymorpha* (1—2 ft tall but flowering profusely; *Korthalsella* often parasitic). Other shrubs are *Myrsine, Styphelia, Ilex, Geranium humile* (not on Molokai), *Coprosma,* and *Vaccinium.* Together with them occur plants like *Astelia, Nertera,* and *Plantago* and several ferns (many also epiphytic): *Amphoradenium Saffordii* and *tamariscinum, Schizaea robusta, Sphaerocionium* (*Hymenophyllum*) *lanceolatum,* species of *Sadleria* and *Elaphoglossum.* Here compact cushions are found, too, not least on low ridges and hills. They are chiefly made up of *Oreobolus furcatus,* the principal peat-forming plant (see Hauri and Schröter 1914, Skottsberg 1916, Hauri 1917), and to a much lesser extent of species of *Panicum.* These cushions become confluent, the hollows between them are gradually filled by plant remains — *Rhacomitrium lanuginosum* and liverworts appear, followed by new individuals of cushion-forming plants. In this way bog hillocks are formed, which sometimes become as much as 3 $^1/_4$ m thick and over 50 m in diameter (see sections, p. 61). There is nothing like the »lagg» of the Boreal raised bogs anywhere though the boundary between a bog hill and a swamp may become quite sharp (Pl. 15 A). The cushions are rarely unmixed. Their surfaces are generally covered by a mosaic of sociations in which several species are found. The principal sociations are the *Metrosideros* sociation (including the species mentioned above in connexion with the shrub vegetation, *Gleichenia linearis, Lycopodium cernuum* and *L. venustulum, Cladium angustifolium, Smilax sandwicensis,* and others), and the *Oreobolus-Panicum*-sociation. They are figured in Pl. 13.

Regional differences occur, and statistical studies of the vegetation will no doubt reveal more differences than are known at present. In Molokai for instance the floristic aspect appears less varied, while on Kauai, and especially in the higher parts of W. Maui, some species are more prominent and new elements met with. With regard to the pollen-statistical comparison, some points of interest have been noted on p. 64.

The genus *Sphagnum*, the leading constituent of Boreal bogs, is of little or no importance in the Hawaiian. We saw no *Sphagnum* except in Kohala, where *S. palustre* forms extensive stands in the swampy forest (Pl. 20 B), or large, loose cushions on the cliffs exposed to the trade wind (Pl. 20 A) but does not form peat.[1] It was observed in Kohala in 1910 by Rock (1920, p. 209; see also Campbell 1927, p. 100). Bartram (1933) knows no other locality and lists only one more species, *S. Wheeleri*, credited to the »mountain bogs» of Mt Eke, W. Maui. This is probably of the same type as *palustre*, a view also held by Skottsberg (1940 d). Bartram adds that »one or both of these species would probably be found in the boggy areas of Waialeale». *Sphagnum* had already been reported from there by Rock (1913, p. 77). Hinds (1930, p. 23) mentions the genus from the Alakai plateau, and Hillebrand (1888 b, p. XXIV), in fact, speaks of it in a general description including Kauai and Maui. The first record from the islands seems to be a note in Sullivant (1859, p. 3): *Sph. cymbifolium* [= *palustre*]. He gives no locality. There is, however, an overlooked note from 1840 or 1841 in Pickering 1876 (p. 435). It refers to the specimen examined by Sullivant. It came from the island of Hawaii: »Sphagnum (No. 1). Rare; found by Mr. Brackenridge at the »saw-mill near Hilo»; (a locality to be suspected, as timber may have been brought there from Oregon)». The specimen appears to be in the Farlow Herbarium, Cambridge, Mass; it has not been available for study, however.

3. STRATIGRAPHY.

Until a close study of the peat-forming plant communities has been published, the particulars of bog stratification cannot, of course, be success-

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[1] It may be added that the pH value of water from a cushion of *S. palustre* (rim of Kawaikoi Valley, 1100 m elev.) was found to be 6.9. The values from soligeneous swamps are between 4.9 and 6.1 (some of these mentioned in Selling 1944, p. 75). All analyses were kindly performed at the Experiment Station of the Hawaiian Sugar Planters' Association.

fully tackled. Only the main stratigraphical features were studied, chiefly in borings. One narrow pit was dug through the peat (close to [E of] boring station no. 1 in Molokai; this should be noted by future investigators to avoid studies of disturbed strata). The peat is chiefly made up of *Oreobolus*, which gives it a reddish brown colour. Parts of leaves, stems, and roots may very often be seen mixed with remains of other bog plants, including occasional branches and roots of lignoses, fruits of for inst. *Myrsine*, etc. Local, dark parts seem to be formed by the *Rhacomitrium*-liverwort community in the hollows, other parts by *Carex*, *Cladium* and *Panicum*. In the *Oreobolus* peat the degree of decomposition also varies in different parts of the strata, but there are no sharp breaks of a general nature anywhere. In what will later be called Period II, a symmetrical arrangement of the more humified parts of the peat can be observed, and in one of the localities (Kauai: Kilohana, Ser. 81) they were found to occur in pairs symmetrically arranged around the culmination of the period. This feature will be discussed in Chap. V: A (Period II) in connexion with the pollen curves, which show partly parallel variations.

In respect of stratigraphical type, these bogs have their closest counterparts in the countries on both sides of the southern Pacific. Thus, Auer writes (1941, p. 652): »Im Gebiet der Regenwälder, vorwiegend im Schärenhof des Feuerlandes, gibt es einen besonderen stratigraphischen Typus, den man zuvor nicht gekannt hat. Er besteht aus *Donatia* und *Oreobolus*, die sich als eine hochmoorartige Erhebung wie ein hartes Polster aufwölben. Doch enthalten die unteren Teile dieser Moore Braunmoos oder Carex-Torfschichten.» Further descriptions and sections presenting similarities to the Hawaiian ones are given in Auer 1933 (Isla Clarence). This stratigraphical type was, besides, described already by Darwin (1839, p. 349—350), from the Chonos archipelago.

The lower limit of the peat of the Hawaiian mires is well marked. At every station there is clay of varying colours, generally gray, sometimes brownish, below the peat. Its thickness varies from $<$ 1 to 36 cm [the latter value in ser. 2 (Molokai)]. Local, very narrow bands of vegetable matter occur occasionally in the clay. These do not necessarily suggest breaks in the clay formation, but rather seem to represent vegetable debris around roots. Pollens and spores very rapidly become very scarce below the upper clay limit, and eventually disappear. A feature worth noting is the frequent occurrence just at this limit of many liverwort spores (Figs. 21—24); these will be destroyed in acetolysis, but are brought out by boiling with dilute KOH or by the hydrofluoric acid method (Assarsson and Granlund 1924). The marked rarity of microfossils in the clay, together with the occurrence of this on ridges and hills below the peat, show that the clay has been formed in situ by chemical action on the volcanic rock below. The gray clay is found everywhere below the organic soil in the humid montane region and transitions to the laterite formations of the lower regions are found only in the lower parts of this. The colours are contingent on the state of hydration of the iron of the soil (see Richter 1931, and the literature cited there), and might therefore be useful for tracing displacements of the climatic zones.

Traces of volcanic ash have been found under the microscope in the *Oreobolus* peat. No ash layers could be detected during the field work. I made notes of the relative amounts of ash found in each slide — which were all made prior to the analyses — to see if any general trend could be deduced from their occurrence. Nothing worth publishing was found, however, most likely because the ash material studied was inadequate. It would seem worth while to try to get a Hawaiian tephrochronology (see Thorarinsson 1944). For a proper investigation, a continuous series of fairly large but low peat samples should be cut out from a wall at right angles to the stratification and analysed for ash (except for a small sample of each for pollen-statistical studies). This might possibly afford an opportunity to connect volcanic activities in the islands with the Late Quaternary chronology of the pollen diagrams and further to elucidate the relation of volcanicity to climatic change (see, e. g., Fuchs and Paterson 1947).

The presence of ash in the peat is not in itself remarkable. In recent eruptions in the island of Hawaii, Lyons says (in Coan 1902), the columns of mineral smoke rose to a height of perhaps 3000 m, and then rolled away to the northeast, and it is quite natural that some of it — in spite of the general anti-trade wind direction — should be deposited in the other islands. Speaking of the Mauna Loa eruption in April, 1868, Brigham (1868 c, p. 42) also says: »Smoke was thrown into the air far above the trade wind, which was blowing strongly until Saturday [11/4], and carried over Oahu and Kauai, some three hundred miles. Vessels near by were sprinkled with ashes.» Only two Hawaiian volcanoes are active to-day (Mauna Loa and Kilauea), but the principal volcanism apparently ceased on Haleakala, Mauna Kea, and Hualalai in the Pleistocene, and Hualalai erupted in 1800—1801 (Hinds 1930, p. 86; H. Stearns and Macdonald 1946, p. 185). Moreover, the activity of the crater of Haleakala ended by cinder-ejections (Dana 1889, p. 87, 1890, p. 279), and some traditions point to a possible subordinate eruption (with ash?) at La Perouse Bay (SW part of E. Maui) about the middle of the 18th century (Dana 1889, 1890, Powers 1920, Hinds 1930, 1931, H. Stearns in H. Stearns and Macdonald 1942, p. 102 ff.) It should also be borne in mind that the Koloa volcanic episode on Kauai is dated to »late Pleistocene or early Recent times» (Hinds 1930, p. 57).

4. LOCALITIES STUDIED.

An account will here be given of the mires in the various islands with particular reference to the areas that I have studied. The particulars referring to the present investigation will be preceded by a survey of topography, history of exploration, vegetation, and available climatic data that are of interest in this connexion but go beyond the scope of the general accounts given above.

a. KAUAI.

Investigations: Alakai: Kilohana, c. 1220 m elev. (13 and 15—16/8) and Waialeale, c. 1300 m elev. (23/8). — Pls. 17—19.

Rock (1913, p. 59 and 75 ff.; 1915, p. 305) distinguishes five mire areas in Kauai:

1) Alakai »swamp» (from a few miles back of Halemanu almost to the edge of Wainiha gorge);
2) Kauluwehi »swamp» (4210 ft elev., back of Kaholuamano on the trail to Waiakealoha waterfall);
3) Lehua maka noe;
4) Waialeale; and
5) Wahiawa bog.

Personally, I have seen only the Alakai mire and Lehua maka noe in the NW and Waialeale near the centre of the island.

The Alakai plateau in the interior of Kauai is the best preserved part of the constructional surface of the old dome. It carries the largest mire areas of the island. Its position is shown on the map (Fig. 14). It is surrounded by submaturely dissected highland. Hinds (1930, p. 22—23) has given a good description of the topography of the area, part of which may be cited:

> »This sector, which has an area of nearly 30 square miles (about one-twentieth of the island) extends for 10 miles northwestward from the center of the island; its northwestern boundary is 2.5 to 3 miles from the coast. The deep gorge of the Koaie River flowing southwestward from the plateau nearly bisects it. Northwest of this gorge, the average width of the plateau is about 2.5 miles; to the southeast, the average width is about 1.5 miles. The elevation of the sector decreases from 5,000 feet along its eastern margin to 4,000 feet along its northwestern margin. On the northwest, northeast, east, and south,

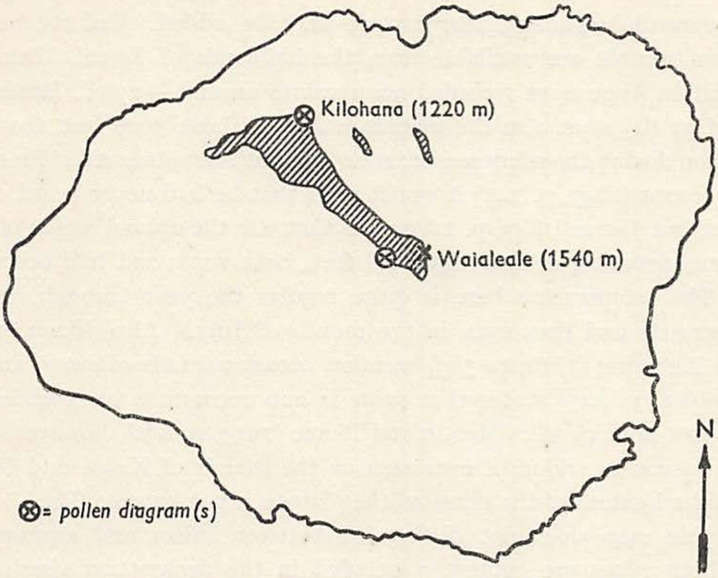

Fig. 14. Map of the boring localities in Kauai and their relation to the summit plateau. This, the principal remnant of the constructional surface of the Kauai dome, is surrounded by submaturely dissected highland. — Scale: 1 cm = c. 5.5 km (= c. 3.4 miles). Physiographic base map simplified from Hinds 1930, p. 22, Fig. 3.

the limits of the plateau are sharply defined by great palis, the cliffed walls and heads of the major canyons. On the southwest side, the upstream growth of the canyons has been slower and more irregular, owing to the lesser precipitation over the leeward slopes of the dome; hence the southwest margin is ill defined. There is, however, a rather sharp change in slope between this sector and the deeply eroded portion of the highland to the west. As is shown by the direction of flow of most of the streams, the general slope of the plateau is southwest. The eastern extremity slopes north and east, and from this section flow the headwaters of the principal rivers of northern and eastern Kauai.»

»The surface of the plateau is traversed by ill-defined drainage lines, which have eroded broad, shallow valleys. Northwest of the deep Koaie gorge, these valleys are somewhat deeper than to the southeast, apparently because of the somewhat higher surface gradient of the former area. Broad, tabular interfluves separate the valleys. Though the topography of the region is youthful, the valley forms are those developed in an upland region of low slope where downward erosion by the small, headward tributaries of the principal streams of the island is relatively slow. Beyond the limits of the plateau, valley cutting has proceeded much more rapidly, hence there is a striking contrast between the gentle rolling topography of the plateau and the highly differentiated relief of the rest of the highland. . . . .».

»On the summit plateau, rain falls almost constantly . . . . . Because of the low relief, drainage is slow, and large areas of the surface are swampy. Low ridges and eminences standing above the general surface are better drained, but, even on these, water stands more or less permanently in every depression. Except on these higher areas, the plateau is practically treeless; the areas separating the pools of water are covered with grass, sphagnum mosses [see p. 49 of the present paper], lichen, sedges, a few shrubs, and other types of small plants. Jungle forest, similar to that of the rainier section of the dissected highland, covers the higher elevations of the plateau. Owing to the extent of the swamp and to the almost ever-present cloud blanket, travel over the plateau is difficult.»

A few words regarding temperature may be added. Unfortunately, no long term records are available from the highlands of Kauai. During our brief visit in August we recorded noon values around +17° C. Hinds (1930, p. 17; cf. p. 62) says: »On the mountain slopes, above 3000 feet, frost is not uncommon during the rainy season; snow has not been observed.» From Bingham's account (1847, p. 141) it would seem that he had never heard of frosts in Kauai, but Jarves (1847, p. 12) asserts that »On the upland region of Kauai, a uniform elevation of four thousand feet, both snow and hail occasionally occur. The temperature here is quite regular the year through, requiring warm garmets and fires even in the month of July.» Also Jouan (1873, p. 26) and Pickering (1876, p. 389) mention occasional falls of snow, and Brigham (1868 a, p. 447) states that snow is not uncommon on Waialeale (see further foot-note p. 58). Martin and Pierce (1913, p. 492), however, emphasize that »snow is seldom if ever seen on the islands of Kauai and Oahu.»

The actual extent of the mires on the plateau is not known. The U. S. G. S. topographic map does not distinguish between mires and swampy rainforest: both types are evidently included in the designation »fresh marsh» (1912 ed., reprinted 1937). A close study of the extent of the mire areas must therefore be postponed. In view of the topographical difficulties such investigations should be based on aerial maps. As far as my experience goes, the miry clearings form a branched system along the northeastern margin of the plateau exposed to the trade winds. From there outrunners follow low ridges, projecting into the forest district to the southwest, where they gradually disappear; small, well defined patches occur down in the forest. Lehua maka noe is one of these (Pl. 19 B, Text-fig. 15), and Kaulowehi (Hitchcock 1919, Pl. 24, fig. 1; cf. 1922, p. 195) another. The bog I studied below Waialeale (ser. 90) is in the same position in relation to the mire at the summit. Bog growth in this and similar outposts was possibly initiated later than in the windward localities.

Unfortunately, I had no opportunity to take a very desirable detailed series of samples at Lehua maka noe (1180 m above sea level), where the peat is very shallow (it is said to have been burnt not long ago). My work here was confined to levelling (see section, Fig. 15) and measuring for a sketch map of the vegetation by Miss Cranwell (now Mrs. Smith). In the period 1919—1932, the average annual precipitation in this locality amounted to 5437 mm (Tüllmann 1936; reduced value; no further data given here).

It is also to be regretted that we could not visit the peculiar Wahiawa bog, situated only 600 m above the sea, in the south. Fosberg (1936 a; cf. Heller 1897, p. 769, 792, 841) describes it as true open bog with *Oreobolus*,

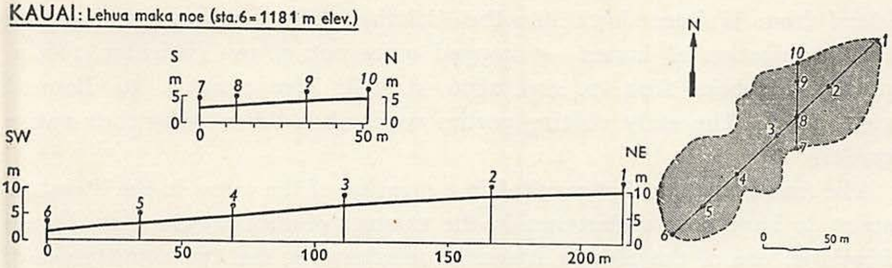

Fig. 15. Sketch map and levellings of surface of Lehua maka noe mire, near Kilohana, Kauai (1181 m elev. = aneroid reading by C. Skottsberg). See further the text (no pollen diagrams from here). Levellings and sketch map by the author, 18/8 1938.

etc. Its vegetation includes *Cassytha* and *Exocarpus luteolus*, however, elements that are not found in the other areas. It would be valuable to know when bog growth started here, and its subsequent history. As regards precipitation, I have seen no values from here; Tüllmann's nearest station is »Wahiawa Mountain» (no. 281), 610 m elev., with an annual average of 4023 mm (1901—1932), annual extremes: 6364 mm (1901) and 2136 mm (1926), monthly extremes: 1542 mm (III 1902) and 19 mm (V 1904).

Alakai: Kilohana, c. 1220 m elev. (Ser. 81, 84, and 87).

Most of our investigations in Kauai were devoted to the northernmost part of the Alakai plateau, near the rim of the Wainiha Valley. The locality is situated immediately W of Kilohana Bench Mark, shown on the U. S. G. S. topographic map and close to the rain gauge [= no. 309 on Tüllmann's map (1936, p. 65)]. According to the topographic map the bench mark is at 4023 ft (= 1226 m). Skottsberg's aneroid reading at the summit of the bog hill from where I got the series 81 and 84 (Text-fig. 16), gave the altitudinal value of 1220 m. This is probably slightly too low but a good approximation.

The average annual precipitation in this locality is about 5000 mm; Tüllmann (1936) has the average of 5042 mm for the years 1919—1920, 1923, 1925—1926, and 1930 (sta. 309, 1226 m elev.; reduced value).

The area is classical in Hawaiian mire research. It was the first mire area to be visited by scientists: from here is the first account of Hawaiian mire vegetation. It appears moreover to be the first montane mire in the islands visited by a non-Hawaiian. One reason for this is that the trail leading up to it — on both sides of which the boring stations are located — is a famous old trail, which was formerly much used by the natives when crossing the island from Waimea down into the Wainiha Valley but has since — after the introduction of horses — dropped quite out of use (Brigham 1868 a, p. 349, Meinicke 1874, p. 209, 1876, p. 288, Rice 1923, p. 46, Bennett 1931, p. 7). The early visiting parties were taken this way by their native guides.

The first excursion that resulted in a mention of the mires in the literature seems to have been undertaken in the summer of 1821 by the Rev. Hiram Bingham, one of the pioneer American missionaries, and two countrymen of his, Whitney and Chamberlain, Jr. Before reaching the pali at Kilohana, they passed »through miry places, and over a tract of high table-land» (Bingham 1847, p. 141). Bingham gives a vivid picture of the scenery at the pali, but says nothing of the botanical peculiarities.

The botanical exploration of the mires began two decades later, on October 30, 1840, when Ch. Pickering and W. Brackenridge, botanists of the United States Exploring Expedition 1838—1842, crossed the island by the same route. Their Alakai collections were published by Brackenridge (1854, 1855), Gray (1854), and Pickering (1876), and their general observations from the excursion, by Wilkes (1845, p. 66). The latter account is the first communication on the botany of Hawaiian mires:

> »After passing this fertile region they reached the table-land which is a marshy district, filled with quagmires, exceedingly difficult to travel through, and in which they frequently sunk up to their knees in mud and water. This table-land was supposed to be upwards of twenty miles square. Here the natives were inclined to turn back; but as they afterwards said, they considered themselves bound to proceed »on so unusual an occasion.» Their fears arose from the report that natives had been lost in crossing by this path. At about 3 p. m., they reached the Pali or precipice, which is like that of Oahu, having a very abrupt, though not dangerous, descent. Many interesting plants were gathered on this route, such as Acaena, Daphne [= *Wikstroemia*], Pelargonium [= *Geranium humile*], Plantago, Drosera, with several interesting grasses.»

More than thirty years later, Pickering himself summarized his impressions (1876, p. 389):

> ». . . . . proceeding by a path not very clearly defined, we found the walking unpleasant, from mud and quagmires, the falling rain, and the cool temperature; the forest-growth being everywhere sufficiently luxuriant to intercept the distant view. . . . . . from the failure of all attempts at cultivation, the occasional falls of snow, and the presence of some real bogs, the Table-land belongs partially at least to the Hawaiian Mountain-region, to be described presently. Natives have perished on the Table-land, in former times from exposure, and more recently, some had been »killed by bands of dogs that have run wild»; so that our route was unfrequented.»

The region has subsequently been visited by several botanists. Its mire vegetation, very briefly described by Wawra (1873, p. 29), was studied by Skottsberg in 1922 and by Skottsberg and Miss Cranwell in 1938.

The treeless parts of the region are filled by swampy flats, in the lowest parts of which there are ± permanent, clay-bottomed pools. Above the

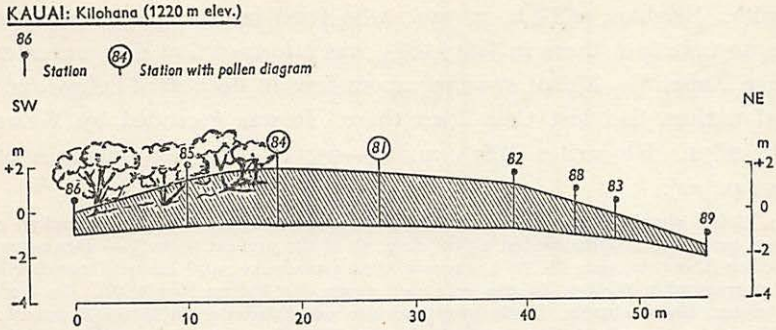

Fig. 16. Section of the bog hill at Kilohana, Kauai (1220 m elev. = aneroid reading by C. Skottsberg; see Fig. 14). Levellings and borings by the author, 15/8 1938.

general surface of the swamp rise occasional, not particularly large bog hills. The general aspect is shown in Pl. 17.

Of the material collected by myself for this work, three series of samples (81, 84, and 87) were selected for analysis.

The two first of these come from a bog hill immediately N of the above-mentioned trail, where this turns to follow the narrow strip of forest separating the locality from Wainiha Valley. Fig. 16 is a cross-section of the hill. The part not exposed to the trade is covered by scrub. The peat is 2.5 m thick.

The third series (87) was taken from the swampy flat about 100 m ESE of this bog hill (Pl. 17). Judging by several borings in other spots, the series may be considered representative of the peat deposits in the swampy flats of the district; they are seldom thicker than this (47 cm, underlain by 3 cm clay). The peat gradually diminishes in thickness towards the shallow pools abounding in the region.

Waialeale, c. 1300 m elev. (Ser. 90).

The summit of Waialeale — one of the wettest spots of the earth, with an annual precipitation averaging 456 inches (Nakamura 1935, p. 189) and sometimes exceeding 600 in. = 15,000 mm[1]) — was long botanically a terra

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[1]) Nakamura's average is based on 12 years of record in the interval between 1911 and 1933. In his series the wettest years (1914, 1918) are lacking, however. Campbell (1917, p. 511) and Henry (1919, p. 37), using the years 1912—1916, got the average 518.4 inches. Larrison (1919, p. 303) computed a value of 476 inches (2/8 1911—26/3 1914, 21/5 1915—13/8 1917 = 1782 days with 2325 inches = 1.3047 inch daily; in 365 days this would make 476 inches). This is quoted by Ward (1919, p. 275), Visher (1922, p. 120), Daingerfield (1926, p. 2) and Brooks (1927, p. 2—3). Tüllmann's (reduced) average for 1919—1932 is 11,843 mm (1936, p. 17). Nakamura's annual values are listed below;

(Cont'd on next page)

incognita. Brigham (1868 a, p. 349), who tried in vain to persuade native guides to take him there in July, 1865, was informed that it is »an extensive bog like Napali [= Alakai swamps] abounding in deep mud-holes» and that several natives had lost their lives there. It was ascended by Wawra in March, 1871. He writes (1873, p. 62—63; cf. Pls. 18 and 19 A of the present paper):

> »Das kleine ziemlich ebene Plateau ist zum grossen Theil von Wasserlachen eingenommen, seine Flora entschieden alpin [cf. p. 37 of the present paper]. — Den schwarzen Moorboden überzieht eine dichte kurzgeschorene Grasdecke, und kleine Sträucher haben hinter vorragenden Steinen Schutz gefunden gegen den kalten Nordwind. In der Grasdecke nisten theils einzeln, theils gruppenweise verschiedene einjährige Pflanzen: eine fingerlange *Astelia* mit steifen, meist lackirten Blättern gibt dem grünen Grasteppich ein gesterntes Muster; *Drosera longifolia*, ein winziges *Plantago*, dichte Büschel von *Acaena exigua* und zweier kleiner Farren, ein zwerghaftes *Lycopodium* und zwei schneeweisse Lichenen — das ist so ziemlich alles, was die gleichförmige Pflanzendecke des Plateaus zusammensetzen hilft. *Cyathodes Tameiameae*, die wir tiefer als baumartige Sträucher und am Haiakala [= Haleakala] als bürstenförmige Krüppelgewächse gesehen haben, schrumpft hier zu fadenförmigen niederliegenden Stengeln ein, im Gras macht sie sich nur durch die gleichfalls sehr spärlichen Beeren bemerkbar.»

It may be added that *Oreobolus furcatus*, the principal bog plant, is recorded by Reichardt (1878, p. 730) from Wawra's collection: »Auf dem Plateau des Waialeale in sehr dichten Polstern ausgedehnte Strecken überziehend.»

J. F. Rock was the next botanist to visit the region; he made the first of

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unfortunately, I have not had access to the values from recent years. I have added in brackets those given by Campbell (l. c.). These records are stated to have been kept by W. V. Hardy, hydrographer of the U. S. Geol. Survey. Acc. to Larrison there is reason to think that in both 1914 and 1918 the rainfall at this station exceeded 600 inches.

1912: 414 [399·35]
1913: 451 [453·00]
1914: — [610.00]
1915: — [590.00]
1916: 521 (539·70]
1917: —
1918: [probably > 600]
1919: —
1920: 549

1921: 367
1922: 452
1923: 360
24—25: 362
28—29: 354
30—31: 528
31—32: 527
32—33: 592
Aver.: 456

Nakamura found here the same coefficient of variation (19 %) as he had found in the wettest parts of Oahu (see Nakamura 1933).

As regards absolute values, the rainfall of Waialeale is stated to be second only to that of Cherrapunji, in the Khasi Hills of Assam, India, where the average annual rainfall, 1851—1920, was 458 inches and for 11 months of 1861 (March excluded) reached a total of no less than 905.12 inches. There are grave doubts, however, concerning the accuracy of this record (see Larrison 1919, Tüllmann 1936; cf. also Henry 1919, p. 34, Brooks 1927, p. 2).

As regards temperature conditions at the summit of Waialeale very little is known. They are probably similar to those of the Alakai plateau (see above). Brigham (1868 a, p. 447) says that [in winter] »snow is . . . not uncommon on Haleakala and Waialeale, but does not extend down the sides below an altitude of eight or nine thousand feet [!].» Waialeale is slightly over 5000 ft high but was at that time estimated at 8000 ft (l. c. p. 342; cf. Dana 1849, p. 157, 262). See further the general notes regarding the Alakai plateau (p. 54).

his three ascents on Sept. 24, 1909. Accounts of the vegetation were published in Rock 1913 (p. 76—77, 219) and 1919 (p. 71—73). Some particulars of the region have also been published by Larrison 1919 (ill.) Rock speaks of an open bog containing i. a. *Oreobolus*, and of turfy soil. We therefore expected to find peat deposits like those at Kilohana when we ascended on Aug. 23, 1938. In the summit region we found the ground — wet rock or wet, gravelly soil approaching shifting earth — partly bare, however, with little humus among the plants. The heavy precipitation seems to wash away the peat. The peculiar plant community is shown in Pl. 18 B. Peat deposits probably occur not far from the summit in other directions, but during our short stay — the fog did not permit but a few minutes of clear sight — we did not come across any that could be bored.

In the forest on the SW. slope a couple of small bogs occur. A series of samples (no. 90) was taken from the first of these along the trail from the summit to Waialae camp.

This bog is situated on a small ridge a few kilometers from the summit and surrounded by heavy rain forest. Its vegetation is dominated by a *Metrosideros-Oreobolus* community; the *Oreobolus* cushions are firm. Ser. 90 comes from the highest part of the bog, on top of the ridge and close to the trail. The deposit is 138 cm thick, with very little clay below. The peat is homogeneous.

The exact amount of precipitation here is unknown. Tüllmann's average annual (reduced) value for the summit of Waialeale in the period 1919—1932 is 11.843 mm (see above, however). The corresponding value for the nearest station on the leeward side of the bog, no. 295 Olokele mauka (2.0 miles SW of the summit of Waialeale), is 3522 mm (1911—1932). This station is situated far below the bog, however, at only 640 m elev. Daingerfield's value for it is 144.48 in. = 3670 mm (average of 1911—1918).

[b. OAHU.]

In 1938, Fosberg and Hosaka discovered a small area in the Koolau Range, at the head of the Kaipaupau and Kawainui gorges, »which, though lacking several of the common bog species, seems to have the floristic and physiognomic aspect of a true open bog» (Fosberg and Hosaka 1938). It is situated on the brow of a bluff at the summit of the range and in one of the wettest regions of Oahu, in 850—860 m alt. In the same year, on July 3, I had an opportunity to visit the locality in Hosaka's company. Judging by the differences in aspect and the general trend of climatic evolution traceable from now published diagrams (fairly recent depression of the belt of maximum rainfall), I have elsewhere (1942) suggested that this may represent one of the initial stages of a bog; I do not think it can be called a true bog. Unfortunately no peat auger was available on our excursion. It might pay to study the strata, though these are not very thick.

c. MOLOKAI.

Investigations: Pepeopae bog, c. 1200 m elev. (7—9, 11, and 12—13/7). — Pls. 13 B and 16.

The bogs and montane swamps are here confined to the eastern part of the island, which alone is high enough — about 1200 m and higher — to provide the requisite conditions for their growth. Hillebrand (1888 b, p. xv) seems to be the first to mention them. His notes may date from the summer of 1870, when he was collecting in the island:

> ».... in one or two parts of Molokai, a thick layer of mosses, liverworts, and sedges covers the moderately heavy soil; being within the reach of perpetual clouds and continually dripping with moisture it has increased to beds of turf, and forms extensive bogs, the habitation of many of the rarest plants.»

He probably visited the bog discussed below, that at Pepeopae. It is situated back of the Kamoku shelter cabin and not far from the head of Pelekunu Valley. Rock (1913, p. 75, Pl. XXIV; cf. 1920, p. 207), who was there on March 17, 1910, considers it to be the only one worth mentioning in the island. He speaks of it as the Kawela swamp, a name also found in other publications (e. g. Rock 1917, p. 31, Mac Caughey 1918 b, p. 7). Forbes calls it the Kawela bog (labels quoted in Hitchcock 1922, p. 195); Kawela is the district where Pepeopae is situated. Degener (Fl. Haw., Fam. 7, 10/12/'34: *Schizaea*) refers to it as »bog east of Hanalilolilo». Bogs seem to occur also farther east, at least to Kamalo (cf. Hitchcock 1922, p. 145). »Fresh marsh» is indicated on the U. S. G. S. topographic map also at Halawa and N of Olokui, but whether this includes true bog vegetation is not known to me. Acc. to Hinds (1931, p. 181) the three slightly dissected summit plateaux of E. Molokai closely resemble »in the character of their ... boggy surface similar areas on Kohala, West Maui, and Kauai.» A picture of the raised bog at the head of Pelekunu Valley is found in Bryan 1915 (p. 218 = Pl. 60, Fig. 6); Bryan 1908 mentions only »bog forest». Forbes (in Brigham 1913, p. 14) speaks of »the so-called swamp country» at Pelekunu Pali but does not enter on particulars.

