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Ecological Features of Climate in High Tropical Mountains

GUILLERMO SARMIENTO

Climate and soil are the basis and substrate of all life, vegetal and animal. High tropical mountain climates, extremely peculiar in their combination of features, are examined here for the first time in intra- and intercontinental comparisons involving all major high tropical mountains of the world.

After defining tropical climates in general I will then discuss tropical mountain climates. This will be followed by detailed analysis of climatic variables pertinent to the establishment and maintenance of life on tropical mountains (the Andes, Mexico, East Africa, New Guinea). Finally I will summarize common patterns and ecologically crucial features, in order to set the stage for the rest of the book, where climate will be discussed only in a more local or regional fashion, or if appropriate to the theme of each chapter.

TROPICAL CLIMATES AND HIGH MOUNTAIN CLIMATES

Particular Features of Cyclic Changes in the Tropics

Cyclic changes in the tropics are best illustrated by comparing solar radiation along a latitudinal gradient from the equator (0°) to middle latitudes (50°) (Table 2–1). On the equator, the daily total amount of solar radiation at the equinoxes, when it reaches its annual maximum, is only about 13 per cent higher than the minimum amount of radiation intercepted at the solstices (Table 2–1, first line). At first this percentage increases slowly with latitude, together with solar declination at the solstices, so that at 23° 27′ (at the tropics) the annual range of extraterrestrial irradiation is still only about 60% of the winter solstice minimum (third line of Table 2–1). This percentage increases sharply outside the tropical belt, and reaches almost 400% at 50° latitude North and South (line four of Table 2–1). That is, at this middle latitude, the amount of solar radiation at the top of the atmosphere on midsummer day is nearly five times that of the daily value at the winter solstice. (At ground level, insolation at low latitudes, though variable locally, also maintains constantly high values throughout the year, in contrast with the strongly seasonal radiation climate of temperate zones.)

These figures help us to understand one of the most essential climatic characteristics opposing the intertropical regions to the rest of the earth's surface, in other words, the relative annual constancy in daily solar radiation, both in the upper atmosphere and at the earth's surface, and its well-known consequence, the low seasonal variability in mean air temperature. Therefore, tropical climates differ sharply from middle- and high-latitude climates in having very reduced month-to-month variation in both mean temperatures and day length, a fact that surely permit us

TABLE 2–1. Annual range of daily solar radiation at the top of the atmosphere at various latitudes.

Latitude	Daily max cal/cm^2/day	Daily min cal/cm^2/day	$\frac{\text{Maximum}}{\text{Minimum}}$	$\frac{\text{Max} - \text{min}}{\text{min}} \times 100$
0°	930	820	1.13	13.4
10°N	905	760	1.19	19.1
23° 27′N	980	610	1.61	60.7
50°N	1030	210	4.90	390.5

Data from List (1971).

to consider tropical environments to be remarkably constant. (Seasons do not have the same meaning in the tropics as in higher latitudes, even when they can be recognized by rainfall patterns or by slight variations in temperature. Summer and winter will be employed here to mean the six-month period when the sun is over the corresponding or the opposite hemisphere.)

Climatic constancy has been utilized to circumscribe the area under tropical climates, either by defining as tropical those regions where differences in temperature between the warmest and the coldest months are smaller than the average daily range, or by applying the criterion of a maximum threshold in annual variation in temperature, usually 10°C. Either criterion produces results that do not differ significantly. Near the oceans, the limits of the tropical zones so defined do not depart much from the tropical parallels, but as one moves to the interior of the continents, increasing continentality and higher seasonality displace the limit of the tropical area toward lower latitudes. The area of tropical climates is thus narrowed.

In contrast to the small variation in daily temperature from month to month, the daily or circadian cycle is quite marked in nearly all tropical regions, making it the major environmental cyclic pulsation. The amplitude between the minimum night temperature and the maximum day temperature (which depends on many factors), is at least 3 times, and frequently more than 10 times, higher than the difference between the means of the coldest and warmest months. Climatic factors such as relative humidity show a regular daily variation inversely correlated with air temperature. As I will discuss later, cloudiness, winds and fogs also vary following a predictable daily pattern according to temperature and air flow induced by heating or cooling of the lower atmosphere.

Besides their year-round constancy in mean temperature, some tropical climates show distinctive patterns in the distribution of precipitation and consequently in relative humidity and soil water availability. Except in the wettest areas where rainfall is more or less evenly distributed throughout the year, or in arid regions (which have a permanent water deficiency), most tropical regions have seasons with heavy rainfall alternating with almost rainless ones. This is particularly true in areas under the direct influence of the trade winds, with their cyclic displacement across the thermal equator. These winds and the atmospheric circulation associated with them are responsible for the widespread occurrence of highly seasonal rainfall climates within tropical latitudes. By contrast, in regions under the influence of the equatorial trough, where air convection predominates, the two rainy seasons correspond with each passage of the sun across the equator, and the two dry seasons coincide with the solstices.

Irrespective of the causes of rainfall seasonality, many tropical areas have either two or four distinct and highly contrasted seasons, including rainless periods that extend from 1 to 6 or 7 months. This annual pulsation may induce slight but significant changes in the temperature regime. Since high cloudiness prevails during the rainy seasons, the total solar radiation at ground level decreases, whereas high relative humidity at night greatly diminishes the coldness due to longwave outgoing radiation from the ground and vegetation. These combined effects decrease the amplitude of daily temperature variation. The opposite conditions prevail during the rainless periods, when low cloudiness, clear skies, and dry atmosphere lead to higher day and lower night temperatures, that is, an increase in the amplitude of daily temperature fluctuations. In this way, seasonality in rainfall brings thermoperiodism, an annual cycle with dampened temperature oscillations and higher night minima during the wet seasons and with greater temperature fluctuations and lower night minima during the dry seasons. I describe later how this variability in daily oscillations of temperature combined with humidity seasons becomes a conspicuous feature of high-altitude climates.

Altitudinal gradients represent the most obvious axes of climatic and ecological variability in the tropical zone. In any large mountain mass, every type of temperature and humidity regime may be encountered along gradients from the warm lowlands to the nival summits. Indeed, the whole range of temperature and rainfall that exists over the nontropical parts of the planet may be found in tropical regions, the values at any tropical site being strongly dependent on that site's altitude above sea level. In wet tropical mountains air temperature decreases at an average rate of about 0.6°C per 100 m elevation, with slight variations according to local conditions. The altitudinal gradient in temperature determines the occurrence of the various thermal belts classically recognized by biogeographers in tropical mountains (van Steenis, 1935; Weberbauer, 1945; Cuatrecasas, 1958; Boughey, 1965).

Without entering into details of vertical zonation, I want to remind the reader that rainfall varies much more than temperature in tropical mountains since rainfall heavily depends on the precise geographic conditions of each mountain system. Lauer (1976) analyzed these patterns along the slopes of various tropical mountain regions. His data show that, as a general rule, the amount of precipitation increases from low altitudes to a maximum at a middle altitude, roughly corresponding to the occurrence of montane or cloud forests, and then decreases more or less steadily to the highest elevations. Later I will consider some of these patterns with particular reference to the upper belts.

Environmental Pulsations in High Tropical Mountains

The position of the tropical belt on the planet and the general circulation of air masses at low latitudes are responsible for the major features of tropical climates. Tropical highlands should therefore have the same kind of environmental rhythm as the lowlands. The relatively high variability of daily cycles, contrasting with the relatively low variability of yearly cycles, are thus the major features of tropical mountain climate. Having emphasized the overwhelming importance of 24-hour cycles, I now want to consider in more detail the specific features that distinguish tropical highlands from tropical lowlands. I will discuss, first the main patterns of temperature and precipitation, then some major trends of geographical variation in the various mountain systems and finally the climatic characteristics of a few well-known localities.

In the tropics high-altitude areas are the sole regions where low temperature predominates and is an important factor in plant, animal, and human life. According to the vertical lapse rate, at about 3000 m mean annual temperature is about 10°C. Average daily ranges remain below 15° in wet mountains up to the altitude of permanent snow (about 4700 m). As month-to-month variation is inconspicuous, the temperature of 10°C roughly corresponds to the climatic boundary between montane and páramo climates, that is, between G and H types in the Koeppen system of classification adapted to mountain climates (Andressen and Ponte, 1973). Irrespective of whether this classification is indeed applicable to tropical mountains, on wet slopes at least this boundary roughly coincides with the first appearance of freezing temperatures, in the form of a few days of frost that can occur at any time of the year.

Frost occurrence can surely be assumed to have great significance as an ecological boundary for tropical, warm-adapted life. On humid slopes, this frost boundary is located between 3000 and 3300 m and corresponds with the upper limit of montane forests, which are replaced by páramo formations (grassland and scrub) higher up. The frequency of frost increases slowly with higher altitudes, to about 100 frost days at 4500 m, and then more rapidly to attain the nival limit between 4700 and 4900 m (Fig. 2–1). On dry mountains, frost starts at somewhat lower elevations, but the limit of permanent snow may be as high as about 6000m. As one approaches the border of the tropical zone, as in the Mexican volcanoes, freezing temperatures begin at much lower altitudes and the altitudinal increase in number of frost days per year is more gradual.

Several outstanding environmental consequences on living organisms follow from these facts. First, temperature remains so low most of the time that adaptations to cold are necessary for survival. Second, perennial species must have mechanisms of frost resistance. Third, these adaptations have to be permanent, since there is no definite growth season in tropical mountains, unlike temperate mountains, and since even with only occasional frosts, the annual frost-free period may be quite short because freezing may occur at any time of the year. This is particularly true in the wettest climates, whereas in sites with a definite dry season, frost days are concentrated in this period. Fourth, as insolation is often fairly low, at least during the rainy periods, and as daylight temperatures remain low also, assimilation and growth in plants may be limited by insufficient light and suboptimal temperatures.

All tropical mountains share the characteristics mentioned above concerning means and oscillations in temperature, but they vary widely in their precipitation regime and hence in humidity conditions. These, in turn, determine the annual regime of frosts. As a general rule, highlands and adjacent windward lowlands have the same rainfall pattern. Thus, in regions influenced by the trade winds, mountain slopes show a clear unimodal seasonality in rainfall, whereas in highlands influenced by the equatorial trough, a distinctive bimodal pattern of precipitation is found. These contrasting precipitation regimes are unrelated to the total amount of rainfall of each locality.

