Hawaii as a Natural Laboratory for Research on Climate and Plant Response[1]

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THE INTERPLAY of genetic and environmental forces has resulted in the process of evolution. The distribution of indigenous plants is a product of the genetic make-up of the successful invaders of a particular area and the total physical and biological environment of that area. Native plants have achieved a point in which their genetic constitution is in a certain degree of harmony with their environment. Plants in extreme latitudes, for example, have a genetic constitution which few, if any, tropical plants possess and so are able to withstand the low temperatures. The successful cultivation of economic plants is in even greater measure dependent upon the harmonious interaction of the plant's genes and its environment. One of the most important components of the plant's environment is climate.

Adaptability studies of plants have been of major concern to research workers from the standpoint of both genetics and physiology. Clausen, Keck, and Hiesey (1940) and Clausen and Hiesey (1958) have emphasized the role of interaction of environment with particular genotypes. Went (1957) has demonstrated the practicability of greenhouses with close environmental control.

Research workers concerned with crop production have been studying adaptability in an attempt to find the best phenotype for a particular environment. Plant breeders try to create highly adapted phenotypes. Recently much emphasis has been placed on agricultural meteorology in an attempt to refine studies on this phase of the plant's environment. Sprague (1959) and others have shown the importance of microclimate in understanding the plant's development.

Experimental work on the relationship of the genotype to its environment points up the magnitude of the problem. Probably more such studies have not been made because of the difficulty of obtaining adequate comparative data. The interest in methods of obtaining controlled environment for research on plant growth and reproduction attests to the need for this type of information.

Two general methods may be used to obtain data on this problem. First, plants may be grown in the field, and, second, they may be grown under controlled environment conditions. Field studies usually provide greater size and number of plants in a test and require small capital outlay. In a controlled environment greater precision of climatic regulations may be obtained plus a greater number of treatments. A combination of both methods gives the most useful information, since field studies may then be confirmed by laboratory methods but few locations provide sufficiently different conditions in the field for studies of this kind. Also, installations on the scale of the Phytotron at the California Institute of Technology are beyond the resources of most institutions.

This study demonstrates that the Hawaiian Islands by virtue of their diverse climatic zones present a natural laboratory for studying effects of environment on plant growth and reproduction. The data reported, for the most part, are concerned with the physical environment, temperature, and rainfall. Concurrent studies were made of growth and reproduction of *Trifolium repens*. These findings will be reported in other papers for which this paper will serve as a reference for the data on physical phenomena.

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There are many stations in Hawaii reporting to the U. S. Weather Bureau (USWB) most of which report only rainfall. Temperature stations are, for the most part, in the low elevations. Relatively little data are available at the intermediate and higher elevations. All Hawaiian temperature data reported herein are from original data except those at the 10,000-ft elevation on Maui. Air temperature data at sea level, 2,000, and 7,030 ft have been extended by data from the USWB in order to increase the length of time of observations. All soil temperature data are original. Air temperatures at 3,500 and 5,000 ft on Maui are reported for the first time.

The importance of islands in the study of biological phenomena has been emphasized by Darwin (1839) and his contemporary, Wallace (1881). In Hawaii Ripperton and Hosaka (1942) have reported the effects of climate on vegetation zones. A bibliography on Hawaiian rainfall was published by Taliaferro in 1959. A summary of the climate of Hawaii was published by the U. S. Department of Agriculture in 1941.

MATERIALS AND METHODS

Air temperatures were obtained at the experimental plots from USWB maximum and minimum thermometers read daily or, at remote stations, from thermograph tracings. The thermographs were checked periodically against a thermometer and at most stations a maximum and minimum thermometer was read weekly for further check. A series of temperature readings was made by exposing a thermometer at 500-ft intervals of elevation while driving to the experimental plots. Corrections for diurnal variations which occurred during the time of travel were made by examination of thermograph tracings at three stations along the route, and by adjusting the temperature to 10:00 AM. Elevations were obtained by an airplane altimeter. Altimeter readings were checked against locations of known elevation.

Soil temperatures were read from soil thermographs (either Friez or Dickson "minicorder") with the sensing bulb 3 inches below the surface of an adapted grass cover. Instruments were housed in standard USWB shelters.

RESULTS AND DISCUSSION

Temperature

The seven major islands in the Hawaiian group represent the eroded peaks of volcanoes which extend from great ocean depths. Two of them, Maui and Hawaii, have peaks over 10,000 ft above sea level. Differences in time since cessation of volcanic activity and in amounts of rainfall on different islands have caused great topographical differences. The islands range from land areas with relatively smooth contours, in one case still actively growing from vulcanism, to highly dissected mountain masses with deep canyons and shore cliffs several thousand feet high.

