Microclimatological Investigations in the Tropical Alpine Scrub of Maui, Hawaii: Evidence for a Drought-induced Alpine Timberline[1]

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ABSTRACT: Micrometeorological measurements were made in the lower alpine zone of Mt. Haleakala on Maui, Hawaiian Islands, in March 1988 to characterize ecologically significant climatological parameters. Daily courses of photosynthetically active and total net radiation; temperatures of air, soil, and plant canopy; wind speed; air humidity; leaf wetness; and precipitation were recorded at an elevation of 2100 m in alpine scrub slightly above the timberline. A battery-powered data-logging system was used, which gave high temporal resolution. Influence of variable cloud cover on microclimate of the study site was evaluated on five selected days with highly differing weather conditions. Based on comparison with data from other high mountains of the humid tropical zone, it is concluded that the alpine timberline on Maui is caused by a complex of factors. Plant water availability is probably the dominating one; temperature seems to be of lesser importance. The possible role of other important factors is discussed. The extraordinary microclimatological conditions of the alpine zone of Maui are examined in the context of the atmospheric circulation system in the region of the Hawaiian archipelago.

TROPICAL ALPINE ECOSYSTEMS HAVE three geographical characteristics: their nearness to the equator, their high elevation above sea level, and their occurrence in a pattern of disjunct or highly isolated small patches in the tropical belt. A review of the field of tropical alpine plant ecology is given by Smith and Young (1987). Most mountain systems of the humid tropics that reach the timberline are situated on the large continents of South and Central America and Africa, as well as on several extended islands of Southeast Asia (e.g., New Guinea and Borneo) that are more or less subject to the "Massenerhebungseffekt" (mass elevation effect) of larger land masses, with its influence on vertical temperature profile, cloud formation, and, consequently, vertical zonation of vegetation (Troll 1959, Grubb 1971). In this context, the high volcanoes of the Hawaiian archipelago in the

middle of the Pacific Ocean represent a marked exception found perhaps nowhere else on earth. On the islands of Hawaii and Maui alpine ecosystems evolved under the influence of highly oceanic surroundings combined with pronounced daytime–nighttime temperature fluctuations and weak seasonal temperature changes typical for the humid tropics. Comparable ecological conditions could feasibly be expected on Réunion in the Indian Ocean, with its Piton des Neiges (3069 m height), and, with some restrictions, on Tenerife (Pico de Teide: 3718 m [see Walter 1968, Höllermann 1978]).

Microclimatological and plant ecological studies in the tropical alpine zone have been conducted in the Andean Paramos (e.g., Troll 1968, Walter and Medina 1969, Vareschi 1970, Lauer 1973, Larcher 1975, Cleef 1978, Sturm 1978, Cuatrecasas 1979, Monasterio 1980, Halloy 1989), the afroalpine region (e.g., Hedberg 1951, 1964, Salt 1954, Coe 1967), and in the Southeast Asian islands (e.g., van Steenis 1964, Lowry et al. 1973, Smith 1977a,b, 1980, Körner et al. 1983). Excepting investigations on subtropical Tenerife

(e.g., Höllermann 1978), no detailed measurements of ecologically significant microclimatological factors have been conducted in the alpine zone of tropical oceanic islands.

On the island of Hawaii special interest has been paid to fog ("horizontal") precipitation in the montane and subalpine region (Mordy and Hurdis 1955, Ekern 1964, Juvik and Perreira 1974, Juvik and Ekern 1978). Furthermore, Mueller-Dombois (1967) and Mueller-Dombois and Krajina (1968) investigated the occurrence of nocturnal frost at different elevations of Mauna Loa and Mauna Kea on Hawaii.

This paper presents the results of a microclimatological study done in March 1988 in the lower alpine zone of the trade wind–intercepting slopes of Mt. Haleakala on the island of Maui (Hawaii).

Site Description

Measurements were taken on a site situated on a slope of Mt. Haleakala, facing north-northwest, at an elevation of about 2100 m (ca. 6800 ft, Figure 1). An almost-level section of the slope halfway between the National Park Headquarters and the park entrance west of the Crater Road was selected to meet the requirements of energy balance calculations.

The vegetation type can be classified according to Mueller-Dombois and Bridges (1981) as xerophytic alpine *Sophora-Styphelia-Vaccinium* shrubland and is situated immediately above the actual timberline. About 1 km north of the selected site at a similar elevation within the upper Waikamoi and Honomanu Stream region there is a closed cloud forest of stunted stature (3 to 5 m high, "elfin woodland") dominated by *Metrosideros collina polymorpha* (Myrtaceae). Within a confined area east of the Crater Road, near the area of Hosmer Grove Campground, plantations of several North American conifers were established above the native cloud forest at the beginning of the century, forming the actual timberline in this area at an elevation of about 2000 to 2100 m. East of the Koolau Gap of Haleakala Crater, the timberline is formed by a *Metrosideros* "tree line ecosystem" at about 2400 m (ca. 8000 ft) above sea level on a north-facing slope.

Directly adjacent to the site, an irregular pattern of xerophytic aggregated individual shrubs, patches of grass and herb cover, and bare lava soil is found (Figure 1). Most shrubs reach a height of 50 to 100 cm, and several small trees of *Sophora chrysophylla* (Fabaceae) are as tall as 180 cm (Figure 2). Beneath the shrubs there are aggregations of herbs, ferns, and mostly introduced grass species (Figure 2). A similar vegetation pattern occurs in the alpine scrub of Mauna Kea on Hawaii and was termed "fog-drip community," referring to the favorable precipitation regime beneath the shrub canopy (Mueller-Dombois and Krajina 1968). Table 1 presents a relevé of the shrubland community in a 400-m^2 plot around the measuring pole.

Flora and vegetation of the alpine zone of East Maui and Hawaii are described in more detail in, for example, Hartt and Neal 1940, Fosberg 1959, Mueller-Dombois 1967, Mueller-Dombois and Krajina 1968, Forehand 1970, Carlquist 1980, and Mueller-Dombois and Bridges 1981.