During the rainy seasons an uneven distribution of rainfall is associated with less sunshine, more cloudiness, less total solar radiation, and less heat loss due to terrestrial long-wave radiation. The opposite characteristics prevail during the dry seasons. In this way, a seasonal regime of temperature exists that is obviously not compar-

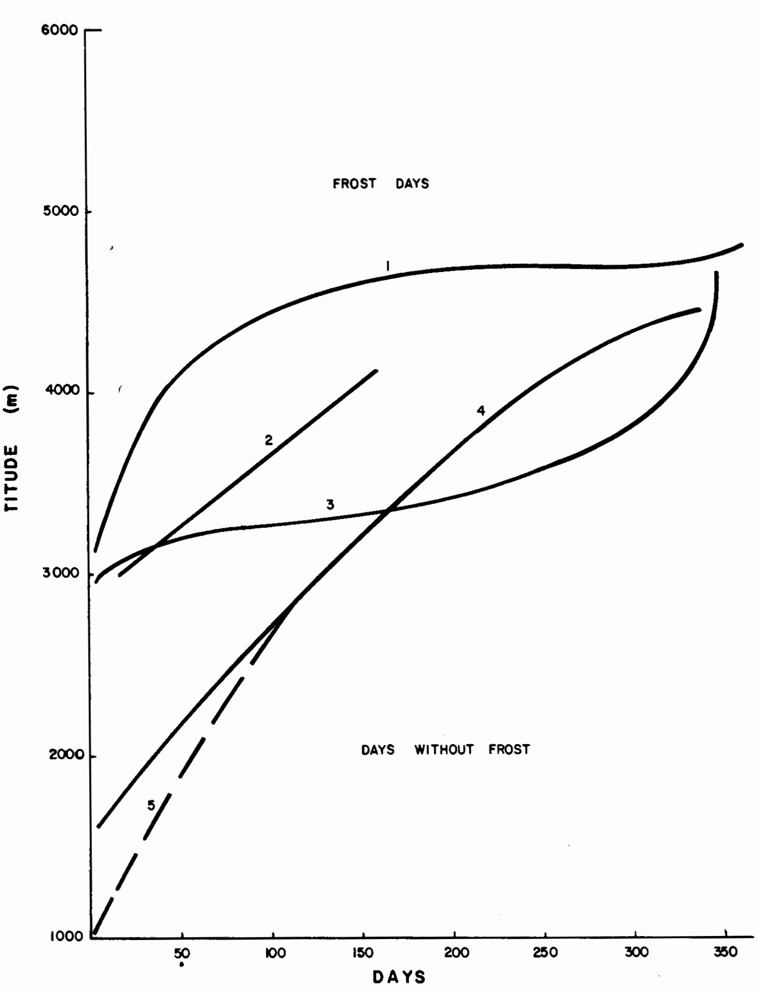

FIG. 2–1. Altitudinal variation in mean number of frost days per year in some American highlands. (1) Sierra Nevada de Mérida, Venezuela; (2) upper Chama Valley, Venezuela; (3) Volcano El Misti, Perú (from Troll, 1968); (4) the Mexican meseta; (5) Sierra Madre Oriental (after Lauer, 1973a, 1973b).

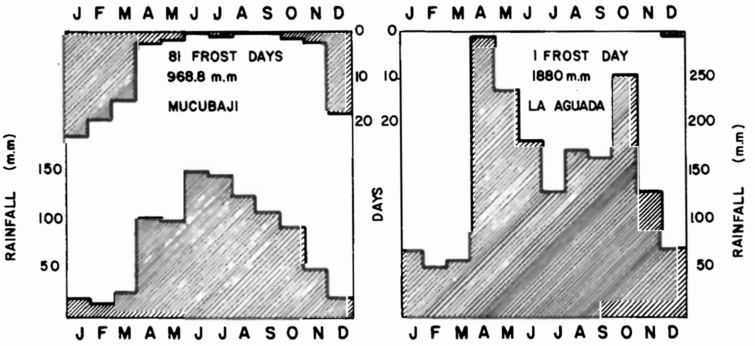

FIG. 2–2. Contrasting patterns of frost distribution in two localities of the Sierra Nevada de Mérida, Venezuela. Both sites are at a similar altitude but differ in amount and distribution of rainfall. Mucubají, the drier site, shows an annual average of 81 frost days, and La Aguada, with almost twice as much rainfall, has a mean of only 1 frost day per year. From Monasterio and Reyes, 1980.

able in intensity with the sharply seasonal mid-latitude climates, but that nevertheless shows a clear annual rhythm since frosts occur mostly during the less rainy periods. A comparison between two sites at similar elevations and only a few kilometers apart in the Venezuelan Andes illustrates this difference (Monasterio and Reyes, 1980). La Aguada has a bimodal rainfall pattern wherein the less rainy months receive more than 50 mm of precipitation, while Mucubají, with a unimodal pattern, has a four-month dry season with less than 100 mm rainfall. Figure 2–2 shows that the dry season at Mucubají is also a very definite frost season, when freezing temperatures occur almost nightly, whereas La Aguada has only very occasional frosts (only three in three years of records, all in December). These differences in frost regime are scarcely reflected in mean monthly temperatures, yet they have great ecological significance. In fact, even in sites with a very strongly seasonal climate, the difference in mean temperature between extreme months is less than 4°–5°C. At Mucubají, for instance, this difference is only 1.2°C; hence seasonality will become apparent only either in the mean minima or in the absolute minimum.

MAJOR GEOGRAPHIC TRENDS IN HIGH-ALTITUDE CLIMATES

After a consideration of the common features of all tropical high-altitude climates, I will provide details concerning the regional patterns of climatic variation within each major tropical highland region. My purpose is not to present a detailed geography of these climates. This would be unrealistic given the paucity of available meteorologic information. Instead, the aim of this section is to sketch the main patterns of climatic distribution and variation to serve as background for the discussions of biogeographic and evolutionary processes occurring in these environments. I start with the Andes, which is the major continuous cordillera crossing the tropics, and will continue with the more discontinuous highlands of Mexico and Central America, tropical Africa, and Malesia.

The Tropical Andes

The Andean cordilleras form a nearly continuous high-altitude chain in western South America, from the southern edge of the tropical zone at 17°–18°S in Bolivia northward to 10°N in western Venezuela (Fig. 2–3). The tropical Andes contain the largest extension of low-temperature areas within the tropical belt of the world. Not surprisingly, in such a huge geographic area that extends latitudinally thousands of kilometers, an amazing variety of climates exists along elevation and latitude gradients. Even restricting myself to the upper belts, I can only sketch a broad picture of environmental variability. As temperature closely depends on the elevation lapse rate, both means and ranges vary with altitude. But as night minima as well as frost frequency are correlated with the timing of rainfall the amount of rainfall and its annual distribution become the two principal climatic factors of ecological importance varying across and along the Andean cordilleras.

Considering altitudinal gradients first, they evidently differ from one latitude to another, and within each main chain, from one slope to its opposite. For example, in the Andes of Mérida (Fig. 2–4), four contrasting slopes have to be considered (Andressen and Ponte, 1973; Monasterio and Reyes, 1980). The southeast slope, facing the llanos, has a unimodal, two-seasonal or tropical rainfall pattern, with a more or less pronounced dry season during the winter, from December to March. Mucubají (Fig. 2–5) shows this type of rainfall pattern. Maximum annual rainfall (about 3000 mm) falls at altitudes between 400 and 800 m (Fig. 2–6). Precipitation gradually diminishes upward to 2200–2400 m, and then more steeply at higher altitudes to less than 800 mm near the summits at 4,200 m. The opposite slope, exposed to the northwest and facing Lake Maracaibo (Fig. 2–4), shows instead a bimodal, four-seasonal or equatorial pattern, with one main dry season in winter and one secondary minimum during the summer months, while the two annual peaks of precipitation correspond to May and

FIG. 2–3. The tropical Andes as delimited by the 2000-m contour. (1) Chita; (2) Aquitania; (3) Chiquinquirá; (4) El Granizo; (5) Chingaza; (6) Popayán; (7) Quito; (8) Izobamba; (9) Cajamarca; (10) Cerro de Pasco; (11) Huancayo; (12) Chuquibambilla; (13) La Paz; (14) Oruro.

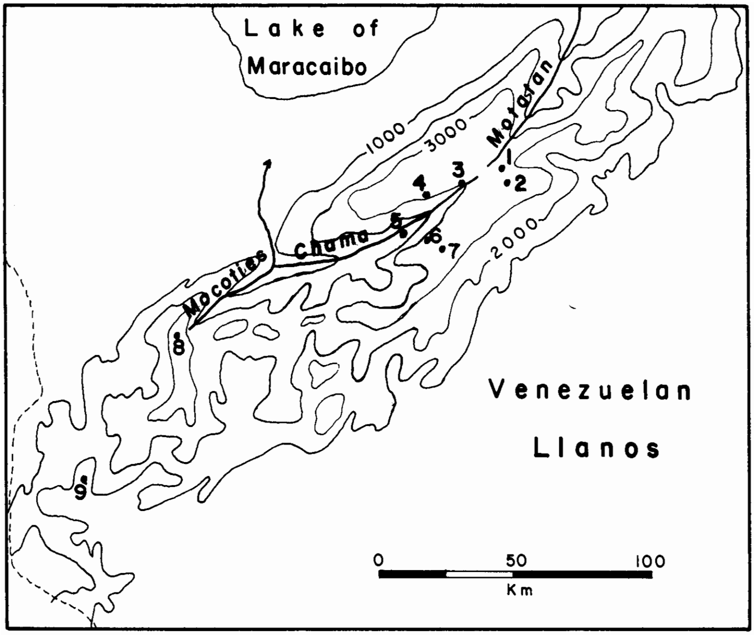

FIG. 2–4. The Venezuelan Andes as delimited by the 1000-m contour. (1) Pico El Aguila; (2) Mucubají; (3) Granja Mucuchíes; (4) La Culata; (5) Mérida; (6) La Aguada; (7) Pico Espejo; (8) Páramo La Negra; (9) San Cristobal.

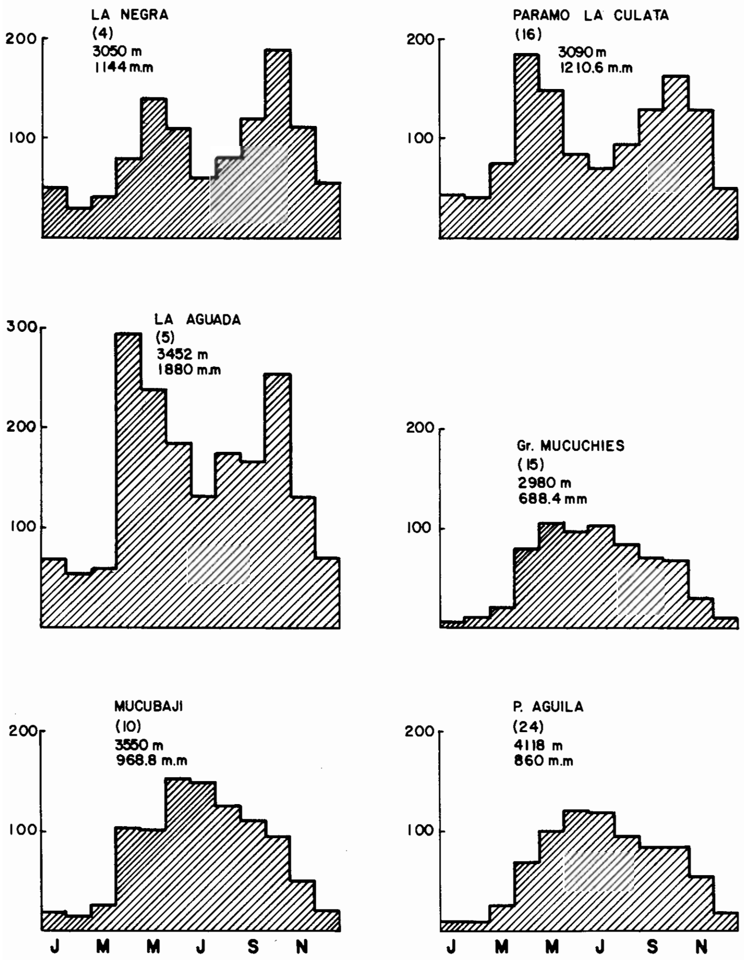

FIG. 2–5. Precipitation patterns in the Venezuelan Andes. Notice the bimodal pattern of La Negra, Páramo La Culata and La Aguada, and the unimodal distribution of precipitation at Granja Mucuchíes, Mucubají, and Pico El Aguila. In both cases the yearly minimum occurs from December to March, that is, in the Northern Hemisphere winter.