Geographically, the islands are just within the northern belt of the tropics, ranging from approximately 19° to 22° 15′ N. They are separated from the nearest continent, North America, by 2,400 miles—thus are probably as little under the direct effect of other land masses as any other land area of the world.

The location within the Tropical Zone plus the insular condition give the islands temperatures which at sea level are warm throughout the year. Excessively high temperatures are not encountered because of the maritime conditions. The highest recorded temperature at Honolulu, which is just above sea level, is 90 F. Increase in elevation tends to be accompanied by a decrease in temperature of approximately 3 F for each 1,000 ft. From the mean annual temperature of 75 F at Honolulu to that of a station at 11,000 ft on Mauna Loa on Hawaii, the temperature range corresponds to that from the southern tip of Florida to a point midway in Maine (U. S. Dept. Agr., 1941).

Mean annual temperatures do not present a complete picture of temperature relationships as far as plant growth is concerned, as they fail to show diurnal and seasonal fluctuations. Mean monthly temperatures at different altitudes are given in Figure 1. Mean temperatures rather than mean maxima and minima are shown so that all may be placed on one graph for comparison. It is possible to select the approximate temperature desired by selecting the altitude.

Mean monthly maxima and minima are given for a number of locations in Figures 2–8. Figure 2 compares the mean maximum and minimum

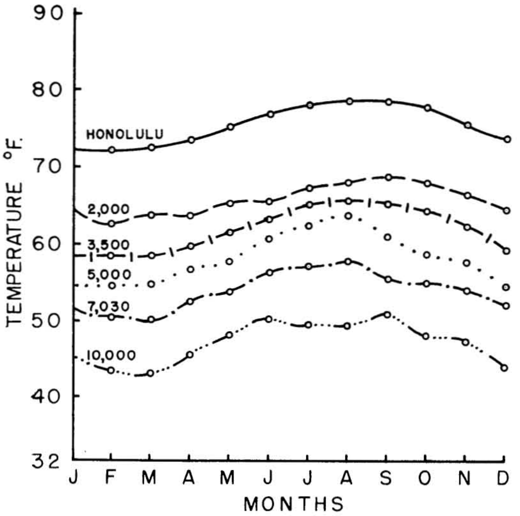


FIG. 1. Mean monthly air temperature of six locations varying in elevation from Honolulu at sea level to summit of Haleakala at 10,000 ft. Increasing elevations bring progressively lower temperatures. Selection of temperature desired may be made by choice of elevation. Note relatively uniform temperatures at each station throughout year.

temperatures of a station at 2,000 ft and one at 7,030 ft. There is some overlapping of temperature bands. If a comparison is made between Honolulu near sea level and the station at 7,030 ft (Fig. 3) there is no overlapping when means are compared, but there would be overlapping of extremes. Range between maximum and minimum increases with altitude.

The temperature of the air is usually measured about 5 ft above the ground surface. However, temperatures taken close to the plant are of great importance. Ideally, a series of readings at soil level and at a few inches above and below soil level would provide complete information on this point. However, instrumentation to this degree was not possible. Accordingly a soil thermograph was installed to record temperatures 3 inches below the soil surface. A comparison of air temperatures at different elevations with corresponding soil temperatures is shown in Figures 4–8.

Temperatures of air and soil follow similar patterns in most cases. The maxima at the 2,000-ft station (Fig. 4) intersect each other twice, the soil maxima being higher than the air maxima during the summer but lower in the winter. The air minima are consistently less than those of the soil. Air temperatures at 3,500 ft (Fig. 5) are cooler than at 2,000 ft, but the range is similar. No soil thermometer was available for this location. The range of temperatures at the 5,000-ft station (Fig. 6) is about the same as at 2,000 and 3,500 ft, but again the temperatures are lower. Air minima are consistently lower than those of the soil. The lower air temperatures may be explained by the cooling of the air to a greater extent than that of the soil because of faster radiation. The condition might be intensified by drainage of air from higher elevations, thus lowering the air temperature but having relatively little effect on the soil.

The pattern of air and soil temperatures at 7,030 ft (Fig. 7) is marked by the greater range between maxima and minima of both air and soil and the higher temperature of the soil than of the air. The soil maximum is actually greater than that of soil at 5,000 ft probably because the 5,000 ft elevation station is within the cloud zone and so may not receive as much direct sun as at the higher station, at the upper edge of the cloud zone.