Unfortunately, the rainfall conditions of E. Molokai are insufficiently known, and I know of no records for Pepeopae. It can be supposed, however (cf. Hinds 1931, p. 182), that the average over the summit plateaux must be about 5000—6000 mm. In Coulter's map (1931, p. 21, fig. 7), reproduced

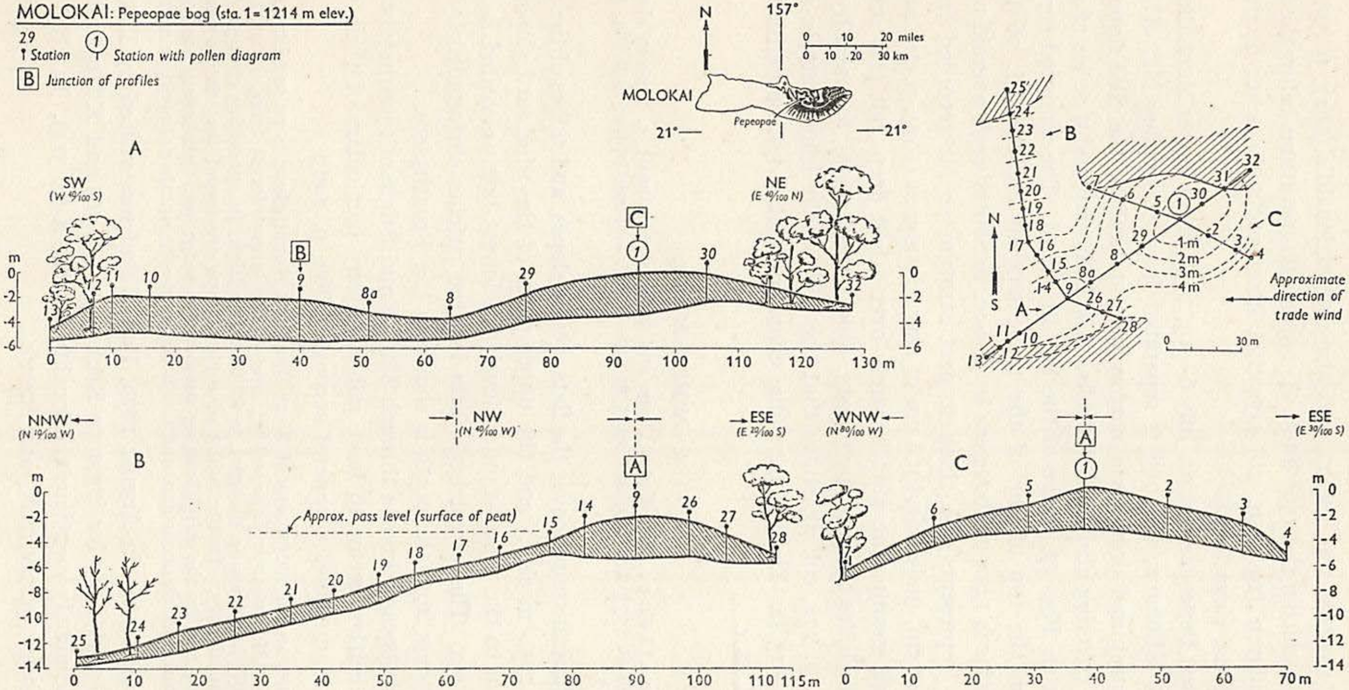


Fig. 17. Map and sections of Pepeopae bog, Molokai (1214 m elev. = aneroid reading by C. Skottsberg). Levellings and borings by the author, (7—) 11—12/7 1938. [Sta. 13 (not 25, as stated in Selling 1947, p. 119) is the locality of *Viola mauiensis* × *robusta*.]

by Jones (1938, p. 196, fig. 2), and also in Macdonald's (1947, p. 39, fig. 6), the region is within the 150″ limit. As regards temperatures below the freezing point, Lindgren (1903, p. 16) says that »frost» probably never occurs, even at the highest elevations.»

We visited Pepeopae bog on July 6—13, 1938, from Upper Maunahui camp. Just as at Kilohana, the bog is separated from the valley NE of it by a strip of forest and occupies a narrow belt at head of the SW slope of the old dome, covering also small hillocks. A sketch map and a series of sections are shown in Fig. 17, views of the bog in Pl. 16. The analysed ser. 1 was taken from the top of one of the trade-exposed hillocks (Pl. 16 A). The surface of this is 1214 m above sea level (acc. to Skottsberg's aneroid reading). The series represents the thickest peat stratum so far recorded from the islands: 322 cm, underlain by 8 cm of clay. Lindgren (1903, p. 19) says that »in the high swamps the mud is rarely over 2 feet deep» but this statement evidently includes the swampy forests. Rock (1913, p. 59), followed by Campbell (1933, p. 172, col. 2), states that the bogs of the islands attain a thickness of 10—15 ft. The highest value given could thus not be verified in the localities I saw.

d. WEST MAUI.

Investigations: Puu Kukui, bogs and swamp at summit, c. 1750 m elev. (23—25/7), bogs at 1575 m (28/7) and 1375 m (27—28/7). — Frontispiece and Pls. 12, 13 A, 14, and 15.

In W. Maui the mires cover the flats, gentle slopes, and ridges of the summit region (c. 1750 m elev.) and the upper parts of the windward slopes of the ridges down to the 1200—1300 m level; the lowest bog we visited is 1375 m above the sea. The lowest bogs form isolated patches surrounded by forest. A general view from the north is shown in the Frontispiece.

The mires became known through Mann's and Brigham's journey in 1864—1865, but neither seems to have published any particulars of their visit to the area. Mann gives a general account (1867, p. 148):

> »Above this, on the mountains of West Maui and Kauai, there is an open tract, where the lehua [= *Metrosideros polymorpha*], one of the largest forest trees, at an elevation of 2000 feet[!] has become dwarfed, a foot or two high, in spreading clumps, but still flowering abundantly. In the midst of such clumps are found the violets peculiar to these regions, and in the neighbouring tussocks of sedge (an Oreobolus) are found the few other plants, which occur here and nowhere else, to the number of eight or nine; . . . . .»

A few years later, in August 1870, Puu Kukui was visited by Hillebrand [see labels quoted by for instance Keck (1936, p. 20) and Kükenthal (1940, p. 70)]. He merely mentions the locality in 1888 a (p. 314). In 1888 b he is also very brief (p. XV, XIX, and XXIV):

> »The flat top, wrapt in a cloud of mist nearly the whole year, is boggy, and harbors a number of rare plants, many of which are altogether confined to this narrow area. No bare lava streams are anywhere to be seen; a thick layer of detritus or arable soil covers the entire surface.» [p. XIX] . . . .» The turfy soil is covered with tussock-like *Gramina-ceae* and *Cyperaceae*, all quite peculiar species, with *Sphagnum*, creeping forms of woody *Metrosideros*, *Cyathodes* [= *Styphelia*], *Geranium*, *Lysimachia*, and a number of rare, mostly single, representatives of genera which have their home in the Antarctic regions, New Zealand, the Falkland Islands, southern Andes, etc.» [p. XXIV; this description refers also to Kauai]. On p. XV he gives the same description as for Molokai.

Hillebrand labelled his specimens »Mt. Eeka», and used the same name in 1888 b (p. 484, 648, etc.). It is now generally considered that this refers to Puu Kukui and not to the somewhat lower Mt Eke N of it — he does not mention *Argyroxiphium*, which occurs in masses in the latter mountain, but is little prominent on Puu Kukui (Lydgate in Forbes 1918, p. 55, note; Rock 1920, p. 206; Degener, Fl. Haw., Fam. 7, 10/12/'34: *Schizaea;* Degener in Keck 1936, p. 20—21). Hillebrand may not have made the distinction between the peaks as we do but applied the name of Eeka to the whole mountain mass, as did for instance, Dana (1849, p. 156; cf. p. 227; 1890, p. 269), Brigham (1866, p. 366), Mann (1867, p. 146), and Jouan (1873, p. 40).

The first more detailed account of a mire area in West Maui was given by Alexander (1883, p. 33—34) from an ascent of Mt Eke (see Pl. 12). It gives a vivid picture of this type of country. Alexander approached the region from Waihee:

> »From this place [Keahikano crater] to the summit of the mountain the country is generally as devoid of trees, on account of excessive moisture, as the steep ridges at the shore were on account of drought. Every where is swamp covered with a sedge of strange, stunted plants, rare ferns and exquisite mosses. The ohia tree [= *Metrosideros*] dwindles from a monarch of the forest to a shrub a few inches in height, still bearing its scarlet plumes. On all sides are pools of standing water and in every hollow rushing streams.
>
> The route now lies upward towards the left over a broad plateau, called from its superabundance of water, Kalanikawai, to the brink of Waihee Valley, and along the dizzy edge of fearful precipices through jungles densely clothed with moss. This is the paradise of mosses. As though nature abhorred absence of life as much as vacuum, they carpet the whole earth and every rock and decaying log with their feathery beauty; they form heavy mantles of bright red or emerald green over the trunks of the trees; they wind their weired locks like Absalom's hair about the branches: and trail long fantastic and exquisite wreaths from tree to tree. Rare plants abound here, a species of violet, called Viola Mauiensis, daisies, dwarf silver-sword plants, schizaeae, and lobelias rising with long red and yellow blossoms like chandelabra of a cathedral.
>
> The Waihee ridge a little further trends away towards the north to the crater of Eeke, which lies at the head of Kahakuloa Valley, and extends half a mile in breadth to the Honokohau Valley. It rises abruptly from the mountain side several hundred feet in height with its sides spangled with silver swords and shining grasses. It is so situated with all its sides higher than the surrounding land that it has received the debris from the wash of the mountain, and therefore has its thirty pits still open and apparently bottomless. I ascended it the first time early one morning after a still and cloudless night, and found columns of steam like smoke rising from several of these pits . . . . . The almost incessant fogs of this region rarely lift to give more than glimpses of the magnificent surrounding panorama, of the water-fall at the head of Honokohau gleaming white against dark mountain walls far away.»

For further notes on the Eke bog the reader is referred to Rock (1921, p. 17) and Degener (1930 = 1945, p. 308). It seems to be a promising locality for pollen-statistical investigations.

Returning to Puu Kukui, we find a somewhat detailed description of the summit bog in Rock 1913, p. 78—79 (= 1915, p. 307—308). A photograph of it, taken in 1922, has been published by Skottsberg (1930 a, p. 71, 1934, Pl. 7). The same view 16 years later is shown in Pl. 14 A of the present paper. Rock writes:

> »Puu Kukui is a large, open, more or less flat plateau, composed of light-gray, heavy, loamy soil. The vegetation is stunted, with the exception of such as occurs in depressions or small gulches, and at the head of Iao Valley, where trees belonging to the middle forest region abound.
>
> The whole of Puu Kukui is a second Waialeale of Kauai, though a number of plants are peculiar to the former. We find the same globose tussocks of *Oreobolus furcatus* and the very interesting *Carex montis Eeka*, besides Gramineae, such as *Deschampsia australis* forma *longius aristata*, *Calamagrostis Hillebrandii* Hack. (nov. nom.), and others, while the juncaceous *Luzula hawaiiensis* var. *glabrata* grows in their company. One of the most striking vegetative features is the great abundance of the very beautiful *Lobelia Gaudichaudii*. In certain parts this plant covers the ground, and in the month of August it is indeed a beautiful sight. .... [mention of *Argyroxiphium*] ....
>
> *Lagenophora mauiensis* is very common in the turfy soil in company with the creeping *Geranium humile* with pink flowers. *Acaena exigua*, which is very scarce on Waialeale, is here exceedingly common, together with *Viola mauiensis*. Remarkable to say, *Drosera longifolia*, so common on Kauai, is here absent. A small creeping *Metrosideros* is also present with *Lycopodium venustulum* var. and *Styphelia imbricata* var. *struthioloides* [= *S. Douglasii*].
>
> The writer met with a single plant of *Lycopodium Haleakalae* ... Several species of lichens grow on the exposed gray loam, such as Cladonia, Stereocaulon and others.
>
> At the extreme eastern end of the bog on the brink of Iao Valley the tree growth is mainly *Cheirodendron Gaudichaudii* [= *trigynum*], *Suttonia* [*Myrsine*] sp.?, *Pelea* sp., *Metrosideros polymorpha*, and the lobeliaceous *Clermontia grandiflora*. All the trees are covered thickly with moss and hepaticae or Liverworts. .....»

Among important bog plants omitted by Rock are *Plantago* and *Astelia*. At the very summit *Astelia Forbesii* subsp. *nivea* forms a conspicuous part of the vegetation (see Pl. 14 A). Lower down on the Amalu-Honokohau ridge (towards the north) no such abundance has been noted. This may possibly be correlated with less extreme variations in rainfall, as is suggested by fossil finds of another *Astelia* in the bog below Waialeale, Kauai (see Part II, p. 358).

In describing the rain forests of W. Maui, Rock adds (l. c., p. 66—67):

> »Immediately below the swampy plateau are one or two miniature bogs [they seem to be several] which harbor *Plantago pachyphylla*, with its many varieties peculiar to high elevations. Here also occurs a creeping species of Lysimachia, together with Lycopods, and other cryptogams, besides *Lagenophora mauiensis*, which has descended from the bogs above.»

The vegetation of the mires investigated during the HBS will be dealt with by Skottsberg and Cranwell.

The summit of W. Maui is the wettest area in the islands next to the summit region of Kauai [H. Stearns (in H. Stearns and Macdonald 1942, p. 32) mentions another locality where the rainfall is stated to be heavier (Kuhiwa Gulch, E. Maui), but I do not know if this holds also for a longer period]. We spent several days and nights in the region and thus got excellent opportunities to experience the continuous soft rain or it may as well be called heavy mist making the air oversaturated with moisture. Though the temperature was not high, it was not felt uncomfortable due to the lack of evaporation. In a few days clothes and notebooks went spotty. Everything was soaked with water, and water dripped from every tree and shrub. This condensation brought about by the vegetation increases the moisture at a given station beyond the amounts recorded in rain gauges. Some rainfall records will be illustrative in this connexion, however:

Three of Tüllmann's rain gauge stations refer to the summit region of W. Maui. Two of these are in the Eke district: sta. 123 »Eke», 1402 m elev., with an annual average of 6810 mm (1913—1932), annual extremes of 9410 and 3823 mm (1918 and 1926, resp.), and monthly extremes of 1816 and 51 mm (XII 1921 and V 1926, resp.); sta. 176 »Mount Eke», 1372 m elev., with an annual average of 6235 mm in the period 1913—1918 (no further values given).

The third station is no. 124 Puu Kukui Upper. It shows a mean annual value of 8832 mm (1911—1932), annual extremes of 14,274 and 3149 mm (1918 and 1926, resp.), and monthly extremes of 2845 and 76 mm (I 1921 and I 1931, resp.) (Tüllmann 1936 and ms.; the values for these three stations reduced). Larrison's annual average for Puu Kukui Upper (1911—1918) was 369 inches (1919, p. 303 and 304), Daingerfield's value for the »normal annual rainfall» 370.07 inches (1926, p. 2 and 44). H. Stearns and Clark (1930, p. 168) state it to be between 370 and 400 inches. H. Stearns (in H. Stearns and Macdonald 1942, p. 31—32, 40) states the rainfall at the very summit — sta. »Puu Kukui (Crest)» — to be 389.05 in. = 9882 mm (250.00 in. = 6350 mm in 1933, 496.00 in. = 12,598 mm in 1937; period of 1928—1940). His Fig. 6 (l. c., p. 34) shows the monthly distribution of rainfall. Unfortunately, I have seen no values for recent years. Larrison (l. c., p. 304, fig. 8) gives a diagram showing the mean for each month in the seven year period ending 31/12 1918: the wettest months are (in descending order): April, November, and July, and the driest are September, February, and May.

Striking contrasts in annual rainfall values are found in comparing Puu Kukui with Olowalu, only about 6 miles distant on the leeward side (alt. 15 ft). The annual amount here is only 8.08 inches (value taken from H. Stearns and Clark 1930). Still more striking contrasts can of course be demonstrated

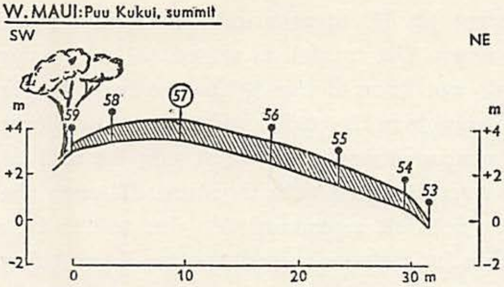


Fig. 18. Section of the bog covering the summit of Puu Kukui, West Maui (1765 m elev., acc. to the U. S. Geol. Surv. topogr. map; Skottsberg's aneroid reading gave a somewhat lower value). Sta. 57 (see pollen diagram) = rain gauge station »Puu Kukui (Crest)»; aver. annual rainfall 389 inches. Levellings and borings by the author, 25/7 1938.

if extremes are used: 562 in. = 14,274 mm at Puu Kukui (in 1918; Daingerfield 1926, p. 2) and 2.00 in. = 51 mm at Olowalu (in 1928), the lowest rainfall ever recorded officially in the islands (H. Stearns in H. Stearns and Macdonald 1942, p. 32; see further rainfall maps of Maui in Hinds 1931, p. 157, Coulter 1931, p. 23, Jones 1938, p. 196, and H. Stearns l. c., p. 29). As emphasized above, I have not been able to consider the more recent values.

I have seen no mention of temperatures below the freezing point in W. Maui. Occasional occurrences of frost are not unlikely, however.

Peat samples were taken in four localities between the summit and Nakalalua, along a line in a N-S direction which comprises an altitudinal belt of about 400 m. This is of particular importance to the discussion of the vertical displacements of the vegetation belts (see Chapter V).

One series (57) comes from the very summit, close to the rain gauge (Fig. 18). Pl. 14 A shows a view of the bog towards the NE.

A couple of diagrams (33, 34, 35, 37) were taken just below the summit, a few hundred metres from ser. 57. Fig. 19 shows a map of and section through the locality with the boring stations. Views from different directions are given in Pls. 14 A and 15. The peat of these bog hills is not particularly thick (up to 142 cm), and in the swamp it is only about 35—40 cm. Still, this swamp has yielded one of the oldest peat strata so far met with in the islands, and the series from there (34) shows much of the subsequent history, too. This is a former habitat of *Schizaea Skottsbergii* and it has therefore previously been dealt with in Selling 1944 (p. 74, ill.). Localities like this should be given particular attention in the future. They seem to have afforded opportunities for peat formation before the truly ombrogeneous *Oreobolus* communities had produced notable deposits.

A single diagram (80) comes from the extensive bog at about 1575 m elev., near Violet Lake (a little pool at which a white-flowered violet is said to

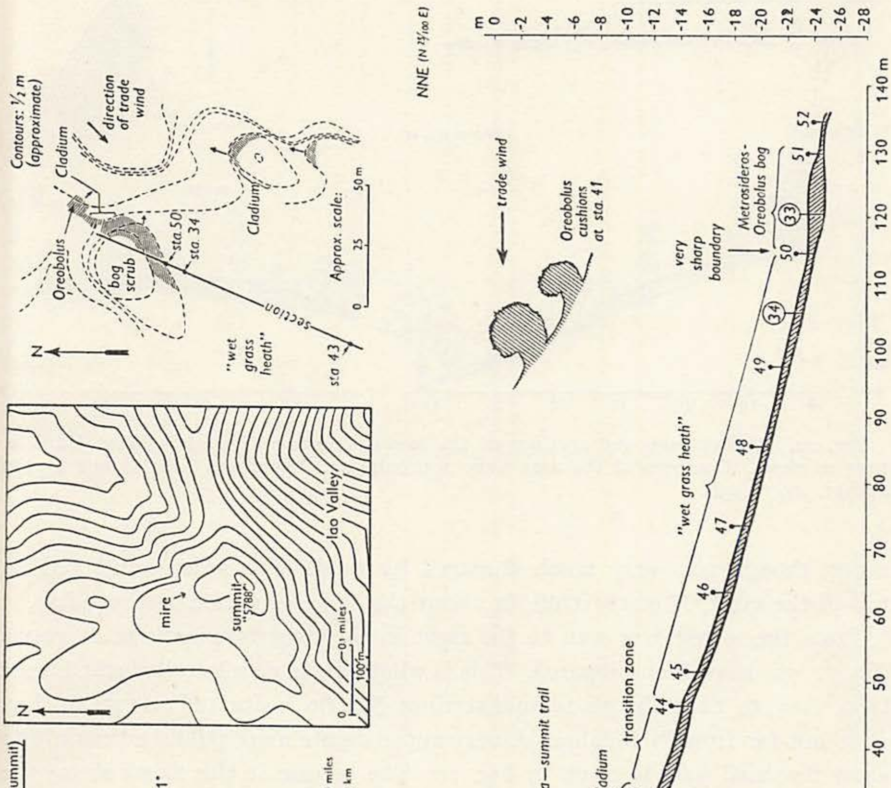


Fig. 19. Maps and section of the mire just below the summit of Puu Kukui, West Maui (c. 1750 m elev.). Left and central maps drawn after U. S. Geol. Surv. topogr. map (ed. of 1933). Sketch map (very approximate), levellings, and borings by the author, 24/7 1938.

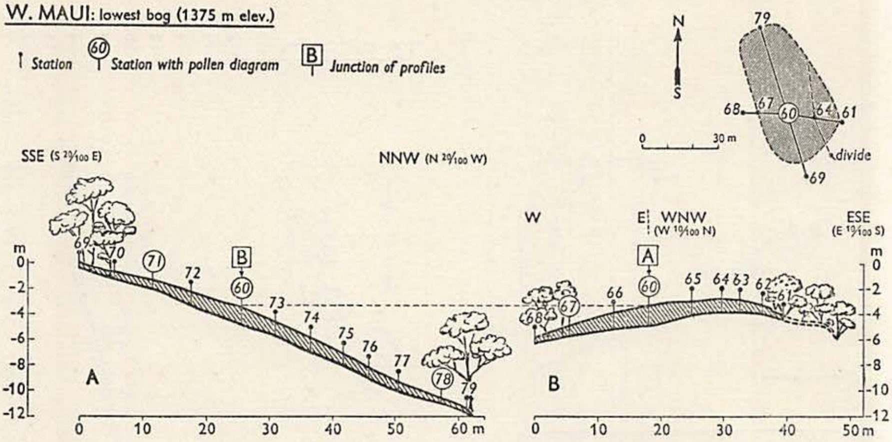


Fig. 20. Sketch map and sections of the lowest bog investigated in West Maui (c. 1375 m elev.). Contours of the map very approximate. Levellings and borings by the author, 27/7 1938.

occur, though now very much damaged by rats). The series was bored on top of the crest, E of the trail, in about the same elevation as the »lake».

From the lowest bog seen to the right in the Frontispiece three diagrams (60, 71, 78) have been prepared. This is what I have simply called »the lowest bog». Acc. to Skottsberg's aneroid reading, Sta. 60 is situated at 1375 m elev. It is not far from Nakalalua. A very approximate map, published mainly to show its small size, is given in Fig. 20. The section in this figure shows the location of the boring series. The vegetation of the bog is rather homogeneous. The *Metrosideros-Oreobolus*-sociation is the principal plant community. The orientations of this and the other bogs are briefly dealt with in p. 47.

[e. EAST MAUI.]

Hillebrand (1888 a, b), Rock (1913, etc.), and Skottsberg (1940 b, p. 522; 1940 d, p. 660) mention no raised bogs from East Maui. Rock only states (1913, p. 75—76) that »it is indeed of interest to note that most of the species of plants found on Puu Kukui are not peculiar to the bog region, but have been found by the writer on the steep walls in Kaupo gap in the crater of Haleakala». In the light of this, Pickering's overlooked report of *Oreobolus:* »Growing in large tufts» and »Abounding on Mauna Haleakala, at an elevation of 7300 feet» [1876, p. 485; Hillebrand (1888 b) knew it only from W. Maui and Kauai] does not prove anything regarding bogs. In 1919, however, Forbes (report in Gregory 1920, p. 175) found a narrow zone with what he calls a bog flora during his excursions from a camp several miles E of Ukulele (about 5000 ft elev.). Down the mountain toward Hana he found a series of cones and flats with »an open bog flora». One of these localities is stated to be below Wai Anapanapa on the N slope of the mountain (label cited by Keck 1936, p. 20). In another connexion Forbes (1920, p. 39) even speaks of »the extensive bogs on Haleakala». On the windward flanks heavy precipitation has been recorded with annual averages exceeding 7000 mm (Tüllmann's stations nos. 138 and 183; cf. map in H. Stearns and Macdonald 1942, p. 29). It is a pity that we had no opportunity of visiting this little explored region. It may yield important material for pollen-statistical studies.

[f. HAWAII.]

The occurrence of raised bogs in this island has been a matter of controversy. On a couple of occasions it has been stated that there are none. Berggren's find of *Oreobolus* in the upper part of the Mauna Kea rain forest in Aug., 1875 (Skottsberg 1940 b, p. 513, note, 1943, p. 371), was probably an isolated outpost that did not form a true bog. On the Kohala mountains the situation is different. Many of the descriptions so far published certainly do not convey a clear impression of true bog vegetation, but judging by other sources we are not entitled to dismiss the idea that it may occur there.

Brigham (1868 a, p. 379) found the summit »swampy like Waialeale on Kauai, and full of dangerous bog-holes», Dutton (1884, p. 171) speaks of »large peat bogs» formed fully a mile above the sea, but these statements may just as well refer to the *Sphagnum* community mentioned below. Rock (1913, p. 76) asserts that »there are several bogs besides the main one at the summit» and (l. c., p. 228) that his *Pelea pseudoanisata* is most abundant in the »swampy jungle bordering a big open bog» on the summit (5500 ft); here he also found *Oreobolus*, the principal bog plant (Rock 1917, p. 31, Kükenthal 1940, p. 70). On the other hand he uses the designation »big open bog» also for the *Sphagnum* community on the Waimea side of the mountain (see Rock 1920, p. 209 and label cited by Pilger 1923, p. 115); Bryan (1915, p. 149) and Campbell (1927, p. 100) use the words bog and boggy formation for the entire swampy forest region (see Pl. 11 A = Campbell 1926, Pl. XXVII: »Tree-fern swamp»). Rock, however, expressly states that the open summit bog visited by him in 1910 »harbors a similar vegetation to that of Puu Kukui, Maui, and Waialeale of Kauai» (1917, p. 64).

The rainfall of both areas (Kohala and Mauna Kea) is abundant. Tüllmann's station no. 15 Kawainui Upper, 1244 m elev. and near the summit of the Kohala Mts, has an annual average of about 6000 mm (1907—1932:

6065 mm), annual extremes of 12,793 and 2526 mm (1914 and 1917, resp.; in inches acc. to Daingerfield 1926, p. 22: 503.69 and 99.46), and monthly extremes of 2139 and 39 mm (VIII 1914 and II 1914, resp.; it may be added that Tüllmann's values for this station are reduced). Similar and partly higher values have been obtained on the eastern flank of Mauna Kea. Maps showing the location of these two areas of maximum precipitation in the island have been published by Coulter (1931, p. 29), Hinds (1931, p. 158), Jones (1938, p. 196), Robyns and Lamb (1939, p. 247), H. Stearns and Macdonald (1946, p. 212), and others.

Our excursions in Kohala did not reach the summit region, and the investigation of the *Oreobolus* bogs of the island of Hawaii is therefore left to future research.

D. SPORES AND POLLENS OF THE NATIVE VASCULAR PLANTS.

With the aid of the literature so far published it was possible definitely to identify just a few genera, and even fewer species, in the fossil material. Slides of recent pollens and spores were necessary for that task. Material only from the leading forest trees was not sufficient, however, since it was not known of whether doubles might not also be present. These, if any, could only be revealed by monographic studies of recent spores and pollens. Much discussion in pollen-statistical research in other countries has been produced, and many good observations neglected, for lack of such studies. As a first step, I therefore found it necessary to attempt to lay a firm foundation as far as the Hawaiian Islands are concerned. The results have been published in Selling 1946 and 1947.

Besides serving as the basis of the present paper, these parts will show how much still remains to be done in respect of detailed pollen morphology and the relation of pollen morphology to systematics. A rich field is open in every family. The reproductions might have been more ample, but that was a question of costs. The ideal would be photographs of habitus supplemented by drawings or — better still — photographs of wall-details from cut and dyed material.

IV. THE BASIC MATERIAL.

A. GENERAL INTRODUCTION.

The 250,000 microfossils that I have recorded in my analyses constitute the basic material of this study. That figure does not include the numerous spores of fungi (incl. lichens) and bryophytes, nor the occasional algae and animal remains that have been found.

Algae. Among the algal remains — like the spores of bryophytes most of them them seem to have been destroyed by the acetolysis — may be noted specimens of a *Tetraëdron* of ± quadrangular outline, averaging 41 μ in min. diam. [25 specimens from sample 178 (33)]. These were found in many of the HF-treated samples (bottom parts of the mire deposits). MacCaughey's list (1918 a) mentions no species from Hawaii. The genus is of world-wide distribution and comprises about 65 species in lakes or brackish water, of which many are much smaller than the Hawaiian species. Some of them are only developmental stages of other algae, e. g., *Hydrodictyon*, *Pediastrum*, and *Oocystis* (Printz 1927). The genus has been reported from Late Quaternary deposits in Europe (see for instance Lagerheim 1902 b), and there is also a record from the Tertiary Green River formation in Colorado (Bradley 1929, 1931). As to *Phycopeltis*, see below.

The diatoms have been made the subject of a preliminary investigation (unpublished) by Mr. Åke Berg, Uppsala.

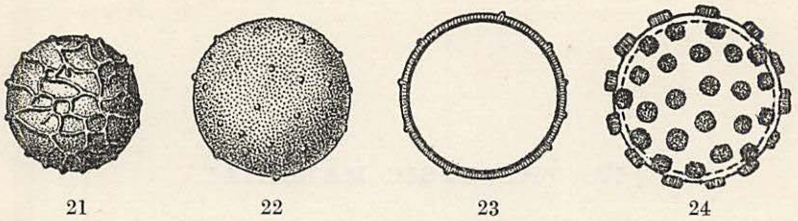
Fungi. Structures which are either single-celled sprouts of *Phycopeltis* or stigmocysts of microthyriaceous fungi, as well as multicellular stages of development of the kind occurring in these groups, are not of infrequent occurrence in the peat. These species are characteristic features of the epiphyllous rain forest vegetation; they are not rare in the corresponding Tertiary deposits. For further particulars of this, and for the possibilities of identification, see Kirchheimer 1942 and Cookson 1947. They occur in about 10 % of the samples, most in Molokai (20 % of the samples there), and least in Kauai (5 %). They were not observed in Ser. 33, 34, 71, 80, 84, and 87, are rare in Ser. 10, 35, 37, and 90, and sparse in the other series. The frequency in each sample — calculated in the same way as for accessory pollen types (see p. 88) — shows relatively small variations: traces to 7 %, generally traces to 1 % (both equally common). 7 % were found in 6 (1), 3 % in 13 (1), 2 % in 2, 4, 33, 36, 37 (all in Ser. 1), and 331 (81). The Maui values thus only reach 1 %.

The fungus spores represent several morphological types; these have not been closely studied.

Bryophytes. The spores seem to have been largely destroyed in acetolysed samples. Notable among them are the various types of liverwort spores met with in the bottom samples treated with KOH or HF (in the KOH treatment the gradual destruction can be followed). Some of them are pictured in Figs. 21—24.

As regards vascular plant spores and pollens, I refer to the accounts given in Selling 1946 and 1947.

Up to about 175 different kinds of pollen and spores may occur in a single sample. To get some general idea of what might be expected to be of importance in investigations of vegetation-historical developments, the fossil



Figs. 21—24. Liverwort spores from Hawaiian peat deposits (no identifications so far possible). 21: From sample no. 91 (ser. no. 2, immediately below the peat), Molokai; 22 (surface) and 23 (section): 158 (10), Molokai; 24: 374 (81), Kilohana, Kauai. Preparation: boiled in 10 % KOH solution. See further the text. — 300/1 nat. size.

materials in the different analyses were first collated by series. As, however, the data obtained were absolute values, the different samples were not commensurable. The next step was therefore to try to obtain a basis for computing relative values, which as far as possible smoothed any disturbances unconnected with the picture of the historical developments. In Boreal regions the problem is easy: tree pollen may there be counted in % of their sum total, pollen from herbs and shrubs in % of theirs. Conditions are not as simple in the tropics. They will be discussed below.

B. THE CONSTRUCTION OF THE DIAGRAMS.

I. DISCUSSION.

A pollen diagram has to be constructed so as to reflect as satisfactorily as possible the principal composition and relative extension of the from time to time leading types of vegetation in a given area, as a rule forests (the upper tree-layer), but — where such are lacking — also communities belonging to lower vegetation layers (low tree, shrub, field, or bottom layers).

As I have already said, there was nothing in the form of previous investigations into the Late Quaternary history of vegetation in the islands that might serve as a guide in determining what pollens should be included in the Hawaiian diagrams. It was by no means obvious which plant communities ought to be represented. Nor could the problem be tackled by analogy, as nothing is known of developments in other parts of the tropical and subtropical zones of the Pacific. The pollens likely to give a picture of the vegetational developments must therefore be selected solely by repeated trials of different combinations of the material of the analyses. The frequency of each species included in the particular combination tried was expressed in % of the total number of pollen grains (in each sample) from the same combination of species.

In Boreal regions, for example, where extensive areas are dominated by only a few species of trees, the chief ecological requirements of which are moreover ± known, the selection of pollen types is not by a long way as difficult as in a region as rich in tree species as the Hawaiian Islands. The number of ligneous species is very large, and some hundred and fifty of these may occur in certain types of forests without any of them being dominant (Rock 1913). Our knowledge of the ecological requirements of these species — which are often variable — is moreover still very superficial. This applies not least to the species dominating the montane rain forests, in which the mires are situated. Two of the most important of these forest-tree genera — *Metrosideros* and *Myrsine* — include not only a series of forest-forming species, subspecies, varieties, and forms, but also shrubby forms which, together with closely related species, form part of the mire communities (see p. 48) as well as the forests. The pollen produced by these shrubs might conceivably constitute local obstacles to pollen-statistical conclusions of a general nature.

When the laboratory work began, it was thus extremely uncertain whether any usable results could be obtained, and in his first reports on my work, Skottsberg (1940 a, p. 22; 1940 d, p. 660) expressed himself very pessimistically.

In planning the laboratory work, the first problem was how to distinguish the local production of primarily *Metrosideros* and *Myrsine* pollen from the pollen rain from corresponding species in the surrounding forest. It was found impossible to distinguish, even by variation statistics, between pollen from forest trees and the corresponding mire forms, and incidentally this is hardly astonishing.

This alone made conclusions from the curves themselves the only criterion by which the question of regional applicability versus local disturbances could be judged. The radical step of excluding say the *Metrosideros* pollen from the diagrams could obviously not be resorted to, as this would be equivalent to disregarding the incomparably greatest part of the rain forest.

I therefore concentrated on obtaining material permitting checking the curves from a given locality by comparison with curves from adjacent as well as distant points.

A skeleton scheme was drawn up on the basis of the rain forest species *Metrosideros*, *Myrsine*, *Cheirodendron*, *Cibotium*, and moreover *Acacia* and

Dodonaea, with the aid of which I tested the relative values of the types of tree pollen — alone or in variously combined groups — occurring in ± low frequencies.

Species which only occasionally occur as trees, but are usually shrubby, as well as obligatory shrubs and a number of herbs, were also tested.

In this way I found that neither all the trees by far, nor any shrubby species, could be taken into account, whether by themselves or in combination with others. Grasses, Cyperaceae, or other species dominating the lower vegetational layers were also found not to occur in such a manner as to justify the assumption that entirely forest-bare districts of considerably larger size than the present mires can have occurred during the period covered by my series of samples in the vicinity of the localities represented by the diagrams. These conclusions are favoured by the fact that the proportion of tree pollens in the total pollen contents (see the F diagrams) shows no marked variations. The only exceptions (in Ser. 33, 57, and 84) are due to mass occurrences of fern spores, which are natural explained by local changes of facies. The first of them are discussed on p. 109, the third is a local concentration of *Polypodium* (*Amphoradenium*) *tamariscinum* or some allied species (see Selling 1946, p. 59).