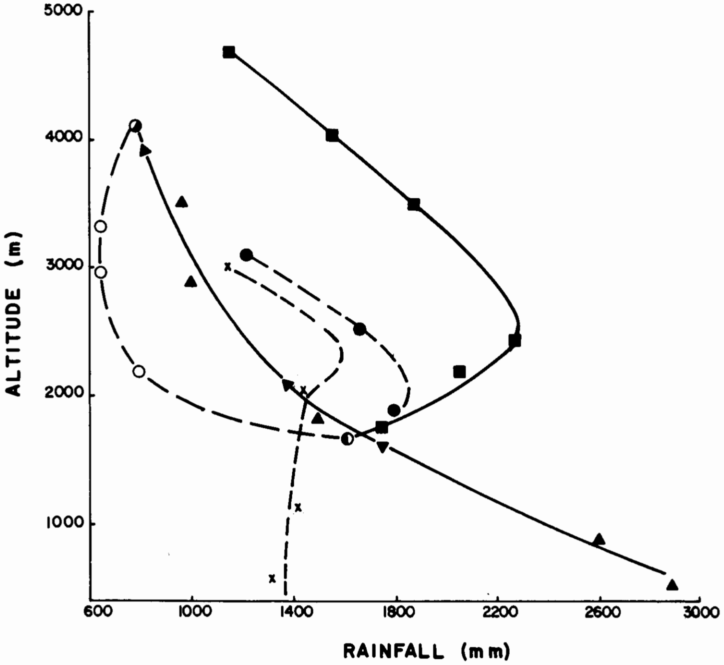

FIG. 2–6. Altitudinal gradients of precipitation in the Andes of Mérida, Venezuela. ▲—▲, SE slope, facing the llanos, where maximum rainfall occurs below 1000 m; ×—×, NW slope, facing the Lake of Maracaibo; ■—■, NW interior slope from Mérida to Pico Espejo; ●—●, SE interior slope from Mérida to Páramo La Culata; ○—○, upper Chama Valley from Mérida to Pico El Aguila.

October, respectively. Páramo La Negra (Fig. 2–5) shows this rainfall pattern. On the Maracaibo side of the cordillera rainfall is about 1400–1500 mm from the lowlands up all along the slope but reaches a small peak between 2000 and 2500 m, where cloud forest occurs (Fig. 2–6).

Furthermore, the Venezuelan Andes are deeply cut by long valleys parallel to the main chains occupying tectonic grabens: the Mocotíes, Chama, and Motatán valleys (Fig. 2–4). Thus, two interior versants appear besides the two external slopes just considered. Both interior versants have a bimodal rainfall distribution like the northwestern side, but the interior northwestern slope is much more rainy than the southeast one, with a maximum of nearly 2300 mm at an altitude of 2400 m in the wettest part of the Chama valley, in the Sierra Nevada National Park. La Aguada (Figs. 2–2 and 2–5), a somewhat higher station within this park, is still a very rainy locality. Precipitation decreases with increasing altitude to 1173 mm at the highest weather station in Venezuela, Pico Espejo at 4765 m, near the glacial tongue of the Pico Bolívar (Fig. 2–6). The southeastern interior versant facing the Sierra Nevada is significantly drier, with a maximum annual rainfall of 1800 mm at about 2000 m, decreasing to 1100 mm at the lower edge of the páramo (3000 m). This amount is nearly 1000 mm less than the opposite slope at the same elevation. Páramo La Culata (Fig. 2–5) is the highest weather station on this slope. As Monasterio and Reyes (1980) pointed out, these contrasting rainfall patterns, together with the vertical and horizontal variation in annual totals, heavily influence minimum temperatures and frost regimes that contribute to the wide diversity of high-altitude environments and to the richness of the biota of the high Venezuelan Andes.

Within the same area of the Andes of Mérida, it is worthwhile to refer to the peculiar situation met with in the upper Chama Valley between 2000 and 3500 m, where under the driest climate of the Venezuelan highlands a diversified agriculture flourishes: irrigation horticulture on alluvial soils, dry farming with potatoes and wheat as main crops on the slopes. In fact, annual rainfall varies from 800 to less than 600 mm with a unimodal pattern where less than 25 mm falls during the four month dry season (Fig. 2–6). Chavez (1962) analyzed the temperature regime in a locality within this area: Granja de Mucuchíes, at 2980 m, where annual rainfall reaches 688 mm (Fig. 2–5). Although the mean monthly temperature varies only from 10.6°C in January to 12.1°C in May, the mean minimum in January is 3.6°C whereas during the rainy season minima always remain above 7°C. In 12 years, an annual average of 16 days with frost was recorded, 15 of them during the dry season. These data corroborate the close association between rainfall pattern and minimum temperature that leads to a sharp decrease in temperature during the nights of the rainless period. In the same area of the Andes, at similar elevations or even 100 or 200 m higher, but with a wetter climate and a less severe

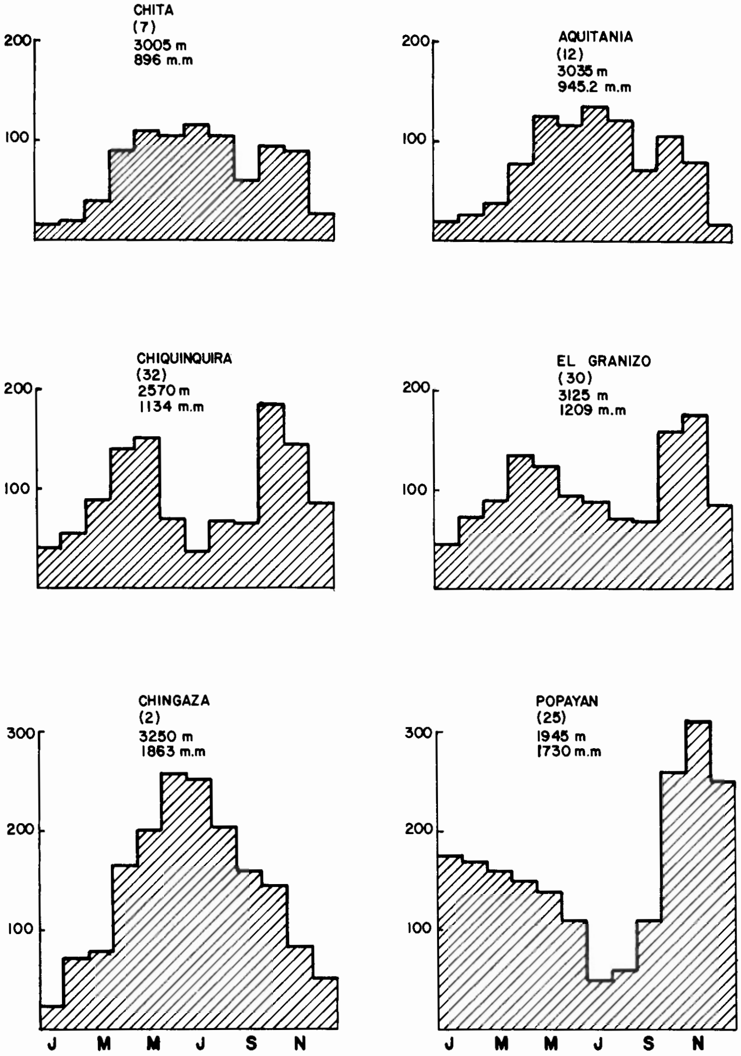

FIG. 2–7. Precipitation patterns in the Colombian Andes. Notice that the bimodal regime with an absolute minimum in the first months of the year, typical of the northernmost localities (Chita and Aquitania), changes to a bimodal pattern with two roughly equivalent dry seasons in the central part of the cordilleras (Chiquinquirá and El Granizo), while Chingaza, on the eastern slope of the Cordillera Oriental, has a unimodal pattern. Popayán, in the southern part of the Cordillera Central, also shows a unimodal pattern but with the minimum during the Southern Hemisphere winter.

drought, there is no frost and cloud forests normally occur. It is not evident what the original vegetation of the dry upper Chama Valley could have been, although the well-known abundance of hard tussock grasses along the roads and in some rangelands and the total absence of trees on the slopes strongly suggest a steppelike plant formation similar to the *pajonales* of the moist Peruvian Andes. This could be one of the rare situations in the generally moist northern Venezuelan Andes where the páramo does not represent the zonal vegetation above the forest, being replaced instead by a punalike grassland.

In the Colombian Andes, an equatorial rainfall regime predominates on the western slope of the Cordillera Oriental (Eastern Cordillera), with the main dry season from December to March and a second scarcely discernible minimum in September. Chita (1 in Fig. 2–3), on the western slope of the imposing Sierra Nevada del Cocuy, and Aquitania (2 in Fig. 2–3), some 100 km to the southwest, may serve to illustrate this pattern (Fig. 2–7). Here the altitudinal belt of maximum annual precipitation extends from 2000 to 3200 m.

The eastern slope of the Cordillera Oriental, facing the llanos, shows an almost biseasonal pattern, since the midyear low is hardly visible or does not appear at all. This windward side, where the air masses coming from the east discharge their humidity, constitutes one of the rainiest parts of the Colombian Andes, with heavy rainfall all the way from their base to their summits. Chingaza (Fig. 2–7) in the páramos to the east of Bogotá, is a representative site from these very wet highlands. Both in rainfall pattern and type of altitudinal gradient, the eastern slope resembles the southeastern side of the Venezuelan Andes, since maximum precipitation occurs at low elevation. Thus, Villavicencio in the piedmont of the Cordillera Oriental at 423 m receives more than 4000 mm of rain (Snow, 1976).

Below 6°N, as we approach the thermal equator, located in this part of South America between 4° and 5°N, the distribution of precipitation on the western slope of the Cordillera Oriental begins to change, stressing first the midyear minimum, so that both dry seasons become comparable in intensity and extension, to displace, farther south, the main dry season to the middle of the year, that is, to the Southern Hemisphere winter. Chiquinquirá in the Altiplano de Boyacá shows this type of bimodal pattern (Fig. 2–7). Weischet (1969) gives a profile through the Cordillera Oriental at 5°N, showing how cloud formation and rains occur all along the eastern slope as well as on both borders of the Sabana de Bogotá. On this plateau at altitudes between 2500 and 2800 m, the rainshadow effect of the eastern peaks decreases the annual totals to 700–1100 mm. However, the summits just bordering the Sabana are somewhat moister, like El Granizo at the Páramo de Cruz Verde (Fig. 2–7), just above Bogotá, while the windward upper side in this mountain area seems to be one of the wettest of all Colombian páramos, with annual totals from 1600 to 2900 mm, the latter figure recorded at Chuza at 3350 m (Cleef, 1981). Chingaza at 3250 m represents one of these moist sites (Fig. 2–7).

Guhl (1968) gives preliminary indications about the climate in the Páramo de Sumapaz, a huge massif in the Cordillera Oriental, immediately south of Bogotá. He concludes from his data that the windward eastern slope is the rainiest, with a maximum of 2368 mm recorded at Santa Rosa at 3400 m (four years). January is the driest month and June the rainiest, when a maximum of 599 mm was recorded in 1964. The lee side of this massif is less rainy, with precipitation from 1200 to 1400 mm between 3200 and 3500 m. Along this slope, the pattern becomes bimodal, April and October being the wettest months and January the driest. Farther downslope, this lee side becomes drier still; rainfall thus attains only 732 mm at El Hato (3100 m), although with the same bimodal pattern. Guhl (1968) remarks that the climatic equator seems to run across this mountain, since its northern part has a typical Northern Hemisphere rainfall regime while its southern areas approach the Southern Hemisphere pattern.