The study site is situated within a steep rainfall gradient on the north-northwest–facing slopes of Mt. Haleakala in the transition zone between the windward and leeward side of the island. According to Giambelluca et al. (1986), maximum precipitation is found at about 1300 m elevation, with more than 6000 mm per year (West Honomanu: 6137 mm) in the belt of the montane *Metrosideros* rainforest, while only 1000 mm of rainfall per year is measured at the mountain's summit, where an alpine desert prevails at an elevation of 3055 m (Haleakala Satellite: 1009 mm). The most intense decrease of precipitation with increasing elevation occurs at an altitude range from 1500 to 2000 m above sea level, which coincides with both the lower limit of the inversion layer and the height of the timberline. The amounts of vertical rainfall recorded at Haleakala National Park Headquarters, which is situated in the alpine scrub at about 2300 m elevation (or roughly 200 m higher than the study site), in the period 1979 to 1987 are given in Table 2.
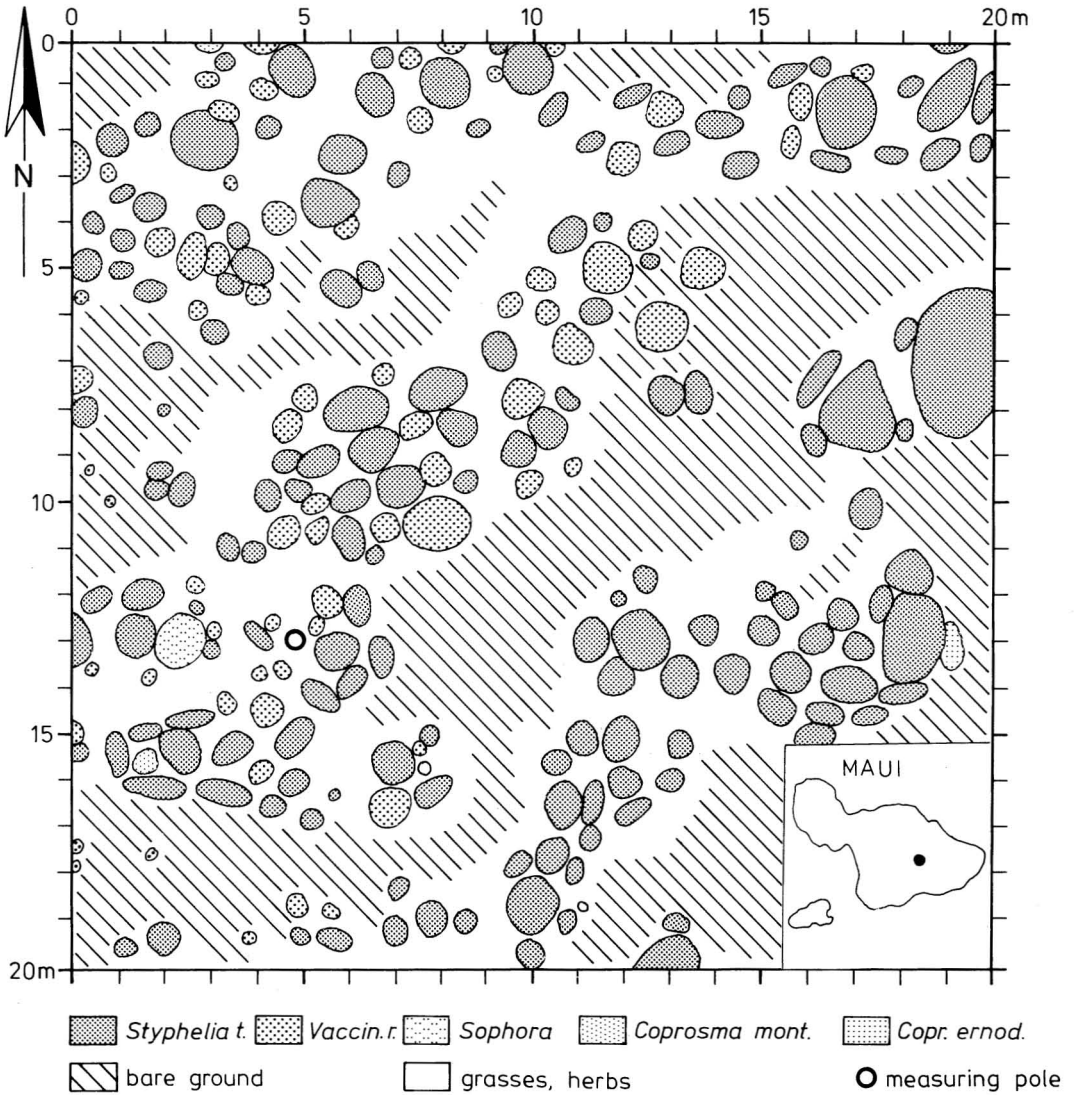
FIGURE 1. Vegetation pattern of alpine shrubland on Mt. Haleakala in the direct vicinity of the micrometeorological measuring pole. The measuring site is situated on a north-northwest–facing slope at about 2100 m elevation in the eastern part of the Hawaiian island of Maui.

As is typical for most parts of Hawaii, a drier summer period (*Kau*) and a wetter winter half-year (*Ho'oilo*) can be distinguished. Extraordinarily dry summer periods are assumed to be ecologically the most influential elements of the precipitation pattern in the alpine zone of Mt. Haleakala.

The vegetation grows on a weakly developed, lava-derived, porous soil of the Inceptisol order. Frequent soil water stress can

be expected. The geological substrate is formed by aa as well as pahoehoe lava flows (Macdonald 1978).

MATERIALS AND METHODS

During the period from 8 March to 25 March 1988, a telescopic pole 6 m high, equipped with a set of micrometeorological
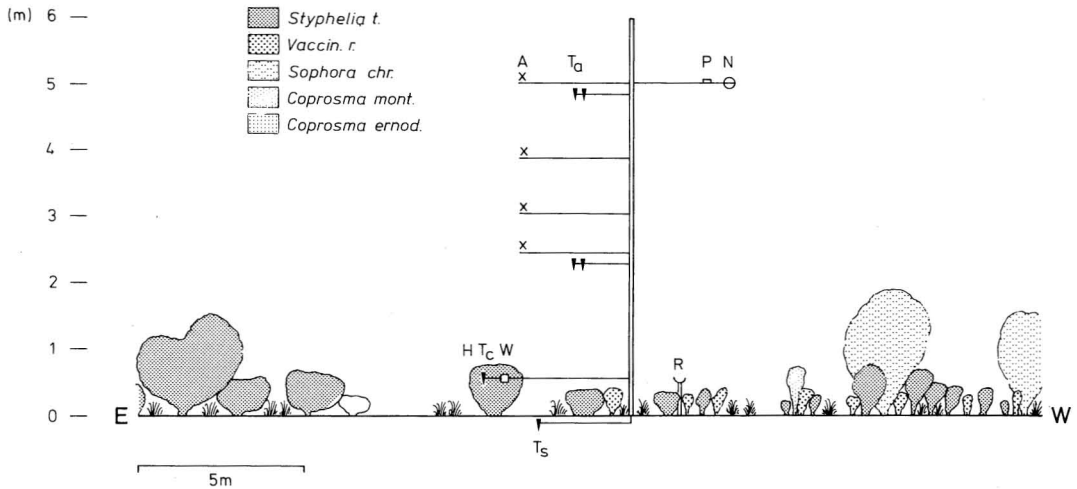
FIGURE 2. The measuring pole with its micrometeorological sensors (N = net radiation flux sensor, P = sensor for photosynthetically active radiation, A = anemometers, T_a = air temperature sensors, T_c = canopy temperature sensor, T_s = soil temperature sensor, H = air humidity sensor, W = surface wetness sensor, R = rain gauge).

TABLE 1

RELEVÉ OF THE ALPINE SHRUBLAND IN THE SURROUNDINGS OF THE MEASURING SITE (20 by 20 m)

	COVERAGE (% OF TOTAL AREA)
Styphelia tameiameiae	35
Vaccinium reticulatum	10
Sophora chrysophylla	1
Coprosma montana	1
Coprosma ernodeoides	<1
Geranium tridens	<1
Deschampsia australis	17
Holcus lanatus	8
Anthoxanthum odoratum	5
Hypochoeris radicata	2
Plantago lanceolata	1
Carex wahuensis	<1
Rumex acetosella	<1
Oenothera stricta	<1
Luzula hawaiiensis	<1
Pinus patula juv.	<1
Dry remnants of a fern	5
Total coverage by vegetation	60
Shrubs/dwarf shrubs	45
Grasses/herbs	30
Mosses/lichens	2–5

sensors, was set up at the measuring site. The following list shows the parameters that were measured continuously and the instruments used.