After testing the whole material, the following 17 genera were ultimately included in the diagrams:

Acacia, Alectryon, Antidesma, Chenopodium, Cheirodendron, Cibotium, Claoxylon, Coprosma, Dodonaea, Ilex, Metrosideros, Myoporum, Myrsine, Osmanthus, Pelea (Type II), *Pritchardia*, and *Sophora*.

Methodologically these belong to the following groups:

Included as a matter of course for phytogeographical reasons as well as on account of conclusions drawn from the diagrams: *Acacia, Cheirodendron, Dodonaea;* also *Metrosideros* and *Myrsine* despite the abovementioned limitations.

Included primarily for phytogeographical reasons: *Alectryon, Antidesma, Claoxylon, Myoporum, Osmanthus*, and *Sophora;* also *Ilex*, notwithstanding certain restrictions (see below).

Included primarily on account of conclusions drawn from the diagrams: *Chenopodium, Cibotium, Coprosma, Pelea*, and *Pritchardia*.

The pollen types of the second group are so weakly represented in the diagrams that this would not in itself lead to their inclusion. *Alectryon, Antidesma, Claoxylon*, and *Osmanthus*, however, are on the whole indicators of forests in low levels, usually on the leeward sides; in spite of their partial occurrence in rain forests and low frequency in the diagrams they are accordingly not insignificant. *Myoporum* and *Sophora* are, together with *Acacia*, the most important elements of the subalpine forest, and are therefore included even though their amplitude is wide — like that of many other species — and they also occur below the subalpine belt. All these species may conceivably assume great importance in diagrams from other localities or periods. *Ilex* is included as the representative of the many subordinate, fairly indefinite rain-forest species, and will therefore tend to give a more correct picture; it is on the other hand uncertain whether anything essential would be gained by excluding it. That it occurs to some extent in mires is obviously no objection.

The pollen types of the third group deserve a fuller discussion.

First among them comes *Chenopodium*, one of the most important and perhaps the most unexpected — to some extent also perplexing — species of the pollen diagrams. In respect of major ecological features, its curve is primarily comparable with those of *Acacia* and *Dodonaea* (although important differences can easily be demonstrated), and its course is as a matter of fact no more local than that of a dominant forest tree. However, the species occurs only occasionally as a tree, chiefly in the subalpine forests: at any rate in present day vegetation it generally becomes shrubby. It is thus quite obvious that the type of vegetation to which *Chenopodium* belonged might be represented both by the tree layer (e. g. *Acacia*) and by the shrub layer, in which case it would possibly be over-represented in the diagrams. If so, it would of course be better not to include it in the 100 % sum. But as a rule the species (whether arborescent or not) forms part of an open vegetation, e. g. in subalpine parklands where the tree layer is relatively sparse. Such a vegetation — (some modification of) which incidentally seems to be the basis of the highest frequencies in Maui — would be greatly under-represented if *Chenopodium* were excluded. The high frequency of *Chenopodium* in the Maui diagrams (those from the higher levels) cannot be satisfactorily explained unless the species had covered a considerable portion of the open areas of the present mire districts or in their immediate vicinity (see also p. 106). Its inclusion in the diagrams seems accordingly justified.

The *Cibotium* species are important, locally dominant rain forest trees, though they generally form a lower layer in the rain forest (see Pls. 6 and 10). The spore type would therefore not as a matter of course be included in the 100 % sum of the diagrams. The shape of the curve in some of the diagrams shows, however, that this genus must at times in the past have dominated the forest flora (see also p. 98). Under such circumstances it would be incorrect to exclude it from those integrated in the main diagrams.

The many *Coprosma* species occur in several types of vegetation, from the mires to the dry localities of the leeward sides and the alpine belt. From the literature it is not even possible to hazard a guess as to where in this series the genus produces most pollen per unit area, but the curves culminate so distinctly at definite points in the succession that they have been included in the diagrams, although they are certainly not composed solely of species that are forest trees. As will be seen from the diagrams, however, variations in frequency that may be due to the mire species are not of a kind to disturb the picture as a whole.

Pelea pollens of Type II appear to differ from those of *Pelea* of Type I in that they occupy a fairly characteristic position in the succession, without any too noticeable disturbances. *Pelea* is included from to some extent the same motive as *Cibotium*, even though its species do not by long way occur as abundantly (see further p. 95).

Pritchardia is found anywhere from rain forests close to mires to relatively dry places. The literature gives no indication where, along a profile like that shown by this genus, the pollen production per unit area it the largest. The diagrams indicate the same relative position as that held by *Coprosma*. Contrary to the latter genus, *Pritchardia* contains only forest trees. Its inclusion in the diagrams is thus not open to any objection as far as life form is concerned.

* * *

The type of diagram thus obtained, however, which includes 17 curves, does not fulfil reasonable demands for perspicuity. It therefore seemed desirable to group the material into main ecological groups that also reflect the fundamental climatic features of the islands. As no absolutely sharp division is possible, several species are carried to the group to which they mainly belong. The objections raised to this from the point of view of ecotype research (see for instance Turesson 1932, 1940) are not conclusive arguments against the use of such material, the most important being where in the series of habitats the principal frequencies of each species occur. In interpreting the pollen diagrams, these curves must not be pressed beyond their main features, however, unless the diagrams themselves, the stratigraphy, or any otherwise known facts render a greater precision possible.

Although the boundaries — of Groups I and III in particular — are rather vague, the following classification will be found useful in interpreting these diagrams:

I. Species mainly of the xerophytic or mesophytic forests in the same altitudes as or higher than the montane rain forests on the windward sides of the islands (see further under B below).

II. Species of the montane rain forests covering mainly the windward sides of the islands (see further under C below).

III. Species mainly distributed in lower levels (see under A below).

This classification allows a clearer survey of any vertical displacements of the vegetation belts (I and II contra III, to some extent I contra II), as well as of variations of the humid and arid types of vegetation in the same general belt (I contra II).

2. THE VARIOUS TYPES OF POLLEN DIAGRAMS AND THEIR CONSTITUENTS.

The material made up of the relative values of the 17 constituents is presented in five parallel diagrams for each series of samples:

A. Total.

This gives a survey of the main features. The unbroken curves represent the above-mentioned Groups I (red), II (dark-green), and III (black). The dotted curve is made up of the two less extreme pollen types of Group II (hence the green colour) and is introduced to show their behaviour in transitions between the major periods (I—II and II—III). The symbols stand for the pollen types of Group III, which are too unimportant statistically to be represented by a separate diagram (the data on recent occurrences have been reproduced with certain abbreviations from Part II [= Selling 1947], and the references in these accounts refer to the bibliography of the same part):

Al = *Alectryon macrococcus* Radlk. (Sapindaceae). — Pollen: Part II, p. 221—222, Pl. 27, Figs. 405—409.

A 6—10 m high tree reported by Rock (1913, p. 277) to grow in »dry regions on the leeward side of the islands». Several specimens subsequently collected in Oahu were met with in dense, wet forests, however. In view of the scattered occurrence of the species, it is hard to fix the upper limit of its distribution. The highest value so far reported, 800 m, may be — or may until quite recently have been — surpassed elsewhere. The species appears to be obsolescent. From West Maui, where it occurs in the pollen diagrams, its has been reported only once, from Olowalu Valley. (Part II, p. 222—223, incl. detailed list of the so far known habitats.)

An = *Antidesma* L. (Euphorbiaceae; in the present diagrams probably *A. platyphyllum* Mann; see Part II, p. 200). — Pollen: Part II, p. 199—200, Pl. 23, Figs. 323—330.

A. platyphyllum is an up to about 10 m high tree recorded from all the large islands. It occurs in both wet and dry forests. Its altitudinal range is given by Rock (1913, p. 249) as 450—900 m. Sherff (1939 b, p. 570) lists a specimen collected at 250 m elev. It is common locally. Rock (l. c. p.) thus states it to be plentiful in certain localities in the island of Hawaii, and Hosaka (1937, p. 223) found it abundant in the Ohia and Cloud zones of Kipapa gulch, Oahu. In the former zone this species occurs in the third of the four layers distinguished there (l. c., p. 205; where notes on associates are found as well as in Rock l. c. p.). For lists of localities, see Sherff 1939 b. (Part II, p. 199.)

The other Hawaiian species, *A. pulvinatum* Hillebr., is a 6—8 m high tree, credited to all the large islands. Unlike the preceding species, it is peculiar to the dry districts of the leeward sides. Rock (1913, p. 253) does not mention higher localities than 600 m; the highest locality with specified altitudinal data in Sherff's recent list (1939 b) is at 800 m elev. The species is locally plentiful. At Kapua, S. Kona, Hawaii (600 m elev.) it thus constitutes 60 % of the forest trees (Rock l. c. p.). (Part II, p. 200.)

C = *Claoxylon* Juss. (Euphorbiaceae; three species in the islands; the fossil material likely to represent *C. sandwicense* Muell. Arg.; see Part II, p. 203—204). — Pollen: Part II, p. 203, Pl. 23, Figs. 335—342.

C. sandwicense is a polymorphous species forming a tree generally 3—5, rarely 6 m high, sometimes shrubby. From Kauai Sherff (1939 b) lists 3 varieties: var. *magnifolium* Sherff, *Degeneri* Sherff, and *tomentosum* Hillebr., the latter reduced to a form by Skottsberg (1944 b, p. 390). Var. *Degeneri* is the rarest of these and known only from the forest and its edges W of Waimea Canyon (Degener, Fl. Haw., Fam. 190, Feb. 10, 1940). Var. *magnifolium* seems to be the only representative in Molokai and W. Maui. Of its habitats, Degener (l. c.) writes: »Growing up to an elevation of about 5000 feet usually in dark, rich, often rainy forests. Though comparatively rare, this variety is the commonest representative of the species.» Judging by Sherff's list of localities (1939 b, p. 552—553) it reaches the 5000 ft level but rarely. It appears to be collected generally between 750 and 1000 m elev. Taken in its widest sense the species occurs (locally plentiful) also in fairly dry forests (see Rock 1913 and others) and so does this variety.

To sum up, the pollens of *Claoxylon* suggest rain forests of less extremely humid types as well as the ± dry forests now found up to about 1500 m elev.; generally the genus apparently occurs about the 1000 m or lower levels. The bulk of the fossil material might be considered likely to represent var. *magnifolium* of the abovementioned species. Only in Kauai might other varieties (or at least one) be expected to be as commonly represented. (Part II, p. 203—204.)

O = *Osmanthus sandwicensis* (A. Gray) Knobl. (Oleaceae). — Pollen: Part II, p. 296, Pl. 43, Figs. 665—668.

A tree, often reaching a height of 20 m, found in all the large islands. According to Rock (1913, p. 397; cf. Degener, Fl. Haw., Fam. 300, 12/24/'34) it is »one of the most common Hawaiian trees, but rarely inhabiting the rain forests or even their outskirts. It is more confined to the lower forest zone, especially on the leeward sides of all the islands, and is usually the predominating tree on the lava fields of Hawaii». Hillebrand (1888 b, p. 302) says that it is »scattering in the lower and middle woods of all islands», but as far as for instance Kauai is concerned, Heller (1897, p. 876) reports it as »common in the lower forest»; similar statements are also found in respect of at least Oahu and Lanai (see Skottsberg 1926, p. 257; Hosaka 1937, p. 226; Fosberg 1936 b, p. 122, 123, with fig., etc.). Notes on its associates in certain drier habitats are found in Wawra 1872 b, p. 362; Rock 1913, p. 39; 1919 c, p. 11, 17; and Fosberg l. c. p. Its altitudinal range (on the leeward sides) is stated by Rock (1913, p. 397) to be 600—4000 ft. The values published elsewhere mostly come within these limits. Wawra, however, reports it from the leeward side of Haleakala at an elevation somewhat above 4000 ft, and the locality Hawaii: Bird Park (Judd 1921 a, p. 258; Skottsberg l. c. p.; Lamb 1936, p. 21) is a similar exception. To return to Kauai (there are no detailed data on the species from E. Molokai and W. Maui), Heller (l. c. p.) did not see it above 2500 ft elev., but it occurs in the woods of Kokee in about 1050—1100 m alt. (Skottsberg l. c. p.). Rock (1913, p. 397) mentions it from the same general region (Halemanu) as well as from Waimea Canyon, Milolii and Kopiwai forest. (Part II, p. 296—297.)

B. Xerophytic (and ± mesophytic) species (= species of Group I).

These frequencies are represented by areas added to each other. The final contour is thus identical with the red curve of Diagram A. *Chenopodium*, that does not enter the rain forest precedes those that do. In materials comprising more of the subalpine development a different arrangement may be preferable. The Diagram is made up of the following species (the accounts of recent occurrences extracted from Part II [= Selling 1947]; their references refer to the bibliography of the said part):

Chenopodium oahuense (Meyen) Aellen (Chenopodiaceae). — Pollen: Part II, p. 89—90, Pl. 1, Figs. 21—24.

A dry district species occurring in all the larger islands as well as on Kaula, Niihau, and some of the Leeward Islands. On the coast and at low elevations in general, it is a much branched shrub about 1 m high (sometimes subherbaceous). In high altitudes it becomes a tree. Thus, Hillebrand (1888 b, p. 380; see also Remy 1862) found it »arborescent, with a woody trunk, and 12—15 ft high», in the subalpine forest of Mauna Kea. Some more data on its life forms are given in Part II.

The vertical distribution of the species is very wide. Hartt and Neal (1940, p. 264) give it from 10 to 8250 ft (= 3—2500 m) elev. The latter value was noted on Mauna Kea, where, however, Pickering noted it at 9000 ft elev. (1876, p. 484; the value possibly less exact); Guppy said 7000 ft (1906, p. 272, 283). It is rather hard to ascertain the levels where the species is most common. Only a few data are given in literature. Heller (1897, p. 819) says that he collected it »on the edge and about the base of the tabular summit above Waimea, Kauai, at elevations of from 3000 to 3500 feet [= 900—1050 m], where it is plentiful». A. S. Hitchcock (Aellen 1929, p. 125) found it in the same region in from 900 to 1330 m elev.; higher up the rain forest supervenes; the species, which is of the dry vegetation types of the leeward sides, accordingly cannot ascend to the summit region of that island. Rock (1913, p. 50) states it to be »very plentiful» at the 900 m level in the Puu Waawaa region, Hawaii. It may be mentioned that Hillebrand (1888 b, p. 380) regarded it as commonest on the high plains of Hawaii, where it was found to be frequent also during the excursions of the HBS in 1938 as well as by Robyns and Lamb (1939, p. 263), who write: »Considerable areas at the eastern end of the plateau, in the vicinity of Huumula, are covered by an association of *Myoporum sandwicense* and *Sophora chrysophylla* (fig. 24 and 25). . . . . *Chenopodium sandwicheum* grows to a height of 15 to 20 feet along the road too Huumula below the *Myoporum-Sophora* association.» Figs. 24, 25, and 42 of the said paper (p. 266 and 291) show localities with abundant *Chenopodium* at elevations of 2000, 1700, and 1700 m, respectively.

To sum up, we find that the species belongs to the lowlands, to the lower and middle elevatations of the leeward sides, and to the subalpine belt up to 2500 m elev., and is possibly most frequent about and below the 2000 m level. It does not belong to the rain forest. (Part II, p. 90.; see also p. 102—110 below.)

Dodonaea L. (Sapindaceae). — Pollen: Part II, p. 224—225, Pl. 27, Figs. 410—416.

Sherff, in revising the Hawaiian material recently (1945 a, p. 202—214), recognizes three species: *D. eriocarpa* Sm., *sandwicensis* Sherff and *stenoptera* Hillebr.

D. eriocarpa, a shrub or small tree from 2.5 to 5 m high, is found in all the large islands (and elsewhere) from almost sea level to about 2700 m elev. or possibly higher. It prefers fairly dry districts, arid lava flows, dry fore hills, and occurs also in semi-dry forest types. One of the twelve varieties credited to the islands by Sherff (l. c.) occurs also in the Wahiawa swamp at 600 m elev. in southern Kauai, the peculiar mire vegetation of which has several features that are not duplicated in the montane mires of higher altitudes. Another is found in the fog swept scrub vegetation of the Koolau Gap region, E. Maui. Some notes on the drier habitats are found in Rock 1913, p. 281, and in Beccari and Rock 1921, p. 16.

D. sandwicensis, mainly corresponding to the *D. viscosa* of previous authors, is described by Sherff (l. c. p. 202) now as a shrub 2—3 m tall, now as a tree about 4—6 m tall and found in all the large islands. Rock (1913, p. 279) mentions trees of his *D. viscosa* about 10 m in height. It is one of the commonest trees in the islands. Rock (l. c. p.) calls it »gregarious at elevations of 1000 to 4000 feet». It plays a dominant part, together with the preceding species, in dry districts. The species occurs also in rain forests, in the outskirts and the moderately wet types, but it is only occasional there. Ripperton and Hosaka (1940, p. 10) give its altitudinal range as 2000 to 5000 ft, and say that it occurs in their zones B (= principally leeward zone just above the very hot and dry areas bordering the leeward coast line) and C (= low to moderate altitudes of moderate temperature and moderate rainfall, 40—65 inches). Hartt and Neal (1940, p. 264) give the altitudinal range as 700—8250 ft (= 200—2500 m) for *D.* »*viscosa*», saying nothing of *D. eriocarpa*.

D. stenoptera was recorded by Hillebrand (1888 b, p. 88) and Rock (1913, p. 281) only from Molokai, but Sherff recently described a variety of it from Oahu, a specimen of which was originally described by Léveillé (1911, p. 155) as a hybrid of *stenoptera* and *viscosa*. The main species was known to Hillebrand (l. c. p.; Radlkofer 1933—1934, p. 1374) from »Kamalo, 1500—2000 ft». Sherff lists it from the same region at elevations of 1500 to 4000 ft (l. c. p. 213—214). »At the two thousand-foot level», Rock writes (in Beccari and Rock 1921, p. 16), »*Dodonaea stenoptera* is very common and especially at Puakoolau and Kamolo proper. The region must be considered a subxerophytic one although a thousand feet higher the rain forest commences.» The diagnosis says »Shrubby, 2—4 ft high». Sherff's Oahu variety is a 4 m tall tree, and occurs in the dry forest of the Waianae range at 650 m elev. (Part II, p. 225.)

Myoporum sandwicense A. Gray (Myoporaceae), in the present diagram (34) marked M, since the values do not form a curve and may therefore easily be overlooked. — Pollen: Part II, p. 286, Pl. 40, Figs. 637—640.

A tree generally 6—10 m high but sometimes, in protected situations, attaining a height of upwards of 20 m; at sea level it is a shrub just a few dm high (Pickering 1876, p. 416; Wawra 1872 b, p. 417; Rock 1913, p. 5, etc.). Among Hawaiian forest trees of wide vertical distribution, *Myoporum*'s range is one of the widest. It occurs from sea level to 3000 m alt. (Hartt and Neal 1940, p. 264). It has been found in all the large islands: Hillebrand (1888 b, p. 339) did not find it in Molokai or Lanai, but from there it was reported by Rock (1913, p. 427; cf. also Degener 1930, p. 263) and Fosberg (1936 b, p. 123), respectively.

Hillebrand (l. c. p.) writes: »Inhabits the high mountains of the group. On Mauna Kea it forms, together with *Edwardsia* [= *Sophora*] *chrysophylla* and *Raillardia struthioloides*, the upper limit of the tree zone at an elevation of about 10000 ft. on the leeside, attaining there its greatest height, ...». Rock (1913, p. 42) also emphasizes that the tree prefers the dry districts of the leeward sides and the subalpine belt. The idea that it should reach its best development in the latter belt is, however, contradicted by his finding trees of 15 to almost 20 m with trunks 1 m in diam. not uncommon in E. Maui, in the dry forest back of Makawao at an elev. of 2500 ft.

Notes on the associates of the species are found chiefly in Rock 1913 (passim). In Kauai Wawra (1873 b, p. 23) lists it among *Alphitonia*, *Bobea*, *Claoxylon*, *Fagara dipetala*, *Santalum pyrularium*, *Xylosma hawaiiense*, etc., from the neighbourhood of Halemanu. I know of no records from more humid forest types. Heller (1897, p. 892) found it only occasionally in gulches on the leeward side of Kauai, below the forest. (Part II, p. 286—287.)

Sophora chrysophylla (Salisb.) Seem. (Papilionaceae). — Pollen: Part II, p. 146, Pl. 9, Figs. 177, 178.

A tree, generally about 6—10(—13) m high, sometimes a shrub, especially at low elevations. It is reported from all the large islands with the exception of Molokai, but is abundant only in Hawaii and E. Maui. According to Rock (1919 b) only shrubby specimens are found in Kauai and Oahu. Degener (1930, p. 179) reported that some years earlier he had seen a few Oahu trees, adding that the species may now possibly be extinct in this island. In Dec., 1929, C. S. Judd (1931, p. 49) found another tree not far away in Makua Valley, Oahu.

The vertical distribution was stated by Hillebrand (1888 b, p. 109) to be from 2000 ft or even less up to 10,000 ft. These data are reproduced by Guppy (1906, p. 147—148), Skottsberg (1931, p. 51), and Hartt and Neal (1940, p. 265), the lower limit value also by W. A. Bryan (1915, p. 226). They might represent a certain frequency (cf. Degener l. c. p.), and most other data fall within these limits. Still, there are occasional occurrences at higher and lower levels. Mann (1868, p. 233) thus says »often at inconsiderable elevation». Rock (1913, p. 18; 1919 b, p. 41) reports the species from »almost sea level up to nearly 10,000 feet». In Jan., 1841, however, Pickering and Brackenridge (Wilkes 1845, p. 203; Gray 1854, p. 459) found the species at 11,000 ft elev. on Mauna Kea, a value which was not mentioned by Pickering in 1876, p. 479, and which does not appear to have been considered by anybody later than Grisebach 1884 (p. 501). Occasional trees might have been planted by the natives (cf. Wilkes 1845, p. 205; Pickering 1876, p. 403—404).

Together with *Myoporum* and some species of *Railliardia* the species forms the subalpine forest belt of the highest islands, (E.) Maui and Hawaii, a belt which Hillebrand (1888 a, p. 311) therefore called »die Zone der Edwardsia» (a designation later changed to »The upper forest-zone»; 1888 b, p. XXIV). *Sophora* is a parallel to *Myoporum* in several respects: they both have the same vertical distribution, they are important constituents of the subalpine forests, but also inhabit the drier forest types in lower elevations. An illustrated account of its occurrence on Mauna Kea is found in Hartt and Neal 1940, to which I refer. It may be added that trees are very rarely found in wet, shaded forests (Rock 1913, p. 69; Degener 1930, p. 179). Possibly such a locality is indicated by Pickering (1876, p. 479): »Observed also on the tabular summit of Tauai [= Kauai, Oct., 1840]». (Part II, p. 146—147.)

Acacia Willd. (Mimosaceae; in the present diagrams apparently represented by *A. koa* A. Gray). — Pollen: Part II, p. 139—140, Pl. 8, Figs. 155—160 (as regards the other two species, see Part II, p. 139, Pl. 8, Figs. 152—154, and p. 141, Pl. 8, Figs. 161—164, respectively).

A. koa is the commonest tree of the islands next to *Metrosideros polymorpha* and occurs on all the large islands, from about 15 m to about 2100 m above sea level, occasionally still higher. Only on the island of Hawaii it is found — represented by the variety *hawaiiensis* Rock 1919 b, p. 21 — in the subalpine parkland forest. Dutton (1884, p. 130) states that on Hawaii it does not flourish »below 4000 feet. From 4000 to 6000 feet, and sometimes higher up, it is the dominant forest tree». Guppy (1906, p. 604) puts its highest limit on Mauna Kea at an altitude of 2000 m, Rock (1913, p. 79; 1919 b, p. 15, 30), and Hartt and Neal (1940, p. 263) give the height of 2100 m (7000 ft), and Pickering noted that scattered shrubs of it occur as high as at 7200 ft elev. (1876, p. 480), a value extended to 2500 m by Krämer (1906, p. 109, 112). On Kauai and Oahu it is common in the lower forests and goes but little higher (cf. Heller 1897). According to Hillebrand the main vertical distribution of the species falls between an altitude of 450 and 1200 m. It forms, or has earlier formed, large forests on the leeward sides of the islands — now to a considerable extent in a dying state [se pl. 21 B of the present paper] — though it can be found also in the rain forest. In the humid Fern forest near Kilauea on the island of Hawaii it occurs thus in specimens 25 m high, with straight trunks (Rock 1919 b, p. 12, pl. II). Degener (1930, p. 173) mentions a specimen from near Bird Park, Kilauea, which measured 118 ft (36 m) in height. Friedländer (1896, p. 72), who described an ascent of Mauna Loa from the Kona side (Honomalino) in 1896, writes also: »The trail for some miles leads into a thick and wonderful forest, in which I saw the largest koa trees and tree ferns I met with in the islands.» It appears as if the species reaches its greatest height in transitional types between strictly dry forests and rain forests. Skottsberg writes (letter 30/12 1942), that the largest koa trees he has ever met with grew at Koa Camp on the W slope of Mauna Loa, Hawaii, in fairly dry rain forest. The species is not, however, characteristic of the rain forest. Only by merging the Koa and Ohia zones, Mac Caughey (1917 c, p. 598) gets it a »representative plant of the Manoa rain forest.» (Part II, p. 140.)

The separate curves of the pollen types constituting Diagram B are shown in Diagram D.

C. Hygrophytic species (= species of Group II).

As in Diagram B, the frequencies are here represented by areas added to each other. Their final contour is identical with the dark-green, full-drawn curve of Diagram A. The pollen types are arranged in a descending series according to the ecological demands of the corresponding species or group of species (see p. 95—98). However, two pollen types, which do not come into the general succession in the same way as the others, are marked separately. *Ilex* of this latter group was for technical reasons put nearest to the ordinate of the diagram, followed by *Pelea*, which belongs to about the same general place in the ecological succession as *Metrosideros* (= no. 3). *Cibotium* follows after *Metrosideros*, to the curve of which it appears to bear an interesting relation (p. 98). The two pollen types at the end of the series are also represented by the dotted green curve in Diagram A, since the variations in their aggregate areas are hard to follow in this diagram. In the following list of constituents the pollen types are mentioned in the order adopted in the diagram. The accounts of recent occurrences have been extracted from Parts I and II (= Selling 1946 and 1947), and their references refer to the bibliographies of the respective parts.

Ilex anomala Hook. et Arn. (Aquifoliaceae). — Pollen: Part II, p. 228, Pl. 28, Figs. 421, 422.

A common forest tree, often also a shrub; arborescent individuals becoming 6—12 m high (Hillebrand 1888 b, p. 78; Rock 1913, p. 265; Judd 1921 a, p. 258). Occurs in the rain forests of all the big islands (Mann 1867 b, p. 171; Hillebrand l. c. p., etc.), also in the bogs, but is occasionally found also in the drier districts (Rock l. c. p.). Rock states that it can be found usually in company with *Perrottetia, Cheirodendron trigynum, Straussia, Bobea, Elaeocarpus*, and other members of the less extremely humid forest types. Its optimal ecological conditions remain to be settled in detail. Hartt and Neal (1940, p. 264) state its vertical range to be 900—6000 ft. I have found no data outside these limits. (Part II, p. 228.)

Pelea A. Gray (Rutaceae): Type II. — Pollen: Part II, p. 213, Pl. 25, Figs. 374—378, Pl. 26, Figs. 379—382.

No survey of the species that have this pollen type can yet be presented, but those of the present diagrams appear to have been rather extreme rain forest species. The numerous and often variable species of the genus are low to medium-sized trees or shrubs of the montane rain forests as well as drier forest types chiefly of the leeward sides, at about the same elevations as the mires or lower. For a more detailed survey, see Rock (1913, 1918 b), Skottsberg (1936 b, 1944 b), and St. John (1944). Several species are common constituents of the forests surrounding the bog areas investigated (cf. Rock 1913, p. 56: »They like heavy, gray, loamy soil, where water is often stagnant, forming small pools all the year round.»). (Part II, p. 213—214.)

Metrosideros Banks ex Gaertn. (Myrtaceae). — Pollen: Part II, p. 161—162, Pl. 11, Figs. 216—225.

The chief species to be considered in this connexion is *M. polymorpha*, the commonest tree of the Hawaiian Islands. *M. macropus* and *rugosa* are confined to Oahu. Hillebrand (1888 b, p. 128) lists the former species also from Kauai and Molokai, and Heller (1897, p. 865) published a supposed locality for it on Kauai. Rock also followed Hillebrand preliminarily (1913, p. 336), but later (1917 b) referred Heller's specimen to *polymorpha* and also disproved the other records outside Oahu. *M. Waialealae* Rock is peculiar to Kauai and considered by Rock to be endemic in the upper part of Waialeale, where it is fairly abundant. Where Heller's *M. tremuloides* from Kauai belongs, I do not know (cf. the var. μ of Hillebrand l. c. p. 127; Rock 1917 b, p. 45). A somewhat doubtful specimen, suggesting affinity to *M. Waialealae*, was found by Skottsberg (1944 b, p. 409) along the Kokee-Mohihi trail. Evidently these forms play but an insignificant part compared with the following species to which *M. pumila* (Heller) Hochr. is to be referred.

M. polymorpha Gaud. not only is the most common tree of the Hawaiian Islands, but also the principal rain forest constituent. Shrubby forms are plentiful in the bogs. It is extremely polymorphous and no satisfactory taxonomy has yet been presented. The bulk of the subspecies, varieties, and forms recognized by Rock and Skottsberg belong to the montane rain forest (habitats pictured in Wawra 1872 b, p. 299; Rock 1913, passim; 1917 b, passim; Hosaka 1937, and others), but there are several outside this, too. Hartt and Neal (1940, p. 264) thus list subsp. *typica* Rock in from 300 to 2700 m elev., and on Mauna Loa it forms the tree limit (Skottsberg 1936 b, p. 147). Subsp. *incana* Lévl. is another example: it ranges from about sea level to high up into the rain forest, but is also, acc. to Rock (1917 b), a colonist on arid lava fields at 2000 m elev. For further details, see Rock l. c. and Skottsberg 1944 b, p. 402—409.

In summing up — and speaking only of Kauai, Molokai, and Maui — the *Metrosideros* curve can be said to be dominated by *M. polymorpha*, and to be essentially indicative of rain forest conditions. Due consideration should be given, however, to the fact that the species occurs also outside rain forest districts from sea level up to the alpine belt, and that local concentrations from shrubs of the bogs themselves may occur. In the diagrams from Kauai *M. Waialealae* may sometimes be expected; ecologically, it comes close to the said species, however. The possibility of *Eugenia malaccensis* not being entirely absent in the diagrams from all three islands should not be entirely disregarded, but the facts mentioned in Part II, p. 159, tend to show that its influence must have been far from important. (Part II, p. 162—163.)

Cibotium Kaulf. (Dicksoniaceae). — Spores: Part I, p. 40—42, Pl. 4, Figs. 68—88.

Of the five species of *Cibotium*, four are known from those islands, where the bogs that I have studied are located. *C. St. Johnii* is known only from Kauai, from whence, on the other hand, *C. glaucum* does not appear to have been reported. *C. Chamissoi* and *splendens* appear to be common on Kauai and Molokai as well as Maui. Particulars of the various species are found in Part I. All the species are mainly found in the rain forest though they are not strictly confined to it. Ripperton (1924, p. 3) states that they occur in all parts of the group where the annual rainfall is 100 inches or more. They occur from 300 up to 1800 m, sometimes also at a height of 2000 m. Bailey (1882, p. 14) gave the general range as 1—3000 ft, Hillebrand (1888 a, p. 312) says: »Ihre höchste Entwicklung erhalten sie erst von 3500 Fuss aufwärts», and MacCaughey (1918 a, p. 205) states them to range »from 1000—6000 ft, sometimes lower». Ripperton (1924, p. 3) also points out that only on the island of Hawaii we find them in almost unbroken stretches from sea-level to an elevation of 6000 ft or more. The highest limit value »ten thousand feet or more», in Degener 1930, p. 27, appears to be exaggerated.

There are no definite data at hand permitting general conclusions as regards the relative and absolute frequency of the species on the different islands as well as different levels. Ripperton (l. c. p.) states that, taken as a unit, the species occur in dense forests only on the islands of Kauai and Hawaii. In the latter island the »windward slopes of Mauna Kea and Mauna Loa are one continuous tree-fern forest, the belt extending from the Puna district to the Hamakua district being about 10 miles wide and 40 miles long. It is estimated generally that there are 400,000 acres of tree-fern forests on the island of Hawaii alone» (l. c.). To this should be added that, as is well known, there are extensive areas of fern forest also in Kohala (see ill. in, e. g., Rock 1913 and Campbell 1926, Pl. XXVII, as well as in the present paper). (Part I, p. 43.)

Myrsine L. (Myrsinaceae). — Pollen: Part II, p. 250—251, Pl. 32, Figs. 505—518.

The 21 endemic species and 4 varieties distinguished by Hosaka (1940) are trees or shrubs of rain forest districts as well as dry, open vegetation types. The trees are (1.5—)3—8(—over 20) m high, and some of them are important rain forest constituents, while a number of shrubby species are also found in the bogs. The number of species in each island is: Kauai: 16 (13 endemic), 1 with a var.; Oahu: 8 (2 end.), 2 with one var. each; Molokai: 5 (no end.), W. Maui: 5 (no end.), E. Maui: 5 (no end.), Lanai: 4 (no end.), and Hawaii: 2 (no end.). Only two species (*M. pukooensis* and *Lessertiana*) are common to the three islands to which my diagrams refer. I have plotted the localities listed in Hosaka's monograph in altitude diagrams for each island, to see whether any of the species could from such data be expected to be the leading contributor to the fossil pollen flora. The attempt gave no reliable result, however, and the question must be left open until settled by field studies of this point.

The individual species are sometimes very variable. Rock (1913, p. 375), for instance, found hardly two trees alike of *M. Lessertiana*, which is one of the commonest rain forest species and one of the species of most importance to the appearance of the *Myrsine* curve of my diagrams. Hosaka 1940 gives further data on this point. The pollen characters noted above accordingly cannot be supposed to be constant in the corresponding species. For lack of material I have had to leave this question unanswered. Even if the variations are found to be unexpectedly small, the task of distinguishing separate species will still meet with considerable difficulties. (Part II, p. 251—252.)

Cheirodendron trigynum (Gaud.) Heller (Araliaceae). — Pollen: Part II, p. 239, Pl. 30, Figs. 476—479.

One of the leading rain forest trees, occurring on all the big islands and reaching individual heights of 12—15 m or even more. It is polymorphous, and a number of varieties peculiar to single islands or small groups of islands have been segregated. A really thorough study, including both morphology and the most local geographical conditions, would no doubt pay. In the present investigation I must deal with this species without further differentiation, admittedly a drawback but still no obstacle preventing the working out of a general pollen-statistical system for the islands, for the diagrams themselves clearly indicate that the general ecological characteristics are the same in the different areas concerned.