In the Cordillera Central and the Cordillera Occidental, precipitation follows a four-seasonal pattern too, with minimum rainfall during the winter months, but even in these two chains both dry seasons tend to be of similar intensity southward from 4° 30′N. The east slope of the Cordillera Central has a very moist cloud forest belt; thus El Paso at 3265 m receives 2296 mm of precipitation, but rainfall decreases again at higher elevations. The páramo therefore receives between 1100 and 1300 mm, that is about as much rain as falls on the opposite slope of the Cordillera Oriental. The highest recording station at El Ruiz (4200 m) registers 1011 mm of annual precipitation. Weischet (1969) also gives a transect of these two chains at 5°N where he shows the altitudinal gradient on the west slope of the Cordillera Central that faces the Cauca Valley, where rainfall decreases from a maximum of 2800 mm at 1400 m (Naranjal) to 2000 mm at 2700 m (Las Palomas), and to 1200 mm at 3250 m (Esperanza). But at about 4°N this west slope of the central chain becomes very rainy all the way to the top, with an annual rainfall up to 2200 mm in the páramos of the Departamentos del Valle and Cauca. Popayán (Fig. 2–7) is located in the southern part of this moister area. Rainfall becomes still more abundant in the lowlands of the Pacific slope of the Cordillera Occidental, where the highest precipitation in South America seems to occur, but unfortunately there are very few data on the climate of the western slope of the Western Andes.

In southern Colombia, below 2°N, the three major mountain chains converge into one single cordillera. In this area, rainfall distribution appears to be almost unimodal, June, July and August being the less rainy months, that is, the Southern Hemisphere winter. Farther south, the Ecuadorian highlands have a bimodal pattern, but also show a pronounced midyear minimum (Fig. 2–8). I want to point out here that the Colombian highlands are moister than other parts of the tropical Andes. Many areas receive more than 2000 mm of rain, which at these elevations certainly represents a very humid climate. But this is by no means the general situation throughout the Colombian Andes, since in most of the areas above 3000 m less rainy climates prevail, with annual totals in the range of 700–1300 mm.

At about 2°S in the Andes of Ecuador, a broad and dry intermontane valley gives way to a high altitude semiarid area comparable to the Chama Valley in Venezuela. The minimum rainfall in this area is recorded at Pachamama, at 3600 m, with only 382 mm. The landscape has a punalike physiognomy that contrasts with the rest of the Ecuadorian Andes (Johnson, 1976).

To summarize the main trends in the timing of rains in the high Andes from Venezuela to Ecuador, a bimodal pattern with the main dry season from December to March characterizes the environmental rhythmicity from Venezuela to central Colombia. The only exception is the slope facing the llanos, where the unimodal pattern typical of these lowlands extends to the highest mountain summits. At about 5°N in central Colombia, the double rainfall peaks occur in the three Andean chains, but the most pronounced dry season shifts from the first months of the year to midyear. Farther south, the secondary minimum that corresponds to the Northern Hemisphere winter tends to disappear and the climate becomes almost two-seasonal with a major dry season during the Southern Hemisphere winter, even though the region is in the Northern Hemisphere. That is, the Southern Hemisphere rainfall regime extends north of the equator to southern Colombia. This climatic trend is reinforced in Ecuador and culminates in a neat two-seasonal regime in the Peruvian Andes.

From central Ecuador to Bolivia, across the whole extension of the Peruvian Andes, the east–west rainfall gradient becomes by far the main axis of environmental variation, dividing the high Andes in quite distinct ecological zones that are roughly parallel to the chains (Troll, 1968). The Amazon-facing eastern slopes and related highlands conform to the wettest climatic zone, to which correspond, as zonal plant forma-

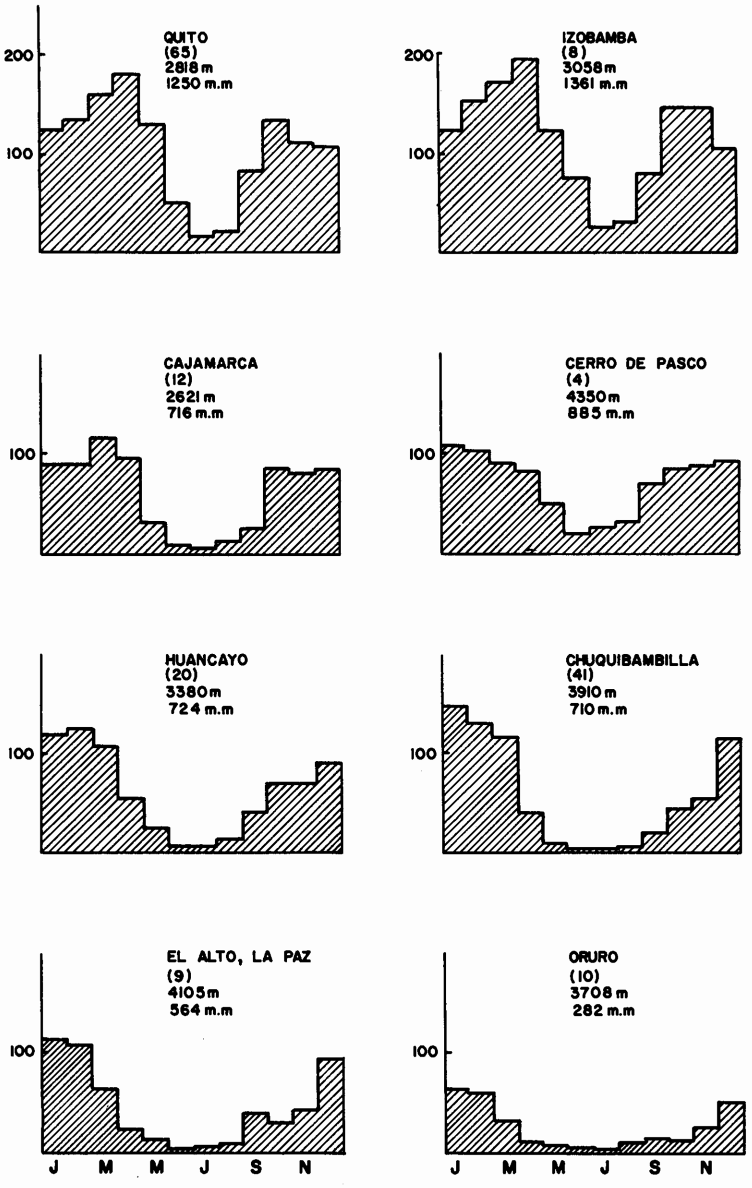

FIG. 2–8. Precipitation patterns in the Andes from Ecuador to Bolivia. The two Ecuadorian sites, Quito and Izobamba, have bimodal regimes with a midyear minimum. The remaining localities in Perú, (Cajamarca, Cerro de Pasco, Huancayo, Chuquibambilla) and Bolivia (El Alto, Oruro) all show a unimodal regime with a pronounced drought during the Southern Hemisphere winter.

tions, first the cloud forests or *yungas*, and above them the mountain grasslands or *pajonales*. High amounts of orographic rain can fall even at high altitudes on the rainside of these eastern chains, as at Talenga (10°S, 3995 m), east of a 5600 m range, with a rainfall of 1968 m (Johnson, 1976). Westward, the Peruvian altiplano or puna lies entirely in the rainshadow of these high chains. Its eastern part, the moist puna, still receives enough rainfall to maintain a rather closed grassy vegetation, while the central and western areas, together with the Pacific slope, are extremely dry and covered with the sparse vegetation of the shrubby dry puna. But disregarding this driest zone, the Peruvian altiplano has a unimodal rainfall regime with a strongly accentuated dry season during the Southern Hemisphere winter from June to August. Cajamarca, Cerro de Pasco, Huancayo and Chuquibambilla (Fig. 2–8), form a north–south sequence of 1500 km along the Peruvian Andes that may be representative of precipitation conditions in the moister part of the altiplano. The eastern border of the puna in northern Bolivia is still drier, La Paz receiving only 564 mm (Fig. 2–8), whereas farther south, the puna becomes exceedingly dry, Oruro receiving only 282 mm. Drought and cold increase southward and westward, reaching their extreme in the Atacama Desert at the boundary of Bolivia, Chile, and Argentina.

According to Johnson (1976), besides the major east–west variation across the central Andes, several climatic gradients are quite apparent along the Andes from Ecuador to Bolivia. The first is a gradient of southward-decreasing total rainfall, smooth from Ecuador to Peru, then more noticeably marked below 15°S. This change toward aridity is accompanied by a second climatic gradient of increasing rainfall seasonality, with a more intense and longer dry season. Thus, in the Andes of Ecuador, about 70% of the annual precipitation falls during the rainy season, whereas in southern Peru and in Bolivia, this figure reaches 80% and even 90%. A third gradient is the gradual occurrence of a cold season during the winter months, giving the climatic characteristics of subtropical latitudes. In Ecuador, the lowest published temperature up to 1969 was −6.8° at Río Pita (3860 m), but in the grassland area of the southern Peruvian altiplano minima of −15° have been recorded (Winterhalder and Thomas, 1978), and in the Bolivian puna a −30° record is not unusual. Further details will be given in the discussion of the climate of the Nuñoa area of southern Peru. A fourth gradient that appears along the Andes relates to rainfall reliability. In Peru and Bolivia, for instance, quite dry years do occur periodically. The coefficient of dispersion in yearly rainfall varies between 10% and 15% in Ecuador and central Peru, to increase to 27% in Cuzco, 19% in La Paz, and 28% in Oruro (Johnson, 1976).

It is not easy to locate the southern limit of the tropical Andes, partly because the eastern border of the Bolivian altiplano is not well known climatologically. It may be said, nevertheless, that between 17° and 18°S, the annual range of temperature sharply increases to 10°C while the daily range increases from a maximum of 25° in the southern Peruvian Andes to 30° or even 40° in the Bolivian puna. Under these conditions of severe winter temperatures, the tropical high-altitude biota give way to a cold-temperate one. An ecological corroboration of a definite change in the environment is the replacement of high-elevation grasslands (*pajonales*) more akin to the páramos of the northern Andes by plant formations of the dry and desert puna.

Climatic Trends in Other Tropical Highlands

Unlike in South America, where a nearly continuous zone of cool climates extends for thousands of kilometers along the tropical Andes, in all other tropical regions high summits may be envisaged as more or less disjunct archipelagos of small cold islands separated by extensive warm lowlands. This is the case in tropical Mexico and Central America, in Malesia, West Africa, and to a somewhat lesser extent in East Africa. I shall consider first Central America, then Africa, and finally Malesia.

Main Climatic Features of the Mexican Meseta and the Central American Highlands

Three mountain areas reach over 3000 m in Central America and tropical Mexico. These are the volcanoes of the eastern Mexican Meseta, namely, Ixtaccíhuatl (5285 m), Popocatépetl (5455 m), Pico de Orizaba (5675 m), and a few others that are several thousand meters higher than the average altitude of the plateau (2000–2500 m). In northern Central America, the Guatemalan highlands culminate in the Tacana (4064 m) and Tajumulco (4210 m) volcanoes. Finally, the most important mountain area in southern Central America is the Cordillera de Talamanca of Costa Rica, with its extensions into Panama. Several peaks in this range rise above the 3000-m level, culminating in Chirripó volcano

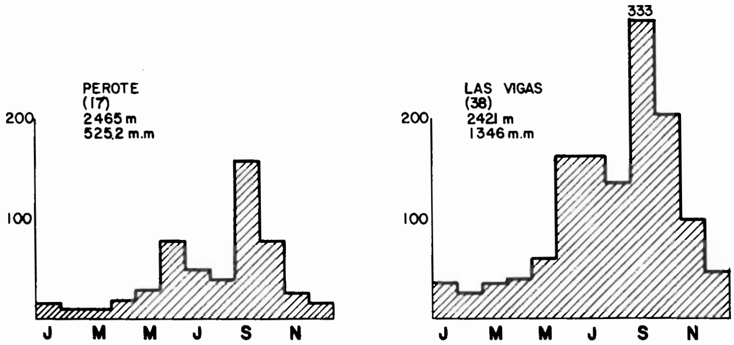

FIG. 2–9. Precipitation pattern in two Mexican localities: Perote, on the windward slope of the Sierra Madre Oriental and Las Vigas, on the eastern meseta, in the rainshadow of the chain. Data from Garcia (1970).

at 3820 m. The Central Cordillera of Costa Rica is hardly lower, its highest peak being the Irazú volcano (3422 m).