TABLE 2

ANNUAL AND SEASONAL AMOUNTS OF RAINFALL FROM 1979 TO 1987 AT HALEAKALA PARK HEADQUARTERS (in mm)

Year	Full year	April to September
1979	1,894	242
1980	3,081	585
1981	1,255	354
1982	2,820	561
1983	420	221
1984	643	153
1985	1,906	379
1986	1,760	968
1987	1,290	522

1. Flux density of photosynthetically active radiation (quantum sensor LI-190 SA from LICOR, Inc., Lincoln, Nebraska)—phar
2. Flux density of total (long- and short-wave) radiation from the upper and lower hemisphere (net radiation sensor no. 8111 from Schenk, Vienna, Austria)—Q_u resp. Q_l, and total net radiation—Q_n
3. Air temperature at 2.3- and 4.8-m height (spherical 10-kOhm NTC resistors of 1 mm diam. protected by a threefold radiation shield)—T_{a2} resp. T_{a4}
4. Canopy temperature (10-kOhm NTC resistor with radiation shield positioned at

0.5-m height within a dense canopy of a *Styphelia tameiameiae* shrub)—T_c

5. Soil temperature (10-kOhm NTC resistor placed at a depth of 5 cm in uncovered soil)—T_s
6. Air humidity at 0.5 m above the surface (Humicor M 5100 capacitive sensor, CORECI GmbH, Freiburg, FRG)—H
7. Horizontal wind speed at 4 heights above the soil surface (cup anemometers, Thies, Göttingen, FRG)—A
8. Surface (leaf) wetness (self-constructed horizontal, metallic sensor plate of 4 cm diam.)—W
9. Intensity of (vertical) rainfall (rain gauge of 50 cm² surface with drip recording)—R

All sensors were read at intervals of 10 sec by a portable data-logging system consisting of a SHARP PC 1500A pocket computer, a 10-bit analog/digital converting unit, and a 12V car battery. Using the individual calibration factors of the sensors, the computer program was able to calculate means of 10-min periods of the measured parameters. In the case of the NTC resistors, individual cubic polynoms were used for each sensor to convert Ohm values into temperature values. This procedure allowed high-accuracy temperature measurements.

RESULTS

Daily courses of microclimatological parameters were recorded for 15 days from 8 March to 25 March 1988. Because dramatic and sudden changes of weather conditions are one of the most distinctive features of the ecosystems above the inversion layer in Hawaii, we chose the results of 5 days that offered a broad spectrum of cloud cover at the site. These ranged from a day with absolutely no cloud cover to one with a permanent presence of fog and continuous precipitation. Consequently, these days showed widely variable levels of humidity and temperature conditions. The following days were investigated in detail:

13 MARCH: No clouds reached the elevation of the study site during the whole day; the insolation was reduced only temporarily at noon by high cirrus clouds; there was no precipitation, and comparatively low wind speeds prevailed.

23 MARCH: No clouds were present at the study site during the morning hours, while at night fog prevailed; high cloud cover profoundly influenced the insolation from noon till the evening; relatively high wind speeds dominated throughout the day, while no precipitation occurred.

16 MARCH: Clouds were present temporarily throughout the day, giving way to a clear sky for only limited periods; there were limited amounts of (vertical) precipitation, and low wind speeds prevailed.

18 MARCH: Clouds were present throughout the day, but only limited amounts of (vertical) precipitation occurred; relatively high wind speed dominated.

15 MARCH: Clouds were present throughout the day; high amounts of (vertical) precipitation occurred and relatively high wind speeds prevailed.

A closer examination of the daily courses of "vertical" precipitation (i.e., rainfall measurable in an open rain gauge), leaf wetness, air humidity, radiation, and vertical temperature distribution on these 5 days follows. Thereafter, conclusions are drawn about the possible underlying causes of the alpine timberline at Mt. Haleakala on Maui.

Precipitation, Leaf Wetness, and Air Humidity

If clouds reach the alpine zone of Maui at Mt. Haleakala during the daytime hours, they are usually the result of orographic uplifting of the northeast trade winds, enhanced by convective lifting of these air masses caused by the heating of the island's surface. During the night, fog may occur regionally in the alpine zone under a clear sky because of intense cooling of the air near the ground. The presence of clouds and fog at the measuring site governs the moisture status of the atmosphere, but does not necessarily lead to (measurable) vertical precipitation.
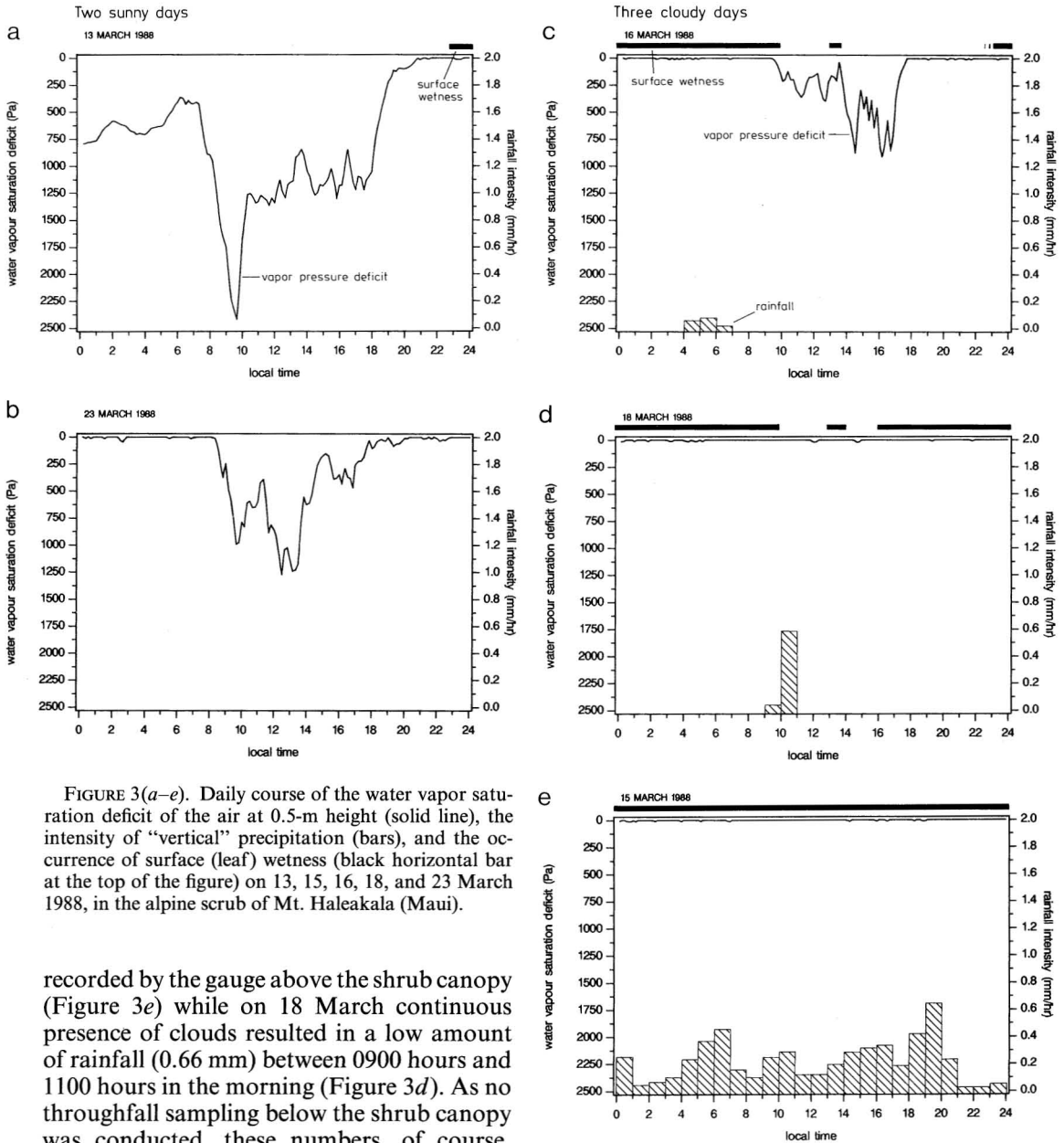
On 15 March about 5.35 mm of rainfall was