As to its relative frequency in the different islands, there is little to be found in literature. Rock alone (1913, p. 363; cf. p. 67, 69) states that it is »most common in East Maui, in the middle forest zone on the slopes of Haleakala at an elevation of 4000 feet, and it is here that it attains its best development».

The altitudinal range of the species is wide. Hillebrand (1888 b, p. 148) and Rock (l. c., p. 363) state it to be common between 600—1200 m (2000—4000 ft) elev. Guppy, who on an excursion to the N flank of Mauna Kea in Hawaii found it from 660 to something over 1900 m elev. (1906, p. 604), lists the same lower limit but considered the upper limit (of its frequent occurrence?) to be at 1500 m elev. (l. c., p. 594), but at the same time he states that it occurs on the SE side of Mauna Kea up to 2100 m elev.; a somewhat similar value had earlier been recorded by Pickering (1876, p. 407; cf. p. 395): »In the forest on Mauna Kea, growing at the elevation of from 4000 to 6700 feet». Hartt and Neal (1940), who made a special study of this mountain, seem to have overlooked these figures. The vertical distribution of the species is by them (p. 264) said to comprise the levels between 450 and 1800 m above the sea. The altitudinal data published by Heller (1897, p. 870), Skottsberg (1926, p. 252—253; 1944 b, p. 416—418), and Hosaka (1937, p. 225) all fall between the above extremes: 450 m and 2100 m above sea level. A close idea of its relative frequency in this belt in the different islands cannot be gained without field studies. (Part II, p. 239—240.)

Coprosma Forst. (Rubiaceae). — Pollen: Part II, p. 315—316, Pl. 48, Figs. 758—764.

The 18 species found in Hawaii (W. R. B. Oliver 1935, 1942) are shrubs or small trees mainly of the rain forests or of dry regions at equivalent or higher elevations. In the island of Hawaii the genus is represented in altitudes of 9600 ft (Hartt and Neal 1940, p. 264). No species is found in all the islands from which peat samples were analysed. Still, the reaction of *Coprosma* to climate is similar in all diagrams. (Part II, p. 316; see further p. 96—97 of the present paper.)

Pritchardia Seem. et Wendl. (Palmae). — Pollen: Part II, p. 335, Pl. 53, Figs. 865—868.

Numerous species (see Part II), mainly of the rain forest. According to Mac Caughey (1918 b, p. 320, note 4) the altitudinal range would be from sea level to 5000 ft, with the chief distribution between 1000 and 3000 ft. Rock (in Beccari and Rock 1921) confirmed this view with a representative material. Mac Caughey called 5000 ft the extreme limit, but he made the remark that this »coincides with that of the middle forest zone; on Maui and Hawaii, which rise high above this zone, the *loulus* do not ascend above 6500 feet.» He also states that »Clumps of aged *loulu* palms are plentiful along the windy precipices of the various islands, at altitudes of 1800 to 3500 feet», which makes his data on the chief altitudinal distribution less distinct.

The supposition, in itself rather likely, that these palms were formerly more common than they are now, particularly at lower elevations (Mac Caughey l. c.,

p. 320) cannot be elucidated by the pollen diagrams so far available — I only speak of the wild occurrences, for it is an open fact that numerous planted groves around old native dwellings are now gone (cf., e. g., Guppy 1906, p. 327). Upon the whole, these palms are not frequent (though they may be locally), but on the other hand they can not be called rare either (all species then taken as a unit) — as Alexander (1883) and Lydgate (1883, p. 30) did — though in certain districts they have been much destroyed by insects in comparatively recent times (cf. F. L. Clarke 1874, p. 20). They occur, mostly as scattered specimens here and there in all the large islands. A survey of the palm flora of each island is given by Rock in Beccari and Rock 1921, p. 12—19. There are 4 in Kauai, 6 in Molokai (a locality at Pelekunu is also mentioned in Fornander 1919, II: 2, p. 496, another, near Kalawao, in Lydgate 1883, p. 30), and 3 in Maui, 2 of them in W. Maui (cf. also Alexander 1883, p. 33). Some species might remain to be discovered in unexplored parts of the mountains, for the Pritchardias are highly local. Many of them occur in one valley only, and none of them in more than one island (Beccari and Rock 1921, p. 19; cf. also Skottsberg 1938, p. 289). (Part II, p. 335—336.)

The separate curves of the pollen types constituting Diagram C are shown in Diagram E.

D. Xerophytic (and ± mesophytic) species (= species of Group I).

This diagram comprises the same pollen types as Diagram B, but all their frequencies are here marked off from the ordinate, and not added together.

E. Hygrophytic species (= species of Group II).

This diagram comprises the same pollen types as Diagram C, but all their frequencies are here — as in Diagram D — marked off from the ordinate, and not added together. The sum total of the light green curves (= the least hygrophytic types) is shown in the dotted dark-green curve of Diagram A.

3. ABSOLUTE NUMBERS OF POLLENS AND SPORES PER SLIDE.

The procedure used to obtain these values has been described above (p. 23). The values are illustrated in Diagram F. The computations include a) the sum total of all pollens and spores of vascular plants, and b) the species of (mainly) forest trees on which Diagrams A—E are based.

The diagram roughly expresses the degree of decomposition of the peat. The proportion of forest trees in the pollen and spore flora is of importance to the question whether open — mire or grassland — vegetation has at any time been considerably more extensive in the vicinity of the point of observation, encroaching upon the area of dense forest and *Chenopodium* vegetation.

4. SYMBOLS.

As the object of this investigation was to give as clear a picture as possible of the results of a relatively complicated working method in a new field — its first full application in the tropics — it was deemed desirable to publish the curves in colours [see Pls. 23 (symbols) and 24—27]. Naturally, they must later be printed in black and white. It is on the other hand uncertain whether diagrams of the B and C types will be necessary at a later stage. Their object is mainly pedagogical as they give the reader at a glance some idea of the general significance of the diagrams. The interrelations of individual pollen types, however, are frequently not readily discernible. In such cases, diagrams of the types D and E are therefore more indispensable, and will for that reason be more used in future, though for the sake of clarity some of the curves may possibly have to be presented in accessory diagrams. It may accordingly be worth while to say a few words regarding their printing in black and white, in the hope that no student of the peat deposits in the islands will in future be content — as has sometimes happened elsewhere — with giving the results of his analyses only in a Table. This would unnecessarily hamper work of this kind.

In 1929 Gams summarized the proposals for tree-pollen diagram symbols made in European pollen research. von Post's fundamental paper on this subject appeared shortly afterwards (1929 b). Gams has also submitted a proposal (1938) for the standardization of the symbols used in European N(on) T(ree) P(ollen) diagrams. A collocation of the symbols of these two groups, enlarged at some points, has also been published by Erdtman (1943). This also includes some symbols for extra-European pollen types. Others have been proposed by for inst. Auer (1933, p. 309, and in Salmi 1941, p. 113).

No standardization, however, can cover the need of distinct and easily drawn diagram symbols for every floral district of the earth. We cannot, in the Hawaiian diagrams, do without the symbols of the Boreal pollen diagrams. Erdtman's symbol for *Myrtaceae* (1943, p. 159) is for instance too complicated to be used for the commonest pollen type of the Hawaiian diagrams. I therefore suggest the symbols of Fig. 25 in place of those that I have used in the colour diagrams.

It would perhaps seem more natural to let the filled symbols stand for rain forest representatives. For the sake of clarity, however, it has been considered preferable to use as many open symbols as possible (see a diagram with crowded curves like 34 E). *Myoporum* and *Sophora* have therefore been placed at the beginning of the series; they moreover largely represent subalpine

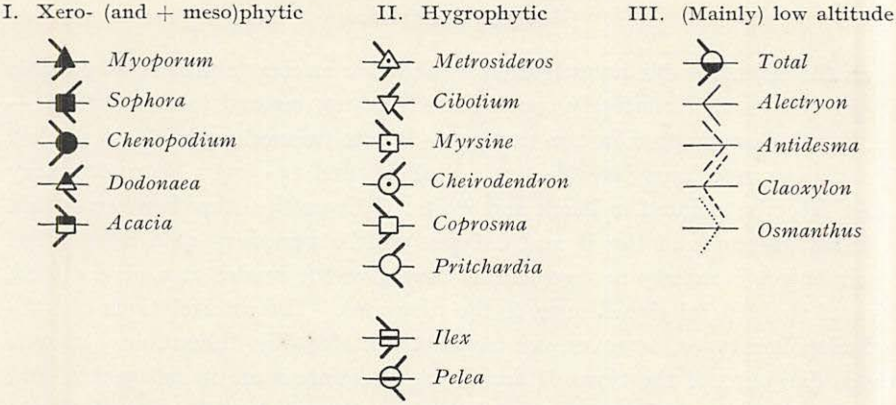


Fig. 25. Proposed symbols for Hawaiian pollen diagrams in black and white.

vegetation. The three other pollen types of Group I are more frequently represented in diagrams from lower vegetation belts. They have been arranged in the same order as in the colour diagrams: *Chenopodium*, that does not enter the rain forest, precedes *Dodonaea* and *Acacia* that do. As the symbols now stand, they are moreover reminiscent of the corresponding pollens: *Chenopodium* round, *Dodonaea* triangular (the pollen tricolporate), and *Acacia* quadrangular.

The sum of the pollens of Group III (species of mainly lower levels) have been marked by a half-filled symbol, but in this case the filled part has been placed on the lower side of the symbol. If desired, the curves of the various constituents can be conveniently put into an accessory diagram and drawn with finer lines.

The principles of the symbols of Group II will be apparent from the discussion in Chap. IV: B: 2: c.

The curves of the constituents of the main diagrams have been drawn with unbroken lines. If all of them are put together into a single diagram, it will perhaps prove useful to have for inst. those of Group I drawn with broken lines.

C. ACCESSORY POLLEN TYPES.

The pollen types selected for the main diagrams constitute about 1/3 of the total number of pollens and spores of vascular plants recorded in my analyses. Apart from scattered rain-forest trees that had to be left out for various reasons, the remainder is chiefly made up of shrubby mire and rain-forest species (no distinct boundary can be drawn between their occurrences in this respect), ferns other than *Cibotium*, and herbaceous dicotyledons. Speaking only of the N(on) T(ree) P(ollens), it proved impossible to represent these by the same methods as in Boreal regions. In the Hawaiian microfossil flora no sharp boundary can be drawn between many of the shrubby species and forest trees, from the pollens of which those of some of the herbs are also indistinguishable. The pollens that can be definitely referred to shrubs or herbs do not seem representative enough to form the basis of a percentage calculation. To get some idea of the relative values of these pollen types, it was therefore found most expedient to refer them all to the sum total of pollen types in the main diagrams (= »the 100 % sum»). The F diagrams (absolute numbers per slide) show that the limits of the closed forest have never been pushed far enough out from the boring stations to affect this basis of calculation to any considerable extent.

Some of the values thus obtained confirm the conclusions drawn from the main diagrams regarding the ecological conditions (see Selling 1947 and below), but most of them are of little interest, and have therefore been omitted.

V. DISCUSSION OF THE DIAGRAMS.

A. THE MAIN PERIODS IN THE LATE QUATERNARY HISTORY OF THE HAWAIIAN VEGETATION.

GENERAL INTRODUCTION.

The diagrams agree exceedingly well as far as the main features are concerned. The agreement is unexpectedly good if the many sources of error are considered that might conceivably disturb their conformity.

Dissimilarities ascribable to differences in exposition may be found in diagrams from adjacent localities, but owing to the very strong variations in the growth of the peat produced by these differences these dissimilarities seem larger than they actually are; peat growth in the raised bogs of the Hawaiian Islands is apparently very sensitive to changes in humidity. Sections well developed in one locality may be entirely absent from another, adjacent locality. Examples of this are found not least in the localities round Stations 33—37 (W. Maui).¹) The differences in the general levels of the pollen curves seen in Diagram 34 are probably to a not insignificant extent due to the fact that each sample in it represents a much longer period, and that the pollen spectra are accordingly smoothed. The influence of local scrub vegetation, the effect of pollen-carrying winds from valleys below (Pl. 11 B), and selective destruction of pollens by trickling water rich in oxygen, are by no means denied by this. Important is, however, that, despite these and other conceivable limitations, the diagrams show the same general development. The good agreement justifies the conclusion that changes common to all the islands are without serious local disturbances registered in this combination of pollen curves. These pollen diagrams can be used with good success in establishing the main phases of the vegetational development. They are, however, confined to

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¹) My material is insufficient for conclusions as to whether these variations in peat growth are useful for studies of changes in the prevailing direction of the rain-bearing winds. Just a slight change in the direction of the free winds may cause considerable local changes; the winds are deflected in the valley systems (see map in Cox 1924, pl. II). Since about 1910 east winds have increased in about the same proportion that northeast winds decreased (Beals 1927 b, p. 217, Tab. 3). This change may perhaps turn out to be connected with the recent world-wide climatic change.

the mountain vegetation. The detailed pollen-floristic investigation presented in Part II shows that species restricted to the lowlands do not appear in the microfossil analyses of the montane peat deposits. Pollen grains and spores of species from the lower levels undoubtedly occur in the montane strata, but in quite insignificant numbers compared with the quantities of pollen from adjacent vegetation.

Three main periods can be distinguished:

I. The area of the rain forest restricted (in comparison with present conditions) in favour of drier vegetation types, at least in the higher levels.

II. The area of the rain forest extended. The boundary between it and the dry forests likely to have been further away from the localities examined than it is now.

III. The rain forest replaced by drier vegetation types in parts of the area occupied in Period II. Conditions more extreme at the beginning of the period than they are now.

Naturally, much still remains to be done before the Hawaiian pollen diagrams can provide a clear picture of the extent of the several types of forests at different times. The features that can now be discerned will be discussed here in so far as they apply to the above periods or any greater parts thereof. Features of development of a lower order will be briefly dealt with in Chap. V: B.

Already now it can be stated that the vegetational changes reflected by the diagrams cannot be ascribed to changes of sea level. During the period concerned, these have been much too insignificant to be of importance in this connexion (see further Chap. VI, with literature references).

PERIOD I.

Strata with a flora fundamentally differing from that of Period II were only met with at Stations 34 and 37 in West Maui. This limitation alone is a strong criterion of the correctness of the conclusions drawn from the pollen diagrams. These seem to show that during this period drier types of forests used to dominate the typical rain forest in the vicinity of the present mire areas in higher altitudes. Limited peat formation and rarity of the corresponding strata in these areas are accordingly natural. From the discussion presented under Period III (see below) it would seem that Period I is also represented in e. g. Diagram 81 (Kauai) though by very wet rain forest (much *Metrosideros*). This will be discussed in connexion with the features of Period III, however. We shall here only deal with the strata containing representatives of drier forest types.

Diagram 34, which comprises one of the oldest hitherto known peat deposits in the Hawaiian Islands, is the most informative. The sample series was taken in a swamp just below the top of Puu Kukui, the highest point of West Maui (about 1750 m above sea level). This locality, the vegetation of which was briefly described by Skottsberg (1940 a, p. 8—9), is depicted in Pls. 14 B and 15; a section is found in Text-fig. 19. On the slopes above it *Oreobolus*-bogs are now found, i. e. ombrogeneous vegetation conditioned by rainfall alone, while the swamp vegetation is soligeneous, i. e. conditioned by both rain and trickling water. The sample series from the tops of these raised bogs (Diagrams 33 and 35), situated 15 and 105 m respectively from Station 34, contain no strata corresponding to Period I. It seems that the local precipitation has been too small to make the occurrence of ombrogeneous bogs possible, but not sufficiently small to prevent the retention of some humidity in the soil. In those parts of the topography which in particular receive trickling water — but hardly anywhere else in the vicinity — the soil has been sufficiently wet to allow peat to be formed. It should be noted that this applies to the later parts of the period, the only ones represented in the diagrams.

Neither *Acacia* nor *Dodonaea*, the dominant species whose frequencies in the diagrams show that they must have grown in the summit region, are exclusively confined to the dry areas; they also occur in moderately humid forests. The evidence provided by peat formation is accordingly not contradictory to that of the pollen flora. The forests were probably not — I only speak of conditions towards the end of the period — pronounced savannah forests, even though a considerable increase in the frequence of grass pollens in these strata (see Part II, p. 347), and the occurrence of for instance *Myoporum* and *Sida* pollens, favour the view that they were of a more open type than the rain forest.

Were the displacements that made room for this less humid type of vegetation in an area which nowadays is one of the wettest places on earth — the precipitation is in some years as much as 14,000 mm — horizontal or vertical? The answer is probably not of the type of either—or, but rather of both—and. In view of the wide vertical range of these species, unequivocal evidence of a vertical displacement cannot be obtained by pollen-floristic means. The frequencies of pollen types of Group III (species from lower altitudes) are moreover too low to justify any conclusions in this respect. Nevertheless, such displacement has undoubtedly played the decisive role in this connexion. The internal conformity of the diagrams from plant-physiognomical points of view, in conjunction with the development of Period III, which apparently can only be explained by a vertical displacement, render this interpretation possible. It must be remembered (see p. 42) that *Acacia koa* may form a forest between the rain forest and the typical subalpine park land consisting of grasslands with scattered stands of *Acacia, Sophora chrysophylla, Myoporum sandwicense, Chenopodium oahuense*, and several other species also found in the pollen flora of Period I. It is more than likely that the summit parts of W. Maui (and the corresponding levels in the other islands) were covered by subalpine forests before peat growth started in this and similar localities. The general bearing of this conclusion will be dealt with below. How far down these forests extended is not known. During the later parts of the period they seem not to have occurred as low as in the 1300 m level (see Diagram 81, discussed under Period III).

As regards the constituents of the raised bog communities, they cannot, on the other hand, have been lacking in the islands before the end of Period I. This is evident from an examination of their relations outside this group of islands. Most of them — including *Oreobolus furcatus*, the most important peat former — are endemic. As Skottsberg (1940 d, p. 660) has also pointed out, this characteristic set of types cannot conceivably have developed in the short period of about 10,000 years.

Where, then, did these species occur during Period I or similar times? The raised bog communities may have occurred at lower levels, even though little is known for certain about the rainfall there before the end of the period. Peat growth appears to start earlier in the lowest bogs than in those of higher elevations but this does not say anything about conditions during the previous culmination of Period I. The bog species may also have been growing without leaving peat — in communities or singly — not only in the rain forest, but also outside this in odd places where the local climate was favourable. Reference may here be made to Rock's finds of bog plants on the steep, fogswept walls of Kaupo Gap in the crater of Haleakala, East Maui (see p. 68 above).

PERIOD II.

This period introduced considerable changes in the Hawaiian mountain vegetation.

Taking the forests first, the dry subalpine forests and the moderately humid transition types were pressed back by the rain forest, which became dominant in all areas examined. During the culmination of the period, its share in the total quantities of tree pollens (as grouped in the diagrams) as a rule exceeded 90 %, and in some localities, especially in the lower ones (Kauai and Molokai), all the tree pollens in the analyses derive from rain forest representatives.

But the changes were not confined to the forests. In all the raised bogs examined, except the few in which peat growth started at the very end of Period I, the peat deposits began to grow in this period, even though the rates of that growth indicate considerable local differences, which will be touched upon later. The raised bog vegetation now characterizing the landscape on the peaks and ridges in the higher parts of present montane belt — especially on W. Maui — is probably no older, or at any rate not much older, than Period II.

The frequencies of pollens and spores that belong to herbs and shrubs also show many changes; some of these have been dealt with in the preceding parts of this work (see e. g. *Sanicula*, Part II, p. 245). A closer evaluation of the N(on)T(ree)P(ollens), particularly those of the mire communities, have had to be excluded from the scope of the present investigation for the reason that no corresponding study of the recent vegetation has so far been published.

On the other hand, raised bogs may have occurred in Period II in places from which the peat deposits have since disappeared. Berggren's find of *Oreobolus* on the slopes of Mauna Kea in 1875 (see Chapter III: C: 4: f) is suggestive, even though it is not possible at present to say anything of its probable history in that locality.

The growth of the forests and the development of the peat deposits during this period display a number of common features in their complex wave-like course of development. These will be dealt with below.

The diagrams give some idea of the most important rain forest tree successions, and — although it has not been possible to identify the species of several genera from their pollens — this is one of the more important results of the investigation, as well as a good criterion that the general conclusions drawn regarding the displacements of the vegetation belts and their causes are correct.

Irrespective of the finer zone divisions, the general outline of the curves in the diagrams gives us the following information. Diagram 81 is particularly illustrative.

In the localities so far examined, the silvi-historical milieu during Period II seems to be the higher parts of the montane rain forest. Rock, for instance, has pointed out (1913, p. 35) that the rain forest (exclusive of the transitional belt towards the next higher belt) becomes more uniform with increased elevation, and this relative uniformity is obvious in the fossil pollen flora, which contains very little of the wealth of species of the lower rain forest sections; the high frequencies of *Elaeocarpus* and *Zyzygium*, which might be expected there, are also absent (see Selling 1947). The curves of Group III (lower levels) are still exceedingly weak; that that Group is occasionally missing at the culmination of the period is not in itself evidence of the rain forest belt having been raised, but is probably, in so far as anything at all can be concluded from these low frequencies, rather due to the increased humidity.

The most important rain forest constituents are *Metrosideros, Myrsine,* and *Cheirodendron,* as well as *Cibotium* and *Coprosma* (+ *Pritchardia*) and occasionally — about the middle of the period — *Pelea* of Type II. Rock (1913, p. 35) also says in his description of the forest in the island of Hawaii (where the zone of maximum precipitation is depressed, however, in relation to the lower islands) that »from 3000 to 5000 feet elevation three species of trees, *Suttonia* [= *Myrsine*] *Lessertiana, Cheirodendron Gaudichaudii* [= *trigynum*] and *Metrosideros polymorpha,* are the principal ones». He says the same of Maui (l. c., p. 67—68); on the first-named island the upper limit is actually above the 5000 ft level (l. c., p. 36).

The mutual relations of these three most important species of forest trees when the humidity changes have not been discussed in literature. Hall (1904) certainly says that *Metrosideros* is always found where the rainfall is greatest, but does not mention the others. The diagrams show, however, that *Metrosideros* actually attains its highest frequencies just at the culmination of this rain forest period; its curve is the nucleus round which those of the other species of the main diagram are grouped. This culmination was most likely characterized by particularly continuous, and perhaps also heavy, tradewind rains. The *Pelea* occurrences appearing mainly at the time of this culmination, or just after, are not unlikely to be due to the same climatic cause; several species are common constituents of the wettest forests today (see Part II, p. 240). Rock's statement (1913, p. 56) may be also repeated here: »They like heavy, gray, loamy soil, where water is often stagnant, forming small pools all the year round».

Next, the diagrams disclose a tendency of the *Myrsine* curves to rise both before and after the *Metrosideros* culmination. Here, as before, minor fluctuations are disregarded. Counting from the middle of the period, we find the maximum *Cheirodendron* values outside the *Myrsine* culminations. This succession of *Cheirodendron* → *Myrsine* → *Metrosideros* would seem to parallel an increasingly pronounced anti-cyclonic precipitation (trade-wind rains), and may perhaps be correlated to its increasing continuity. In forest areas where conditions correspond to those obtaining at the beginning and end of Period II, *Cheirodendron* is thus ± dominant in relation to the other leading forest trees. Such conditions may be assumed to have obtained until quite recently, or are still obtaining, in these districts (see the most recent part of Period III). This is of interest to the interpretation of one of Lyon's observations (1919, p. 3). He included this species in his theory that the Hawaiian forests are doomed on account of their inability to subsist on old soils, and found that it »shows evidence of more tenacity in our old soils than does the general run of native trees». This observation might possibly indicate a transitory climatic favouring of the species, such as had previously led to a strong increase in its frequency. I will briefly revert to the question of old soils on p. 126.

The said tendency of the *Cheirodendron* curve is particularly well marked in Kauai and Maui. The species is still playing a great part in the forest at the rim of Vainiha Valley, Kauai, as well as in the small forest stand on the very summit of West Maui (first described by Rock 1913, p. 79), and particularly large occurrences in E. Maui are mentioned by Rock (see Part II, p. 239—240). We do not yet know the cause of this and other peculiarities of the Molokai diagram, which seems to reflect more stable conditions than have been found in the other localities. The net of observations of pollen spectra, as well as of recent precipitation, must be extended before this point can be further elucidated. It should be noted, however, that the largest peak of the humification curve in Molokai (Ser. 1: F) is accompanied by the largest peak of the *Cheirodendron* curve.

There is another curve which — like the *Cheirodendron* curve — shows maximum frequencies at the beginning and end of the period in Maui, viz. the *Coprosma* curve; so does the *Pritchardia* curve. The two combined are shown by a dotted curve in the A diagrams, in order to indicate the precision with which the maxima of this summation curve appear; in this case there can accordingly be no question of their being due to merely local influences (see Part II, p. 316), with the possible exception of sample 60:264. I have said above that at the present stage it is impossible to say with any certainty whether these *Coprosma* species were trees or shrubs, and have therefore preferred to discuss the succession phenomena of this curve separately here. Rock mentions that the undershrub in the uppermost part of the forest behind Naalehu, Hawaii, is mainly composed of *Coprosma* and species of some more genera (1913, p. 36), but on the other hand he includes this species among the commonest forest trees in the E. Maui rain forest described in l. c., p. 67—68.

In the general series of successions outlined above, the *Coprosma* culminations seem on the whole to fall between those of *Myrsine* and *Cheirodendron*. The *Coprosma* maxima take up no fixed positions in relation to the summation curve of the B diagrams (xerophytic and ± mesophytic species = Group I). They quite naturally vary with the distance of the boring stations from the general rain forest zone, where *Coprosma* is abundant. In localities essentially differing in this respect, the maxima accordingly mark metachronous levels. The curves of Group I and *Coprosma* synchronize fairly well during the culmination of Period II. At that time the localities concerned were situated so relatively far from the respective centres of dispersion that when these advanced none of them reached the vicinity of the station point. When the »*Coprosma* zone» had once been reached or passed, this simple congruence disappeared. In the Maui localities these »large» maxima of the *Coprosma* curve are quite close to the ascending part of the Group II (*Chenopodium*) curve, constituting relatively good indications of the transition stages I—II and II—III (more particularly the latter).

In the diagrams from Waialeale (90) and from Molokai (1) the top frequencies of the *Coprosma* curve were only reached in Period III; the localities seem never to have passed any pronounced *Coprosma* stage at the end of Period II. These two diagrams have also other features in common which cannot yet be satisfactorily explained in detail. Among these are the relatively high *Metrosideros* and *Coprosma* frequencies (and the relatively retarded *Myrsine* frequencies) on either side of the culmination of Period II; The F (= humification) curves have much in common; the peat growth was much steadier than in the corresponding sections elsewhere. Features which might elsewhere be expected to represent a boundary (*Coprosma*) zone of the rain forest have for a long period been combined here with others which rather indicate a more even precipitation. This apparent dualism might possibly be confined to areas where the vegetation belts are more compressed or areas in which the trade-wind rains have been fairly well supplemented by cyclonic precipitation; this is only a working hypothesis. It is also possible that the ecology of the leading *Coprosma* species in Molokai is somewhat different (cf. below). Be that as it may, the relatively ample representation by the middle of the period of *Chenopodium* in Molokai seems almost inexplicable at our present state of knowledge, unless one assumes a relative proximity to the vegetation on the leeward sides also at times when the vegetation belts were not depressed and the trade-winds dominated in the Pepeopae region. This effect on the leeward sides might possibly have been promoted by a rise in the lower limit of the cloud belt at the middle of Period II (see Fig. 28: C). Nothing of this sort can yet be definitely proved, however.

In connexion with the *Cheirodendron* discussion above, I emphasized that in the Molokai diagram the largest peak of the humification curve (= the F diagram) is accompanied by the largest peak of the *Cheirodendron* curve. *Coprosma,* on the other hand, seems to have its largest culminations in less extreme rain-forest periods than those of the *Cheirodendron* culminations. It is then of interest to note that the next largest culminations of the humification curve in Molokai are accompanied by *Coprosma* peaks and that they flank the said *Cheirodendron* peak. Moreover, this group of culminations, partly accompanied by *Chenopodium,* seem to correspond in a general way to the fairly high frequencies of *Chenopodium* on the other side of the largest and central *Metrosideros* peak of the diagram. Rhythmically, these groups form counterparts, though the silvi-historical result in each case has been different.

A few words remain to be said of the place of *Cibotium* in the succession. In most of the diagrams the curves show no striking peculiarities. Many of the variations occurring give the impression of being fortuitous, and seem to have little to do with the changes in the forests outlined above. The amplitude of the relevant species is moreover wide (see Part I). They are common in the under storey of the rain forest in various altitudes (Pls. 6 and 10 B). Nor would *Cibotium* have been included in the 100 % sum unless Diagram 81 (to some extent supplemented by Diagram 84) had shown that at certain stages this genus must have appeared as an independently area-forming element of the post-Glacial forests; *Cibotium* occasionally dominates in the fossil flora, with values close on 50 %. This indicates conditions like those now found on the NE side of the island of Hawaii, where extensive areas are covered by *Cibotium* forests (see Part I, p. 43—44, and Pls. 10 A and C, 11 A, and 20 A of the present paper).

What can have caused the high frequency of *Cibotium* in the past?

To begin with the fossil finds in Diagram 81, we find that their culminations are symmetrically arranged in relation to the highest value. They are, however, not synchronous with the culminations of the *Metrosideros* curve. Each of them seems to correspond to the beginning of a *Metrosideros* culmination. This would imply that during a few periods, apparently characterized by a transition towards particularly wet conditions and regularly spread over the post-Glacial, conditions have been unusually favourable to the growth of *Cibotium*. This applies at least to Kauai. We may ask if the particularly rich (recent) occurrences in the island of Hawaii can be due to a similar cause. The lack of similar frequencies in the intervening islands may not be fortuitous. Ripperton (1924, p. 3) emphasizes that the genus is found »on nearly all the mountains, but occurs in dense forests only on the islands of Kauai and Hawaii». There is a slight trace of a similar tendency in Molokai (Ser. I: 45—46), in the interval between the largest peak of *Cheirodendron* and the largest *Metrosideros* culmination, but the *Cibotium* frequencies here do not reach higher values than 10 %.

In a study of New Zealand conditions, Pope (1924) found that pure stands of tree-ferns are fairly frequent in ordinary rain-forests, but that on cleared land they occur mainly as a first stage in the natural forest rejuvenation; settlers at Ship's Cove, Marlborough, N. Z., tell how tree-ferns came up where Captain Cook once sowed wheat. The fronds of the growing young tree-ferns suppress any foreign growths for a considerable time, even after they have been dropped, thus maintaining the purity of the stands. The same thing seems to have happened in Hawaii, where *Metrosideros*, with its peculiar mode of establishing itself in a closed community (see, for instance, Hall 1904, p. 13; Rock 1913, p. 333, Pl. 131; 1917, p. 23—24, Pl. III; Judd 1936, p. 111, with ill.; cf. Carse 1902, p. 361), is their only large scale successful competitor: the seeds of *Metrosideros* germinate on top of the tree ferns, the young plant sends down aerial roots to the ground, and in the long run the epiphytic tree kills its supporter. The natives have an old saying that the tree fern is the mother of the ohia lehua (= *Metrosideros*).

We may, in fact, ask whether the unusually high *Cibotium* frequencies are due to some natural clearings of forests in the immediately preceding periods, and whether *Cibotium* has given place to *Metrosideros* owing to a succession of the kind described above.

I think that the hypothesis of natural clearings cannot be dismissed. The question is whether these were due to heavy winds or unusual droughts (or both) during part or some parts of the year, or if other factors — e. g. increased temperature — have had any influence. Two of the said culminations have occurred towards the peripheral parts of Period II, when the cyclonic tendencies were more pronounced, but the largest of them all was in the most highly developed stage of the period, when anticyclonic conditions were presumably particularly prominent. Heavy winds seem to be mainly associated with cyclonic situations; as pointed out by Hillebrand (see p. 32 above), they are »heftig genug, um alte Bäume zu entwurzeln», and may on occasion develop into actual cyclones. Strong, often destructive, trade winds are, however, mentioned by Hillebrand (1888 a, p. 305) and Fornander (1920, p. 534 and 476); it should be added, however, that NE winds of cyclonic situations (see Chapter III: A: 1) might have been mistaken for trade winds.

Such clearings may accordingly have been the result of strong winds. Nor need these have been exceptionally strong, seeing that the root systems of many rain forest trees, for example *Metrosideros*, are shallow (see Hall 1904, and others).

But this does not solve the question. Diagram 81: F shows that the peat is very unevenly decomposed; its symmetrical relations are of the same general kinds as those of the rain forest species. It must be noted, however, that the humification curve cannot be quite synchronized throughout with the curve of any rain forest species. What is interesting is its good agreement with the *Cibotium* curve. The three highest *Cibotium* culminations have their exact counterparts in the humification curve. The latter has three very distinct double-topped culminations. The *Cibotium* peaks fit exactly with the first peak of each pair. The second peak of the same pair also corresponds to a *Cibotium* peak, but this is much less pronounced. For reasons connected with sampling density and methods of preparation nothing can at present be said with any certainty of the interrelation in size of the two peaks in each peat curve pair; of these, however, the middle group seems to be stronger than those on the flanks. This, too, corresponds to conditions in *Cibotium*.

This puts the hypothesis of uprooting by storms in the background, even though it cannot yet be entirely dismissed. The *Cibotium* culminations reflect changes that are not limited to the tree layer. The organic soils of the mires are also affected. The peat curve reflects complex interferences of constructive and destructive factors, probably represented here primarily by humidity and temperature. After a comparison with the *Metrosideros* curve, one would in this case be inclined to regard the more strongly humified layers as expressions of relatively pronounced either drought or warmth (or both), for if the insignificant growth had been due to excessive precipitation, the tendency would hardly be reversed at the time of the highest *Metrosideros* culmination (Ser. 81: 351—352).

If this interpretation is correct, the montane rain forests would have become more open in some places during certain relatively short parts of Period II, possibly owing to reduced relative humidity (drought, increased warmth, or both), with or without fairly heavy storms uprooting the forests. Dense stands of *Cibotium* would then have grown up in these clearings. The climate has then again rapidly become more humid, and everything points to *Metrosideros*' having gained the upper hand of the fern forest in the manner outlined above on the basis of present day conditions.

After this, it seems worth while to consider a question which was mooted earlier in this chapter, viz. why the fern forests are so abundant just on the southernmost island, Hawaii. It should be seriously investigated whether these recent fern forests are not developmental facies of the kind found in Kauai in the post-Glacial Period II. Droughts such as are known to have occurred at intervals in this region (see for instance Hall 1904, p. 19, Guppy 1906, p. 212) might be suspected of having at least some effect in this respect. Judging by the occurrences of *Sphagnum* (such as we saw them during our brief visit in 1938: Bartram 1942, p. 322), it would on the other hand appear as if the climate were at present becoming more moist in this region. There is accordingly some possibility of conditions in Kauai in bygone times being duplicated here. The question will no doubt be solved by pollen statistics, however. The above suggestions will therefore suffice to draw attention to the problem.