Lauer (1973) indicated that the eastern Mexican plateau bears only a rim-tropical character, with a tropical climate during the moist warm season and a strictly extratropical climate during the dry cool season. Cold continental air masses from North America (*nortes*) produce appreciable temperature decreases for several consecutive days during the winter. This influence is particularly noticeable on the northeastern slopes of the Sierra Madre Oriental. But in spite of these periodic intrusions of cold continental air, temperatures are higher over the Mexican meseta than in the free atmosphere over the Pacific and Gulf coasts at similar altitude. For instance the mean annual temperature at 3150 m over Tocubaya exceeds by about 3° that of the free atmosphere over Veracruz (Hastenrath, 1968). The causes of these higher temperatures are not yet clearly understood. The average absolute frost limit lies at about 1900 m on the meseta, while on the eastern slopes of the Sierra Madre Oriental, under more direct and frequent influence of the nortes, this limit probably lies 500 m lower. At 2500 m on the eastern meseta, with January temperatures at 10–12°, there are more than 50 frost days per year (Fig. 2–1), this number increasing at a rate of about 10 days of frost for every 100 m (Lauer, 1973). More details about temperature and rainfall will be given in a later section when I discuss the case of Pico de Orizaba, the highest volcano in this area.

Concerning altitudinal gradients in rainfall, a maximum up to 3000 mm or more is reached at the tropical montane forest belt from 2000 to 2300 m. On Ixtaccíhuatl at 3000 m, rainfall is about 1100–1200 mm, depending on exposure, the annual total decreasing to 800 mm at 4000 m in the pure grassland belt (*zacatonales*) (Lauer, 1978). Rainfall regime is tropical: the central volcanoes receive only 9% of annual rainfall during the winter, and at Orizaba, at the eastern edge of the meseta, the winter rains amount to just 12% of the annual total (Lauer, 1973). The rainshadow effect of the eastern high chains is quite noticeable. Two contrasting situations (Fig. 2–9) are met with, for instance, in Las Vigas (19° 38′N) and Perote (19° 38′N), at about the same altitude (approximately 2400 m), but the former site is on the windward slope of the Sierra Madre Oriental and Perote is on the meseta at the leeward side of Cofre de Perote, one of the highest peaks of this chain (4282 m). Table 2–2 shows the sharp decrease in precipitation in the meseta locality where the annual, January, and May temperatures are higher, both because of the aforementioned effect occurring on the meseta, and because of the far greater insolation reaching this dry locality.

Little is known about highland climates in Central America. The main generalization concerning these peaks is that they certainly are very

TABLE 2–2. Temperature and rainfall in two contrasting highland localities in southern México. January and May are the two extreme months concerning temperature.

	Temperature					
	Mean	January	May	Annual range	Rainfall (mm)	Winter rainfall (%)
Las Vigas (2421 m)	11.5	8.4	13.8	5.4	1346.4	7.2
Perote (2465 m)	12.7	9.5	14.9	6.4	525.2	6.7

Data from Garcia (1970).

rainy and cloudy. At the highest weather station in Costa Rica, Villa Mills at 3003 m in the Cordillera de Talamanca, more than 2500 mm has been recorded. Notwithstanding this high annual total, the regime is neatly bimodal, with four dry months (January to April), but during the rainy seasons rainfall peaks to more than 300 or even 400 mm per month (Weber, 1959).

A last point to remark on, related to the climate of these highlands, is the amazing lowering of the upper tree line from Mexico to Panama (Hastenrath, 1968). On the Mexican volcanoes, it lies at 4000 m, where *Pinus hartwegii* forest gives way to pure grasslands or *zacatonales*. At Mount Tajumulco in Guatemala, some 1000 km farther south, the upper tree line is at about 3800–3900 m. The climatic timberline is not reached in El Salvador, Honduras, or Nicaragua, but farther south, on the southernmost peaks of Central America, in Costa Rica and Panama, the upper tree line is found at about 3100 m only. This poleward rise in the altitude of timberline was associated by Hastenrath with a rise of the same order in isothermal surfaces, as I previously mentioned. But the northward drop in precipitation also seems to influence the elevation of both tree line and snow line.

East Africa, West Africa, and the Sahara

The Ethiopian plateau, with average altitudes over 2000 m, represents the largest highland area of tropical Africa, where several chains and peaks surpass 3000 and even 4000 m, to culminate in the Ras Dashan at 4620 m. As the climates at the highest altitudes in Ethiopia are scarcely known, I will refer mostly to the better known climates of the plateau (Brown and Cocheme, 1973). In East Africa rainfall increases with elevation up to an altitude between 2600 and 3400 m (Nieuwolt, 1974), so one may surmise that the high mountains of Ethiopia would have moister conditions than the lower plateau nearby. On the summits rainfall would probably decrease as is the rule on most mountains.

A major climatic gradient runs from the northeast ranges facing the Red Sea, with 400 mm or less rainfall, to the southwest plateau where annual totals attain 2500 mm. Consequently, the long dry period in the north and east decreases south and west to a minimum at about 7°N. Thus in Asmara (2325 m), in the northern highlands, annual precipitation barely reaches 550 mm and the dry period lasts ten months (September to June). Southward, Gondar (2120 m) has 1250 mm and seven dry months, Debra Markos (2313 m) 1350 mm and five dry months, whereas Addis Ababa (2370 m), 200 km to the southeast, has 1070 mm and six dry months. The most abundant rainfall is recorded in the southwestern plateau; thus Gore (2005 m) receives 2240 mm and shows only two dry months, January and February. But eastward, precipitation decreases again: Goba (2730 m), 300 km southeast of Addis Ababa, receives 730 mm and has four dry months. All these plateau areas exhibit a tropical rainfall regime with summer rains.

Less is known about temperature than rainfall in the Ethiopian highlands. At Addis Ababa, the coldest minima were recorded during the driest month, November, with a mean minimum of 4.2°. Rare cases of frost have been recorded in January (Brown and Cocheme, 1973). The warmest minima were noted during the rains. One may presume that the drier climates also have the greater daily and yearly temperature ranges and the lower limit of frost. In the southwestern highlands (Lauer, 1976), the cloud forest belt occurs between 2000 and 2500 m, where rainfall exceeds 2000 mm, decreasing gradually upward to 1600 mm at almost 3000 m, in the montane or "subalpine" *Hagenia-Hypericum* woodland. Few data are available on the climate of the páramo or afroalpine above this woodland formation, but Lauer (1976) indicated snowfall above 3800 m.

The other high mountains of East Africa, almost at equatorial latitudes, are either isolated volcanoes, like Mt. Kenya (5195 m), Kilimanjaro (5899 m), Elgon (4324 m), and a few others, or short volcanic chains on the Zaire-Uganda-Rwanda border, where the Ruwenzori (5119 m) and the Virunga (4500 m) have several summits above 3000 m. In spite of the very scarce records existing from the higher parts of many of these East African massifs, there appear to be substantial differences between them that are reflected in their vegetation zonation. Hedberg (1951) used this zonation to arrange these mountains in a series according to increasing dryness. Ruwenzori is the wettest mountain, followed by the Virunga volcanoes, Mt. Kenya, Aberdare, Elgon, Kilimanjaro, and Meru. With regard to timing of the rainfall seasons, all these highlands seem to have a bimodal regime with the main dry season in winter; that is, it changes from December to March north of the equator, to June through August in the southern mountains (Fig. 2–10). A more detailed consideration of the climate of Mt. Kenya and Mt. Kilimanjaro is offered in a later section.

It must be pointed out that exposure is a most important climatic factor in the high mountains of East Africa. Figure 2–11 shows the situation around Mt. Kenya. Similarly, on Kilimanjaro,

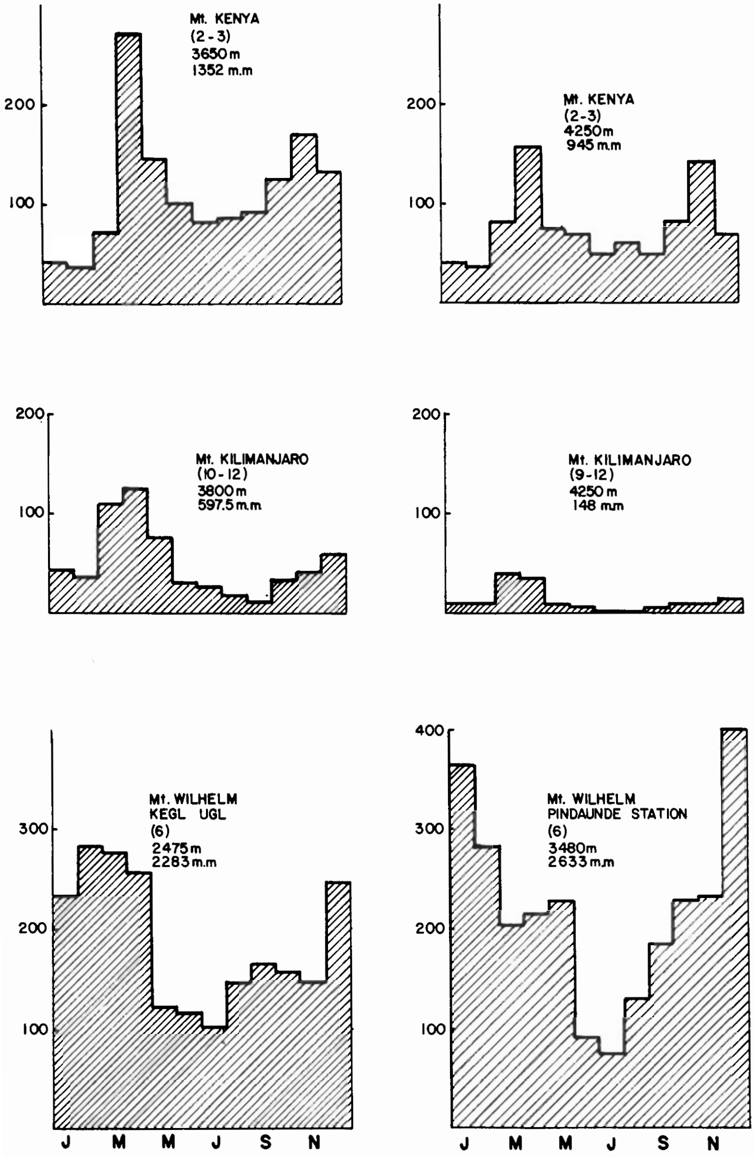

FIG. 2–10. Precipitation patterns in high African and Malesian mountains. Mt. Kenya has an equatorial regime, moist to its highest elevations, whereas Mt. Kilimanjaro, with the same regime, becomes increasingly dry toward its summits. Mt. Wilhelm is fairly humid throughout, though with a well-defined midyear drought. Data for Mt. Kenya and Mt. Kilimanjaro from Hedberg (1964); Mt. Wilhelm data from Hnatiuk et al. (1976).