FIGURE 3(a–e). Daily course of the water vapor saturation deficit of the air at 0.5-m height (solid line), the intensity of "vertical" precipitation (bars), and the occurrence of surface (leaf) wetness (black horizontal bar at the top of the figure) on 13, 15, 16, 18, and 23 March 1988, in the alpine scrub of Mt. Haleakala (Maui).

recorded by the gauge above the shrub canopy (Figure 3e) while on 18 March continuous presence of clouds resulted in a low amount of rainfall (0.66 mm) between 0900 hours and 1100 hours in the morning (Figure 3d). As no throughfall sampling below the shrub canopy was conducted, these numbers, of course, considerably underestimate the total amount of precipitation captured by the soil surface at the measuring site (see Ekern 1964, Juvik and Ekern 1978). Because the amount of intercepted mist ("horizontal precipitation") is clearly a function of the leaf area index of the vegetation, much smaller quantities of intercepted water can be expected in the alpine scrub compared to those found in cloud forests (e.g., Baynton 1969, Vogelmann 1973, Juvik and Ekern 1978, Caceres 1981, Herwitz 1982).

The persistence of clouds on these 2 days (15 and 18 March) is reflected in continuous saturation of water vapor in the air (Figure 3d

and *e*). In contrast, remarkably high saturation deficits can develop under conditions of clear sky (see 13 March, Figure 4*a*) and elevated air temperatures (Figure 6*a*), when up to 2500 Pa were reached (13 March, Figure 3*a*). Because air humidity was measured within the canopy of a *Styphelia* shrub, the values can be considered as affecting the plants directly.

On clear days, the saturation deficit corresponds to the daily course of air temperature. Moreover, saturation deficit seems to be influenced by the conditions of the previous night: full atmospheric saturation overnight as on 23 March (Figure 3*b*) or 16 March (Figure 3*c*) yields lower daytime saturation deficits than nights with deficits as on 13 March (Figure 3*a*).

During daytime hours, marked overheating of leaves, combined with high saturation deficits in the surrounding air, result in large leaf-to-air vapor pressure differences and point to situations in which the plants face high water vapor demands of the atmosphere. Such steep gradients, which are perhaps typically endured by high-elevation plants, are reinforced by a high diffusion constant of water vapor in air. The diffusion constant, which is dependent on both temperature and air pressure, shows, in most cases, greater values at high than at low elevations (Smith and Geller 1979).

Leaf wetness may influence leaf temperature and transpirational water loss during daytime hours. In this alpine environment, diurnal leaf wetness seems to be a consequence of mist precipitation. This is evident from data taken on 15, 18, and 16 March (marked as a black horizontal bar at the tops of Figure 3*c*, *d*, *e*). During the night both dewfall and mist precipitation from moving fog may cause leaf wetness. Zero or small temperature differences between the plant canopy and the surrounding air, as observed during the night on 15 and 18 March, and even around midnight on 13 March, indicate the presence of overnight clouds or fog that caused surface wetness (Figure 7*a*, *d*, *e*). On the other hand, the pronounced lower temperature of the plant canopy as compared to the air temperature during the night hours of 16 March points to dew rather than fog as the cause of leaf wetness (Figures 7*c* and 3*c*).

Radiation

The two most ecologically important components of radiation are photosynthetically active radiation, which supplies the energy for photosynthesis, and total net radiation (i.e., the difference between the incoming and outgoing short- and long-wave radiation fluxes), which governs the process of evapotranspiration. Both components were investigated directly in this study. In the case of the net radiation only positive values (from daytime periods) are depicted in the figures, since no negative voltage input (which occurs overnight) was recorded by the data-logging system.

As expected for high tropical mountains, maximum flux densities of photosynthetically active radiation were high, with 2500 μmol photons $(\mu E) \cdot m^{-2} \cdot s^{-1}$ recorded, for example, on 23 March (Figure 4*b*, solid line). Such high values are comparable to those obtained for desert regions in California (Björkman et al. 1972). They may be even higher on Mt. Haleakala under the sun's zenith in June.

A more surprising result is the relative high radiation flux density even on days with closed cloud cover and precipitation, such as on 15 and 18 March, when average daytime values passed 800 μmol $\cdot m^{-2} \cdot s^{-1}$. Peak values under these conditions reached at least 1800 μmol photons per square meter and second (Figure 4*e* and *d*). This is also demonstrated by the daily sums of photon gain per square meter, which are shown in absolute values (mol photons $\cdot m^{-2} \cdot s^{-1}$) and as percentage values of the brightest day (13 March) in Table 3.