PERIOD III.

Strata from this period were found in all the islands. In Kauai, Period III is thus represented in Series 81, (84), 87, and 90, in Molokai in Series 1, in W. Maui completely in Series 57, 60, and 78, and partly in Series 34, 35, 37, 71, and 80.

Conditions reminiscent of Period I appear in this period. The rain forest was partly retreating from previously invaded areas. Judging not least by the conditions governing peat formation, the changes were not so great as in Period I. The frequencies of pollen types of Group II rise as high as 80 % in Series 34 (W. Maui), i. e. higher than in Period I, but it must be remembered that this time the curves are not derived from the same species. Then it was *Acacia* and *Dodonaea*, now it is *Chenopodium*. If we make the experiment of excluding *Chenopodium* from the 100 % sum of the main diagram, we get *Acacia* and *Dodonaea* values which barely come up to those in the last stage of Period I (Fig. 26). This is possibly of some interest in connexion with the interpretation of the *Chenopodium* occurrences to which I shall revert below.

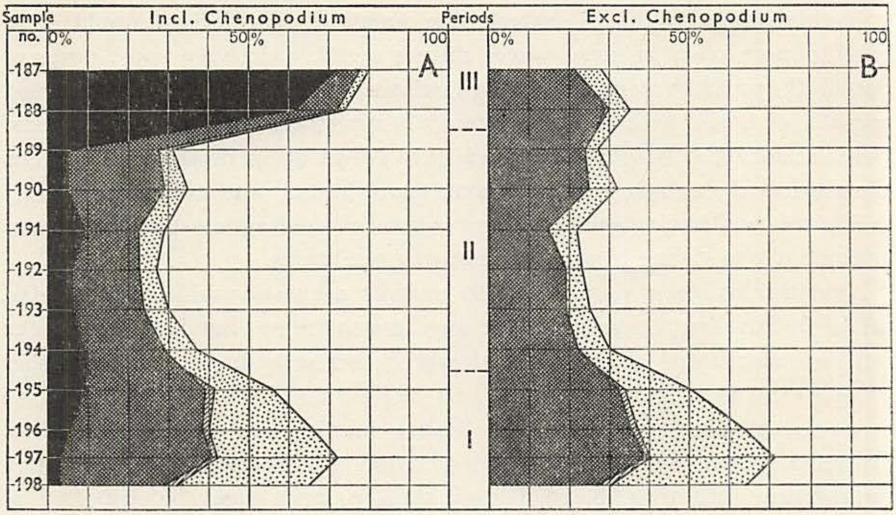

Fig. 26. Detail of the B diagram from sta. 34 (West Maui, near summit; Pl. 24). Values with *Chenopodium* included in (A) and excluded from the 100 % sum (B) for comparison between Periods I and III. Black: *Chenopodium*. Cross-hatched: *Dodonaea*. Ruled: *Sophora*. Dotted: *Acacia*. See further the text.

The diagrams from Kauai and Molokai cannot be used for such comparisons, as Period I is not similarly, or not at all, represented in them.

There is then the question of what *Chenopodium* implies regarding environment. Do the rich occurrences in the higher parts of W. Maui represent a vegetation near or immediately above the inversion limit or is another interpretation more likely? In 1947, p. 90, I dealt with the information available in literature, from which we may conclude that the species belongs to the lowlands, to the lower and middle leeward elevations, and to the subalpine belt up to 2500 m altitude, and that it is probably most frequent around and below the 2000 m level. Also that it is not a rain forest species.

Not being satisfied with this too general result, I asked Professor H. St. John of the University of Hawaii, Honolulu, for more detailed data. He had the kindness to map the distribution of the species in these islands (Fig. 27; the list of localities is published below) and to prepare the following account, based on his own field experience as well as herbarium material and other sources:

»*Chenopodium oahuense* is abundant and characteristic of one of our driest vegetational zones, Zone B of Ripperton & Hosaka (Hawaii Agric. Exp. Sta., Bull. 89. 1942). The plant occurs mostly on rocky soils on the dry leeward sides of the mountains, though there are a few localities on the windward shores. However, at these places, it is relatively dry, as on Oahu: from Moku Manu, Popoia, and Waimanalo; as on Lanai at Maunale and Kaohai; as on Maui, near Makawao. These windward localities are not

> exceptions as they accord with the details of our microclimatic zones. But on Hawaii, there is an unusual occurrence, for the *Chenopodium*, along with *Argemone alba* var. *glauca*, occurs in the Mauna Kea Saddle from Humuula towards Waikii. Though cold, it is there barren and dry and these xerophytes look very much at home, as they do in the arid soils near the shore. This locality is on the lee of Mauna Kea, remote from the wet forests. All the other localities (except the similar one on Haleakala), including all extensive areas are at low elevations at from 0 to 3,500 feet elevation. They grow in the zone characterized now by *Opuntia megacantha, Leucaena glauca, Heteropogon contortus*, etc. This lies below the dry forest zone, and far below the wet forest zone. It receives 20 to 40 inches of rainfall annually, poorly distributed throughout the year. On Oahu the *Chenopodium oahuense* is most abundant on the drier, southern end of the Waianae Mts., a region so parched and sunburnt that it is treeless.
>
> On West Maui there are few records, the one at Lahainaluna at 500 ft., the one at Hanaula near Waikapu, being on the low dry foothills.
>
> On Kauai there is but a single record [in the Honolulu herb.; cf. below], the species being collected at Kaholuamanoa (Kaholuamanu) at the edge of the summit, 3000—3500 ft., Heller 2788. Mr. Hosaka tells me that this approach ridge is arid.
>
> On Molokai there are but two records, one on the dry, barren gulches, above Kamalo. The other on the dry shore flats at Mapulehu.
>
> On Hawaii there are two areas of occurrence, both very arid, rocky regions. The saddle area on Mauna Kea has already been discussed. The other is an area of abundant occurrence at 2300 to 3200 ft. from Huehue to Puu Waawaa, one of the barrenest areas of rough, dry aa lava on the islands.
>
> The absence of the shrub from the arid region of west Molokai and from most of the Kona shore of Hawaii is strange. On Molokai, the deep loamy soil and absence of rocky sites may well explain it. On Hawaii much of the Kona side at low altitudes is dry enough and rocky enough so that the absence of the plant is difficult to explain. I doubt if the absence is due to lack of collecting.»

With respect to the problems raised by the pollen diagrams, Professor St. John adds (spaced type introduced by O. H. S.):

> »The two high altitude localities, Mauna Kea saddle, and Haleakala Crater may represent relicts of a former general subalpine range under a drier climate. The Haleakala Crater region in rainfall and barren rocky soils is eminently suitable. The species may well have spread from or to Koapolu by the rocky arid Kaupo Gap, though it is not now known to grow there. However, the spread to or from Auahi would be across grasslands and scrub forest. The spread to or from Makawao would be across extensive grasslands and wet forests. On Hawaii the Mauna Kea saddle region is cut off from the Puu Waawaa region by a broad band of mesic grasslands, so at present there is no obvious open route of migration between the two areas.
>
> Nothing in the present occurrence of *Chenopodium oahuense* indicates any connection with mesophytic or wet areas. It occurs mostly to leeward and at lower elevations than the zones of wet forest or of bogs. Its abundance in earlier times would doubtless indicate conditions similar to the present habitat — those of deficient rainfall and dusty, arid, rocky conditions.»

A list of the localities in the windward section of the archipelago is given below. H (in brackets) = herbarium material in Honolulu quoted by St. John. I have added the material in the herbaria of the Royal Botanic Gardens, Kew (K), the Laboratoire de Phanérogamie, Museum National d'Histoire Naturelle, Paris (P), the Riksmuseum, Stockholm (S), and the U. S. National Museum, Washington (W), and the literature references. If not found in the bibliography of the present paper, these refer to the one of my 1947 paper. Some ± doubtful records have been excluded.

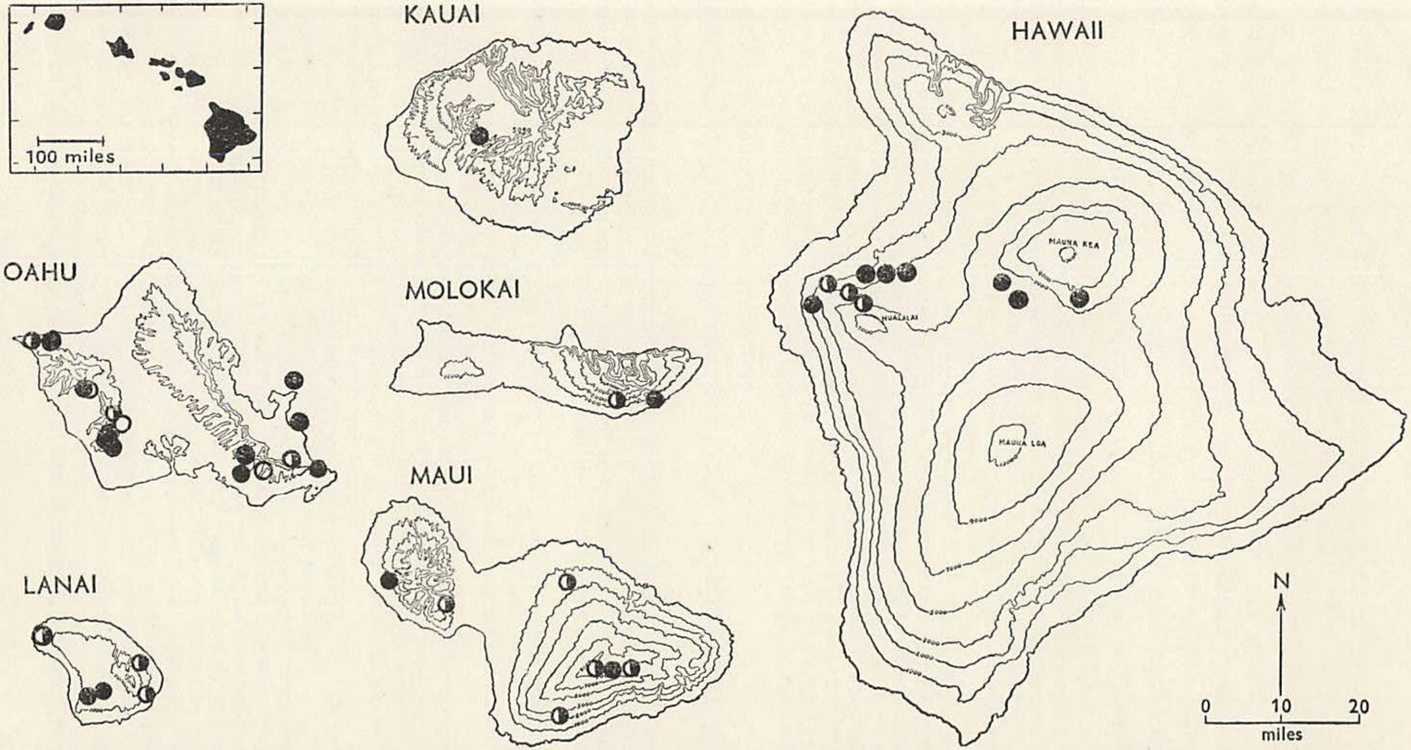

Fig. 27. Distribution of *Chenopodium oahuense* (Meyen) Aellen in the six largest islands of the Hawaiian group. ● = herbarium specimens with precise data; ◐ = do., data incomplete; ○ = localities based on field observations by H. St. John. The mass occurrence in the saddle between Mauna Kea and Mauna Loa represented by too few dots. See further the text. — Mapping by H. St. John; data from the literature added by the author.

LOCALITIES OF *CHENOPODIUM OAHUENSE* (MEYEN) AELLEN IN THE WINDWARD SECTION OF THE HAWAIIAN ISLANDS.

NIIHAU. »Oneeheow. Beechey» (K).

KAULA. »Very common and widely distributed». Coll.: 17 VIII 1932; E. L. Caum 8 (H; Caum 1936, p. 7). [Kaula is 540 ft high.]

KAUAI. Waimea. »On the edge and about the base of the tabular summit above Waimea», 3000 to 3500 ft, plentiful. Collected »on Kaholuamanoa» (= Kaholuamanu) 2 IX 1895; A. A. Heller 2788 (H, K, P, W; Heller 1897, p. 819—820; Aellen 1929, p. 125). »Waimea», 900—1330 m, weed along road, 1916; A. S. Hitchcock 14320 (W; Aellen 1929, p. 125).

W. OAHU. 2 miles W of Kawaihapai, on rocky slope near sea level, 3 XI 1929; St. John 9989 (H, P). Kealia trail, lower part, among rocks, 18 IX 1938; Selling 3841 (H, S; Skottsberg 1944, p. 364: abbreviated data). Do., 150 m alt., steep rocky slope; Fosberg 13308 (H). Puu Kalena, W side, 625 m alt., bare face of precipice; Fosberg 9262 (H). Main divide S of Puu Kalena; field observ. by St. John. Kaloi Gulch, 700 m alt., »moist forest» (remark by St. John: »It must have been raining, for only during a rain is any forest in that southern part of the Waianae Mts. to be called moist»), Fosberg 110 (H). Mauna Kapu — Puu Kuua; observed by St. John. Ridge above Kupehau, 500 m alt., dry open ridge; Fosberg 10994 (H). Palehua, 1—4 IV 1911; C. N. Forbes 1699—O (H, K). Do., 1500 ft alt., bare ridge top; Ewart 20 (H). Waianae Mts, »auf waldigen Hügeln» (no specified loc.), 21—26 IX 1872; Philipp and August of Sachsen-Coburg-Gotha n. I. 152 (Wawra 1875, p. 189: »in den Mendanabergen» only; Beck 1888, p. 58: the mts here called »Kaala-Gebirge», a name also used in for inst. Wawra 1873, p. 94).

E. OAHU. Moku Manu Island, guano covered basaltic rocks, 40 m alt.; Fosberg 14104 (H). Do., guano covered rocks 60 m alt.; Fosberg and Egler 14077 (H). Popoia Island, XI 1915; J. F. G. Stokes s. n. (H). Do., sand covered rocks, 1 m alt.; Fosberg 8892 (H). Do., coral flat, 2 m alt.; Fosberg 13298 (H). Waimanalo, no data; J. F. Rock 12929 (H). Do., dry ridge, top of cliffs, 375 m alt.; Fosberg 13167 (H). Manoa-Palolo Ridge; field observ. by St. John. Nuuanu Valley, at some distance from the Pali, c. 1200 ft, 26 VI 1831; F. J. F. Meyen (type of the species; Meyen 1835, p. 127, with notes on associated species). »Honolulu», 1855; E. Jardin 26 (P).

MOLOKAI. Mapulehu, open plains [dry shore flats]; Rock 6171. Dry gulches above Kamalo; Rock 7029 (H, K). Poholua (a locality that cannot be located); Forbes 106-Mo (H).

W. MAUI. Hanaula (near Waikapu on the low dry foothills); Forbes 121-M (H). Lahainaluna, 500 ft, VIII 1910; Forbes s. n. (H, K, P).

E. MAUI. Koapohu (»Koopahu» in P) (remark by St. John: »This locality name is unknown now. I have mapped it by inference from associated data in Forbes' field notebook.»), 9 XII 1919; Forbes 1770-M (H, P). »On Mauna Haleakala, at the elevation of 6000 feet», 1841; Ch. Pickering and W. Brackenridge (Pickering 1876, p. 484). Haleakala Crater; Forbes 300-M (H) and 1098-M (H), also observed by St. John. Auwahi (S slope of Haleakala), 18 III 1920; Forbes 2013-M (H, K).

LANAI. Maunalei Gulch; St. John 18814 (St. John: »From my notes, this number not readily at hand now»). Kaohai; Munro (H). NW edge of Palawai Basin, 1350 ft alt.; Munro 704 (H). Miki, 1200 ft alt., pasture weed; Munro 126 (H) and 524 (H). »Lanai, west end, open grassy ground, 1916; A. S. Hitchcock 14717 (W; Aellen 1929, p. 125).

HAWAII. »Ins. Owhyhee, ad montem Kaah» [= Manua Kea], VI 1825; Macrae (K). Mauna Kea, »in the pastoral district, to the elevation of 9000 feet, the stem shrubby and sometimes two inches in diameter», 1841; Pickering and Brackenridge (W: no detailed data; Pickering 1876, p. 484; Aellen 1929, p. 125). Manua Kea-Humuula trail, 8250 ft, C. E. Hartt and M. C. Neal 767 (H; Hartt and Neal 1940, p. 264). E of Pohakuloa, 6000 ft; Bryan s. n. (H). Between Humuula and Waikii, 6000 ft; Neal 686 (H; Ibid., p. 256: in pastures). Great central plain near Humuula, 6600 ft, in Plateau Parkland, *Sophora-Myoporum* association (Robyns and Lamb 1939, p. 266, Fig. 24). Do., along the road to Humuula, 5500 ft, growing to a height of 15—20 ft, below the *Myoporum-Sophora* association, associated with bunch grass (Ibid., p. 263, 266: Fig. 25, and 291: Fig. 42). »Slope of Maunakea in Hamakua, 6000 ft» [»upper woods»], tree 20—30 ft high; W. Hillebrand 409 (K, recd VII 1865; cf. Hillebrand 1888 b, p. 380). Hualalai; Mann and

Brigham 315 (H; no loc. in Mann 1867, p. 199). Do., 1859 flow, 2300 ft, on old lava, very dry; Fosberg 10168 (H). Huehue, 3000 ft; Meebold (H). Vicinity of Huehue near main road, lava fields, abundant, 11 IX 1938; L. M. Cranwell, O. Selling and C. Skottsberg 3200 (H, S; Skottsberg 1944 b, p. 264). Between Lind's and Puu Waawaa (near Huehue), 26 IX 1926; Skottsberg n. 1948 (H; Skottsberg 1936 b, p. 107). Puu Waawaa, 9—14 VI 1911; Forbes 19-H (H, K, P). At the foot of Puu Waawaa hill, c. 800 m, open forest, rare, 26/9 1922; Skottsberg 672 (S; Skottsberg 1926, p. 228). Puu Waawaa, 3000 ft alt., a small tree and very plentiful (Rock 1913, p. 50).

Menzies' collection (K, type of *Ch. sandwicheum* Moq.) says only »Sandwich Isles». The labels of Baillieu s. n. (P), Gaudichaud [Voy. Uranie] 26 (P), Gaudichaud s. n. (P), and Kastalsky (P, ex hb. Petropol.) are no more detailed. Four Oahu collections lack specified localities: Macrae's from May 1825 (K), Andersson's from 1852 (S), Remy 208 and 210 from 1851—1855 (P). Pickering (1876, p. 421) says only: »On the arid leeward portion of Oahu»; the U. S. Expl. Exped. specimen in Paris (Oahu or Hawaii?) lacks locality. Hillebrand 460 (K) and Remy 209 (P, S; Mann 1867, p. 199; cf. Remy 1862, p. XXIII, quoted in Part II, p. 90) come from the island of Hawaii.

The idea that the mass occurrence of *Chenopodium* in West Maui might represent the lower portion of the subalpine belt, i. e. the region immediately above the inversion limit, can be better judged on the basis of the detailed data presented above.

That the rain forest must have retreated in the higher levels of West Maui is obvious, not least from St. John's account. The suddenly increased influence of *Chenopodium* in all the diagrams from there cannot be exclusively due to abundant pollen production in distant localities, in spite of the pollen being no doubt easily dispersed by the wind. The species must have covered a considerable portion of the open areas in the present mire districts, at least those of higher elevations, or their immediate vicinity. However, seeing that the species is found right down to sea level (viz. on the leeward sides), a consideration of its altitudinal amplitude alone will settle nothing as regards the question of a vertical displacement. It would seem that the changes might as well have been mainly horizontal, due to a reduced influence of the trade wind rains in a ± stable altitude belt.

The great rarity of the species in the present vegetation on the leeward sides of Maui is remarkable. Only two localities are known in West Maui. If a leeward vegetation had been advancing in the montane and inferial belts in Period III, one would expect to find more of *Chenopodium* in it at the present day. The mass occurrence especially between Mauna Kea and Mauna Loa, Hawaii (see above), on the other hand, supports the view that in suitable localities in our days, too, the species occurs in stands as large as those apparently reflected by the pollen diagrams.

This recent mass occurrence appears to be of particular interest to the present discussion. When, therefore, I heard that Professor C. Skottsberg had visited the region in January, 1948, accompanied by Dr. F. Fagerlind, I asked him for a close description of this locality, and he kindly in response to my request revisited it in April. Below I have summarized his account; it refers to Pohakuloa Camp, situated 1970 m above sea level on the eastern slope of and about 50 m below the saddle of the pass between Mauna Kea and Mauna Loa. The spot is relatively dry. H. Stearns and Macdonald (1946, p. 216) state that the annual precipitation at Pohakuloa is 31.78 inches. Frost is not unusual in the winter; the night temperature at the beginning of April was + 4° — + 5° C. Skottsberg came up from the Hilo side along the Cross Road or »Saddle Road», as it is also called:

> »*Chenopodium* first appears here and there a good way below Pohakuloa, but becomes more common a few miles before reaching that place (i. e. near Humuula), and in the vicinity of the Camp it is so dominant that the whole area looks blue-gray-green (Pl. 22 A). Along the road the *Chenopodium* vegetation extends at least 8 or 10 miles NW-wards beyond Pohakuloa; on the slope of Mauna Kea it seems to extend a little above and below the road, but increasingly scattered, and disappears completely some distance outside the fence of the forest reserve.
>
> The ground at Pohakuloa is old lava, largely covered by a usually brown or browny-yellow soil produced by weathering. There is little or no slope. The vegetation is park-like, trees — in groups or solitary — with open soil between them. The small stands are occasionally fairly dense, but often consist of only 3 or 4 trees, and sometimes the trees are scattered over a slightly larger area. The trees (often of irregular growth) are not very high, 7—8 m being generally the maximum, but many are much smaller.
>
> *Chenopodium*, which is extremely variable in habit and leaf size, has always — even though it mostly looks like a shrub — a short main trunk, and pure tree forms are also met with. Flowering specimens are generally 1—2 m high, but heights of 3 m are by no means unusual [cf. Robyns and Lamb 1939, p. 263: 15—20 ft]. The species may be covering, but grows more sparsely towards the open tree-less sandfields, where it disappears ± completely and *Eragrostis atropoides* becomes all the more common. Grasses and annual weeds are prominent in this area. They usually form a border around *Sophora-Chenopodium* groups.»

Ten sample plots were laid out, five (I—V) around trees or groups of trees, five (VI—X) in the open, tree-less space between the tree groups. The analysis gave the following result:

TABLE II. CHENOPODIUM-VEGETATION IN FOREST RESERVE AT POHAKULOA, HAWAII (c. 1970 m alt.).

(I—V near trees or groups of trees, VI—X in areas without trees; anal. C. Skottsberg 4/4 1948.)

	I	II	III	IV	V	VI	VII	VIII	IX	X
Chenopodium oahuense	**3**	**3**	**3**	**4**	**5**	**2**	**1**	**5**	**4**	**5**
Myoporum sandwicense	1	—	4	—	5	—	—	—	—	—
Sophora chrysophylla	2	2	1	3	3	—	—	—	—	—
Eragrostis atropoides	—	—	—	—	—	1	3	—	2	1
Erigeron canadensis	—	—	—	—	—	1	1	1	1	1
Lepidium virginicum	—	—	—	—	—	2	2	3	2	2
Senecio sp.	—	—	—	—	—	—	—	—	2	1
Verbena litoralis	—	+	+	+	+	+	+	2	+	+
Bromus catharticus *Bromus rigidus* *Hordeum murinum*	patches at margin of tree group					+ (patches), or lacking				

Note: Cover degree acc. to the five-graded Hult-Sernander scale (see Christophersen 1927, p. 5). In January, 1948, also a few small specimens of *Colubrina oppositifolia* were observed by Dr. Skottsberg.

As mentioned, Pohakuloa lies 1970 m high, in the lower part of the subalpine belt. A somewhat similar place in the vertical succession can probably be assumed for *Chenopodium* in Maui during Period III, though the conditions have not been quite so extreme. The experiment which was made above (Text-fig. 26) with *Chenopodium* excluded from the 100 % sum, also seems to show that *Acacia* and *Dodonaea* do not during the corresponding period attain higher values than those which at the previous change of period represented fairly dry parts of the transition zone. This transition zone shows in general in the ordinary diagrams (Ser. 34, cf. 33, 37, and 57) a slight frequency increase for *Chenopodium* also during Period I.

As regards the *Chenopodium* curves, two features in the diagrams point to the accuracy of the above interpretation.

The first refers to the shape of the curve at the very period boundary in the Maui diagrams. The violent, almost explosive increase of the *Chenopodium* values in the highest localities in Maui is in itself suggestive of the localities having witnessed a shift of a boundary between two atmospheric layers. A boundary as sharply defined as this hardly seems to be explained by only horizontal displacement.

The other is the striking fact that the high percentage values of *Chenopodium* on West Maui during Period III has no equivalent on Molokai and Kauai. A rise can certainly be noted even there, but it is rather slight: the species in Group I never got the upper hand of the rain forest representatives in the pollen rain on the localities in the latter islands. In Molokai their share does not exceed 28 %, and the highest value in Kauai is 33 %. The Maui localities are from about 1375 to 1765 m above the sea, those in Molokai and Kauai are between 1200 and 1300 m. This seems to indicate that the really high values in the present diagrams are connected with a pressing down of the trade wind belt. Topographical differences between the islands nevertheless make the idea of horizontal displacement perhaps still seem to have at least theoretical interest: a dwindling in the influence of the trade wind precipitation could be thought to have allowed greater proximity to the leeward side vegetation in an island of Maui's more conical shape (cf. vegetation maps in Chap. III: B). A more moderate frequency increase can probably be assumed to be connected with the changes in the rain forest's part on the leeward sides. [Conditions on the leeward sides of the islands are not easily investigated because of the lack of suitable strata. The extent of the rain forests on the leeward sides in the course of time can therefore only be estimated in a very general way. The rise of the *Chenopodium* curve in the Molokai and Kauai localities show, however, that during Period III there has been an increase in the part played by the leeward vegetation in the pollen rain. Still, it is not definitely known whether this means an advance of the leeward vegetation or more luxuriant growth (irrespective of boundary shifts) due to increased cyclonic precipitation. It can be assumed that one has to reckon with both cases.]

To the list of arguments in favour of the theory of vertical displacement comes one of the most important ones: this is the evidence the *Metrosideros* curve bears on the conditions on Kauai and Molokai. To avoid breaking off the discussion too much I will not enter into details here; these I will revert to below. Of importance for the matter in question is that on the 1200—1300 m levels the rainfall seems to have increased simultaneously with the advance on the higher levels of the drier vegetation types. The high frequencies of ± xerophytic species in the W. Maui localities, especially of *Chenopodium*, apparently reflect conditions above or in association with the inversion limit, which has then become considerably depressed. The influence of the border zone does not seem to have reached as far down as the 1200—1300 m level, however. Towards the end of the period it again rose above the 1765 m level. At the present time it is not unlikely below the level it had in Period II.

Before we go over to the detailed discussions on the further development of the period and its representation on lower levels, the picture of the presence of *Chenopodium* vegetation should be supplemented on some points.

If we consider the pollens of species which are not included in the main diagrams, and confine ourselves to W. Maui, we find that Period III is characterized by a marked increase in the frequencies for certain partially subalpine shrubs such as *Vaccinium* and *Styphelia*, but the value of these frequencies as proof of regional displacement is less; they may perhaps indicate a richer scrub vegetation on boggy ground. Of interest further are the high frequencies of *Coprosma* and the exceptionally plentiful occurrence of monolete fern spores in certain (33, 57) localities during a short time at the actual transition to this period. The ratio tree pollens (Groups I—III)/smooth monolete fern spores, generally about 3/1, reaches a value of 1/135 in Ser. 57: 231. The spores do not permit of a definite determination, since they lack perispore (Part I, p. 62). Judging from form, size (largest equatorial diameter $= 46\,\mu$; aver. of 100 in Ser. 33: 162) and the thickness and slightly reddish tint (after acetolysis), the presence of *Elaphoglossum* might possibly be assumed. How these occurrences are to be explained is difficult to say. A mass occurrence in the thinning forests in the upper part of the rain forest belt is in itself not unlikely. Other explanations are possible, too. The plants may have grown in the bogs or on the cliffs below. I have not found the spores useful to check the idea of changes in the prevailing wind direction which was briefly mentioned in l. c. p.

That *Dodonaea* and especially *Acacia* this time recede in the diagram picture for *Chenopodium* cannot be wholly explained without closer knowledge of the ecology of the species. *Chenopodium* must have been especially favoured this time, possibly by the climatic conditions. The influence of ground changes in connexion with the introduction of drier conditions is more difficult to postulate. I have no proof that the species can appear on humus ground, where the changes could first of all be thought to take place. In any case, it is obvious that a similar mass occurrence as on W. Maui has not occurred at the transition between Periods I and II, though a frequency increase even then can be traced on the respective localities. The rapid rally within the district has possibly been obviated by the fruit not improbably being spread by granivorous birds (see Guppy 1906, p. 284) and that its production on a large scale is effected much more quickly than is the case with for example *Acacia*.

As regards *Chenopodium*, it remains to be explained how these plentiful occurrences, which certainly do not belong to the rain forest, can make their appearance with a by no means scanty peat growth in the strata also on higher levels. The peat on the summit itself actually seems to have grown more rapidly than before. The lowest bog (c. 1375 m) exhibits during this period the same intensity of growth, marked by a distinctly paler colour of the peat.

If a lowering of the temperature has retarded the disintegration of the plant remains cannot yet be settled. From the peat formation it would seem indisputable that the locality has not been completely dry. Perhaps the humid patches have been ± local. One could imagine a relatively diffuse zone of frequent mountain fogs near the upper, uneven boundary of the cloud belt (see Pls. 1 and 2) in which these exposed parts have received more moisture than others; within these districts the peat formation could have continued. But at the same time it seems reasonable to assume that the moisture has not been equally distributed over the year but that periods of drought have occurred. *Chenopodium* could thus be thought to exist, on bare rocks, etc., not far from the peat strata in question. I have, as mentioned, no proof that the species can exist on a (periodically or consistently) dry peat surface. Perhaps the somewhat slower rise of the *Chenopodium* curve in the lower Maui localities has some connexion with the fact that these dry periods there — nearer the cloud belt centre — have not occurred with quite the same frequency. It is also possible that the inversion limit was less well developed than at present.

Before we deal with that part of the period which leads over to present day conditions, we should review those on lower levels. These are represented first by Diagram 81 (Kauai: Kilohana, 1220 m alt.) and 1 (Molokai, 1214 m); Diagrams 84 and 87 (Kauai: Kilohana) are too rough for the purposes in question. Diagram 90 (Kauai: Waialeale) seems to occupy a position between the diagram groups from Maui previously discussed and the group now named. This also seems natural: the locality is situated on the leeward side, protected from the exposure to the trade wind which characterizes the diagrams from Molokai and Kilohana.

The regional parallelism, which lies in the fact that these lower localities record an increase of *Metrosideros* values at the same time as *Chenopodium* assumes dominance on the higher localities, has already been pointed out above. *Metrosideros* marked the culmination stage of the rain forest conditions characterizing Period II, and there is no reason to interpret the *Metrosideros* culmination during Period III otherwise. Everything points to that we have to do with a marked increase of precipitation (probably trade-wind rains) in the lower bog localities, especially that at Kilohana. The connexion with the *Chenopodium* curve in higher localities is not evident from the shape of the same curve in the diagrams from the lower localities without considering the local conditions. The *Chenopodium* curve certainly rises somewhat also in these diagrams, but the curves do not agree with those from West Maui. There we had two clear maxima on the *Chenopodium* curve. These maxima seem to be developed in Diagram 90 (Waialeale). Here they are accompanied by the largest *Metrosideros* peak since the culmination of Period II, whereas in West Maui the largest of the flanking peaks occurs just before the rise of the *Chenopodium* curve (see for inst. Diagrams 71 and 80). It will thus seem that the zone of maximum rainfall has been pressed down. If we continue towards Kilohana, the *Metrosideros* peak of the Waialeale diagram seems to correspond to the very strong *Metrosideros* culmination near the top of Diagram 81 and not unlikely to the weaker culmination in Diagram 87 (Samples 477 and 478), too. The following *Chenopodium* culmination would thus be the same in both diagrams. The differences in other respects between these two diagrams may seem greater than they actually are, owing to differences in sample intervals. At any rate it seems that the *Chenopodium* culminations are suppressed here by the (at least broadly speaking) simultaneous *Metrosideros* culminations. The exact connexions with the Maui curves are accordingly difficult to establish, and the queries in the diagrams cannot yet be avoided. This holds true especially of the Molokai diagram (1), where the location of the period boundary is still more uncertain. It has had to be left as it is, pending further investigations. Further discussion of this location and its bearings seems rather unnecessary at the present state of knowledge; detailed studies will provide the much to be desired facts. It is important, however, to bear such regional differences in mind when interpreting Hawaiian diagrams from widely different altitudes. *Chenopodium* probably showed an increase only on the leeward sides of the lower islands (note the rarity of the species in these islands at present). On the windward sides (exposed to the trade wind) the precipitation increased, and with the consequent local increase of *Metrosideros* influence, the *Chenopodium* pollen carried from afar has not been able to compete, despite its own increased frequency.

The increase of trade wind precipitation, especially on Kauai, can be thought to be attributable to at least two causes. One is temperature changes; though secular changes cannot be deduced from the variation by seasons, Wallén's account of this variation in Chap. III: A: 2 may give some hints as to the possible effects of temperature changes. The other is connected with the free space of the trade wind between the inversion limit and the respective islands. If the space is small the trade wind becomes compressed and the rainfall high, in analogy with what is the case at present above West Maui. During Period III, as towards the end of Period I, when similar conditions have obviously ruled (see Diagram 81), the inversion limit seems to have been pressed down, as mentioned. Above the Kilohana locality the space has therefore been less, and the possibility of increased precipitation in connexion with the compression of the trade wind consequently follows. Perhaps both circumstances have contributed. On West Maui the trade wind at this time seems to have had to find its way round the summit. In analogy with present-day conditions on East Maui and Hawaii, where the trade wind also has to find its way round, the zone for the maximum rainfall has thereby probably been pressed down more than on the somewhat lower islands, i. e. more than corresponds to the general lowering (as regards present-day conditions, see Wallén in Chap. III: A; cf. Martin and Pierce 1913, p. 462, Henry 1919, p. 37, H. Stearns and Clark 1930, p. 168, Tüllmann 1936, p. 30); perhaps on W. Maui at that time there were two ± lateral districts for greatest precipitation as is the case now on E. Maui (see rainfall map in Chap. III: B). What the conditions have been on Kauai it is more difficult to say. If the summit of Waialeale (1540 m) has constituted a hindrance, though but a slight one, to the fairly free passage of the trade wind, which may be possible, a similar ± lateral concentration of precipitation might ultimately have to be reckoned with at Kilohana. However, the conditions at the summit of Waialeale during this period are unfortunately unknown.