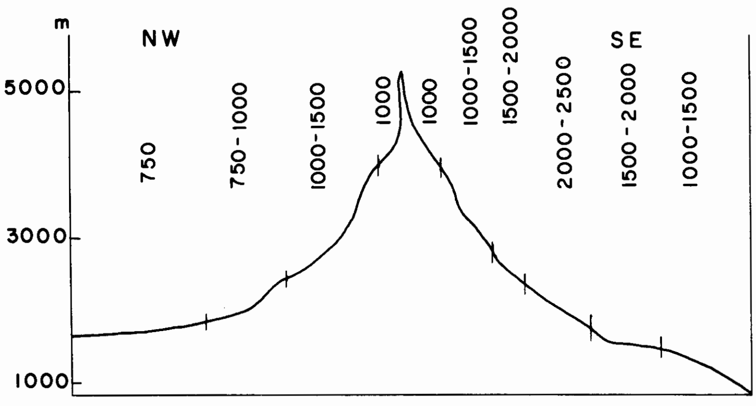

FIG. 2–11. Rainfall profile (in mm) in the Mt. Kenya area. Notice the strong rainshadow effect on the NW slope. Adapted from Thompson (1966).

the southern and southeastern sectors receive at least twice as much rain and have much more cloud during the rainy season, as the western and northern slopes at comparable altitudes (Hedberg, 1951). That is, according to the movement of the humid air masses, not only are the easternmost mountains the wettest, but in every single chain the southern and southeastern slopes are the rainiest.

On isolated Mt. Cameroon (4070 m) in West Africa, the upper belts are exceptionally wet (Lauer, 1976), with more than 8 m of precipitation at 1000 m and more than 2000 mm up to the highest peak. Indeed, this mountain, together with Mt. Kinabalu in Borneo, seems to be the rainiest tropical mountain in the world. Quite the opposite situation is met with in the Ahaggar and Tibesti, two isolated ranges reaching 3000 m in the middle of the Sahara. There, the summits receive only 100–200 mm rainfall (Yacono, 1968).

Malesia

Islands in Malay Archipelago (Java, Celebes, Borneo), and New Guinea all have peaks above 3000 m, but only Borneo and New Guinea have a tropical-alpine belt above the limit of upper continuous forest (Smith, 1977). The mountains of New Guinea are the largest and highest of the whole of Malesia. Their climate has been reviewed recently by Barry (1978a, 1980). Unfortunately, high-altitude meteorological records are lacking, and the only highland site consistently recorded for several years is the Australian National University research station on Mt. Wilhelm. This mountain will be taken as a case study representing high-altitude climates in this region. Besides these data, Allison and Bennett (1976) have given a preliminary characterization of the climate and microclimate of Mt. Carstensz, in West New Guinea, about 1000 km west of Mt. Wilhelm.

Barry (1979) remarked that Malesia is one of the most persistently cloudy regions in equatorial latitudes, a fact associated with the equatorial trough. Mainland New Guinea in particular is an area of maximum cloudiness in all months. Considering the New Guinea highlands as a whole, an east to west gradient of increasing precipitation and perhaps of narrowing temperature extremes seems to exist (Smith, 1980). Mt. Wilhelm (4510 m) has an annual precipitation of about 3000 mm or more throughout its summits (Hnatiuk, Smith and McVean, 1976), whereas Mt. Carstensz, the highest mountain in New Guinea (4804 m), would be rainier still and its temperature regime milder still. In fact, in three months of records, the mean maximum and mean minimum temperatures at 4250 m were 6.8° and 1.5°, respectively, with extremes of 9.3° and 0.1°. According to Allison and Bennett (1976), the most striking feature of the climate of Mt. Jaya, in the Carstensz area, is the lack of any seasonal differentiation. Mean temperatures have a very small annual range, and the diurnal temperature range is also very small: 3.4° at 3600 m, and 2.7° at 4250 m. Furthermore, precipitation and cloud cover probably have little seasonal variation also. This constancy is due to the high moisture content of the air, resulting from the closeness of a warm sea. The minimum daily relative humidity at 4251 m was above 70% in all recorded days.

In spite of the mild character of this highland climate, exceptional periods of frost have been recorded during equally abnormal droughts (Brown and Powell, 1974). In one such year, 1972, when monthly rainfall in most stations was less than 20% of normal values, six frost days were recorded at Tambul (2250 m) and ground frost occurred even down to 1600 m in some valleys. But records are not long enough to give a clear picture of the incidence of extreme temperatures, particularly the frequency of frosts.

Precipitation seasonality is almost absent in western Papua New Guinea toward the border with West New Guinea (Irian Jaya), but in the Eastern Highlands June and July show a relative decrease in rainfall (Fig. 2–10). This pattern also characterizes West New Guinea, but the equatorial pattern occurs only in a narrow sector along the southern edge of the central cordillera (Barry, 1980). Another interesting feature noted by this author is that the decrease of total precipitation with altitude at the highest elevations is less pronounced in the mountains of New Guinea than in many equatorial mountain areas.

Mt. Kinabalu (4101 m) in northern Borneo, is the highest mountain between Burma in Southeast Asia and New Guinea. On the basis of very short periods of observation, Smith (1977b, 1980) suggested that precipitation probably exceeds 3000 mm per year at 3350 m, and it has been estimated to be over 5000 mm at the summit. Rain falls throughout the year, with a wetter season from November to January. Ground frosts seem to be frequent but the absolute minimum temperature recorded at 3350 m was 0.6°. The number of frost days on this mountain is probably the lowest in Malesia. Forest is virtually continuous up to 3350 m, then begins an almost bare rocky summit area, where dwarf trees occur only on less steep slopes and in gullies and crevices up to 3950 m.

Although the climatic data available from the Malesian highlands are scanty, these mountains

TABLE 2–3. Climatic data from selected high Andean localities from Venezuela to Perú.

	Latitude	Altitude (m)	Rainfall (mm)	Evaporation (mm)	Temperature °C				Frost days	Insolation (h)
					Mean	Mean max warmest month	Mean min coldest month	Annual range		
Pico El Aguila, Venezuela	08°52′ N	4118	869	851	2.8	7.8	−1.0	2.7	156	–
Mucubají, Venezuela	08°48′ N	3550	969	763	5.4	11.5	−1.0	1.2	81	1638
Granja Mucuchíes, Venezuela	08°04′ N	2980	688	741	11.5	18.5	3.6	1.5	17	–
Quito, Ecuador	00°13′ S	2818	1250	–	13.0	23.0	7.0	0.3	0	2049
Izobamba, Ecuador	00°22′ S	3058	1361	–	11.5	19.0	4.0	0.8	A few	1895
Huancayo, Peru	12°07′ S	3380	724	–	11.8	20.5	0.5	3.6	62	2488
Chuquibambilla, Peru	14°47′ S	3910	830	–	7.1	18.0	−10.0	6.5	161	–

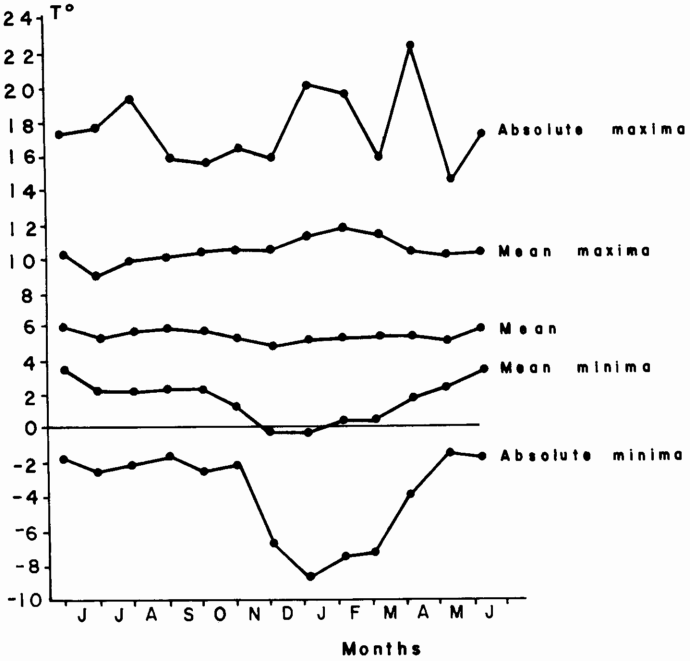

FIG. 2–12. Yearly pattern of temperature at Páramo de Mucubají, Venezuela. Notice the sharp decrease in the minima, especially absolute minima, during the dry season (December to March). From Azócar and Monasterio (1980a).

appear to be among the wettest in the tropics, with very heavy and almost evenly distributed precipitation. Smith (1980a) believes that these climatic conditions, less harsh than in other tropical ranges, may explain the exceptionally high altitude reached by tropical montane forests in these islands. Because the forest reaches such high altitudes, the páramo or tropical-alpine belt is quite reduced even on the highest massifs. It is practically nonexistent on Mt. Kinabalu, both because of a high upper tree limit and a conspicuous bare rocky summit.

SOME CASE STUDIES

Páramo de Mucubají, Venezuela

The meteorological station at the Páramo de Mucubají is located at 8°48′N and at an altitude of 3550 m in the Sierra Nevada de Mérida; it stands in a glacial valley about 900 m below the local summits of the Andes. The valley descends first to the northeast, but a few kilometers down it makes a 90° angle and opens south to the llanos. Mucubají shows the two-seasonal rainfall pattern characteristic of this side of the Venezuelan Andes. The whole area is covered by páramo vegetation, except for some patches of *Polylepis sericea* forest restricted to rocky slopes. Mucubají is at the upper limit of agriculture in the area (potatoes, wheat), although at this elevation field crops are cultivated only once every few years (Monasterio, 1980b).

My climatic analysis is based primarily on the detailed study of Azócar and Monasterio (1980a, 1980b). Two complementary aspects will be treated, namely, the annual variation and the daily cycles. Mean annual temperature is 5.4° (Table 2–3), with a range of only 1.2° between the coldest (December) and the warmest month (June). Monthly mean maxima range between 9° and 11.5° (Fig. 2–12), and mean minima vary from −1° to 3.5°. The highest recorded temperature in nine years was 22.2°, in March, and the lowest was −8.6° in January. The frost regime has already been discussed (Fig. 2–2). On average there are 81 frost days per year, varying between 56 and 96 days from year to year. These frost-change days are fairly concentrated in the driest period of the year, that is, from November to March, when 71 days occur. January has the greatest number, 22 days, and September is the only month totally free from freezing temperatures. Snow has never been recorded at this elevation.

Rainfall distribution is shown in Fig. 2–5. The ten year average is 968.8 mm, with an interannual variability of 13%. Between November and March, rains do not attain 30 mm per month. Relative humidity maintains itself between 60% and 70% during these dry months, but during the eight rainy months it is nearly always above 80%. Annual evaporation is 763.3 mm and calculated annual potential evapotranspiration is 540 mm.

Only during the dry season does monthly evaporation exceed precipitation.

Insolation records for seven years give a mean of 1637.7 sunny hours, that is, an average of almost 4.5 hours per day. During the dry season, insolation is above 200 hours per month (6.6 hours per day), but it decreases to less than 100 hours per month (3.3 hours per day) during the rainy season. Wind speed at 10 m above the ground ranges from 2.5 to 3.5 m/sec.

In summary the annual climatic regime at Mucubají is a fairly seasonal high-altitude tropical climate, with a four-month dry and cold season, when frosts are frequent, and a milder rainy season, with lower maxima but only sporadic freezing temperatures. However, there is no frost-free season, or at least it does not last more than one month. Insolation during the cloudy, rainy season is about half that of the sunny days of the dry season. Wind velocity is low, and does not seem to have a significant ecological effect on plant and animal life.

It is of interest to find other areas of the world with climatic conditions comparable to those of Mucubají. These places are far away from the tropics, in austral South America and its neighbouring islands. Thus in Ushuaia (Argentina) or San Isidro (Chile), at 54–55°S, mean annual temperature lies between 5° and 6°, and annual rainfall attains 800 mm. Similarly, in the Malvinas (Falkland) Islands, at 52°S, temperature and rainfall are within the same ranges. In these austral localities, yearly temperature fluctuation is greater than at Mucubají, although because of their oceanic nature it does not exceed 8°. Wind, however, does play a crucial ecological role, because it is strong and sustained.