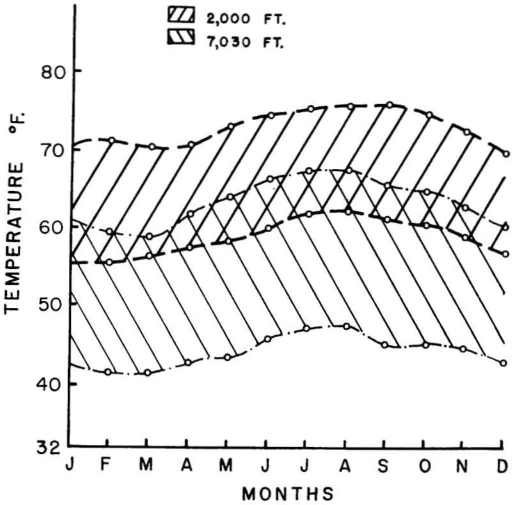


FIG. 2. Mean monthly maxima and minima air temperatures at 2,000 ft and 7,030 ft, Maui. Temperatures at higher elevation are lower and show greater range than at lower elevation. Maxima of 7,030 station exceeds minima of 2,000-ft station; i.e., temperature ranges overlap. Years of records: 2,000 ft, 13–14 years; 7,030 ft, 15–18 years.

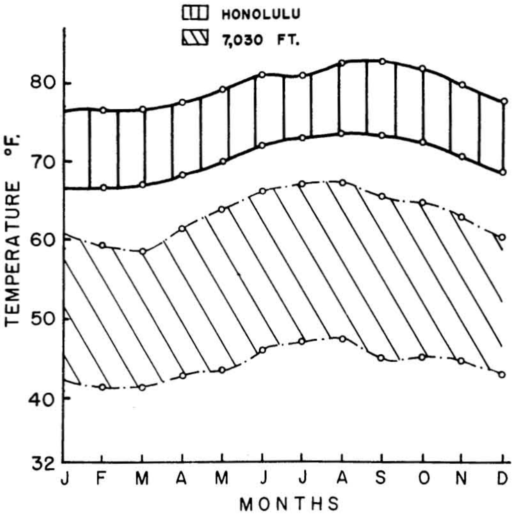


FIG. 3. Mean monthly maxima and minima air temperatures near sea level (Honolulu) and at 7,030-ft station shown in Figure 2. Note complete separation of temperature ranges. Years of record: Honolulu, 1951–53.

The anomalous situation of higher soil temperatures at 7,030 than at 5,000 ft might be used to argue against the validity of using a mountain slope to obtain progressively lower temperatures with increasing altitudes. However, this particular situation is exceptional and shows that temperature measurements are necessary, regardless of station. An investigator of the effect of temperature on plants would certainly measure not only the elevation of experimental plots but also the temperatures.

Temperature records at the summit of Haleakala have recently been available on a continuous basis. The air temperatures in Figure 8 (courtesy of USWB), show lower temperatures than any at the other stations. Rainfall in this area is sparse and no experimental plots have been established.

Where both air and soil temperatures are shown (Figs. 4–7) the period covered is approximately the same for both and is for about 2 years. Other graphs (Figs. 1, in part; 2, 3, 12, 13) showing air temperatures of these locations have been taken from long-term USWB records. This accounts for slight discrepancies between air temperatures for the same location in different graphs.

Island temperatures fluctuate less than those in continental areas. The mean diurnal change in Honolulu is 9.3 F (USWB, 1960*a*). The mean maximum of Sep, the warmest month, is 82.9 F and for both Jan and Feb, the coldest months, is 76.4 F. The difference between maximum of the coldest and the warmest months is then only 6.5 F, which is less than the diurnal change. The significance of this relatively stable temperature relationship throughout the year is that plants can be grown at any season and that somewhat similar temperatures are found at all times, particularly at the lower elevation stations.

The stabilizing effect of the ocean on temperatures produces highly predictable temperature conditions for a given location and time of year. The temperature of any location tends to be a function of elevation, but this is modified slightly by the cloud cover and the presence of an inversion layer. Clouds may cover certain areas more than others. At a given elevation, the temperatures may be about one degree higher in one location than in another because of the effect of local insolation. The inversion layer varies in altitude depending on the day and the time.

The change in temperature with elevation was investigated by periodically recording temperatures while driving up Haleakala Mountain.