The connexion with the present day both on the higher and lower levels is effected by a reversion from the conditions ruling during the period. The rain forest regains its dominance in the pollen flora on higher levels (see W. Maui, Diagrams 57, 60, and 78), the influence of *Chenopodium* in localities on the leeward side likewise subsides (Kauai: Waialeale, Diagr. 90), and in the localities on the lower levels exposed to the trade wind *Metrosideros* recedes to the advantage of less extreme trees as *Cheirodendron* (Kauai: Kilohana, Diagr. 81). The Molokai diagram here shows a gap (the roots of the recent vegetation here prevented the collection of reliable samples). The regional parallelism of this reversion of the rain forest to higher levels on Maui is a further reason why we have no cause to suspect in the rise of the *Metrosideros* curve near the present day an influence of the *Eugenia malaccensis* introduced by the Polynesians, which has similar pollen and which now forms forests here and there on lower levels; I have previously (1947, p. 158—159) advanced reasons supporting this negative conclusion.

With the last-mentioned changes the Hawaiian mountain vegetation got the appearance which has mainly persisted to our days. Judging from the diagrams, the present-day conditions most nearly correspond to the transition between Periods II and III. It can be assumed, too, that the vegetation of the lower belts was now framed such as it appeared up to the 19th century when through the agency of man large areas were occupied by plants quite foreign to the original vegetation of the islands.

B. PERIODS OF LOWER ORDERS.

The diagrams show that within the main periods the development has taken a complex undulating course. Waves of several orders can be distinguished both in the curves of the various rain forest species and in the changes of the boundary between rain forests and drier forest types. Diagram 81 (Kauai: Kilohana) — slightly simplified in Fig. 28 (p. 118) — is particularly illustrative. It will unquestionably be possible to make a detailed zonation of the Hawaiian Late Quaternary by means of pollen statistics. Detailed features can already be recognized throughout the islands, not least with the aid of the F diagrams. The humification curve is particularly useful for connexions in each island, and although a certain metachrony is conceivable, it seems to be useful for inter-island connexions too.

However, it seems advisable to defer a detailed zonation until further links have been forged in the chain of observations. Manifestly the regional variations already mentioned have differed in magnitude during different periods: even the relative height of the curve peaks does not always provide guidance as to how the connexions should be made. One peak may correspond to two or more in another locality in so far as the curve there is overshadowed by another curve; though this may be merely an expression of regional parallelism. Moreover, there is always a possibility of occasional overrepresentation, the definite elimination of which in a detailed context such as this would necessitate more diagrams than those which could be made from the material I had the opportunity to collect.

A good starting point for investigations aiming at a detailed general zonation seems to be Diagram 81, with its clear symmetry. This could be made one end of a series of diagrams towards the leeward side of the island. Another series could be made along a line from Kilohana to Waialeale. Of fundamental importance is that the samples be taken at very short intervals so that none of the peaks are neglected. Even the first series is likely to furnish a good basis for connexions between Kauai and other islands, provided the diagrams from the latter are no less detailed (this matter of connexions may possibly be simplified by studies of the volcanic ash in the peat). Similar series across other islands are likely to be required in due course. When one turns to details, the history of the Hawaiian vegetation is naturally no less varied than the rainfall conditions. The pronounced regional variations which they show, even during short periods in recent times, have previously been touched upon. There are in the islands, to quote Dutton (1884, p. 88), »almost as many climates as there are square leagues».

C. BRIEF SURVEY OF THE GENERAL RHYTHM.

It has been shown above that the vegetation development of the islands has proceeded in waves of different orders. Among those of lower orders that have been dealt with in Chapter V: 2 because they verify the interpretation of the main periods, a symmetrical arrangement round one of the largest peaks has been shown to occur. All diagrams show, however, that this symmetry is not total, not even in the diagram (81), where it is particularly clear. In general the *Metrosideros* values thus seem to be somewhat higher during the earlier part of the period than during the later part. In the case of *Myrsine* and *Cheirodendron* the conditions are reversed, the Molokai diagram (not necessarily Molokai in general) excepted. If we analyse, in a sufficiently detailed diagram, the appearance of the greatest *Metrosideros* culmination of this period, it would seem as if the initial parts of the curve are steeper than its final parts. This is particularly marked in the Maui diagrams, but can also be seen elsewhere (e. g. Diagr. 81: Colour plate 26 and Fig. 28 in the text). Something similar can possibly be traced in the Group I curves during Period III. If these indications can be verified, the great changes will prove to have taken place more or less by leaps, though not without forerunners, and to have subsided more smoothly. As regards the conditions characterizing Period III, I think there can be little doubt about their having come more or less as a climatic shock. However, the observations hitherto available are certainly inadequate to settle the question as a whole. Before reliable conclusions in this respect can be reached, the successional conditions of the forest trees under various conditions ought to be investigated. An absolute chronology is also needed. Even so, this question of the general rhythm is still worth every attention (see for inst. the discussion in Brooks 1926, p. 416 ff.). The possibility of introducing an absolute chronology will be dealt with in the next Chapter.

VI. COMPARISON WITH EXTRA-HAWAIIAN REGIONS. DATINGS.

As shown above, the vegetational changes reflected in the Hawaiian diagrams are ascribable to climatic changes which are common to all the islands, even though their local effects may vary. Is it then possible to connect the course of development with dated phenomena and thus get an absolute chronology? The first step would be to make comparisons with the post-Glacial period or shorter parts of it.

In the Introduction it has been pointed out that no datings are available regarding the post-Glacial development in the Islands, or its probable course. Nor are any datable isolated features known from there during the same period.

The youngest landmark belongs to the Glacial period. Traces of a Wisconsin glaciation have been found on the summit of Mauna Kea, Hawaii, the highest mountain of Oceania (Daly 1910, Gregory and Wentworth 1937, Wentworth and Powers 1941, H. Stearns 1945 c, H. Stearns and Macdonald 1946). An icecap several hundred feet thick extended down to an altitude of 10,500 ft (3200 m); in our days the summit (4210 m) does not reach the glaciation limit.

It has not been possible to determine the relation of this glaciation to the peat deposits or other strata at lower altitudes. Nothing more than rather vague assumptions have been made possible by studies of coral reefs (Daly 1916, Pollock 1928 a, Setchell 1928, etc.), shore lines (Wentworth and Palmer 1925 a, b, Wentworth 1926, Pollock 1928 b, Hinds 1930, Johnson 1931, Daly 1934, H. Stearns 1935 a, b, H. Stearns in H. Stearns and Vaksvik 1935, H. Stearns 1938, 1939, Wentworth and Hoffmeister 1939, H. Stearns 1940 a, b, 1941, H. Stearns in H. Stearns and Macdonald 1942, H. Stearns 1945 a, 1946, H. Stearns in H. Stearns and Macdonald 1946, 1947), fossil dunes (see especially H. Stearns 1935 a, 1939, and H. Stearns in H. Stearns and Vaksvik 1935), or the general morphology of the islands (see e. g. Hinds 1930, 1931). Their quite naturally hypothetical character is exemplified by the following quotation from Hinds (1930, p. 43), who — inspired by Daly 1927 — writes:

> »The stupendous cliffs of western Kauai, 500 to 2,000 feet high . . ., suggest that they were cut when the prevailing wind direction in this region was different from that

of today, as it may well have been during portions of the Glacial Period. A narrowing of the tropical belt as the chilling of the earth's climate progressed may have brought the stormy westerlies as far south as the latitudes of Hawaii, so that the principal wave attack for a time was along the western coast.»

We still know nothing about conditions during the culmination(s) of the glaciation(s). However, H. Stearns (1935 a, p. 1944; cf. 1939 and 1940, p. 53) does not find the above explanation quite satisfactory. He found that large fossil dunes had been formed by north-east winds at a time when the sea level was considerably lower than it is today, and he is inclined to think that this low level was contemporaneous with the fall that has elsewhere been shown to have occurred during the Glacial period. Since high dunes had also been formed at the same time on the leeward side of Oahu, he found that the NE trade winds possibly had not been so predominant as they are today, but that southwesterly winds may have had a greater effect. »The high lithified dunes near Diamond Head, Oahu, may mean that the Kona winds blew more strongly at that period than now», he adds. He emphasizes, however, that the Hawaiian Quaternary chronology is very vague, and therefore abstains from a detailed discussion of the question.

Although it will perhaps be possible to interpret Periods I and III — during which the pollen diagrams indicate a similar development — as times of lowered temperature, the chronological position of these periods has not thereby become settled.

It remains, therefore, to compare the development of the Hawaiian vegetation with similar features in other regions.

Taking Pacific countries first, pollen diagrams for such a comparison have been published from North America (numerous papers; see particularly Hansen 1947), Tierra del Fuego and Patagonia (von Post 1929 b, 1931, 1944, 1946, Auer 1933, 1941, 1946, and Auer in Salmi 1941), and New Zealand (Cranwell and von Post 1936, Cranwell 1938, von Post 1944, 1946). Jimbo's studies from Japan (1932; cf. Sears 1933) unfortunately are not sufficiently representative in this connexion. For Europe a voluminous literature is available. A representative set of synchronized diagrams from Europe, together with some from South America and New Zealand, has been published by von Post (1944, 1946). The majority of these have been collocated in Fig. 29 of the present paper for comparison with the Hawaiian diagrams in Fig. 28.

A comparison between the vegetational development in the Hawaiian Islands and the development elsewhere — in Europe, North and South America, and New Zealand — shows such close agreement,

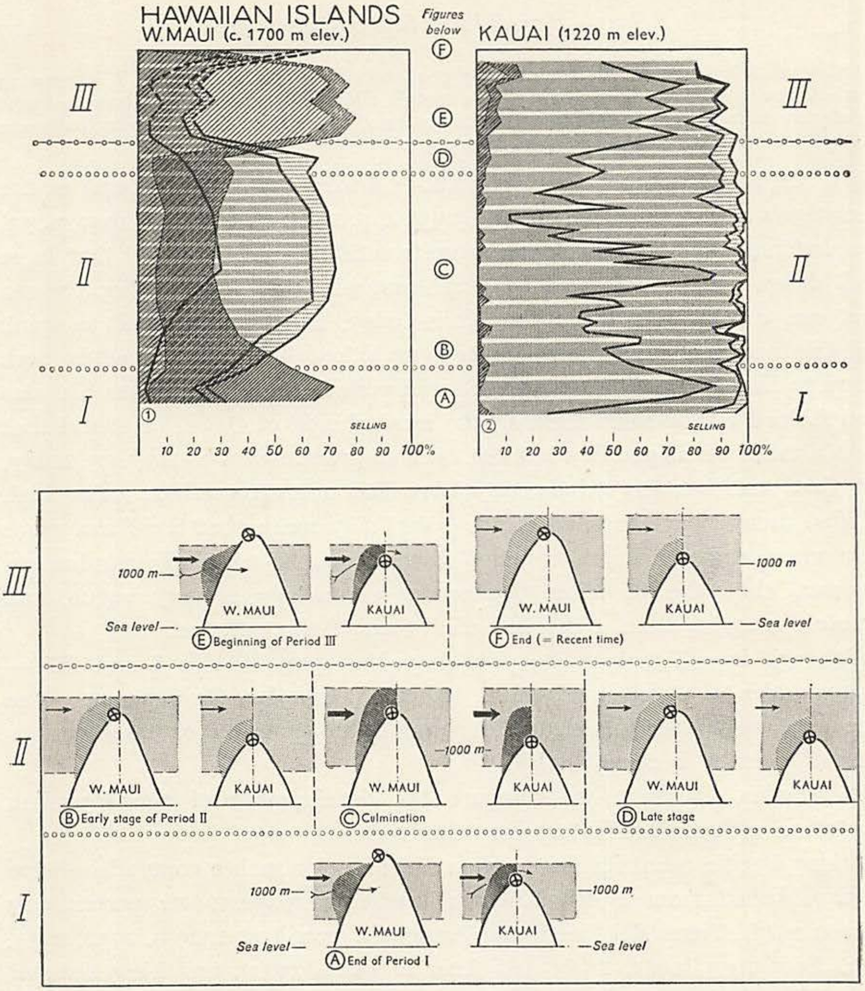

Fig. 28. The two main types of Hawaiian pollen diagrams (in the present paper) and their parallelization. In the diagrams thick lines delimiting areas with horizontal bands mark mediocratic elements (thick bands: *Metrosideros* and — of minor importance — *Cibotium*, *Pelea*, and *Ilex;* medium thickness: *Myrsine* and *Cheirodendron;* thin bands: *Coprosma* and *Pritchardia*); thin lines and obliquely ruled areas: terminocratic elements (spaced oblique lines: *Chenopodium;* close do.: *Dodonaea*, *Myoporum*, *Sophora*, and *Acacia*). The diagrams provide beautiful examples of revertence and regional parallelism. The one from the 1700 m locality shows, during Periods I and III, a retreat of the rain forest, while at the 1200 m locality the rain forest species of the Period II culmination (*Metrosideros*) reappears as a dominant species also during Periods I and III. The parallelization does not include details. The Group III curves (lower levels) have been omitted. Due to sampling conditions, the values of the 1700 m diagram represent much longer periods and are accordingly much more smoothed than those of the 1200 m diagram, which shows waves of lower orders, too.

The bottom part gives a schematic representation of the tentative interpretation of the various stages in the diagrams. Shaded part: cloud belt. Ruled areas and the corresponding arrows indicate the rain-forest forming effect of the trade wind rains (thicker arrows and lines: winds more constant or more rain-bringing). The positions of the diagram localities are shown by crossed circles. The thin arrows in A and E show the

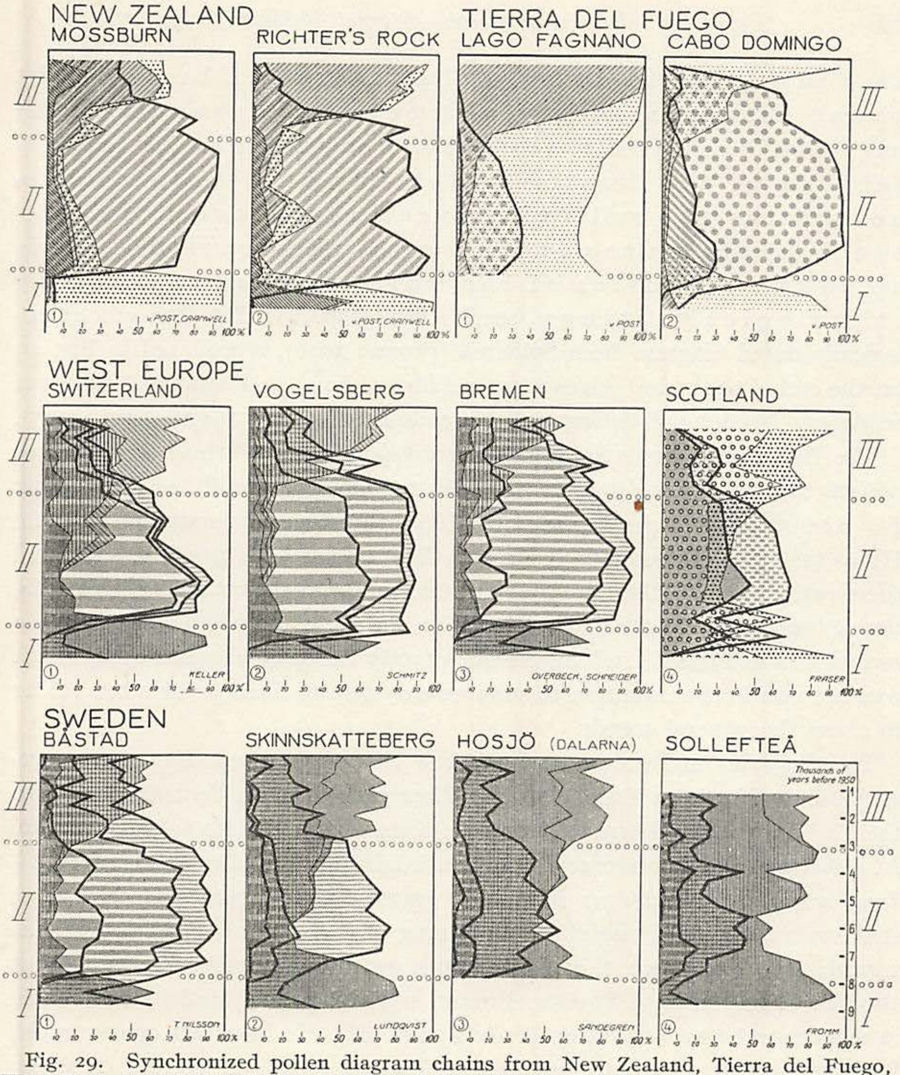

Fig. 29. Synchronized pollen diagram chains from New Zealand, Tierra del Fuego, West Europe, and Sweden, for comparison with the Hawaiian diagrams in Fig. 28. The Sollefteå diagram (geochronologically dated) has served as a vertical standard scale. Areas bordered by thick lines: mediocratic elements (in New Zealand: *Dacrydium*, *Phyllocladus*, and *Podocarpus* = lowland rain forest, in Tierra del Fuego: Caryophyllaceae and grasses, in Scotland: »wood» and hazel, in the rest of West Europe and Sweden: *Quercus* + *Tilia* + *Ulmus* = mixed oak wood, *Alnus*, and *Betula*. Areas bordered by thin lines: terminocratic elements (in New Zealand: *Metrosideros umbellata*, *Nothofagus Menziesii* etc., and grasses + Cyperaceae, in Tierra del Fuego: *Nothofagus pumilio* + *N. antarctica* and Cyperaceae, in Scotland: *Calluna* and grasses + Cyperaceae, in the rest of West Europe and Sweden: *Pinus*, *Picea*, *Fagus* + *Carpinus*, and *Abies*; *Abies* not in the Swedish diagrams). For further details, see von Post 1946, p. 200—206. — Compiled from von Post 1946, Figs. 5—8.

course of the trade winds in relation to the summits. The figure shows only the general trends deduced from the diagrams; the limits of the cloud belt and the vertical variations of the rainfall are merely hypothetical. Conditions on the leeward sides are omitted.

also in regard to details, that there can be no doubt about the courses having been synchronous. In this way it thus becomes possible to introduce into the Late Quaternary of the Hawaiian Islands an absolute chronology for the millenia since Late Glacial times — the first absolute chronology of the Central Pacific up to the centuries of the Christian era covered by ethnological datings (see further Chap. VII: D). The geochronologically dated diagram from Sollefteå (Fromm 1938), reproduced in Fig. 29 (at the end of the series), gives a general idea of how the Hawaiian events can be dated. No detailed datings will be made here (see my 1947 paper, p. 115).

The Hawaiian Periods I—III thus correspond on the whole to the three periods that von Post (1929 a, p. 10 ff.; 1930, p. 53) established for Europe: I = the stage of increasing warmth, II = the stage of maximum warmth, III = the stage of decreasing warmth. Chiarugi has later (1936, p. 55) called these periods the anathermic, the hypsothermic, and the catathermic periods, respectively. The limits in the Hawaiian diagrams, as will be seen from a comparison of Figs. 28 and 29, are not exactly the same as von Post's; but it was not von Post's intention to propose a system of fixed periods but rather to show the general trends.

The diagrams in Figs. 28 and 29 show that the *Chenopodium* curve corresponds in Northern Europe to the *Picea* curve and in Central Europe to the *Fagus* curve. In Tierra del Fuego its place is taken by *Nothofagus pumilio, N. antarctica*, and Cyperaceae; in the South Island of New Zealand by *Metrosideros umbellata, Nothofagus Menziesii*, grasses, and Cyperaceae. Not least striking is the sudden rise at the beginning of (the Hawaiian) Period III (as regards the *Picea* curve, this rise has been geochronologically dated to about 1000 B. C. in Northern Sweden; Fromm 1938, p. 379 ff.) and its subsidence in more recent times (cf. Chap. V: A: Period III). To take just one example, Sauramo's average diagram for Western Finland (1941, p. 580, Fig. 1) shows during Period III two large *Picea* maxima which are reminiscent of the *Chenopodium* culminations in West Maui during the same period. Similar cases have been demonstrated elsewhere (see, e. g., Rudolph 1930, Pl. 1: *Fagus* in Bavaria and Rhön, and Brooks 1926, Fig. 37, Curves V and VI: Climatic fluctuations in Western U. S. A.), but it is not worth while as yet to attempt a detailed comparison. It may be added, however, that the recent subsidence of the *Chenopodium* culmination in the Hawaiian diagrams seems to be an additional indication that the fairly recent decrease of the *Picea* and *Fagus* values in Europe has not been caused (primarily) by man. A similar rapid retreat of *Nothofagus* has been shown by Auer (1933, p. 250, etc.) to have occurred in South America.

In von Post's terminology (1944, p. 93; 1946, p. 203), *Chenopodium oahuense* is a terminocratic element [preponderance in the beginning and (or) final phases of development after the Ice Age]. If we turn to the mediocratic elements (those predominating in the middle phases of development), we find that *Alnus, Betula,* and the mixed oak wood representatives of Western Europe, the Caryophyllaceae and grasses of Tierra del Fuego, and the Lowland rain forest species in New Zealand — to quote examples from Fig. 29 — have their counterparts in Hawaiian rain forest trees. Although the European and North American mediocratic elements conclusively prove a higher temperature for Period II as compared with the others, and although the South American diagrams seem to show the same, only more abundant precipitation is indicated in the South Island of New Zealand. Due to their wide range in this respect, none of the Hawaiian mediocratic elements by themselves prove more than the New Zealand ones. It is significant that, because of the local rainfall conditions, we have in Kauai (Fig. 28: 2) a mediocratic element reappearing as a terminocratic one, namely *Metrosideros.* The temperature question cannot be settled until more is known of the factors governing the shifts of the inversion limit in this area. The advance of drier vegetation types in Periods I and III appears to be best explained by a decreased influence of the North Pacific high pressure area; this would then have shown features more or less recalling present-day winter conditions (Fig. 3). But it cannot therefore be concluded that the temperature has also been lowered in the Hawaiian Islands. A fall of temperature in the high pressure area may possibly correspond to a rise of temperature in the Islands (see map in Brooks 1926, p. 108, Fig. 9). It is therefore necessary to look for local evidence. Further study of the pollen curves of Group III may give useful hints in the future, but at present they are insufficient for an elucidation of the problem (see also Chap. V: A: Period II). I have no purely botanical evidence settling it. An approach via the shifts of the inversion limit appears rather promising, however.

As regards the mediocratic elements, it may be mentioned here that conditions suggestive of the course of the *Cibotium* curve in the Kauai diagram No. 81 (see p. 98—101) are found in the contemporary summation curve for *Nothofagus* in Auer's diagram from Lago Lacar in Northern Patagonia (Salmi 1941, Appendix I, Diagr. 7). It would be premature, however, to try to establish the possible interrelationships of the two curves.

Another individual feature of the period during which the mediocratic elements predominated is the well-marked temporary retreat of those elements (and a corresponding advance of the terminocratic ones) towards the end of the Hawaiian Period II (see e. g. Diagrams 60 and 80, possibly also 34). Several of the diagrams reproduced in Fig. 29 exhibit the same feature (see e. g. New Zealand: Mossburn). It appears rather likely that it marks a synchronous level.

Further studies of these waves of secondary and lower orders are likely to reveal additional similarities between distant areas. In each region an independent survey of their generally applicable features should be made for comparison with one another as well as with the recurrence surfaces of Granlund (1932) and the changes in sea level (see e. g. von Post 1944, p. 107—109, and 1946, p. 213—214). During the time that corresponds to the Hawaiian Period III, Granlund has distinguished three recurrence surfaces, indicating setbacks in the spontaneous development of the bogs towards drier conditions. The first of these is the largest. It corresponds to the great climatic deterioration of Northern Europe and was dated by Granlund to about 600 B. C. The others, dated to about 400 and 1200 A. D., are less pronounced. At least in some regions, the one occurring circa 1200 (—1300) A. D. seems to be more strongly developed than the one occurring circa 400 A. D. Sauramo's average diagram (1941), already referred to, shows two large *Picea* maxima during Period III but none that corresponds to a climatic stress about or after 400 A. D. (see also von Post 1944, p. 105, 1946, p. 212, etc.), and the same holds true of the curves from Western U. S. A. in Brooks 1926, Fig. 37. It is not unlikely that at least part of the last culmination of the Hawaiian »B» diagrams is contemporaneous with the climatic stress following Granlund's recurrence surface no. I (c. 1200—1300 A. D.).

As regards the occurrence of such waves before the period now dealt with, Granlund established two recurrence surfaces that could be dated to circa 1200 and 2300 B. C. As has previously been pointed out in this paper, similar forerunners to the great climatic change in Period III are reflected in the Hawaiian diagrams. How they can be compared with Granlund's system is not yet clear, however. Granlund (1932, p. 157) emphasized that the discovery of additional, not least older, recurrence surfaces could be expected. As far as the Hawaiian waves of development are concerned, the occurrence of older ones is clearly shown by the diagrams. Their placing into a general system will be one of the tasks of Hawaiian pollen statistics.

There remains to add a few words on the bearing of the parallelization of the Hawaiian diagrams and diagrams from other, widely dispersed, parts of the world. The close agreement between their courses of development not only affords possibilities of introducing an absolute chronology and all that this implies; it is also of importance in the determination of the ultimate causes of the vegetational changes. Since the surface of the Earth has not undergone any considerable changes during the fairly short period concerned, explanations limiting these causes to the Earth itself are not sufficient; they must probably be sought in variations of solar (and cosmic) energy. Further discussion of this is beyond the scope of the present investigation, however.

VII. CONCLUDING REMARKS.

The significance of the pollen diagrams in the study of the Late Quaternary development of vegetation in the islands is indicated by the foregoing account. Their importance to an understanding of the general mechanism of the circulation of the Late Quaternary climate has also been touched upon. It goes without saying, that the insight thus gained in the composition of the vegetation, and the climatic fluctuations demonstrated by its changes, also bear upon the interpretation of many other biological, geological, geographical, and ethnographical phenomena. A few examples of this will be given below.

A. SPONTANEOUS IMMIGRANTS AND EXTINCT SPECIES IN THE HAWAIIAN FLORA.

One object of these studies was to ascertain if the pre-historic flora of the islands contains any new immigrants, and if traces could be found of any species that are now extinct, or at any rate have not been found growing there now. Rock (1917, p. 23; 1919 b, p. 17) felt justified in assuming that *Metrosideros polymorpha*, the leading rain forest tree, is a »comparatively speaking new arrival in the Hawaiian group, of course by far antedating the arrival of the race which we call Hawaiians». Even though after this investigation there is reason for thinking that the differences of frequency on which his theory was based is due to climatic rather than to historical causes, the question nevertheless remains whether new floral elements were introduced in Late Quaternary times or not. As far as the montane forest flora is concerned (and that is what we are primarily discussing here), nothing has been found to indicate an immigration of new elements into the Hawaiian Islands in that period. That conclusion cannot be drawn with the same certainty in respect of other species, plants that are more unevenly represented in the microfossil flora, but among the species observed the conditions seem to be the same. One exception must be made for *Drosera*, however, in respect of which there is still a theoretical possibility of remote dispersal during this period (see Part II, p. 115). Ihering's statement that it belongs to an old element in the Hawaiian flora (1893, p. 28) must be classified as a guess. A strongly reduced frequency — possibly beyond climatic fluctuations — has, on the other hand, been demonstrated in a few cases — *Alectryon* (Part II, p. 223), *Sanicula* (ibid., p. 245), and *Schizaea Skottsbergii* (Selling 1944, 1946) — suggesting that some stenotropic populations have to some extent been eliminated. In at least one case (*Schizaea*) there is a possibility that a species has become extinct, in this case during the great change of the climate in Period III. In the Hawaiian Islands it should be easier than elsewhere to trace, with the aid of Parts I and II of these Studies, any other species that may have disappeared. Such investigations would apparently be worth while, not least in deposits from Period I. My notes contain a few solitary finds, which I have not been able to identify with any indigenous Hawaiian species; one of them (Sample 285) is a tricolporate pollen, 30×24 μ, with crowded, fairly slender, about 1 μ long papillae (not reminiscent of *Ilex*); its wide and deep colpae almost reach the poles, and have distinct, rounded pores about 3 μ broad. Still, these finds may just as well be foreign elements in the respective slides, and I do not wish to stress them too much.

In this connexion it should be noted, however, that I discovered no gymnosperm pollens in the Hawaiian peat deposits, though I looked especially for them (cf. Ihering 1893, p. 28, Guppy 1906). Nor were pollens observed of any other of the plants dealt with by Guppy in his chapter on The Absentees from Hawaii (l. c., p. 375—378).

In conclusion it may be mentioned that Hillebrand (1888 b, p. 408) records a native tradition of a tree, which is now apparently extinct in the islands:

> »On the island of Molokai a tradition is preserved of a poisonous tree which grew somewhere about the middle of the island, not far from the southern shore, but has been long extinct. It had a sacred character, but was resorted to by »kahunas» and men in power, when they wanted to get rid of obnoxious persons. As it is said to have bled when cut, it may have belonged to this Sub-order [*Artocarpeae*] which in the *Antiaris toxicaria* includes one of the most formidable poison trees.»

What this plant really was is of course hard to tell, and pollen statistics are not likely to be of any great help. There is the possibility of the tree being one of the aboriginal introductions.

B. TRACES OF CLIMATIC CHANGES IN PRESENT DAY VEGETATION.

Judging by the Hawaiian diagrams, the recent land flora (and fauna) ought to be systematically examined for the occurrence of possible influences of climatic changes in the Late Quaternary. Obviously, these have been much more far-reaching than has been hitherto supposed.

A greater stressing of the results of climatic changes should not be without significance to Hawaiian forestry. The rapid destruction of native forests in the last century seems to have been ascribed to direct or indirect human interference (see for inst. Clarke 1875, Schauinsland 1900, Lindgren 1903, p. 23, Hall 1904, Lyon 1929, etc.), even though a change of the climate may not unlikely have contributed to it (see p. 113). The Hawaiian forests, and especially their marginal parts, have probably not been as static — even when untouched — as authors on the subject are generally inclined to postulate. It would perhaps be useful to make a comparison between forests in areas where the pollen diagrams show similar trends during the post-Glacial. Is the abundance of dying *Metrosideros* in the Pepeopae and Waialeale regions (see Text-fig. 17 B and Pls. 9 and 16) due to a common climatic cause of the kind that the diagrams reflect towards the end of Period III? If so, reverse conditions could be expected in other areas. At any rate, the diagrams show that a generalized study is not likely to yield any useful results and may even be confusing. It would also be of interest to recheck, from the point of view of climatic changes, Lyon's hypothesis that the degeneration of the forests is due to old soils (1918, 1919). This question is of some practical importance, not least to the policy of long term water conservation (see Giffard 1918, Lyon 1926, and others).

C. ON THE APPLICATION OF POLLEN-STATISTICAL RESULTS TO MARINE BIOLOGY, GEOLOGY, AND GEOGRAPHY.

What has been said so far refers to the land flora. Various phenomena of marine biology (see Ostergaard 1935, etc.), among them particularly the growth and extinction of coral reefs (see for instance Bennett 1840, p. 196, Daly 1919, Pollock 1928 a, Setchell 1928, p. 325), also call for discussion on the same lines. A change of the climate such as has now been shown to have occurred in Period III cannot have failed to affect the growth of coral reefs. There might perhaps be a connexion between this climatic stress and the reason why the weak and therefore obviously young coral reefs round Oahu and Kauai have died.

The application of pollen-statistical results to geology need not be discussed. Obviously, the demonstrated changes in the type and vertical incidence of precipitation are also of importance to geomorphological research (cf. Hinds 1930, 1931). The knowledge that the inversion limit was during considerable portions of the Quaternary at far lower altitudes than now must naturally affect our opinion on the manner in which the higher mountain massifs have been eroded (constructional surfaces preserved, etc.) and on any age determinations based on them.

D. LATE QUATERNARY VEGETATION HISTORY AND PACIFIC ETHNOLOGY.

For lack of suitable localities, my investigations could throw no light on the time when the Polynesian food plants were first introduced, and the question whether man's arrival in the islands can be dated with the aid of pollen statistics (see Selling 1947) is therefore still awaiting its solution. The investigation seems to prove that the occurrence in the islands of some species hypothetically supposed to have been introduced by the natives had nothing to do with man, assuming, of course, that man is a comparatively late arrival in the islands (Churchill 1911, Best 1918, S. P. Smith 1921, Stokes 1921, Handy 1930, Buck 1938, etc.) These species are: *Alectryon macrococcus* (see Part II, p. 223) and *Marattia Douglasii* (Part I, p. 28). Mac Caughey once said of the latter (1919, p. 2) that it is »not at all unlikely that the *pala* was deliberately introduced, by the natives, during this epoch. Its present distribution in the islands is in no way incompatible with this hypothesis.» Its spores have been found, however, in the strata of Period I.

But there is also another aspect of the diagrams, which appears to be of interest to Pacific ethnology. I refer to the effect on Polynesian life of the vegetational and climatic changes deduced from the pollen diagrams. A brief consideration of some suggestive features seems worth while.

Hawaiian traditions and legends contain nothing which seems likely to provide definite evidence of secular climatic changes of the kind demonstrated by the diagrams. I have vainly looked for notes that might allude to displacements of the vegetation belts, and the only mention of *Chenopodium* that I have met with (Story of Pikoiakaalala in Fornander (I): III, 1917, p. 454: the rats »at the outskirts of the aweoweo» .... »Aweoweo made red by the sun») is of no use in this connexion. A good deal of attention is given to the weather conditions in the legends and traditions collected by ethnological students. This is quite natural for a people living by agriculture and fishing. Heavy storms and years of famine are mentioned, but such have also occurred occasionally in recent centuries. Nor must this material, on account of its general limitations, be overemphasized as sources of historical information in individual cases. The true significance of the evidence must be left to the consideration of ethnological specialists. Some general contributions to the discussion from the point of view of the researches into the climatic changes in the Hawaiian Islands would seem to be justified, however.

It has long been assumed that the Polynesian race occupied the Pacific islands by stages. Several chronologies have been suggested. That of Fornander 1878 will be given later. The following schedule was given by Churchill (1911; see also Wissler 1921):

1) The first proto-Polynesian migration	0 A. D.
2) The Tonga-Fiji migration	600 A. D.
3) The great Polynesian migration	1000 A. D.