Considering now the daily rhythms, I will discuss the average conditions in two contrasting months: January, indicative of the dry season, and August, representative of the rainy season. Azócar and Monasterio (1980b) recorded air temperature at 10 cm above the ground during one year, several hundred meters away from the meteorological station, but at almost the same elevation. In January, the average hourly temperatures ranged between −3° and 17° (Fig. 2–13). After the daily minimum at dawn, air warms quickly as the sun rises, the temperature increasing 12 degrees between 08.00 and 10.00 hours. Between 10.00 and 16.00 hours, under a clear sky, air temperature remains above 14°. The evening cooling is slower than was the morning warming. Average temperature during the sunlight hours was almost 10°. Night cooling is intense due to high reirradiation under a cloudless sky. Average night temperature is about 1°, but below-freezing temperatures persist for eight consecutive hours. Relative humidity (February) increases at night to 90%, while it reached its minimum at noon with values of 30% to 40%. Mean daily evaporation is 2.2 mm.

In August, average hourly temperature varied only between 3° and 8.5°. Because of the lack of direct isolation, either the morning warming or the evening cooling of the air proceeds slowly. The average daylight temperature is only 6.5°, but the mean night temperature exceeds 4°. As

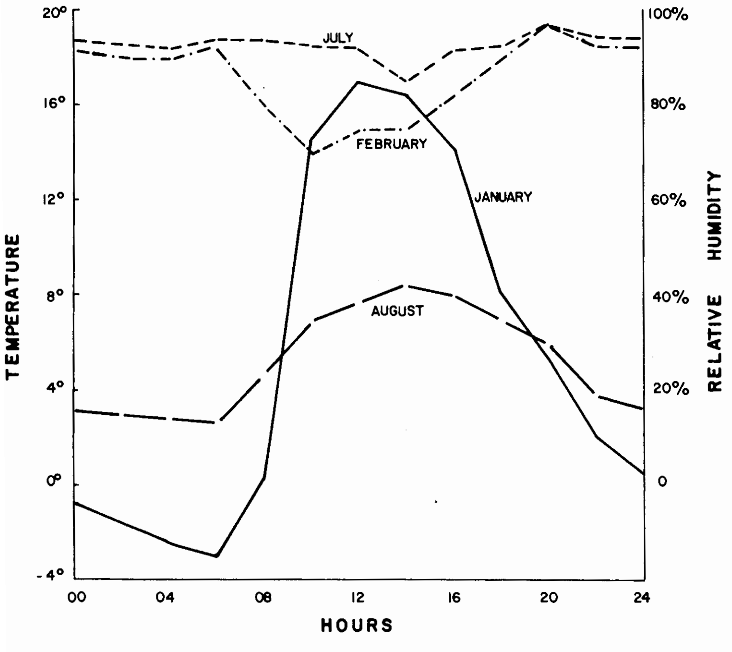

FIG. 2–13. Daily cycles of temperature (—— ; — — —) and relative humidity (– – – – – ; –·–·–·) at 10 cm above the ground in the Páramo de Mucubají, Venezuela. Averages from months of the dry season (January and February) and of the rainy season (July and August). Data from Azócar and Monasterio (1980b).

has already been said, the average number of frost-change days in August is less than one per year. Relative humidity (July) decreased from 90% or 100% at night to about 70% at noon. Mean daily evaporation is 1.8 mm.

During the wet season, high cloudiness and low insolation, together with fogs, mists, and rains, determine a fairly stable moist and cool climate. Both air temperature and relative humidity have low amplitudes. By contrast, differences in temperature and humidity between day and night become sharper during the dry season. In this four-month period, freezing temperatures were recorded during more than half of the nights. Climatic conditions in daylight hours may be comparable to those of clear winter days in many temperate areas.

Pico del Aguila, Venezuela

Pico del Aguila (8°52′N) lies at an altitude of 4118 m in the Andes of Mérida, 5 km as the crow flies from Mucubají. About 300 m higher than this mountain pass, the surrounding summits are known as páramos of Mucuchíes and Piedras Blancas. This high Andean area is characteristically covered with desert páramo vegetation (Monasterio, 1979, 1980a; Chap. 3). The upper limit of agriculture is found several hundred meters below. I refer to Monasterio (1979), who discussed the climate and microclimates of this region.

With an annual precipitation of 869 mm, the unimodal seasonal pattern leaves four dry months, December to March, with only 72 mm rainfall (Fig. 2–5). In 22 years, the interannual variability attained 12.5%. Snowfall is common, particularly during the wet season, but rarely persists more than a few hours. Mean annual temperature is 2.8°. Monthly maxima range between 4.7° and 7.8°, being highest in the dry months. Mean minima vary from −1.0° to 1.1° and are lowest in the dry season. Relative humidity remains close to 100% all day during the rainy months but decreases to minimum values of 20% to 40% on clear days. Annual evaporation, rather high given the prevailing low temperatures, amounts to 851 mm, varying from 111 mm in March to 47 mm in August. Incoming radiation under clear skies frequently reaches a peak of 1.6 or 1.7 cal/cm^2/min, but normally the rapid variations in cloudiness produce numerous sharp oscillations in radiation throughout the day. Monthly totals during the rainy season are in the range of 10–13 kcal/cm^2, increasing to 14–15 kcal/cm^2 in the dry months.

The most outstanding feature of the frost regime in the Pico del Aguila area is its large variation from year to year, which depends mostly on humidity and rainfall. In effect, given that mean temperatures are quite near 0°, a slight increase in the night cooling of the air may produce freezing temperatures. As cooling is directly related to cloud cover and rain, a period with precipitation below the mean has fewer rainy days, and thus becomes a relatively cool period with an increased number of frost nights. On the contrary, a rainier year than the average is also a year with many fewer frost days than the mean. In this way, even a decrease smaller than a couple of degrees in the night temperature may produce a freezing night, increasing dramatically the annual number of frost-change days. For this reason, the number of days of frost differs widely from year to year. Thus, one year with a precipitation 100 mm above the average may have only 100 frost days, whereas the following year with a rainfall 100 mm below the mean may have 200 frost days. The mean number of frost days thus does not have much ecological meaning, its variability being more significant for the survival of plant and animal populations. It should be noted that this frost regime refers to screen temperatures 1.5 m above the ground. The near ground conditions are much harsher and ground frost may be observed on most days throughout the year.

To show the daily cycle of temperature and humidity, I will consider two contrasting days, one in the dry, the other in the rainy season. The average daily cycles in two contrasting months are depicted in Fig. 2–14. A typical pattern during the dry months (for example, March) begins with a clear sky. Minimum temperature before dawn is about −1° and occasionally may be as low as −2°. Air warms rapidly between 08.00 and 10.00 hours, to attain maxima of about 7°–8° between 12.00 and 14.00 hours. Maximum temperatures rarely exceed 9°. The evening cooling is more gradual, so that during most light hours temperature persistently remains above 4°. Relative humidity peaks at 100% in the afternoon as the sky closes and fog may be formed. However, clouds tend to disappear after sunset, and the night is cloudless. Minimum relative humidity may be attained between 24.00 and 08.00 hours, when values as low as 20% or 30% are not infrequent. Evaporation in such a clear day may exceed 7 mm. As an example of daily weather in the rainy season during a typical rainy day in July, the minimum temperature is quite close to or slightly below zero, freezing depending mostly on rainfall duration. Maxima range from 4° to 5°, but the average temperature is 2°. Persistently high

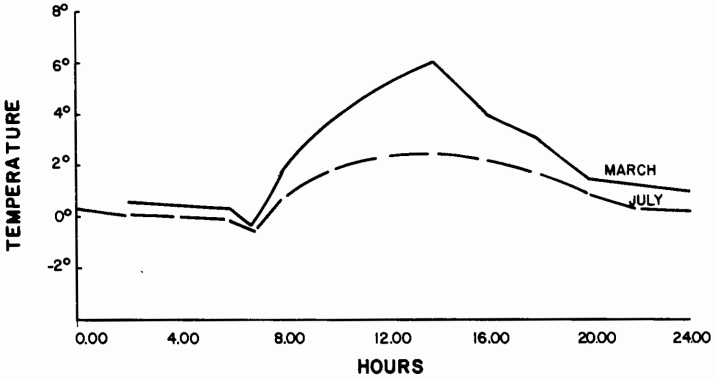

FIG. 2–14. Daily cycles of temperature at Pico El Aguila, Venezuela. Hourly means from a month of the dry season (March) and of the rainy season (July).

humidity is maintained all day. There is hardly any daily cycle, and fairly cold and humid conditions prevail the whole day. Evaporation on a rainy and constantly humid day may be lower than 0.5 mm.

Páramo de Monserrate, Colombia

I mentioned in a previous section that the leeward slope of the Cordillera Oriental above the Sabana de Bogotá has a bimodal rainfall pattern with annual totals of 1100 to 1300 mm. Fig. 2–7 shows the distribution of precipitation at one locality, El Granizo, at 3125 m, in a formerly forested zone now covered with low trees. The páramo begins 100 or 200 m above (Páramo de Monserrate). The midyear dry season is almost equivalent in length and intensity of drought to the first months of the year, which at this latitude correspond to the astronomical winter. Rainfall reliability seems to be somewhat higher than in other highland localities of northern South America, with 17 per cent variation in 30 years of records.

There are very few continuous records of temperatures. Bernal and Figueroa (1980) gave some air temperature data for the Páramo de Monserrate at 3025 m. They recorded temperatures at 100 cm above the ground for nine months. Their data show a mean of 11.5°, a mean maximum of 19.3°, and a mean minimum of 3.8°. January and February are the driest and coldest months, when the absolute minima reach −1° and a few frost days occur.

Bernal and Figueroa (1980) also measured daily cycles of temperature and humidity. Figure 2–15 shows their data for three days in Sep-

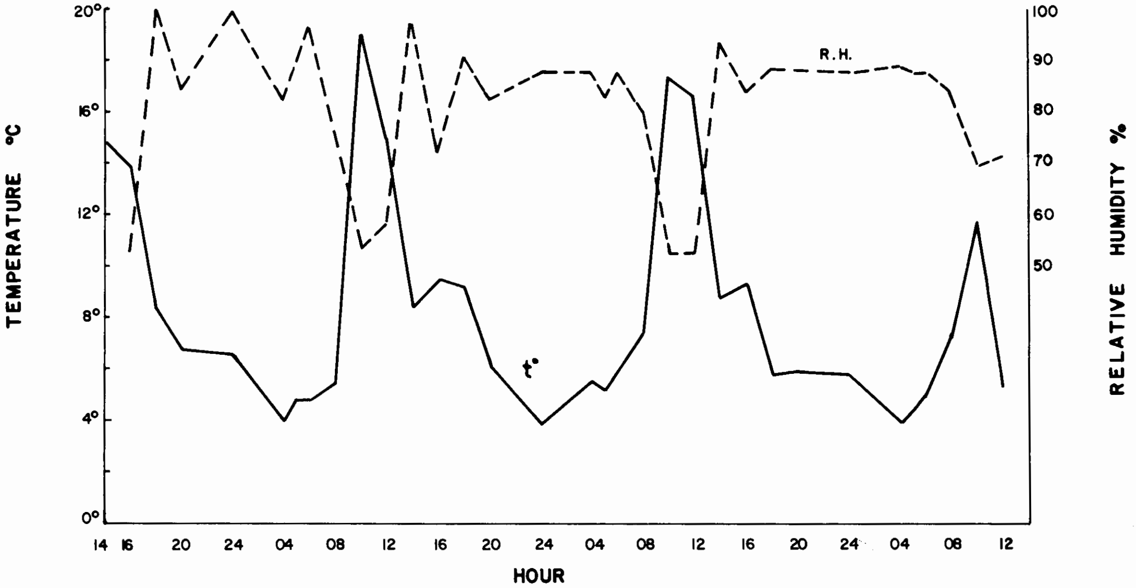

FIG. 2–15. Daily cycles of temperature (———) and relative humidity (— — —) during three days at the Páramo de Monserrate, Colombia. After Bernal and Figueroa (1980).

tember. Minima were above 4° while maxima reached 17° or 18°. Morning warming, as usual in the páramo, was remarkably rapid, whereas afternoon cooling, due to increased cloudiness and fog, began very early in the afternoon and proceeded much more slowly. Relative humidity attains high values, except in the morning when it decreases to 50% or 60%.