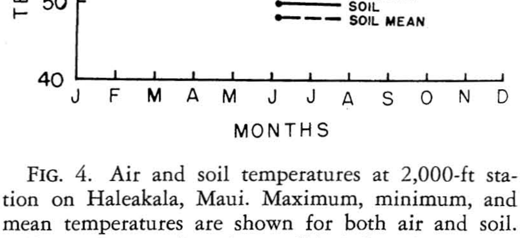


FIG. 4. Air and soil temperatures at 2,000-ft station on Haleakala, Maui. Maximum, minimum, and mean temperatures are shown for both air and soil. Soil temperatures lines have solid circles, air temperatures are designated by clear circles. Generally soil temperatures are higher than air temperatures, but both follow similar patterns. Period of record, 2½ years.

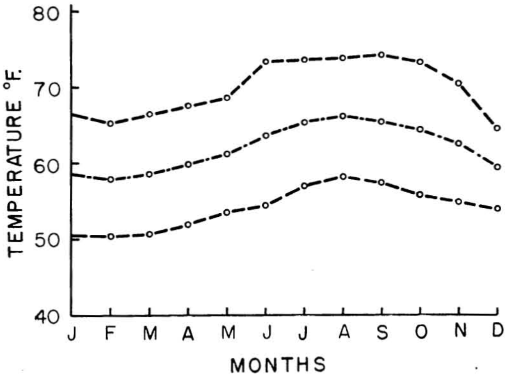


FIG. 5. Air temperatures, maximum, minimum, and mean at 3,500-ft station. Temperatures are lower than at 2,000 ft. No soil thermograph was available. Period of record, 2½ years.

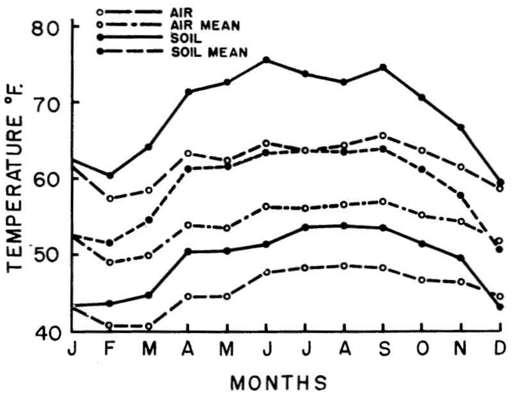


FIG. 7. Air and soil temperatures at 7,030-ft on Haleakala. Soil temperatures exceed air temperatures and range between maxima and minima is greater than at lower elevations. Period of record, 2½ years.

Because of relatively small horizontal distances in Hawaii, it is possible to plot temperatures against altitude within a reasonable time. Air temperatures are shown for two different dates in Figures 9 and 10. To compensate for diurnal changes in temperature which occurred during the drive, thermograph tracings for stations on the route were examined. Appropriate corrections were then made to the original readings to adjust all temperatures to 10:00 AM. In the two instances given, temperature inversion occurred between 4,000 and 4,500 ft in one case and between 6,000 and 6,500 ft in the other. The most frequently encountered inversion was between 5,000 and 5,500 ft. In two instances inversions occurred between 1,500 and 2,000 ft. The records confirmed previous reports that for each 1,000 ft increase in altitude, a drop of approximately 3 F occurred. This figure represents the total drop including the inversion layer. The location of the inversion layer may often be identified by clouds (Fig. 11).

Comparisons of temperatures in Hawaii with those of certain continental locations are instructive. The headquarters of the Haleakala National Park at 7,030 ft and 20° 46′ latitude

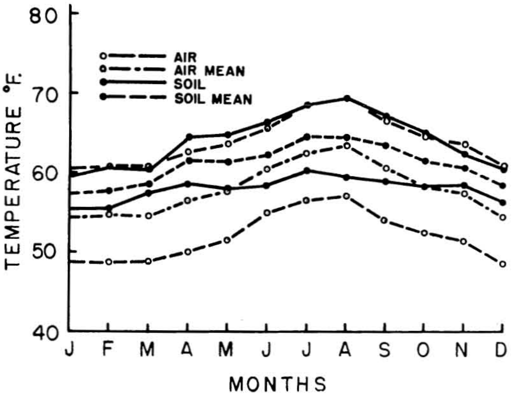


FIG. 6. Air and soil temperatures at 5,000-ft on Haleakala. Temperatures of both air and soil are very similar except that air minima are consistently less than minima of soil. Period of record, 2 years.