In contrast, values as low as 350 μmol photons $\cdot m^{-2} \cdot s^{-1}$ at 1500 hours on 23 March indicate weather conditions in which the radiation attenuation was much more effective (see Figure 4*b*). It is obvious that, depending upon its thickness and density, a closed cover of clouds or fog only in some cases reduces
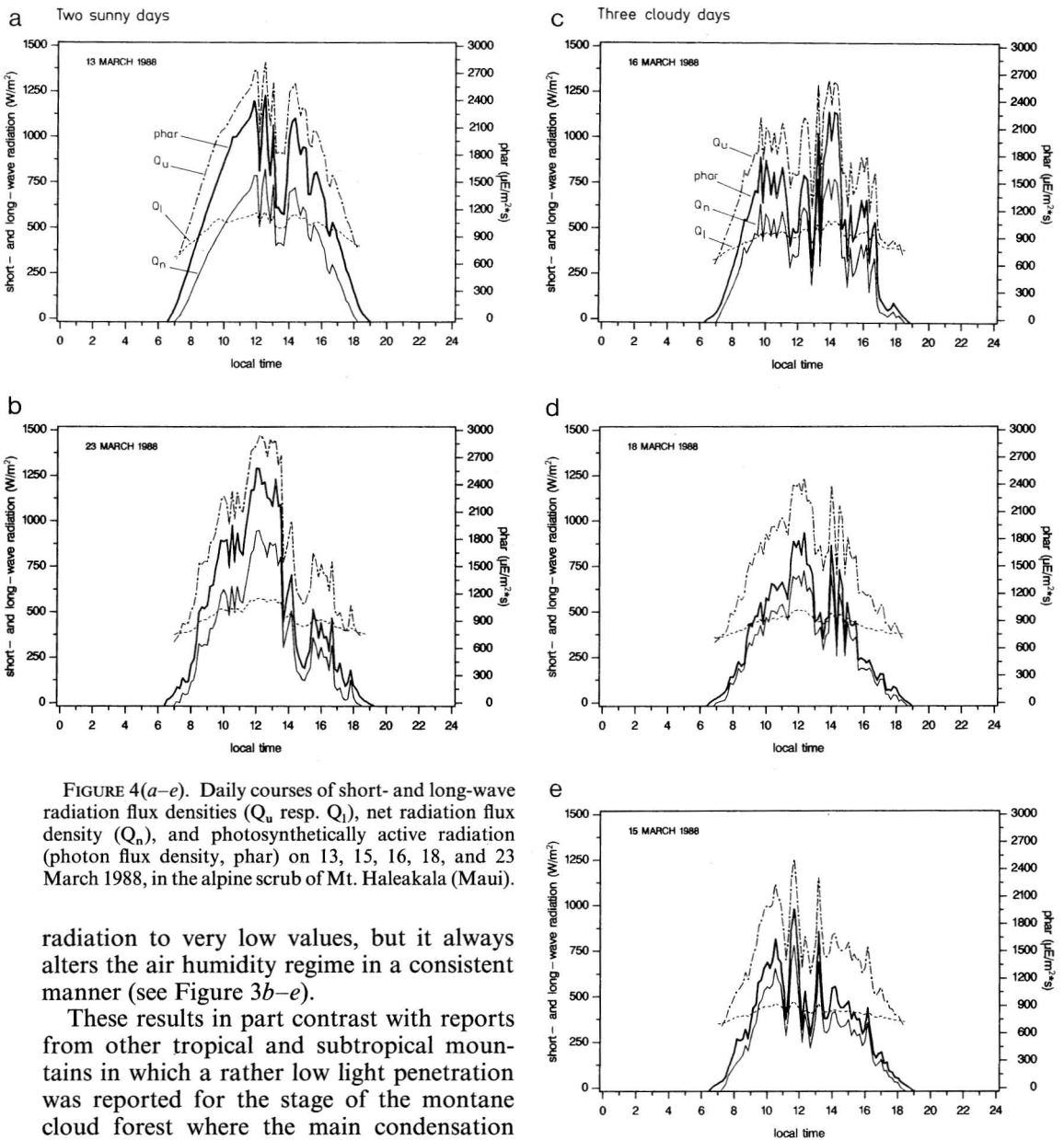
FIGURE 4(a–e). Daily courses of short- and long-wave radiation flux densities (Q_u resp. Q_l), net radiation flux density (Q_n), and photosynthetically active radiation (photon flux density, phar) on 13, 15, 16, 18, and 23 March 1988, in the alpine scrub of Mt. Haleakala (Maui).

radiation to very low values, but it always alters the air humidity regime in a consistent manner (see Figure 3b–e).

These results in part contrast with reports from other tropical and subtropical mountains in which a rather low light penetration was reported for the stage of the montane cloud forest where the main condensation occurs (e.g., Budkowski 1966, Grubb and Whitmore 1967, Huber 1976). The particularly high phar values found under cloud cover at Mt. Haleakala may in part be explained by the location of the measuring site close to the average upper limit of the condensation level that coincides with a thinner cloud cover.

Radiation flux at the measuring site was subject to marked changes over short time spans even in the absence of cloud cover. High-altitude cirrus clouds can cause reductions in light gain at high elevations on Mt. Haleakala. Such clouds may explain the fluctuations seen in Figure 4a and b.

TABLE 3

DAILY SUMS OF PHOTON GAIN (Mol Photons per m^2 and Day) AND DAILY MEANS AND EXTREMES OF AIR (T_{a2}), CANOPY (T_c), AND SOIL TEMPERATURE (T_s, °C) OF THE FIVE INVESTIGATED DAYS IN MARCH 1988 AT THE STUDY SITE

	PHOTON GAIN		T_{a2}			T_c			T_s		
DATE	Sum	%*	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.
13 March	56.52	100.0	11.0	17.2	2.9	11.9	26.0	0.9	10.9	19.9	5.7
23 March	47.49	84.0	11.4	17.5	8.0	12.7	22.5	8.0	12.6	19.9	9.1
16 March	43.03	76.2	9.5	16.3	4.0	9.6	19.9	2.3	11.0	16.5	7.2
18 March	33.48	59.2	10.6	14.6	5.5	11.2	17.3	3.7	13.1	18.7	10.1
15 March	32.05	56.7	8.9	12.6	4.6	9.4	14.4	4.8	12.0	16.6	9.3

*Percentage values of the total on 13 March.

The flux densities of total incoming and outgoing radiation of 0.3- to 60-μm wavelength are also depicted in Figure 4a–e. The curve of incoming radiation (upper hemisphere of the sensor, Q_u) includes short-wave solar radiation and long-wave sky radiation, whereas the curve of outgoing radiation (lower hemisphere of the sensor, Q_l) consists of reflected short-wave solar radiation and long-wave surface radiation. The difference between both fluxes (total net radiation, Q_n) represents the energy to be converted on the surfaces of vegetation and soil. A major part of it is consumed by the process of evapotranspiration and through heating of plant material.

Surprisingly high net radiation flux densities were recorded under complete cloud cover (see 15 and 18 March, Figure 4d and e), a relationship found applicable also for the photosynthetically active radiation. On cloudy days, lower values of incoming total radiation corresponded also to smaller values of outgoing total radiation, mainly due to a lowered long-wave surface radiation. This led to only moderately lower values for the net radiation flux density on cloudy or misty days as compared to sunny days (420 to 850 W·m^{-2} for sunny days and 220 to 780 W·m^{-2} for misty days around noon). Consequently, even under conditions of permanent cloud cover, high amounts of energy were available during daylight hours at the study site, which caused either high evapotranspiration rates or a pronounced heating of the vegetation and exposed soil surface.

Temperature

The temperature regimes of air, vegetation, and soil on tropical mountains are governed mainly by the net radiation flux density at the site, which is also a function of elevation. A characteristic feature of the vertical temperature gradient on mountains intercepted by trade winds in the subequatorial tropics is the presence of a marked and relatively stable temperature inversion that ranges from about 1000 to 2500 m above sea level and shows a temperature increase with elevation of ca. 0.0115 K·m^{-1} (Ficker 1936). This inversion layer marks the upper limit of the orographic lifting of trade wind air masses and is usually found at about 2500 m on Hawaiian mountains (Lavoie 1967). The study site must be close to the lower limit of the inversion layer on Mt. Haleakala.