The dating of these eras of expansion and emigration — especially of those before the last one — is naturally very difficult. What is important, however, is that the cultural development of this region was not a continuous process, but proceeded in waves, and that these waves bear some resemblance to the climatic changes. In other words, seeing that it is now proved that climatic changes have actually occurred in this region, there is reason to pay special attention to their effects on the life of the Polynesian race. The three stages in the history of Polynesian migrations might perhaps in part be correlated to the — possibly universal — climatic waves that have been demonstrated in Period III. Huntington spoke of »The Pulse of Asia» (1907), and one might just as well speak of The Pulse of Polynesia, climatic and cultural.

Reverting to the Hawaiian conditions, I give below Fornander's tentative scheme (1878, p. 168—169), the dates of which have subsequently been amended:

»1st. At the close of the first and during the second century of the present era the Polynesians left the Asiatic Archipelago and entered the Pacific, establishing themselves on the Fiji group, and thence spreading to the Samoan, Tonga, and other groups eastward and northward.

2nd. During the fifth century A. D. Polynesians settled on the Hawaiian Islands, and remained there, comparatively unknown, until

> 3rd. The eleventh century A. D., when several parties of fresh emigrants from the Marquesas, Society, and Samoan groups arrived at the Hawaiian islands, and, for the space of five or six [about 8] generations, revived and maintained an active intercourse with the first-named groups; and —
>
> 4th. From the close of the above migratory era, ... Hawaiian history runs isolated from the other Polynesian groups until their re-discovery by Captain Cook in 1778.»

Many authors have already pointed out that the dating of the first occupation of the islands is exceedingly vague. Stokes, for instance, quotes (1921) some notes placing it between 390 and 650 A. D., and Buck (1938, p. 249) says of the dating at c. 450 A. D. that »until some other writer has the temerity to propose another date, we may accept it with reservations». Nor is this necessarily a question of only one colonizing period. The whole era, and all that happened before it, is exceedingly obscure. The more or less complete isolation of the islands was, however, undoubtedly broken by a period of activity in the centuries around 1200 A. D., even though all dates are fluid, being based on the statements of the genealogies as to how many generations ago this took place. Buck (1938), to quote a modern authority, puts the beginning of this period at »somewhere about the beginning of the twelfth century», and its end at c. 1300 A. D. Emory (1928, p. 120; see also Cartwright 1933) also says that these centuries, 1100 to 1300 A. D. (32 to 24 generations respectively before 1900, allowing 25 years to a generation) »witnessed a sudden beginning and abrupt ending of a period of remarkable voyaging between the Hawaiian group and the islands to the south. From the close of this period to the appearance of the Europeans no more is heard of adventurous navigators from the southern islands: there is mere mention of a few castaways between 19 and 15 generations ago» (a period roughly corresponding to about 1425—1525 A. D.).

To quote Fornander (1919, p. 339):

> ». . . . after a period of comparative quiet and obscurity, the Polynesian folk-lore in all the principal groups becomes replete with the legends and songs of a number of remarkable men, of bold expeditions, stirring adventures, and voyages undertaken to far-off lands. An era of national unrest and of tribal commotion seems to have set in from causes not known. A migratory wave swept the island world of the Pacific, and left its traces on the genealogies of chiefs, in the disuse of old and substitution of new names for places and landmarks, in the displacement of old, and setting up of new tutelar gods with enlarged rites of worship and stricter kapus. Chiefs from the southern groups visited the Hawaiian group, and chiefs from the latter visited the former, accompanied by their relatives, priests and retainers . . . .»

There is ample evidence that the climatic conditions in Europe were exceptional in the fourteenth century (see survey in Huntington and Visher 1922). Similar phenomena are proved to have occurred also in North America (Huntington 1912, 1914, etc.) though the results of the changes of climate in respect of humidity or aridity vary in different regions, and the time limits of the changes also vary to some extent. Huntington infers (1925, p. 202) that one of the coarse gravelly beaches of Owens Lake (Southern California), suggesting heavy rainfall and probably also severe storms, corresponds to the period of rapid growth of the sequoias culminating in 1350 A. D. and ending about 1500 A. D. There is abundant evidence of this climatic stress elsewhere, also in Europe and Asia. On the other hand, Huntington thinks that periods of drought occurred in the interior of Asia and America about 300, 600—700, 1200, and 1700 A. D. Of the two latter, the one about 1200 was the most severe (see also Brückner 1912, etc.).

The general rhythm of the Hawaiian pollen curves makes it seem at least very probable that the last nadir of the climatic stress there in Period III corresponds to this the latest great stress of climate that has been demonstrated on both sides of the Pacific. A connexion between that fluctuation of the climate and the last great Polynesian migration is thus in sight, even though at the moment it is impossible to settle the question of how it worked.

The Hawaiian diagrams indicate that this period was characterized by a depression of the vegetation belts, and probably also by increased cyclonic activity. This would presumably produce somewhat more frequent precipitation on the leeward sides and on the otherwise unwatered lowland tracts of the islands, thus making these more suitable for cultivation than in periods of mainly anti-cyclonic character; we may here quote Hillebrand (1888 a, p. 205), who, speaking of the trade wind, says: ». . . bleibt dieser, wie das ausnahmsweise der Fall ist, das ganze Jahr über stationär, so ist die Regenmenge unbedeutend, ja es hat Jahre gegeben, wie z. B. der Winter 1856—1857, in welchen beinahe gar kein Regen fiel. Das gesagte gilt aber natürlich nur für das Klima der Ebenen . . .». Now deserted cultures like those mentioned by Wilkes 1845, p. 76 and 99, and Lindgren 1903, p. 24—25, might perhaps in part be evidence of a climatic change.

In other respects the weather during the cyclonic periods cannot have favoured agricultural pursuits. An initial stage which from an agricultural point of view was still fairly favourable may have been followed by bad harvests and consequent insecurity as and when conditions gradually grew worse. This might to some extent explain the cultural disquiet of which the traditions speak. They mention the flooding of fertile valleys as well as prolonged droughts and famines in those days (Fornander 1916, p. 136, 156; (I): III, 1917, p. 562—564; cf. 1918, p. 192—198, foot-note p. 198; Cartwright 1933, p. 8—9; etc.), and hint at heavy gales in a subsequent period (Fornander (I): II, 1917, p. 270; 1918, p. 90—122), but an undoubtedly correct interpretation of them is — as I have already said — difficult. One might be tempted to see in the cessation of the long voyages and the renewed isolation of the Hawaiian Islands a consequence of particularly bad weather conditions lasting long enough to break their contact with the south (see a passage in the legend published by Fornander 1918, p. 90—91).

In all questions of this nature, however, a multitude of factors other than those of a navigational and agricultural nature must be taken into account. The ultimate question is how the variations in the solar (and cosmic) energy affected, directly and indirectly, the lives of the island populations. The problem is indeed complicated, and no more than these hints can now be given.

SUMMARY.

Chap. I. Introduction.

1. The Late Quaternary history of the Hawaiian vegetation has hitherto been unexplored. The object of the present investigation has been to elucidate it by means of pollen-statistical studies in the montane peat deposits of the islands. Part of the results have been published previously (Selling 1942, 1944, 1946, 1947).

2. No group of islands in the vast expanse of the Central Pacific offers better opportunities for pollen-statistical research than the Hawaiian Islands. Nowhere else between Alaska and New Zealand are the facilities equally great. The island peat deposits are unique in many respects. The investigation adds weight to the plea for their being declared National Monuments.

3. The possibility of similar studies elsewhere in the Central Pacific is discussed: deposits of crater lakes (various islands) and peat deposits in Washington Island, Nukuhiva in the Marquesas, Raiatea in the Society Islands, and possibly also in Mangaia, Rarotonga, and Atui in the Cook Islands, and Taveuni and Moala in Fiji.

4. Other possibilities of approach in the Hawaiian Islands are surveyed. They refer to (a) plant remains deposited under water (fossils in the sediments of rivers, lagoons, and the few small pools), and (b) impressions, casts, and carbonized remains in lavas and volcanic ash.

Chap. II. Methods.

5. The methods of the field work and of the laboratory investigations are described in p. 21—24.

Chap. III. Data for comparison.

6. The present climate of the islands is dealt with in four sections: General circulation (by C. C. Wallén), Precipitation (do.), Winds, and Temperature. The two first sections contain results of unpublished researches by T. C. Yeh and C. C. Wallén.

7. A survey of the principal vegetation belts of the Hawaiian Islands (p. 35—46, Pls. 3—22) and a Table of the various interpretations of these

in the course of time (Tab. I, facing p. 36) are given. The leading rank in the zonation system of the »Bog zone» of authors is withdrawn. The more neutral name of »inferial» is proposed to substitute »basal» for the lowest belt. The necessity of treating the rain forest belts of the windward and leeward sides separately (because of their being conditioned by different rainfall types) is stressed.

8. A special account is devoted to the Hawaiian montane mires. They include two types: raised bogs (ombrogeneous) and swamps (soligeneous). In this connexion a note is added on the occurrence of *Sphagnum* in the islands.

9. The stratigraphy of the Hawaiian mires is briefly described. The peat (up to 322 cm thick) is chiefly made up of *Oreobolus furcatus* (Cyperaceae); other peat formers are species of *Panicum, Cladium, Carex,* and *Rhacomitrium.* The degree of humification varies in different parts of the strata but there are no sharp breaks of a general nature anywhere. In one of the periods the more humified parts of the peat are symmetrically arranged around the culmination, and in one of the localities (Kauai: Kilohana, Ser. 81) they were found to occur in pairs showing the same symmetry. Traces of volcanic ash have been found under the microscope but no ash layers could be detected in the field work. Still, a Hawaiian tephrochronology should be attempted. The lower limit of the peat is well marked. At every station the peat rests on clay of varying colours, from $<$ 1 to 36 cm thick, formed in situ, at least below the raised bogs. In respect of stratigraphical type the Hawaiian raised bogs have their closest counterparts in the countries on both sides of the South Pacific.

10. The localities studied are described by islands. They refer to Kauai: Kilohana (1220 m) and Waialeale (1300 m), Molokai: Pepeopae (1200 m), and W. Maui: Puu Kukui (1375—1765 m). A survey is given of the topography, history of exploration, vegetation, and climatic data of each locality. Peat occurrences in Oahu, East Maui, and Hawaii are also dealt with. Contour maps and sections of some of the mires are presented for the first time.

11. As regards the spores and pollens of the Hawaiian vascular plants, their morphology, distinguishing characters, ecological significance, and fossil occurrences, the present paper builds on Selling 1946 and 1947, where every genus in the pre-European flora of the islands has been considered.

Chap. IV. The basic material.

12. The possibilities of constructing Hawaiian pollen diagrams were investigated on the basis of analyses of the entire microfossil flora of the peat samples collected. After a consideration of the curves themselves as well

as the recent features of distribution (see Selling 1946 and 1947), 17 pollen and spore types were selected to constitute the main diagrams. They were arranged in ecological groups:

I. Species of the xerophytic or ± mesophytic forests in the same altitudes as, or higher than, the montane rain forests on the windward sides of the islands: *Chenopodium oahuense* (Chenopodiaceae), *Dodonaea* (Sapindaceae), *Myoporum sandwicense* (Myoporaceae), *Sophora chrysophylla* (Papilionaceae), and *Acacia* (Mimosaceae).

II. Species of the montane rain forests covering mainly the windward sides of the islands: *Metrosideros* (Myrtaceae), *Cibotium* (Dicksoniaceae), *Myrsine* (Myrsinaceae), *Cheirodendron trigynum* (Araliaceae), *Coprosma* (Rubiaceae), *Pritchardia* (Palmae), *Ilex* (Aquifoliaceae), and *Pelea* (Rutaceae).

III. Species mainly distributed in lower levels: *Alectryon macrococcus* (Sapindaceae), *Antidesma* (Euphorbiaceae), *Claoxylon* (Euphorbiaceae), and *Osmanthus sandwicensis* (Oleaceae).

The recent occurrences of these species are surveyed in p. 77—86, where the five parallel diagrams (A—E) for each series of samples are explained in which the relative values of the 17 constituents are presented. A sixth diagram (F) gives the absolute numbers of pollens and spores per slide; this roughly expresses the degree of humification of the peat.

13. A system of symbols for pollen diagrams in black and white is proposed in addition to the colour symbols used in the present paper.

Chap. V. Discussion of the diagrams.

14. The pollen diagrams presented can be used with good success in establishing the main phases of the vegetational development. They are, however, confined to the mountain vegetation. The lowland flora does not appear in the microfossil analyses of the montane peat deposits. Three main periods can be distinguished:

I. The area of the rain forest restricted (in comparison with present conditions) in favour of drier vegetation types, at least in the higher levels.

II. The area of the rain forest extended. The boundary between it and the dry forests likely to have been further away from the localities examined than it is now.

III. The rain forest replaced by drier vegetation types in parts of the area occupied in Period II. Conditions more extreme at the beginning of the period than they are now.

15. During Period I the summit parts of West Maui (and the corresponding levels in the other islands) were covered by subalpine forests becoming substituted by more humid types of vegetation towards the very end of the period. The raised bog constituents were no doubt present in the islands before that time. They may have occurred at lower levels — in communities or singly — not only in the rain forest but also outside this in odd places where the local climate was favourable.

16. During Period II, the dry subalpine forests and the moderately humid transition types were pressed back by the rain forest, which became dominant in all areas examined. During the culmination of the period, its share of the total quantities of tree-pollens (as grouped in the diagrams) as a rule exceeded 90 %, and in some localities, especially in the lower ones (Kauai and Molokai), all the tree pollens in the analyses derive from rain forest representatives. The raised-bog vegetation now characterizing the landscape on the peaks and ridges in the higher parts of present montane belt (especially on West Maui) is probably no older, or at any rate not much older than Period II. The frequencies of pollens and spores that belong to herbs and shrubs also show many changes.

17. The diagrams give an idea of the most important rain forest tree successions as well, verifying the conclusions drawn from the shifts of the boundary between the rain forests and the drier forest types. In the localities so far examined, the silvi-historical milieu during Period II appears to be the higher parts of the montane rain forest. A succession of *Cheirodendron* → *Myrsine* → *Metrosideros* (the three leading genera in these areas; their ecological interrelations previously unknown) can be demonstrated, which would seem to parallel an increasingly pronounced anticyclonic precipitation (trade-wind rains). In a locality like Sta. 81 (Kauai) *Metrosideros* attains its highest frequencies just at the culmination of the rain forest period; this was most likely characterized by particularly continuous, and perhaps also heavy trade-wind rains. The *Pelea* occurrences appearing mainly at the time of this culmination, or just after, are not unlikely to be due to the same climatic cause; several species are common constituents of the wettest forests today. After the culmination, the reverse succession is found. Like the *Cheirodendron* curve, the *Coprosma* and the *Pritchardia* curves show, in general, maximum frequencies at the beginning and end of this period. This holds true especially of the Maui localities. The *Coprosma* culminations seem on the whole to fall between those of *Myrsine* and *Cheirodendron*, but they take up no fixed positions in relation to the summation curve of the B diagrams: they vary with the distance of the boring stations from the general

rain forest zone where *Coprosma* is abundant. In localities essentially differing in this respect, the maxima accordingly mark metachronous levels.

18. A special place in the general succession outlined above is taken by *Cibotium*. Diagram 81 (Kauai: Kilohana) shows that at certain stages the genus must have appeared as an independently area-forming element of the post-Glacial forests; *Cibotium* occasionally dominates the fossil flora, with values close on 50 %. The culminations of its curve are symmetrically arranged in relation to the highest value. They are, however, not synchronous with the culminations of the *Metrosideros* curve. Each of them seems to correspond to the beginning of a *Metrosideros* culmination. This would imply that during a few periods, apparently characterized by a transition towards particularly wet conditions and regularly spread over the post-Glacial, conditions have been unusually favourable to the growth of *Cibotium*. At the same time, the three highest *Cibotium* culminations have their exact counterparts in the humification curve. The latter has three very distinct double-topped culminations. The *Cibotium* peaks fit exactly with the first peak of each pair. The second peak of the same pairs also corresponds to a *Cibotium* peak but this is much less pronounced. The middle pair seems to be better developed than those on the flanks.

It is supposed that the montane rain forests have become more open in some places during certain relatively short parts of Period II, possibly owing to reduced relative humidity (drought, increased warmth, or both), with or without fairly heavy storms uprooting the forest trees, and in these clearings, dense stands of *Cibotium* have grown up. The climate has then again rapidly become more humid; it is likely that *Metrosideros* has succeeded *Cibotium* in the way it does today: the seeds germinate on top of the tree ferns, the young plant sends down aerial roots to the ground, and in the long run the epiphytic tree kills its supporter.

The question is raised why the fern forests are so abundant just on the southernmost island, Hawaii. It should be seriously investigated whether these recent fern forests are not developmental facies of the kind found in Kauai in Period II.

19. Period III shows conditions reminiscent of Period I, though — judging not least by conditions governing peat formation — the changes were not so great as in the latter. The frequencies of pollen types of Group II rise as high as 80 % in Ser. 34 (W. Maui), i. e. higher than in Period I, but this time the curves are not derived from the same species. Then it was *Acacia* and *Dodonaea*, now it is *Chenopodium oahuense*. A detailed investigation is

made to elucidate the question of what *Chenopodium* implies regarding environment. It is considered that the mass occurrence of the species in the higher parts of West Maui represented the lower portion of the subalpine belt or the region in the immediate neighbourhood of the inversion limit which has then become considerably depressed. (Remarkably enough the species is now very rare in West Maui, only two localities being hitherto recorded.) On the 1200—1300 m levels the rainfall (probably the trade-wind rain) seems to have increased simultaneously with the advance on the higher levels of the drier vegetation types. The zone for maximum rainfall seems to have been pressed down. The influence of the border zone around the inversion limit (which was possibly less well developed than at present) does not seem to have reached as far down as the 1200—1300 m levels. Towards the end of the period it again rose above the 1765 m level, but at the present it is not unlikely below the level it had in Period II. Where once the pollen flora was dominated by *Chenopodium* (which shows no connexion with mesophytic or wet areas), we now find one of the wettest places on Earth with an annual rainfall sometimes exceeding 14,000 mm. *Chenopodium* has retreated from the higher levels comparatively recently and given place primarily to *Metrosideros*. At the same time the extreme rainfall conditions of lower levels have there been replaced by less extreme ones. With the last-mentioned changes the Hawaiian mountain vegetation got the appearance which has mainly persisted to our days. Judging from the diagrams, the present-day conditions most nearly correspond to the transition between Periods II and III. It can be assumed, too, that the vegetation of the lower belts now got the appearance it had up to the 19th century when through the agency of man large areas were invaded by plants quite foreign to the original vegetation of the islands.

20. Conditions on the leeward sides of the islands are not easily investigated because of lack of suitable strata. The extent of the rain forests on the leeward sides in the course of time can therefore only be estimated in a very general way. The rise of the *Chenopodium* curve in the Molokai and Kauai localities show, however, that during Period III there has been an increase in the part played by the leeward vegetation in the pollen rain. Still, it is not definitely known whether this means an advance of the leeward vegetation or more luxuriant growth (irrespective of boundary shifts) due to increased cyclonic precipitation. It can be assumed that one has to reckon with both cases. The same would apply to Period I. As regards Period II, it is possible that the rain forest belt has then been somewhat elevated.

21. The reason for the increased trade-wind precipitation that can be supposed to have occurred at Kilohana (windward side of Kauai, 1220 m elev.) in Period III is discussed. It can be thought to be attributable to at least two causes: (a) an increase in the intensity of the trade-wind rain (or more continuous rainfall) due to temperature changes, and (b) features connected with the free space of the trade-wind between the inversion limit and the respective islands. The inversion limit has been pressed down (as is shown by the Maui diagrams), and above the Kilohana locality the space has therefore been less. The rainfall there may accordingly have increased due to the compression of the trade wind making its way above the island. Perhaps both circumstances have contributed.

On West Maui the trade wind at this time seems to have had to find its way round the summit. In analogy with present-day conditions on East Maui and Hawaii, the zone of maximum rainfall has thereby probably been pressed down more than on the somewhat lower islands (i. e. more than corresponds to the general lowering). Perhaps on West Maui at that time there were two ± lateral districts for greatest precipitation as is now the case on East Maui. What the conditions have been on Kauai is more difficult to say. If the summit of Waialeale (1540 m) has constituted a hindrance, though but a slight one, to the fairly free passage of the trade wind, which may be possible, a similar ± lateral concentration of precipitation might ultimately have to be reckoned with at Kilohana and similar localities.

22. Within the main periods (I—III) the development has taken a complex undulating course. Waves of several orders can be distinguished in the curves of the various rain forest species as well as in the shifts of the boundary between the rain forests and the drier forest types. It will be possible to introduce a detailed zonation of the Late Quaternary of the Islands by means of pollen statistics. Detailed features can already be recognized all over the group. However, it seems appropriate to leave the diagrams without a detailed zonation until the net of observations has been still better tied together. Some suggestions regarding this are made.

23. A brief survey of the general rhythm of the vegetation development of the islands is given: the wave-like course and the symmetrical arrangement of the waves in Period II are briefly referred to. The symmetry is not total. It would seem that the great changes have been brought about more or less by leaps, though not without forerunners, and that they have ended with a more gradual dying out. The conditions characterizing Period III are considered to have come more or less like a climatic shock.

Chap. VI. Comparison with extra-Hawaiian regions. Datings.

24. The Hawaiian diagrams can be synchronized with Late Quaternary pollen diagrams from countries around the South Pacific as well as North America and Europe. There is a close similarity, also as regards details, in the courses of development. Since the European diagrams are dated, an absolute chronology can in this way be introduced into the Late Quaternary of the Hawaiian Islands, resulting in the first chronology of the Late Quaternary of the Central Pacific up to the centuries of the Christian era covered by ethnological datings. Period I corresponds to the end of the last Glacial period. The depression of the vegetation belts at that time demonstrated by the diagrams can thus be connected with the last stage of the comparatively weak glaciation on the summit of Mauna Kea in the Island of Hawaii, the highest mountain of Oceania. Period II corresponds to the post-Glacial warm period, and Period III to the cooler period succeeding this and involving the well-known climatic deterioration of Boreal (and Austral) regions; the local temperature conditions are still obscure, however. The diagrams reflect vegetational changes that have not hitherto been recorded from the tropics and thus provide a connecting link between the pollen-statistical results derived from the Northern and the Southern Hemispheres. The ultimate factors governing the Hawaiian course of development must probably be sought outside the Earth.

Chap. VII. Concluding remarks.

25. As far as the montane forest flora is concerned, nothing has been found to indicate an immigration of new elements into the Hawaiian Islands in the Late Quaternary. Among other species observed the conditions seem to be the same. An exception must be made for *Drosera*, however, in respect of which there is still a theoretical possibility of remote dispersal during this period (the oldest find is from Ser. 81: 348; Selling 1947, p. 115). A strongly reduced frequency — possibly beyond ordinary climatic fluctuations — has, on the other hand, been demonstrated in a few cases, suggesting that some stenotropic populations have to some extent been eliminated. In at least one case (*Schizaea Skottsbergii;* Selling 1944, 1946) there is a possibility that a species has become extinct, in this case during the great climatic stress in Period III.

26. No gymnosperm pollens have been discovered in the Hawaiian peat deposits, though they have been especially looked for, nor were pollens observed of any other of the plants dealt with by Guppy in his chapter on The Absentees from Hawaii (1906).

27. The recent Hawaiian land flora (and fauna) ought to be systematically examined for the occurrence of possible influences of climatic changes in the Late Quaternary. Obviously, these have been much more far-reaching than has been hitherto supposed. A greater stressing of the results of climatic changes should not be without significance to Hawaiian forestry. The diagrams show, however, that a generalized study of the forests is not likely to yield any useful results and may even be confusing. Comparisons should be made between forests in areas where the pollen diagrams show similar courses of development during the post-Glacial.

28. The application of pollen-statistical results to marine biology, geology, and geography is briefly touched upon, and a few examples are given.

29. The investigations seem to prove that the occurrence in the islands of some species previously supposed to have been introduced by the natives (*Alectryon macrococcus* and *Marattia Douglasii*) had nothing to do with man, assuming that man is a comparatively late arrival in the islands.

30. The climatic and vegetational changes deduced from the pollen diagrams have not failed to affect Polynesian life. A general similarity between the climatic waves and the stages in the history of the Polynesian migrations is emphasized. A connexion between the last nadir of the climatic fluctuations in Period III and the end of the last great Polynesian migration (estimated at about 1300 A. D.) is in sight even though at the moment it is impossible to settle the question of exactly how it worked. Some agricultural and navigational factors which may have been important to the migrations and their cessation are discussed.

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APPENDIX I.

LIST OF DIAGRAMS, WITH SUMMARIES OF GEOGRAPHICAL DATA FOR EACH LOCALITY.

KAUAI.

Kilohana. NW end of Alakai swamps, near the rim of Vainiha Valley, c. 1220 m elev. Average annual precipitation about 5000 mm. See further p. 52—57, Text-fig. 14 (map) and Pl. 17; cf. Text-figs. 8 (vegetation map of Kauai) and 9 (rainfall map of Kauai) and Pl. 18 A (Alakai plateau from Waialeale).

Ser. 81. Colour Plate 26 and Text-fig. 28 (diagram). — Bog hill immediately N of the trail from Lehua maka noe, near the U. S. Geol. Surv. bench mark. Text-fig. 16 (section).

Ser. 84. Colour Plate 27. — Same bog hill. Text-fig. 16 (section). *Pritchardia* and *Pelea* of Type II not specified in the analyses and therefore not represented in the diagram; sample intervals moreover too great.

Ser. 87. Colour Plate 27. — Swampy flat about 100 m ESE of the abovementioned bog hill. Pl. 17.

Waialeale. Small bog in forest a few km W of the summit, along the trail from Waialae Camp, c. 1300 m elev. Exact average annual precipitation unknown (see p. 59). See further p. 52—54, 57—59, Text-fig. 14 (map); cf. Text-figs. 8 (vegetation map of Kauai) and 9 (rainfall map of Kauai).

Ser. 90. Colour Plate 27.

MOLOKAI.

Pepeopae bog. SW of Pelekunu Valley, near rim, 1214 m elev. (sta. 1). Average annual precipitation unknown, probably about 5000—6000 mm. See further p. 60—62, Text-fig. 17 (maps and sections), Pl. 13 B (detail of vegetation), and 16 (views of the bog); cf. Text-figs. 10 (vegetation map of Molokai) and 11 (rainfall map of Molokai).

Ser. 1. Colour Plate 24. — Top of bog hill shown in Text-fig. 17 and Pl. 16 A (as well as 13 B). Thickest peat stratum so far known from the islands (322 cm).

WEST MAUI.

Puu Kukui. Four localities between the summit and Nakalalua (Honokohau-Amalu ridge), along a line in a N-S direction which comprises an altitudinal belt of about 400 m. See p. 62—68, Text-figs. 12 (vegetation map of Maui) and 13 (rainfall map of Maui) and Frontispiece (cf. Pl. 12).

Ser. 57. Colour Plate 25. Bog covering the very summit, 1765 m elev. Average annual precipitation 389.05 inches (= 9882 mm). See further p. 64—66, Text-fig. 18 (section), Pl. 14 A (view towards the NE).

Sers. 33, 34, 35, and 37. Colour Plates 24 (33—35) and 25 (37). Text-fig. 28 (diagram). — Bogs and swamp just below the summit, a few 100 m from Ser. 57, c. 1700—1750 m elev. Average annual precipitation: see Ser. 57. See further p. 66, Text-fig. 19 (maps and sections), Pls. 13 A (detail of vegetation near sta. 41), 14 B, and 15 (views from different directions).

Ser. 80. Colour Plate 26. — Bog at about 1575 m elev., near Violet Lake, on top of the crest E of the Nakalalua-Summit Trail at about the same elevation as the »lake». Exact annual precipitation unknown (see map, Fig. 13). See further p. 66 (and Frontispiece).

Sers. 60, 71, and 78. Colour Plates 25 (60) and 26 (71, 78). — »Lowest bog» on Honokahau-Amalu ridge, near Nakalalua, c. 1375 m elev. (sta. 60). Exact annual precipitation unknown (see map, Fig. 13). See further p. 68, Text-fig. 20 (map and sections), and Frontispiece (aerial photograph).

APPENDIX II.

ADDITIONS TO »STUDIES IN HAWAIIAN POLLEN STATISTICS», PARTS I AND II.

Part I (1946):

p. 5 ff. For nomenclature changes, see E. B. Copeland, Genera Filicum. — Ann. Crypt. et Phytopathol., V (1947).
p. 9. Note. Undescribed fern = *Asplenium Kaulfussii* Schlecht. f. *paradoxa* Selling in B. P. Bishop Mus. Occ. Pap. XIX: 6, 1948.
p. 10 (line 11 from bottom) ff. For Miss read Mrs.
p. 14. The spores of *L. phyllanthum* figured in [Ch.] Gaudichaud, Voy. Bonite, Hist. nat., Bot., Atlas, tab. 34 (1841).
p. 20. The spores of *S. arbuscula* figured in [Ch.] Gaudichaud, Voy. Bonite, Hist. nat., Bot., Atlas, tab. 12 (1841).
p. 28. Brief notes on the spores (»very small, bilateral or tetrahedral, and yellowish-brown») and recent habitats of *M. Douglasii* are given by Mac Caughey in Torreya 19: 1, 1919.
p. 29. *Trilites major* Cookson in B. A. N. Z. Antarct. Res. Exp. Repts, Ser. A, Vol. II, Pt 8 (1947), p. 135, pl. XV, fig. 56, is not unlikely a *Schizaea* of the *australis-tenella* affinity.
p. 41, line 37. For *honoluluensis* read *honolulensis*.
p. 43, Lines 10—13 are left out.
p. 54. The spores of *Doryopteris* also dealt with by Tryon in Contr. Gray Herb. Harvard Univ., CXLII, 1942.
p. 62. Genus inc. sed. = *Asplenium* (see above).
p. 62, line 11. For provided read often provided.
p. 62, line 13. For absent read almost always absent (cf. p. 46).
p. 71. The values for *Nephrolepis* should be bracketed.

Part II (1947):

p. 6, line 6 from bottom. For 1943 read 1944.
p. 13. (Ka and b:) »Sculpture absent» should be put under K.
p. 30. (**: x : + :) »exine brown» is left out.
p. 41 and 67: *Zemisne* is left out (see below).
p. 88. For pollens of *Polygonum*, see Hedberg in Svensk Bot. Tidskr., 40: 4, 1946 (with ref. to Part II for the Hawaiian species).
p. 99, line 9 from bottom. For grains read granis.
p. 108. For the affinities of the Hawaiian *Argemone*, see Fedde in Engler's Pflanzenreich, IV. 104, 1909. From this account it would seem that the natives had nothing to do with its arrival in the islands.
p. 109, line 14. For se read see.
p. 115, line 21 (and 132, line 6, etc.). For Post-Glacial warm period read Period II.
p. 116, line 8 from bottom. For 35 read 35).
p. 118, line 16 from bottom. For endemic read endemic:.
p. 119, line 22. For 25 read 13.
p. 151, line 9 from bottom. For endemic read native.
p. 155. For pollens of *Wikstroemia*, see also Venkateswarlu in Jour. Indian Bot. Soc., XXVI: 1, 1947.
p. 166 f. For a revision of the Hawaiian species, see St. John in Proc. Calif. Acad. Sci., (4) XXV: 16, 1946. It should be investigated whether *Tricolpites reticulata* Cookson in B. A. N. Z. Antarct. Res. Exped. Repts, Ser. A, Vol. II, Pt 8 (1947), p. 134, pl. XV, fig. 45, is not a *Gunnera*, to the characteristic pollens of which it appears to bear a close resemblance.
p. 175. Acc. to Stearn in Jour. Arnold Arb., 28: 4, 1947, the name of the Hawaiian *Pseudomorus* should be *P. pendulina* (Endl.) Stearn var. *sandwicensis* (Deg.) Stearn.
p. 180. For *S. freycinetianum* and an account of the sandalwood trade, see St. John in Pac. Sci., 1: 1, 1947.
p. 183. For *K. Remyi* read *K. Remyana*.
p. 188. Degener considers Caum's *Abutilon eremitopetalum* (*cryptopetalum*) typically an *Abortopetalum* (Fl. Haw., sheets K_7 and K_8, Jan. 15, 1936).
p. 200, line 3. *Antidesma* has later been found to occur also in ser. 1 (Molokai) and 34 (Maui).
p. 218. Degener informs me (letter of 12. XII 1947) that in 1928 he collected *Rhus* in Molokai: Wailau Valley, on grassy slopes near sea level.
p. 242, line 2. For male read pollen-bearing.
p. 249. Degener considers *Plumbago* to be probably native.
p. 258, line 16 ff. For tetrahedral read tetrahedral (and cross).
p. 264. *Manilkara* correctly excluded (see Neal in Pac. Sci., 1, 1947).,

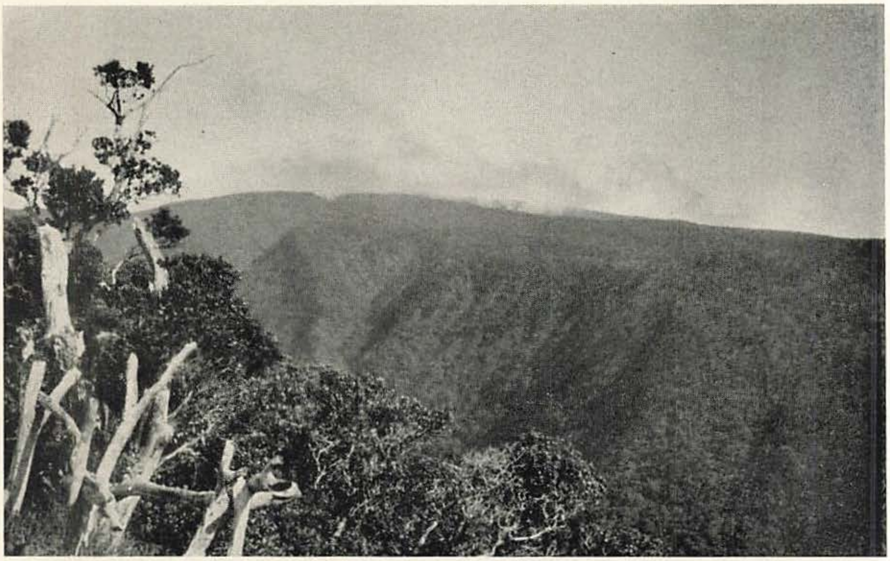
p. 279, line 19. For colpae read furrows.
p. 290, line 5 from bottom. For tie fund read tief und.
p. 297, line 18 from bottom. *Kokonoria* = *Lagotis brachystachya* Maxim. (Scrophulariaceae); see Li in Jour. Wash. Acad. Sci., 36, 1946.
p. 329. *Zemisne* will possibly have to be excluded from the list of Hawaiian plants; see [Degener and] Sherff in Bot. Ser. Field Mus. Nat. Hist., 23: 7, 1947.
p. 331. Acc. to Degener, *Raillardia* should be spelled *Railliardia.*
p. 356, line 1. *D. lanaiensis* Deg. (nom. nud.) = *Pleomele Fernaldii* St. John in Contr. Gray Herb., CLXV, 1947.
p. 391, line 3 from bottom. For Honfg read Honig.