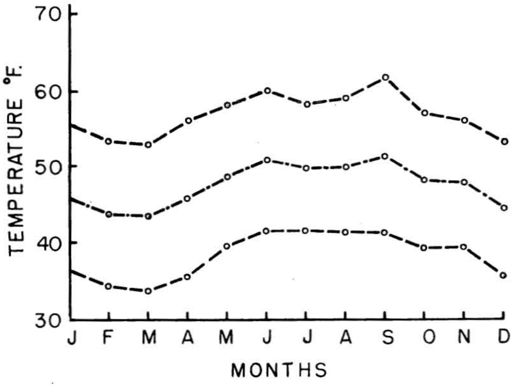


FIG. 8. Air temperatures near summit of Haleakala at approximately 10,000 ft. Temperatures are lower than at lower elevations. Period of record, 3 years. Data courtesy USWB.

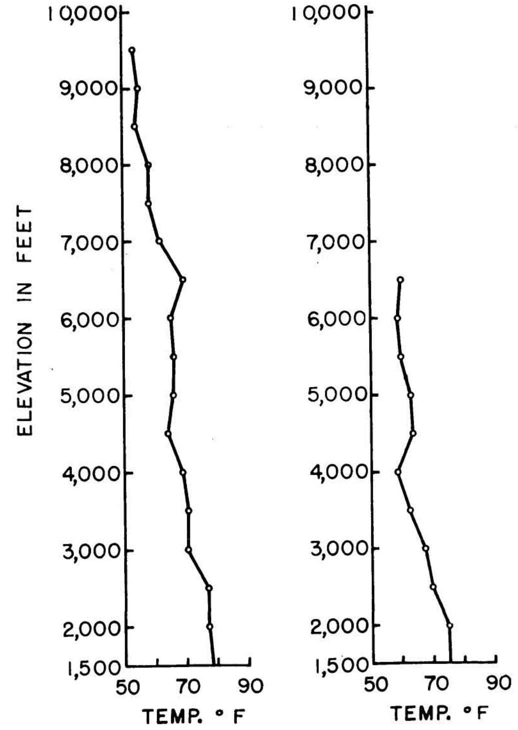
has the same annual mean temperature (54 F) as Beltsville, Maryland, at 120 ft and 39° 40′ latitude (USWB, 1957, 1960*b*). Graphs showing mean monthly maxima and minima for the two locations are in Figure 12. The Beltsville station has colder winters and warmer summers than its Hawaiian thermal counterpart. The cooler summer of the Hawaii station indicates that it is more favorable to plants adapted to cool conditions than is Beltsville, nearly twice the distance from the equator. Experiments with white clover (*Trifolium repens*) have shown that at 7,000 ft in Hawaii growth is virtually stopped for about 2 months in the winter but except for some damage to the edge of the leaves, the clover remains green and flowers continuously. Summer growth is excellent. Frost is frequent in the winter but snow never falls. From 9,000 ft to the summit at 10,025 ft snow may sometimes cover the ground but does not persist. On Hawaii, with two peaks over 13,000 ft snow frequently occurs and may last for days. Because of relative inaccessibility, low rainfall, and lack of soil, the higher elevations have not been used for plant research.

The 7,030 ft Hawaiian location and a continental location at about the same elevation are compared in Figure 13. Marshall, Wyoming, has an elevation of 7,010 ft and latitude of 39° 03′. The mean annual temperatures differ markedly, being 54 and 38 F (USWB, 1955, 1960*b*) for the Hawaiian and Wyoming locations, respectively. Despite the higher mean annual temperature of the Hawaiian station, the summer maximum in Wyoming is actually higher than the maximum in Hawaii at the same elevation. This indicates that even though Hawaii is in the Torrid Zone, at the higher elevations low temperatures may be more limiting for growth than are places within the Temperate Zone.

These differences between the two locations are reflected in the plant life of the two areas. The temperate zone station is characterized by extremely cold winters and relatively warm summers. Perennial plants in such an area must possess genes for cold resistance. Perennials in Hawaii do not need the genes to withstand a rigorous winter. But there is not the same heat energy in the Hawaiian high-altitude summer which proves so favorable for annuals in the mountains of the Temperate Zone, where, besides adapted perennials there is a profusion of annuals. The Hawaiian mountain flora, on the other hand, is predominantly perennial.

RAINFALL

The rainfall pattern in Hawaii is extremely complex. Rainfall in different localities ranges from less than 10 to 456 inches on a mean annual basis. Rainfall is determined by exposure to the prevailing wind, elevation, and local topography. During the major part of the year, the northeast trades are the main factor governing precipitation in most parts of the islands. Areas exposed to the trades, if backed by high mountains (10,000 ft or more), receive heavy rainfall. Conversely the lee sides of such mountains (and any other smaller island to the leeward) may be very arid.