The daily courses of air temperature at heights of 2.3 (T_{a2}) and 4.8 m (T_{a4}), canopy temperature (T_c), and soil temperature at a depth of 5 cm (T_s) during the 5 days analyzed are depicted in Figure 6a–e. The two sunny days, 13 and 23 March, and also 16 March, show higher daily temperature maxima, higher daily temperature amplitudes, and, generally, higher daily mean air and canopy temperatures (see Table 3) than days with prolonged misty or cloudy periods (15 and 18 March). Temperatures below freezing did not occur during the measuring period, and, because March is one of the colder months of the year, it can be assumed that frost is a rare event at that elevation on Mt. Haleakala. The lowest
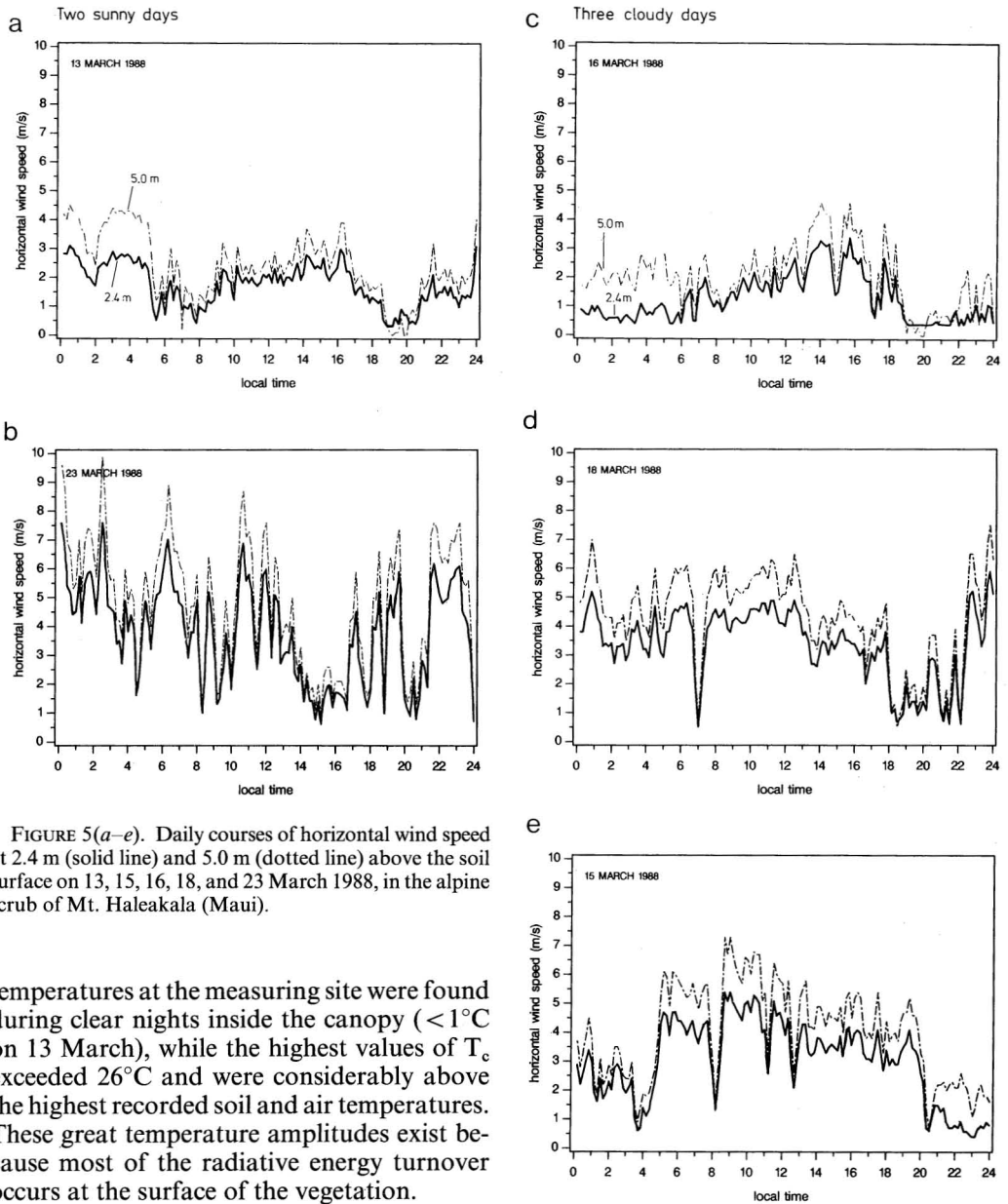
FIGURE 5(*a–e*). Daily courses of horizontal wind speed at 2.4 m (solid line) and 5.0 m (dotted line) above the soil surface on 13, 15, 16, 18, and 23 March 1988, in the alpine scrub of Mt. Haleakala (Maui).

temperatures at the measuring site were found during clear nights inside the canopy ($< 1°C$ on 13 March), while the highest values of T_c exceeded $26°C$ and were considerably above the highest recorded soil and air temperatures. These great temperature amplitudes exist because most of the radiative energy turnover occurs at the surface of the vegetation.

Temperature gradients between air and vegetation, between air and soil, and between the air at different heights above the soil reveal insights into the processes of energy turnover under different weather conditions (Figure 7*a–e*). On a clear day the shrub canopy may show a temperature of up to 10K (degrees Kelvin) higher than the surrounding air. [In this paper degrees Kelvin are used in the case

of temperature differences, degrees Celsius (°C) in the case of actual temperature values ($0°C = 273.15K$).] High radiation loads and a comparably low thermal conductivity of the air at these elevations are considered the main causes. Considerable overheating of plant surfaces at high elevations on tropical and sub-
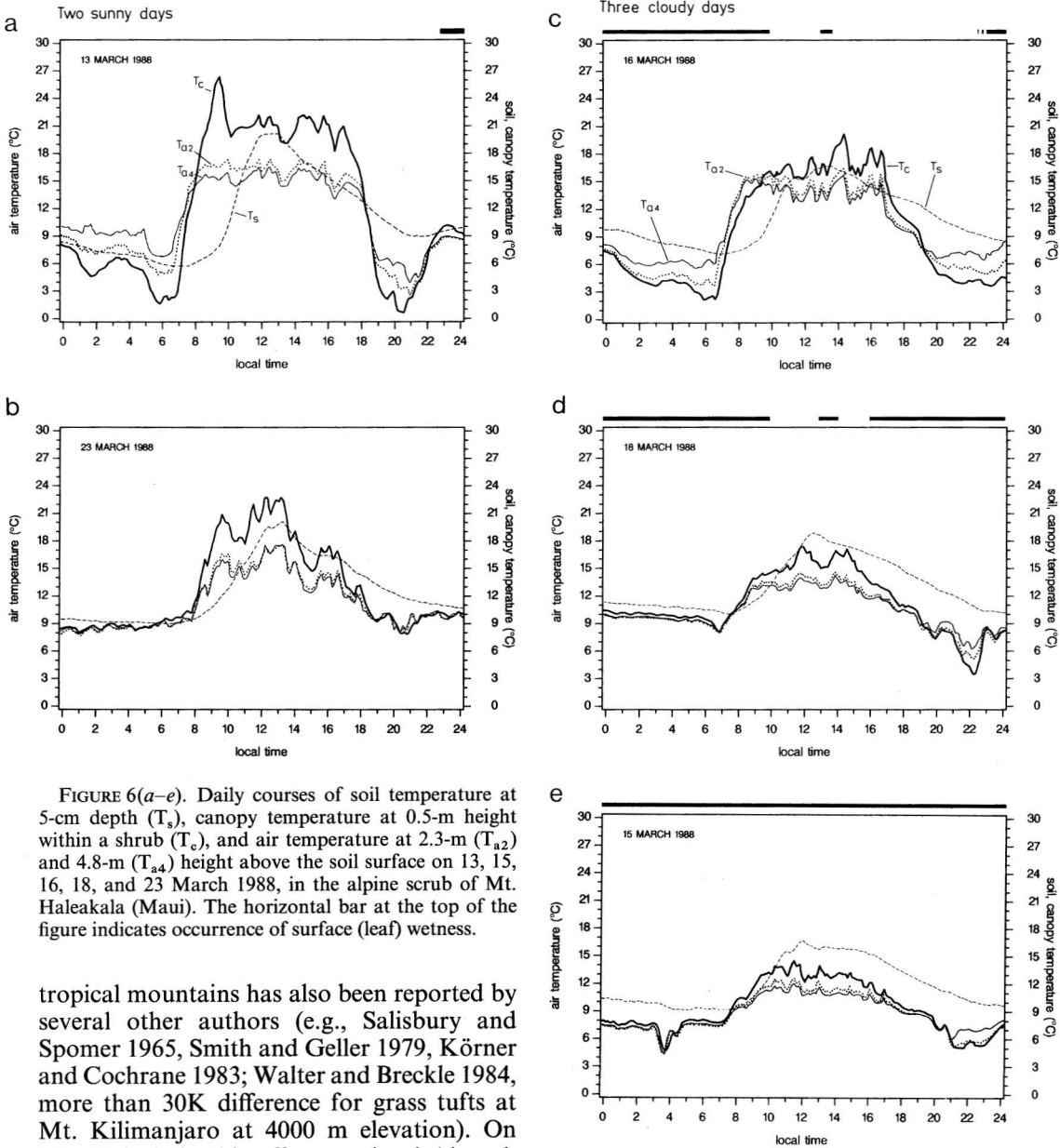
a   Two sunny days