Unless otherwise stated, Pls. 1—22 are from photographs by the author.

(Plates printed by Kartografiska Institutet, Ltd, Stockholm. — Pl. 9: "2" in "23/8" is reported to be lacking in part of the edition.)

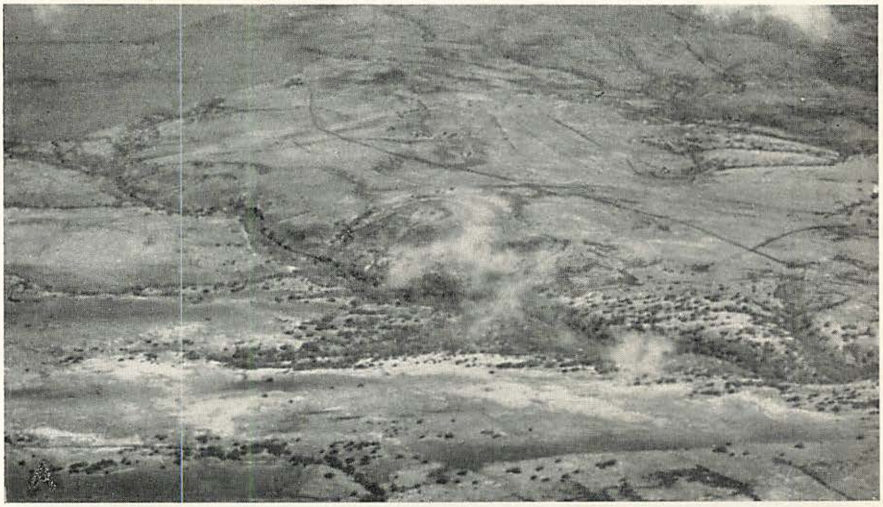
Clouds. — **A**. Cloud cap of E. Molokai, with a very distinct lower limit. View from Haelaau, W. Maui. 29/7 1938.

Clouds. — **B**. The cloud belt seen from above. View from the upper part of Haleakala, E. Maui (commercial photograph).

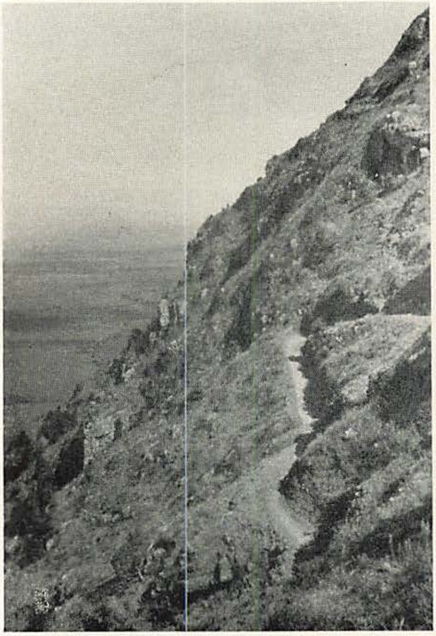


Cloud conditions of W. Maui. — **A.** Almost no cloud formation. View towards the summit (1765 m elev.) from Haelaau on its western side (910 m elev.). 1/8 1938.

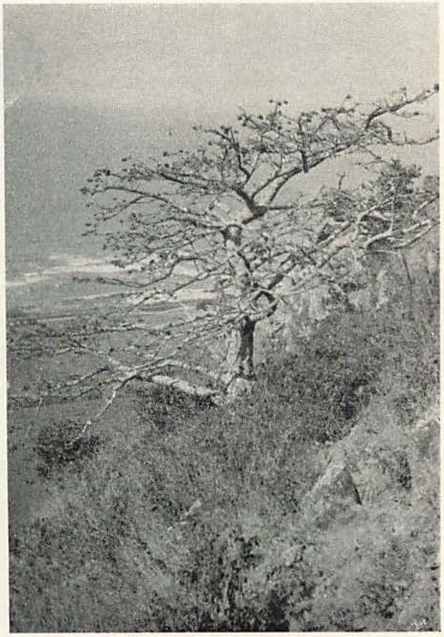
Cloud conditions of W. Maui. — **B.** Well-developed cloud cap. View from the lowlands below Ukumehame Canyon on the leeward side of the island. 3/8 1938.



Vegetation in the lowlands. — **A**. Arid lowlands. Kakaako Gulch, W. Molokai, seen from the air. $^{14}/_{7}$ 1938.

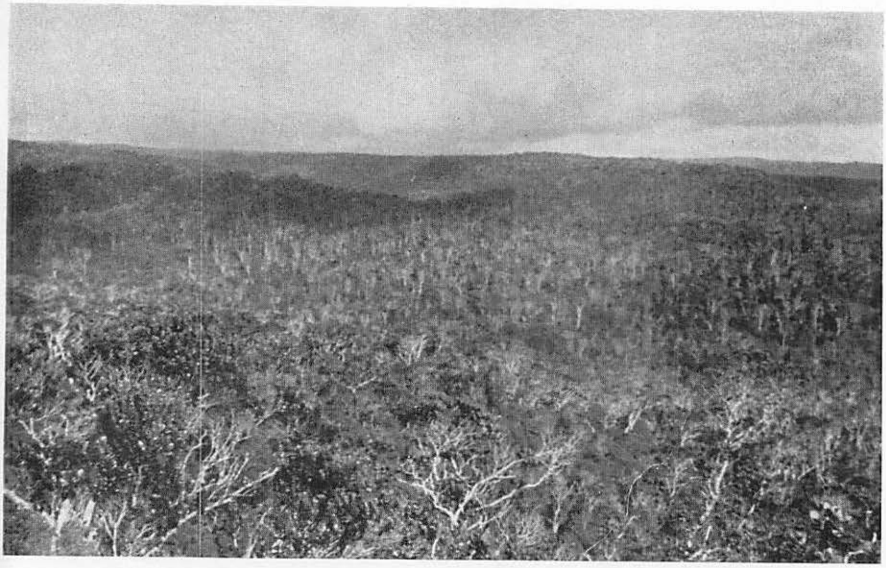


B. View from Kealia trail, Waianae Mts, Oahu. $^{18}/_{9}$ 1938.



C. *Erythrina sandwicensis* (brick-coloured flowers, no leaves). Same locality and date.

Montane rain forests. — View from Pig God Trail, Punaluu, Koolau Mts, Oahu. Rich rain forest with numerous stands of bananas, etc. 27/9 1938.



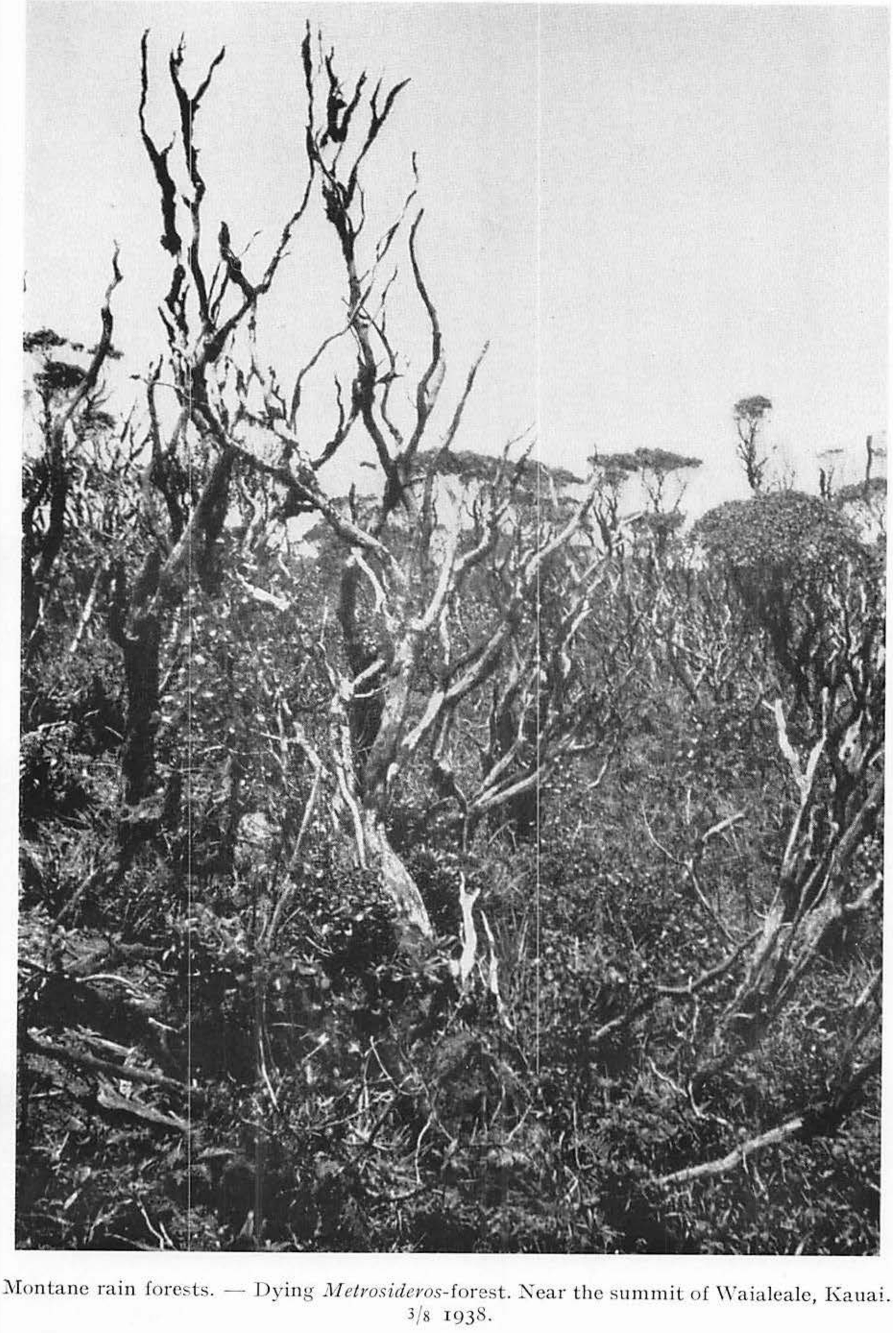
Montane rain forests. — **A.** View towards the Alakai plateau from the Kokee — Lehua maka noe trail, (leeward side of) Kauai. 15/8 1938.

Montane rain forests. — **B.** A typical occurrence of *Gleichenia glauca* (*Hicriopteris glauca;* see Selling 1946, p. 34). Kawaia trail (Kohua ridge), Kauai. 19/8 1938.

Montane rain forests. — Interior of fairly dry *Metrosideros*-forest with under storey of tree ferns (*Cibotium*), etc. *Freycinetia arborea* climbing the trees (cf. Pl. 20 B). Between Haelaau and Nakalalua, c. 1100 m elev., W. Maui. 1/8 1938.

Montane rain forests. — Interior of very wet forest. Trunks, branches, and roots covered with thick layers of emerald and reddish brown liverworts and mosses. The ground covered by about 50 cm of mud. No distinct boundary between undergrowth and epiphytes (*Cibotium*, *Sadleria*, *Astelia Forbesii*, *Pelea*, *Clermontia*, *Cyanea*, etc.). Just above Nakalalua, alt. c. 1350 m, W. Maui. 23/7 1938.

Montane rain forests. — Interior of the wettest type of rain forest (scrub forest, often too dense for photographing). Summit of Mt Kaala, Waianae Mts, Oahu. $^{25}/_{9}$ 1938.



Montane rain forests. — Dying *Metrosideros*-forest. Near the summit of Waialeale, Kauai. 3/8 1938.

Montane rain forests. — A. Fern forest (*Cibotium*) along Upper Hamakua ditch trail (between the Koiawe and Waima Valleys), Kohala, Isl. of Hawaii. $^{10}/_{9}$ 1938.

B. Interior of *Metrosideros*-forest showing under storey of tree ferns (= Pl. 6).

C. Interior of pure fern forest. Near Kilauea, Hawaii. $^{13}/_{9}$ 1938.

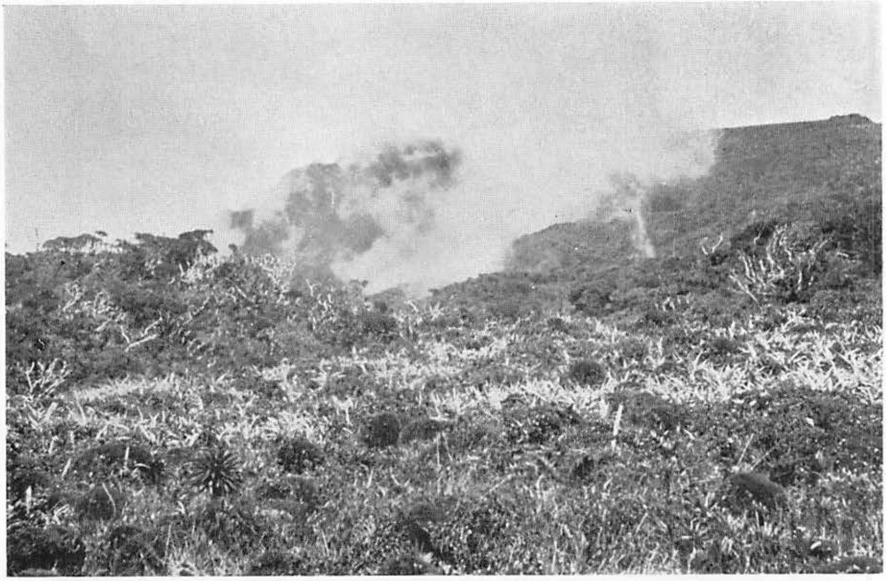
Montane rain forests. — **A.** View of the same fern forest as in Pl. 10 A. Photo by H. L. LYON 9/7 1919.

Valley topography below certain montane mires. — **B.** Valley topography on the windward side of W. Maui. Upper parts of ridges hidden in clouds. Several mires of W. Maui are situated at the heads of valleys like this, which is one of the tributaries of the Iao Valley. 6/8 1938.

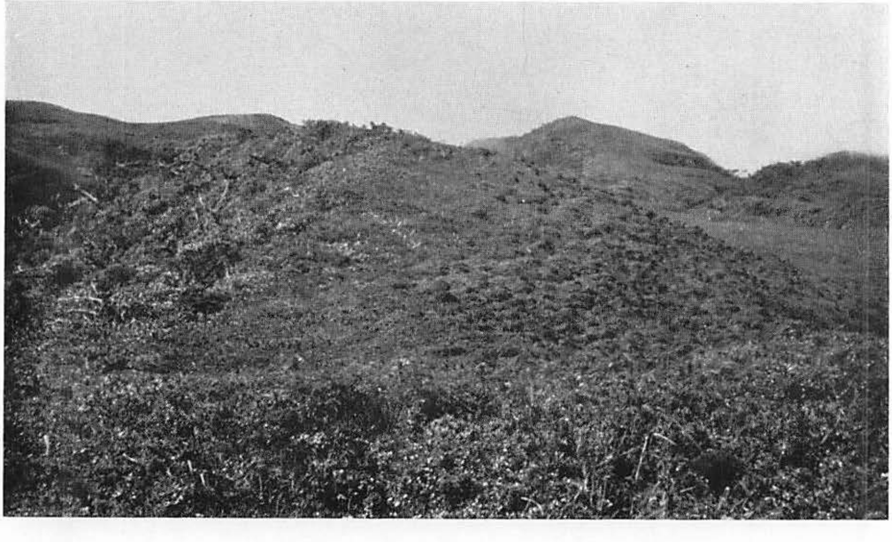
Montane mires: general topography. — Mires of the Eke Crater (1365 m elev.) and the ridges adjoining it, W. Maui. The right part of the picture corresponds to the left part of the frontispiece. Photo by the 18th Wing Photo Lab., U. S. Army.

Montane mires: details of their vegetation. — A. Cushions of *Oreobolus furcatus* with *Metrosideros polymorpha*, *Rhynchospora spiciformis*, and *Lobelia gloria-montis*. Bog below the summit of Puu Kukui, W. Maui. 25/7 1938.

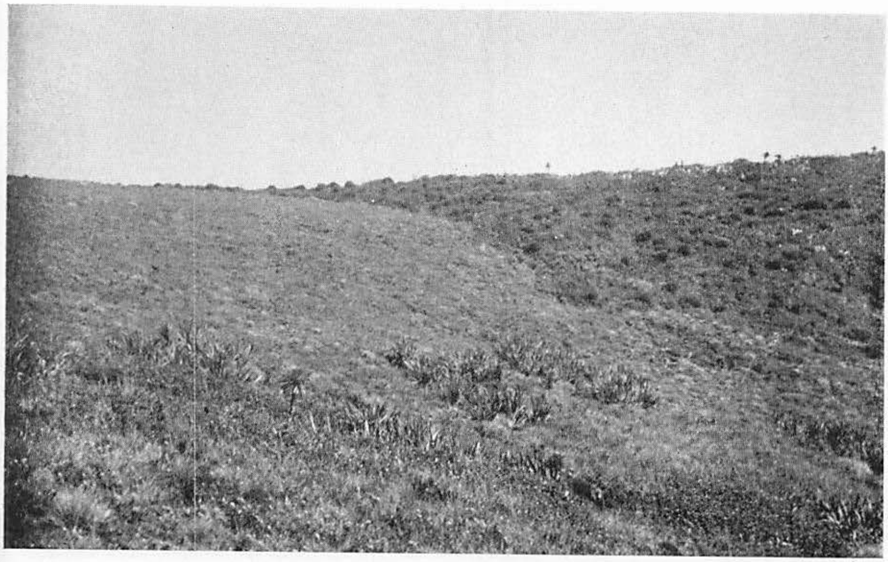
Montane mires: details of their vegetation. — B. *Metrosideros*-sociation (with *Lycopodium cernuum* and *Gleichenia linearis*) near sta. 1, Pepeopae bog, Molokai. 9/7 1938.



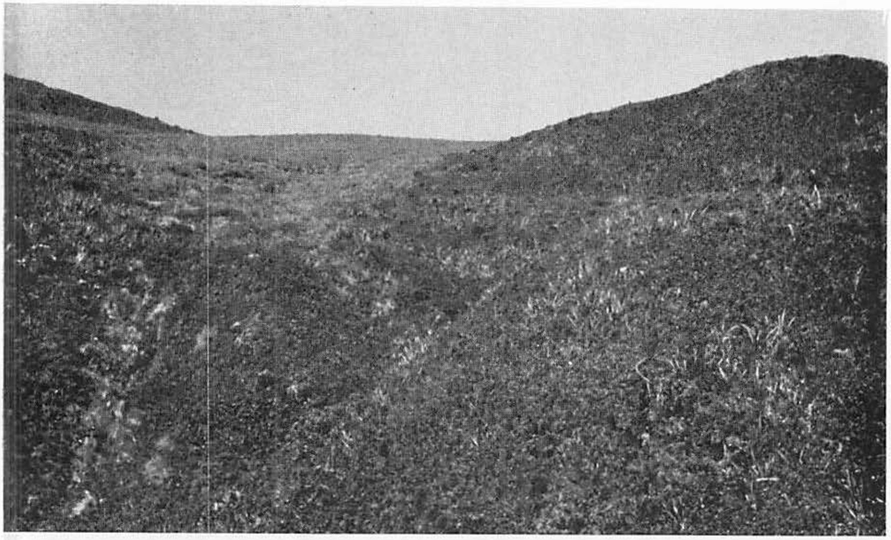
Montane mires: W. Maui. — **A**. Summit bog (with sta. 57); view from the rain gauge towards the NE. Dark cushions of *Oreobolus furcatus*, silvery white leaves of *Astelia Forbesii* subsp. *nivea*, rosettes of *Lobelia gloria-montis*, etc. *Metrosideros*-scrub in the background. $^{22}/_{7}$ 1938.



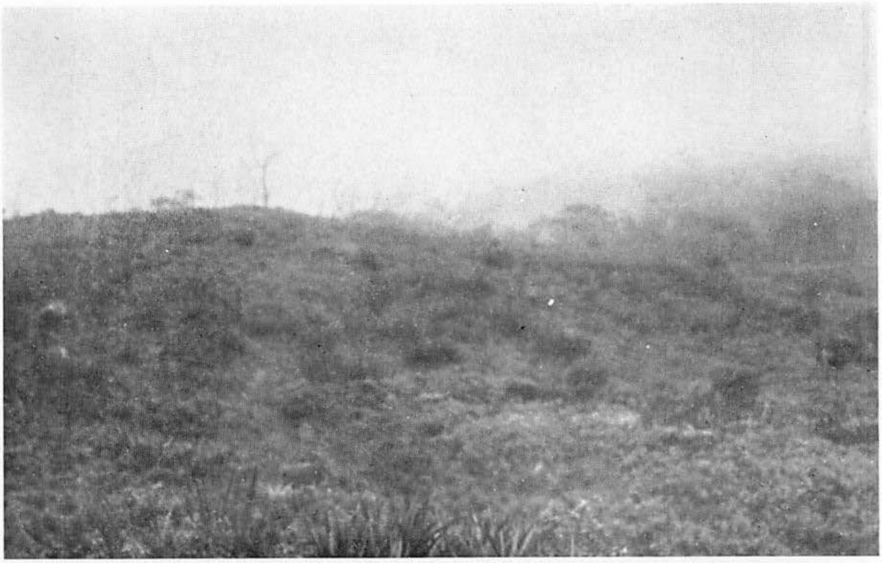
Montane mires: W. Maui. — **B**. The locality just below the summit (incl. sta. 35, etc.). *Oreobolus* bog on the windward side of the ridge. $^{22}/_{7}$ 1938 (cf. section in the text, and Pl. 15).



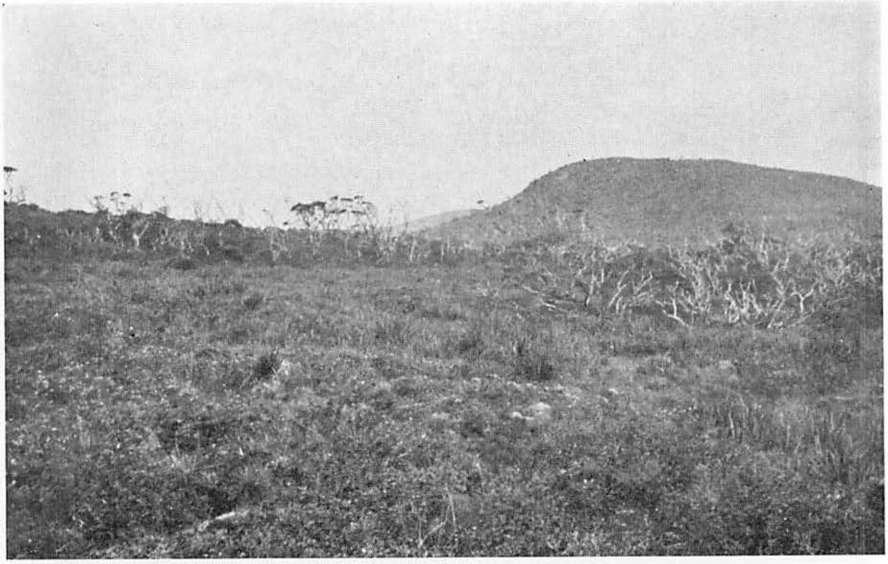
Montane mires: W. Maui. — **A**. View of the swamp just below the summit of Puu Kukui (with sta. 34, etc.). The swamp, situated at the edge of a deep gorge, is dominated by species of *Rhynchospora* and *Deschampsia*. Note the sharp boundary line between the swamp and the bog. 25/7 1938 (= SELLING 1944, Fig. 8).



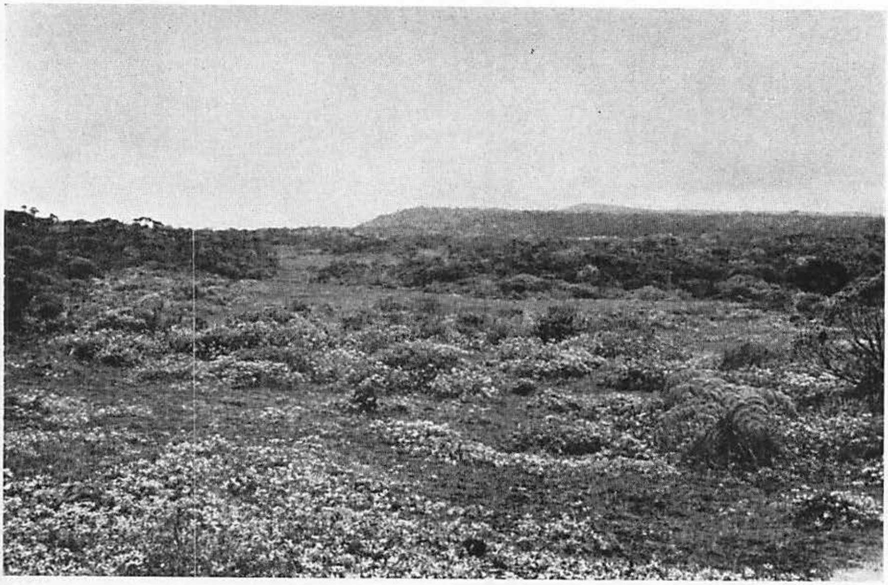
Montane mires: W. Maui. — **B**. The same swamp seen from below. The bog hill to the right is the same in both pictures. Here sta. 33 is situated. 25/7 1938 (= SELLING 1944, Fig. 9; cf. section in the text of the present paper).



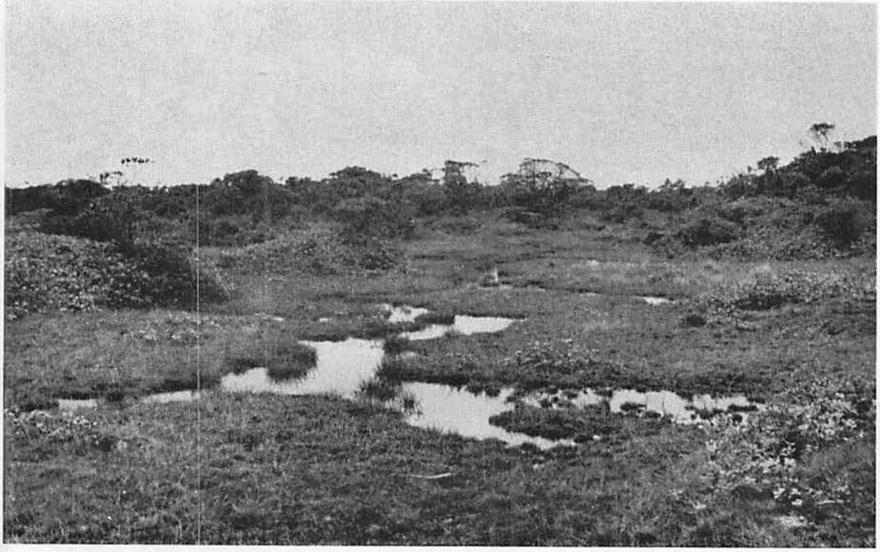
Montane mires: Molokai. — **A**. The bog hill with sta. 1 seen from the W. 13/7 1938 (heavy rain).



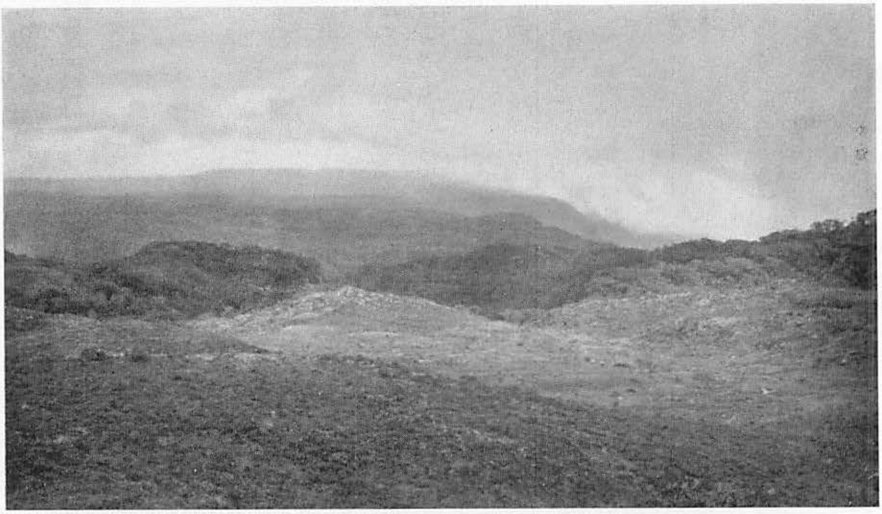
Montane mires: Molokai. — **B**. View of Pepeopae bog from sta. 1 towards the head of Pelekunu Valley. The trees in the background are *Metrosideros polymorpha*. 9/7 1938.



Montane mires: Kauai. — **A.** View of the Alakai swamps, looking from Kilohana towards Waialeale. Occasional bog hills rise above the swampy flats. Wainiha Valley to the left. 13/8 1938 (cf. Pl. 18 A).

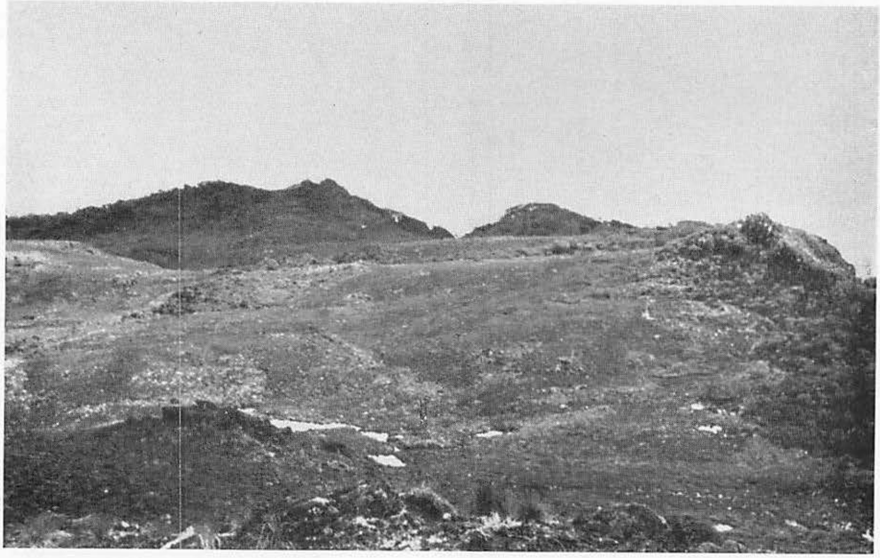


Montane mires: Kauai. — **B.** One of the numerous pools of the Alakai swamps. Near the Kilohana bench mark. 13/8 1938 (= SELLING 1944, fig. 10).



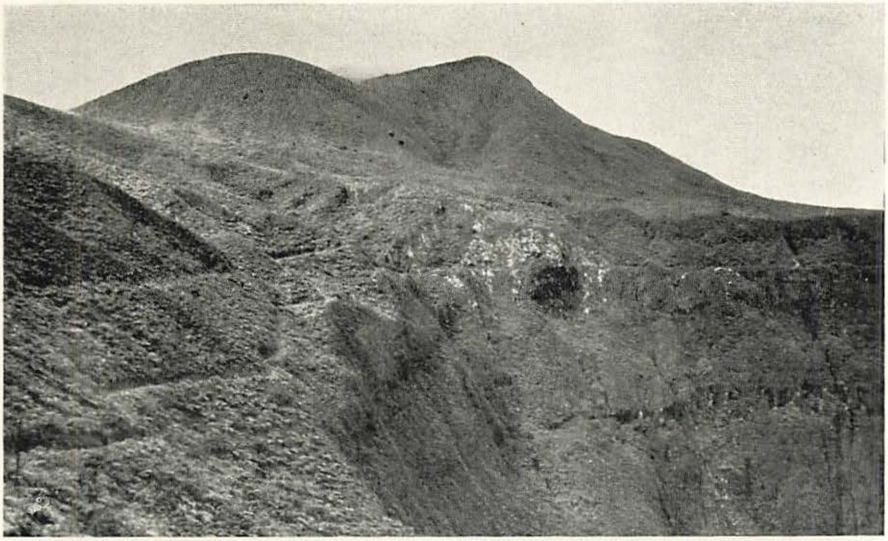
Montane mires: Kauai. — **A**. View of the Alakai swamps, looking from the summit of Waialeale towards Kilohana. Wainiha Valley to the right. The trade wind (coming from the right) is just forming clouds. 23/8 1938.

Montane mires: Kauai. — **B**. Plant community on the summit of Waialeale. Bare gravel with scattered cushions of *Oreobolus furcatus*, *Plantago grayana* (incl. varieties), *P. Krajinai*, *Lagenophora Erici*, *Stereocaulon pilophoroides*, various bryophytes, etc. 23/8 1938.



Montane mires: Kauai. — **A**. View from the summit of Waialeale towards the NE (a continuation of the view in Pl. 18 A). The light-coloured areas in the foreground are pools. 23/8 1938.

Montane mires: Kauai. — **B**. Lehua maka noe seen from the SW. The forest trees and the shrubs in the foreground are *Metrosideros polymorpha*. 15/8 1938 (cf. section in the text).



Occurrences of *Sphagnum*. — **A**. A locality at (the trade-exposed part of) the head of Koiawe Valley, Kohala, Hawaii. *Sph. palustre* forms light-coloured patches in the dark green fern forest and on the wet cliffs just at the rim of the valley. 9/9 1938.

Occurrences of *Sphagnum*. — **B**. The same species invading the scrub at the head of Alakahi Valley, Kohala, Hawaii. The *Sphagnum* carpet is 75 cm thick. Flowering *Freycinetia arborea* (with bright red bracts), *Polypodium pellucidum*, *Marattia*, etc. 8/9 1938.

Subalpine vegetation. — **A**. View from the slope of Mauna Loa, alt. about 2 100 m, towards Kilauea. Scattered trees of *Acacia koa* in favourable places. 14/9 1938.

Subalpine vegetation. — **B**. *Acacia koa* in grasslands on the same slope. Many stands now dying. 14/8 1938.

Subalpine vegetation. — **A**. Mass occurrence of *Chenopodium oahuense* (Meyen) Aellen northwest of Pohakuloa (between Mauna Kea and Mauna Loa), Hawaii. Note arborescent specimen in the foreground. Photo by C. SKOTTSBERG 7/1 1948.

Alpine vegetation. — **B**. Cinder cone with numerous, partly flowering, specimens of *Argyroxiphium sandwicense*. Haleakala Crater, E. Maui. 4/8 1938.