FIGS. 9, 10. Air temperatures at 500-ft intervals, Haleakala, Maui. Temperatures adjusted to 10:00 AM. Fig. 9 (left) data obtained on Sep. 24, 1959. A temperature inversion was encountered between 6,000–7,000 ft. Fig. 10 (right) data were obtained on Jan. 29, 1959. A temperature inversion was found above 4,000 ft. An average 3 F drop in temperature occurs for each 1,000 ft increase in elevation.

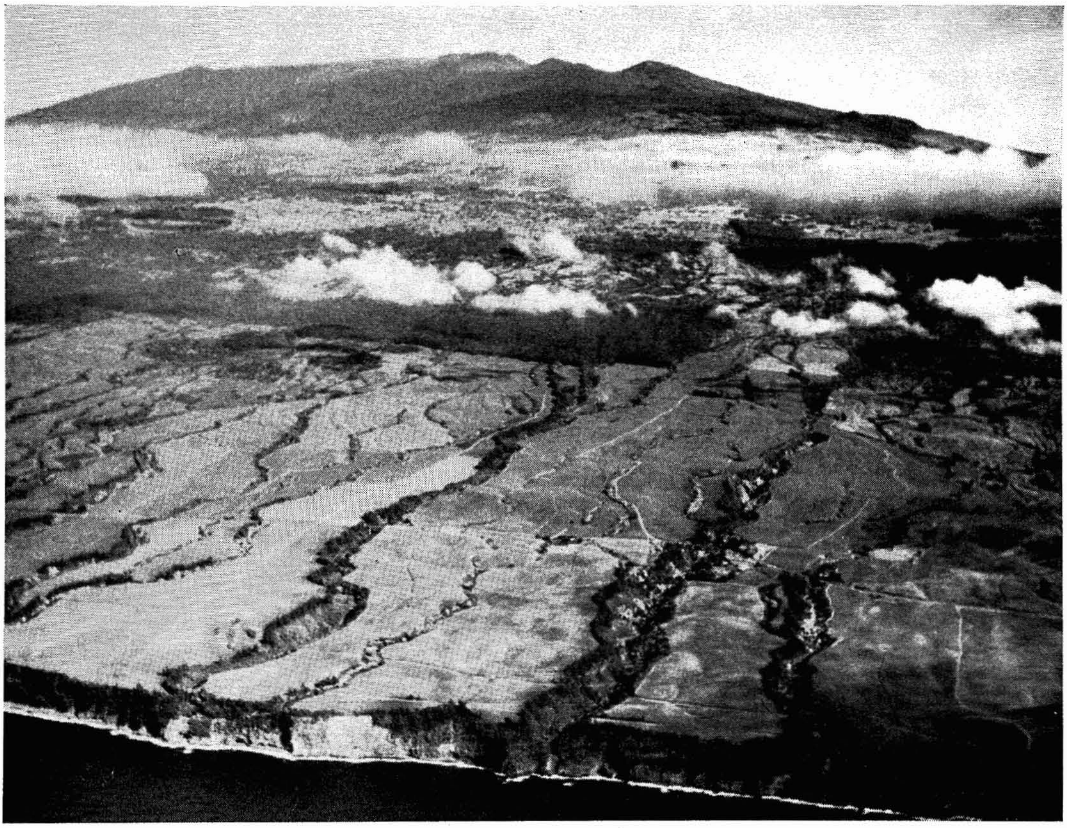


FIG. 11. Few locations afford an opportunity to observe a mountain stretching from sea level to 13,796 ft elevation, as in this photograph of Mauna Kea on Hawaii. The inversion layer is marked by the line of clouds.

Where the mountains are not as high (i.e., less than 5,000 ft), the rainfall on the windward side is not as heavy at the base as on the high mountains. Rain increases toward the crest, and is swept over the summit and down the lee side. Lee slopes therefore receive heavy precipitation which falls off rapidly with distance from the peak. Honolulu is on the lee side of a low mountain range. Rainfall on the windward side at sea level is 40 inches; at the crest it is over 200 inches. Rainfall at the head of the lee valleys is over 100 inches. At the head of the valley in which the University of Hawaii is located it is 150 inches; at the lee shore, about 5 miles from the mountain ridge, it is about 25 inches. The vegetation on the adjoining ridge parallel to the valley changes from the arid type of prickly pear cactus and associated plants to rain forest within a distance of 2 miles. Lawns become visibly greener block by block as one goes up the valley.