c   Three cloudy days

b

d

FIGURE 6(*a–e*). Daily courses of soil temperature at 5-cm depth (T_s), canopy temperature at 0.5-m height within a shrub (T_c), and air temperature at 2.3-m (T_{a2}) and 4.8-m (T_{a4}) height above the soil surface on 13, 15, 16, 18, and 23 March 1988, in the alpine scrub of Mt. Haleakala (Maui). The horizontal bar at the top of the figure indicates occurrence of surface (leaf) wetness.

e

tropical mountains has also been reported by several other authors (e.g., Salisbury and Spomer 1965, Smith and Geller 1979, Körner and Cochrane 1983; Walter and Breckle 1984, more than 30K difference for grass tufts at Mt. Kilimanjaro at 4000 m elevation). On Mt. Haleakala this effect persisted (though mitigated) even during periods of closed cloud cover, which reflects the high net radiation fluxes under these weather conditions (see above). Cover by fog or clouds at night prevents the shrub canopy from cooling to temperatures lower than that of the surrounding air.

Because of the high heat capacity of soil, cooler soil (at 5-cm depth) prevails in the morning hours, while the afternoon and night generally show a soil temperature greater than the air temperature. These results are in agreement with the findings of Walter (in Walter & Breckle 1984) on tropical mountains of South America, where the temperature of the soil surface averages about 2 to 3K greater than the air temperature while temperatures of soil
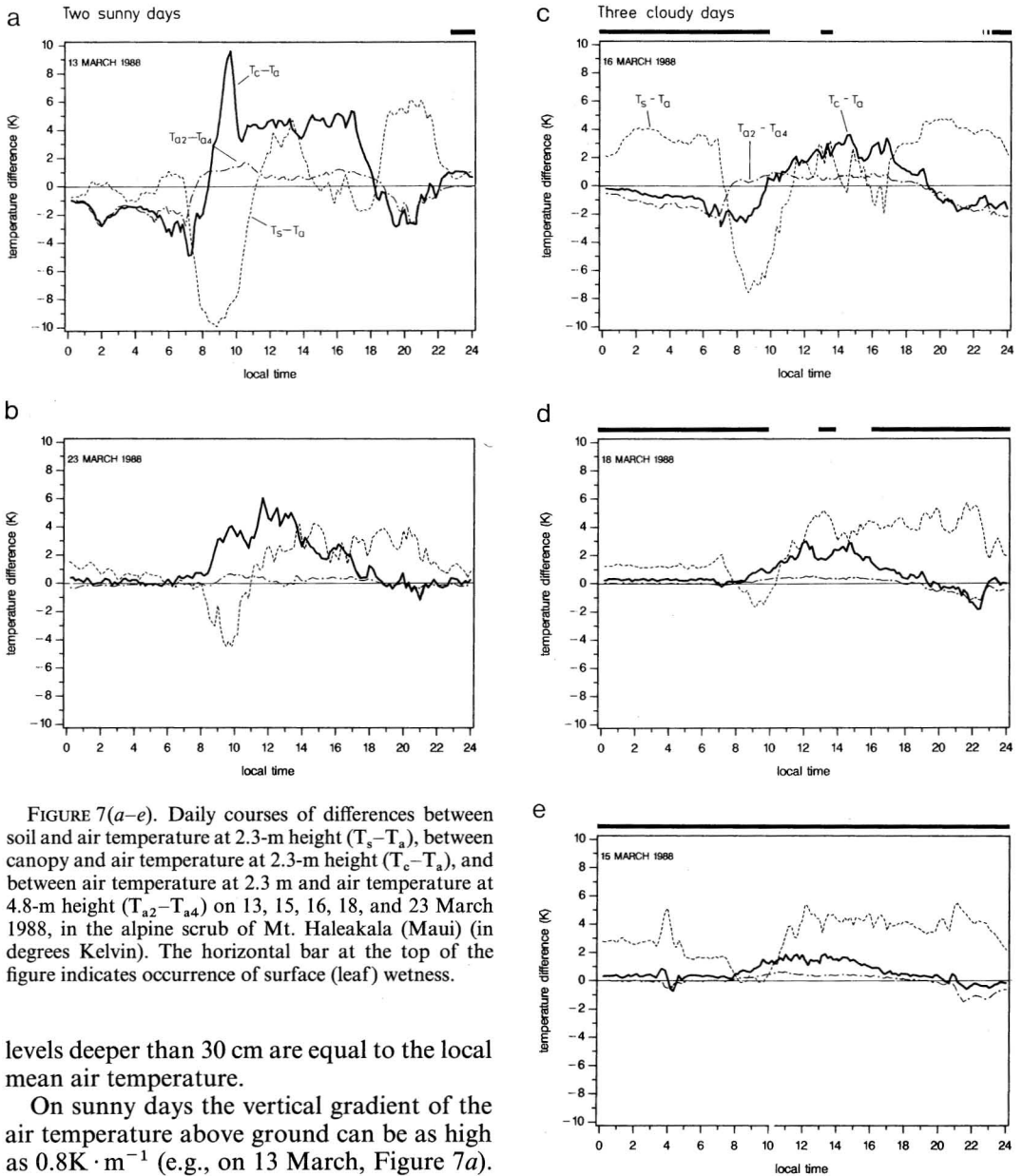
FIGURE 7(a–e). Daily courses of differences between soil and air temperature at 2.3-m height (T_s–T_a), between canopy and air temperature at 2.3-m height (T_c–T_a), and between air temperature at 2.3 m and air temperature at 4.8-m height (T_{a2}–T_{a4}) on 13, 15, 16, 18, and 23 March 1988, in the alpine scrub of Mt. Haleakala (Maui) (in degrees Kelvin). The horizontal bar at the top of the figure indicates occurrence of surface (leaf) wetness.

levels deeper than 30 cm are equal to the local mean air temperature.

On sunny days the vertical gradient of the air temperature above ground can be as high as $0.8 \text{K} \cdot \text{m}^{-1}$ (e.g., on 13 March, Figure 7a). This points to high vertical transports of sensible heat from the overheated plant and soil surfaces.

Alpine Timberline on Maui: Possible Causes

In tropical regions, both temperature and water regime show distinct air pressure–induced alterations as elevation increases. Temperature generally decreases with eleva-

tion and seems to be the major limiting factor for tree growth at the upper timberline in mountains of the humid tropics (Troll 1959, Ellenberg 1966, Walter and Medina 1969, Lauer 1975, Lauer and Klaus 1975, Walter and Breckle 1984).