The rainfall pattern on Haleakala, Maui (Pineapple Res. Inst., 1955), a 10,025 ft mountain, is simpler. Topographical and rainfall contours (isohyets) are given in Figure 14. The seacoast area, being in the direct path of the trade winds, records precipitation of about 125 inches. Rainfall at this location increases rapidly with elevation until maximum amounts of 400 inches are received at about 3,000 ft. From this point, rainfall falls off rapidly so that at the summit it is less than 30 inches. Here rainfall increases then decreases with altitude. However, the isohyets describe ever enlarging ellipses as they approach that part of the mountain which is somewhat sheltered from the prevailing winds but not yet in its lee. The rainfall tends to be constant from sea level to near the summit.

Therefore, in this region, indicated by the arrows (Fig. 14), rainfall tends to be constant while temperature tends to decrease with altitude. This situation is of interest since one variable is changed at a time.

The foregoing discussion refers to annual means. It is apparent that at any one time there may be a departure from the mean which may or may not be significant. There are also seasonal differences. In parts of the islands sheltered from the trades, winters tend to be wetter than summers.

Important in studying plants in relationship to their environment is accessibility. On Maui paved roads extend to the summit (10,025 ft). On Hawaii automobiles may be driven to 9,000 ft and 4-wheel-drive vehicles to the summit of Mauna Loa (13,680 ft).

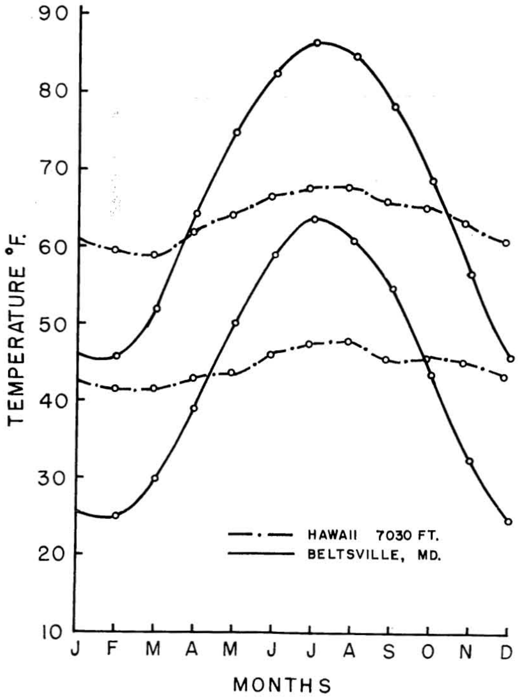


FIG. 12. Air temperatures at 7,030 ft, Haleakala, Hawaii, and Beltsville, Maryland. Both stations have same mean annual temperature. Winter temperatures at Beltsville are much lower than at Hawaii location and summer temperatures correspondingly warmer. Beltsville station is about twice the distance of Hawaii location from equator. Period of record: Beltsville, 5 years; Haleakala, 15–18 years.

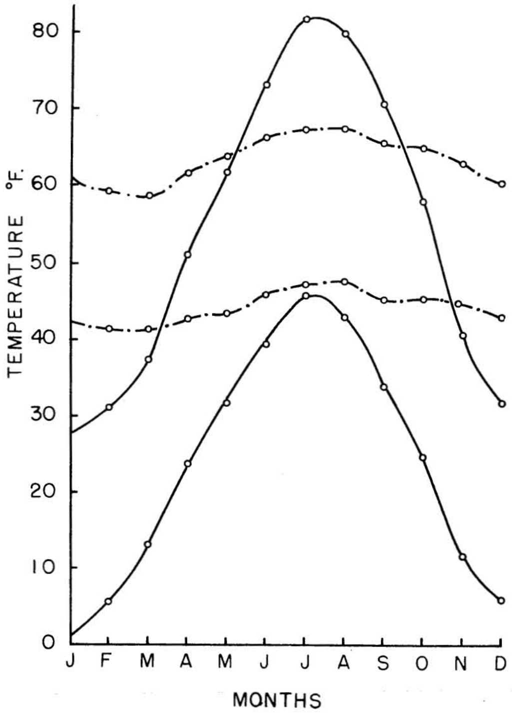


FIG. 13. Air temperatures at 7,030 ft, Haleakala, Hawaii (broken line) compared with a location of similar elevation (7,010 ft) in Marshall, Wyoming (solid line). Winter temperatures in Temperate Zone station are extremely low compared with Hawaii. Even though both stations are at same elevation and Hawaiian station is within Tropical Zone, summer maxima are greater for Temperate Zone station than for Hawaiian location. Period of Marshall record, 20 years.

Experiments utilizing the unique conditions of the Hawaiian Islands have been described by Britten (1960, 1961) who has investigated the role of genotype and temperature in flowering of *Trifolium repens*. The combination of a natural field laboratory and controlled environment facilities offers an opportunity to study fundamental and applied problems of plant growth and reproduction.

SUMMARY

The Hawaiian Islands are in the northern fringe of the tropics. Elevations range from sea level to over 13,000 ft. Mean annual temperatures associated with differences in elevation compare with those ranging from southern

Florida to Maine. By selection of elevation, desired temperature conditions may be secured. The unique conditions obtained by a high oceanic island can be utilized for research on plant response to climate.

Details of air and soil temperatures are given for different locations at different elevations. Comparisons are made between two Temperate Zone stations with a location in the islands. Rainfall patterns are discussed and attention is drawn to a situation where rainfall remains constant but temperature changes with elevation from sea level to high elevation. Utilization of such conditions in conjunction with controlled environment cabinets makes possible integration of field and laboratory experiments.

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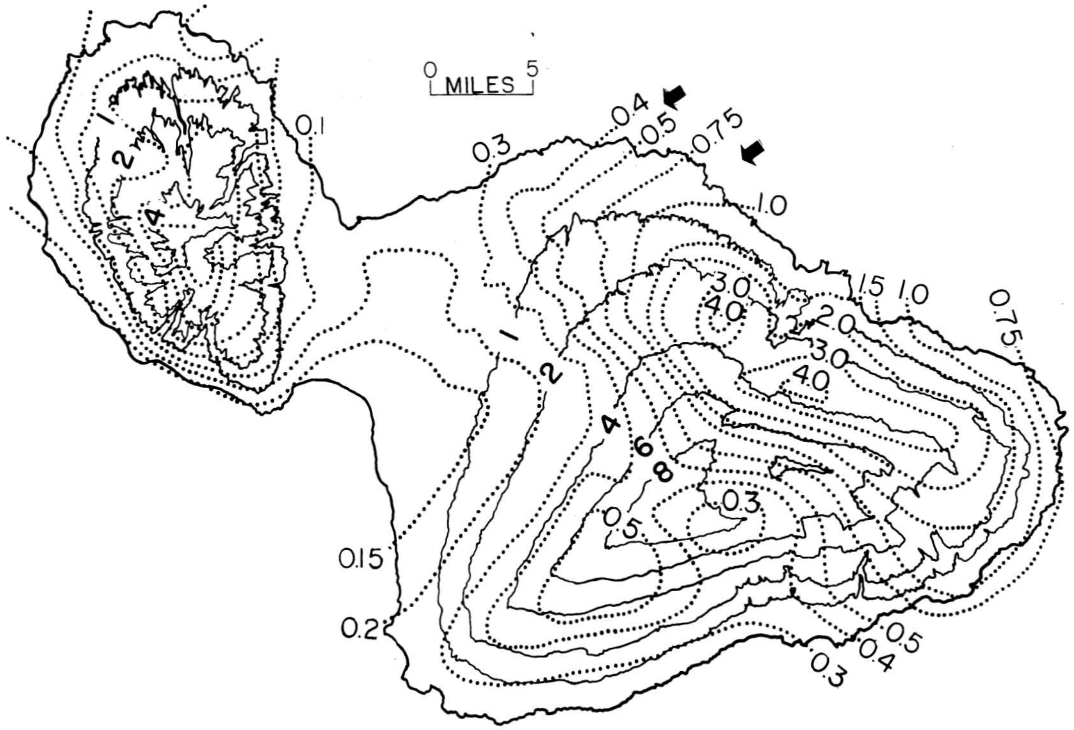

FIG. 14. Map of Maui. The 10,025-ft mountain, Haleakala, forms southeastern part of island. Topographical contours are shown as solid lines and mean annual rainfall contours (isohyets) as dotted lines. Figures for elevations are shown in thousands of feet and for rainfall in hundreds of inches. Rainfall figures for Haleakala only are given. Rainfall ranges from 10–400 inches in about 20 miles. In region denoted by arrows, rainfall is constant from sea level to approximately 6,000 ft. In this region, temperature varies with elevation while rainfall is constant. Rainfall data from Pineapple Research Institute, 1954.

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