Plant water availability reveals a much more complicated dependence on elevation,

because several ecologically significant factors are interconnected. In general, tropical mountains show a vertical rainfall distribution pattern with a maximum level that falls between the mountain base and an elevation of more than 2500 m, depending on the climatic regime and the regional atmospheric circulation system (Lauer 1976). According to Weischet (1969) this level is found on humid tropical mountains predominantly at elevations between 900 and 1300 m (as on Mt. Haleakala, see above), whereas in semiarid subtropical mountains the maximum level can move to heights of up to 2500 m above sea level. A constant decrease of precipitation with rising elevation above this maximum is probably only to be found on isolated mountain peaks. In contrast, extended mountain systems on the larger continents are subject to a pronounced heating of mountainous plateaus, resulting in a further convective uplifting of air masses and consequently a second, less remarkable, rainfall maximum at greater heights (e.g., at 3000 m elevation in Mexico [Lauer 1976]).

To assess plant water availability in alpine environments, one must consider not only the amount of precipitation but also the intensity of evapotranspiration and the water-holding capacity of the soil. In a mainly theoretical investigation, Smith and Geller (1979) compared plant transpirational fluxes at high elevations with those of desert sites at sea level. They found that for alpine ecosystems "plant transpiration may be potentially as severe as at low elevation desert sites, even though plant temperatures may be considerably lower." Under most conditions, a decrease of the saturation vapor pressure of the air with rising elevation is balanced by a simultaneous increase of the water vapor diffusivity in the air and the leaf-to-air temperature difference so that little or no decrease of evapotranspiration occurs as elevation increases. It must be remembered that Smith and Geller compared high-elevation evapotranspiration to conditions at low-elevation desert sites.

Following these theoretical considerations, both temperature and plant water availability (or drought) could act as limiting factors of tree growth on high mountains, especially on oceanic tropical islands, and might be responsible for the tropical alpine timberline. Although it is assumed that drought plays a decisive role with respect to the alpine timberline in several semiarid subtropical mountains such as Tenerife (Walter 1968, Höllermann 1978) and central Mexico (Walter 1964, Lauer and Klaus 1975), until now no clear evidence has been reported that points to a drought-induced alpine timberline in a trade wind–intercepting mountain of subequatorial tropical islands.

Though only covering a rather limited period during the colder months of the year, the results of this microclimatological study provide evidence that the thermic conditions probably are not the most decisive cause of the upper height limit of tree growth on the windward slopes of Mt. Haleakala on Maui. Daily mean air temperatures of 8.9 to 11.4°C (with soil temperature averaging between 10.9 and 13.1°C at a depth of 5 cm) in the colder months of the year in the vicinity of the timberline are at least 2 to 3 degrees higher than timberline temperatures reported on other tropical mountains. Walter and Medina (1969) concluded that an annual mean soil temperature of 7°C (which equals the local mean annual air temperature) seems to be typical for the Andean timberline of Venezuela. For the subalpine belt on Mt. Kilimanjaro a mean temperature of about 8°C is assumed at the timberline (Walter and Breckle 1984). H. Ellenberg (pers. comm.) found a mean soil temperature of about 5°C at the upper timberline in various parts of the Peruvian and Bolivian Andes. Similar to what is found on Hawaii (where Mueller-Dombois and Krajina [1968] specify 2900 m and 2450 m for Mauna Kea and Mauna Loa, respectively, as the height of the treeline), the diurnal frost boundary is situated several hundred meters above the actual timberline within the alpine scrub at Mt. Haleakala on Maui.

The vertical distribution of rainfall on the windward slopes of the extremely oceanic Hawaiian Islands of Maui and Hawaii shows a pattern that differs from that of most of the other humid tropical mountains in two ways: (1) The high moisture content of the ascending trade winds together with minor convective uplifting forces result in a relatively low

height (maximum at about 1000 to 1500 m on Mt. Haleakala) of the condensation level on these relatively small islands compared to that of continents or other larger islands, while no second rainfall maximum occurs at higher elevations (compare Lauer 1976). (2) The temperature inversion that limits uplift of the trade winds in the mountains shows great stability in the maritime subequatorial tropics, while it is less stable on continental mountains in the equatorial tropics (Blüthgen 1966, Dohrenwend 1972, Riehl 1979). This leads not only to a very steep decrease in precipitation above the inversion layer at about 2200 to 2500 m on Maui (Giambelluca et al. 1986), but also results in elevated temperatures at that height.

The alpine shrubland on Mt. Haleakala is marked by high net radiation fluxes, relatively high temperatures (at least in its lower section), a regional minimum of precipitation (though in part compensated by an unknown amount of "horizontal" precipitation), and a soil of low water-holding capacity on young lava flows. Consequently, climatic aridity, defined here as the relation between rainfall and potential evaporation, greatly increases above the elevation of the timberline and the inversion layer. The climatic aridity seems to be reflected in the gradual change from dense alpine shrubland at about 2200 m elevation to an alpine desert at 3000 m height. Lava-derived soil types, rich in crevices and poor in fine-grained substrate, should greatly enhance the effect of aridity on this shield volcano. This should especially be valid for aa lava flows that are found in the vicinity of the study site.

Comparing the east-flank vegetation on Mauna Loa and Mauna Kea on Hawaii, Mueller-Dombois and Krajina (1968) found the treeline on Mauna Loa to be 450 m lower than that on Mauna Kea. The substrate at the treeline on the younger Mauna Loa is lava and on older Mauna Kea it is soil derived from cinder. It appears that a more favorable soil water regime on older soils can lower the effect of drought in this alpine environment.

The fact that the timberline is situated about 300 to 400 m higher on northeastern windward slopes of Kalapawili ridge (where clouds are common) compared to adjacent arid southern slopes inside Haleakala Crater seems to provide further evidence for the lesser role of temperature as a cause of the timberline on East Maui.

We conclude that the alpine timberline on Maui is caused by a set of interacting factors, with plant water availability the most important. Other factors, such as browsing by feral goats (see Mueller-Dombois 1967, Yocom 1967, Stone and Loope 1987) and fire, doubtless have influenced the timberline on a regional scale, but their contribution in general is unclear. In contrast to most other humid tropical mountains, temperature regime seems to be of lesser importance, probably because of the highly isolated, oceanic situation of the Hawaiian Islands, which causes a characteristic vertical distribution pattern of rainfall. With its relatively dry summer season, the climate of the alpine zone of the Hawaiian Islands shows similarities to the Mediterranean climate. Periodic water shortage is enhanced by an "edaphic aridity" in lithosols and young lava-derived soils with high infiltration rates (Schwarzbach 1964). Under the extreme radiation regime of the tropical alpine region, both climatic and edaphic aridity result in at least occasional drought that restricts tree growth at higher elevations. Finally, the very limited number of native tree species in the highly isolated flora of the Hawaiian archipelago may by itself contribute to the extraordinary situation with respect to the alpine treeline. One could speculate that woody species fully adapted to the unique climatic conditions of the tropical alpine treeline are lacking in these islands, leaving the field to the dominating Hawaiian rainforest species *Metrosideros collina polymorpha* (Myrtaceae) and, in the case of Mauna Kea on Hawaii, to *Sophora chrysophylla* (Fabaceae) (Mueller-Dombois and Krajina 1968).

Further investigation is required to attain a more comprehensive explanation of the alpine treeline and its causes in the Hawaiian Islands.

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