These Colombian sites seem to have a milder climate than the two sites in the Venezuelan Andes previously considered, and are closer to the Ecuadorian sites I will discuss in the next section. As was the case along the humid slopes of the Sierra Nevada de Mérida, such as La Aguada, the localities in the forest–páramo boundary either in Venezuela and Colombia or in Ecuador, have very few frost days occurring during the less rainy period of the year. Under these temperature and humidity conditions, the upper limit of cloud forest is exceptionally high for the Andes, since it may reach 3300 m or more. High cloudiness and low sunshine appear to be more crucial limiting factors than low temperature minima and frosts.

Quito-Izobamba Region, Ecuador

Quito (0°13′S, 2818 m) and Izobamba (0°22′S, 3058 m) illustrate climatic conditions in the equatorial Andes (Table 2–3) and permit one to compare two neighboring sites almost at the same altitude, but in two contrasting environments: montane forest and páramo. Quito (Fig. 2–8), situated in an area formerly covered by montane forest, has an average annual rainfall of 1250 mm, with a variation between 890 and 1366 mm in 65 years of records (Johnson, 1976). The pattern is equatorial with the main dry season in July and August, that is, during the Southern Hemisphere winter. As I have mentioned in an earlier section, this midyear drought becomes more pronounced as one proceeds southward through the Peruvian Andes.

Mean annual temperature is 13.0°, with a month-to-month variation of only 0.3° (30 years). Absolute extremes are 28° and 2°, and frost is totally unknown. Relative humidity remains above 70 per cent all year long, with medium to high cloudiness and very low winds. Insolation attains 2049 hours per year, with a seasonal variation from 131 hours per month in April to 212 hours in July. During the rainy seasons, daily temperatures fluctuate between 8° and 21°, while during the driest period of the year the mean daily range varies from 7° to 22°. These figures show how constant the climate is, with daily cycles of temperature and humidity almost similar throughout the year in spite of the seasonal differences in sunshine and rainfall.

Izobamba (Fig. 2–8), situated above the continuous forest line, has an overall climate quite similar to that of Quito, with the same equatorial rainfall pattern but a slightly higher annual total: 1361 mm. Mean annual temperature is 11.5° and yearly amplitude is less than 1°. The absolute maximum and minimum temperatures recorded are 0° (September) and 24° (December and January). September is the only month when occasional frosts may occur. Insolation attains 1895 hours per year, with seasonal variation from 118 hours (April) to 193 hours of sunshine per month (July and August). The mean temperature range in the dry seasons days is 15 degrees (4°–19°) while during the rainy seasons it decreases to 11 degrees (6°–17°).

The two sites thus have quite similar climatic conditions, with the differences due to a 230-m difference in altitude. These equatorial highlands have one of the most equable climates in the South American mountains, with fairly tenuous seasonal rhythmicity given by the rainfall seasons. But however similar the two localities may appear, they represent sharply contrasting ecological zones: montane forest and páramo. The major qualitative difference between the two environments seems to be the total absence of frost from the lower site and its occasional occurrence in the páramo locality, but it is hard to believe that this sporadic factor could have such an important ecological consequence. Nevertheless, the same feature has been repeatedly found on moist Andean slopes, where the frost line runs quite close to the upper forest line.

Altiplano of Southern Peru

The last case study in the Andes is used to discuss climatic features in the moist puna of southern Peru, where environmental conditions are more severe than in Venezuela or Colombia because of increased continentality and the transition toward the extratropical zone. Tosi (1957) analyzed the climate in the Mantaro Valley around Jauja and Huancayo in the central puna. Johnson (1976) gave a general outline of the climates in the Peruvian Andes, while Brooke Thomas and Winterhalder (1976), and Winterhalder and Brooke Thomas (1978) discussed in more detail the climate in the Chuquibambilla-Nuñoa region of southern Peru (see Figs. 2–3 and 2–8, and Table 2–3).

With an annual precipitation in the range of

700 mm to 850 mm, the eastern Peruvian puna, between 12° and 15°S, can be compared with the driest sites in the Venezuelan páramo. However, the altiplano has a more seasonal pattern with a unimodal regime. During the three or four dry months corresponding to the Southern Hemisphere winter, monthly precipitation is very low or even nil. As a consequence of this prolonged period of sharp drought, minimum temperature is much lower than in the driest páramo at comparable altitudes, so that freezing temperatures occur almost daily (Figs. 2–16, 2–19). In the rainy season, frost is less frequent: one to five days per month; thus Nuñoa, at almost 4000 m, has 161 frost days per year. But already at Huancayo (3380 m), with just 62 frost days per year, there is no predictable or extensive frost-free period. Moreover, not only do the number of frost-change days seem to be somewhat greater in the moist puna than in the driest páramos, but the minima may be up to 10 degrees lower.

Strong interannual variability in total rainfall characterizes the altiplano, with certain years well below the mean. At Chuquibambilla, for instance, during one such dry year, minimum temperatures in June and July frequently reached −15°. Although mean annual temperature in the moist puna may be similar to, or even several degrees higher than means in northern Andean localities at the same altitude, suggesting warmer conditions for the altiplano, the daily ranges here are much wider and the night minima lower. At Chuquibambilla, during the dry season, the mean daily range is 25 degrees, with mean minima of −10°. These amplitudes seem, however, to become somewhat smoother with altitude (Fig. 2–19).

Another factor contributes to make dry season temperatures still more severe. Antarctic air masses, after crossing southern South America, penetrate northward to near equatorial latitudes and regularly move through the altiplano. Under such conditions, temperature drops abruptly to −12° or −15°, with daily maxima of only 3° or 4°. This situation may persist for a few days.

Less total rainfall and clearer skies lead to higher annual insolation in the puna than in the páramos. Thus, Huancayo has an average of 2488 hours of sunshine per year, a value almost twice that of the sunshine recorded in the Andes of

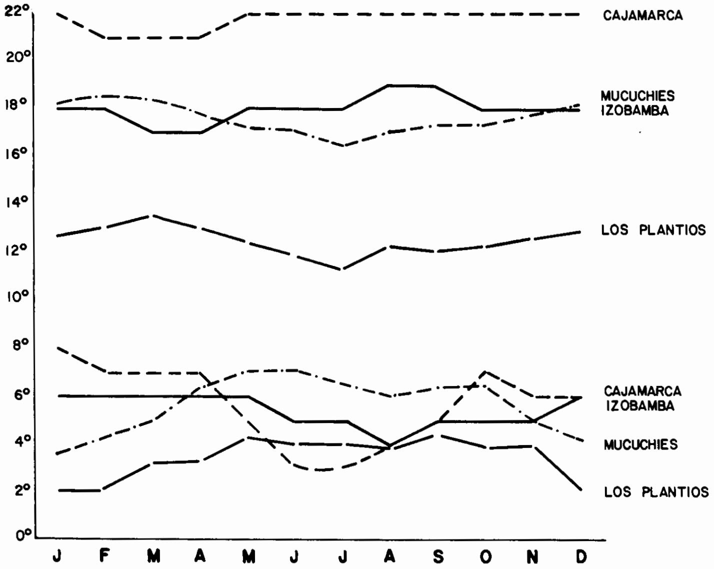

FIG. 2–16. Monthly maximum and minimum temperatures in four Andean localities at about the same elevation (about 3000 m), but differing in rainfall and latitude. Notice how the páramo site (Los Plantíos) has the lowest maxima and also the lowest minima, except during the two rainiest months (June and July). Mucuchíes, a dry site in the upper Chama Valley in Venezuela, and Izobamba, a páramo site in Ecuador, are intermediate in their maxima, whereas the Peruvian locality of Cajamarca has persistently the highest maxima but shows sharp contrast in the minima between the rainy and the dry season.

	LATITUDE	ALT. (m)	RAINFALL (mm)
Cajamarca	07° 08'S	2621	716
Los Plantíos	08° 49'N	2878	1003
Mucuchíes	08° 43'N	2980	688
Izobamba	00° 22'S	3058	1361

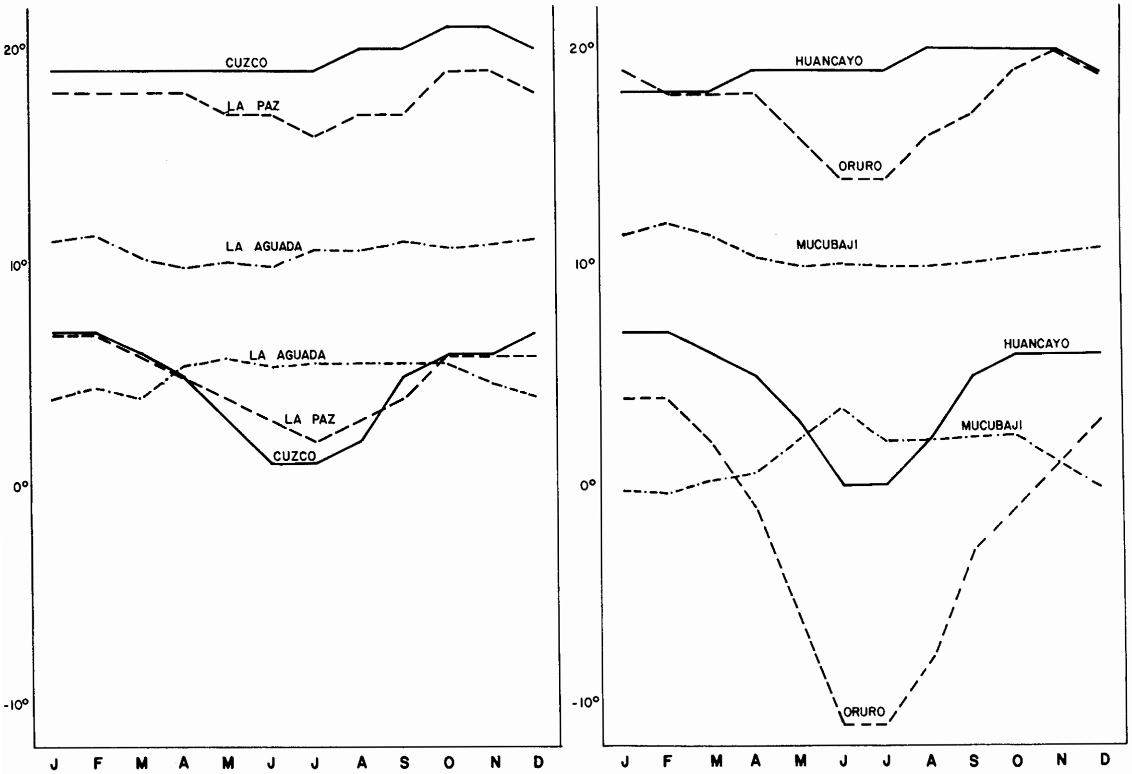

FIG. 2–17. Monthly maximum and minimum temperatures in six Andean localities at about the same elevation (about 3500 m), but differing in rainfall and latitude. Mucubají and La Aguada, in the Venezuelan páramo, have the lowest maxima and rather constant minima throughout the year, whereas Huancayo and Cuzco, on the Peruvian altiplano, and Oruro and La Paz, in the Bolivian puna, have higher maxima as well as a sharp decrease in minima during the winter months. At Oruro, the driest and southernmost locality, the winter decrease also affects the maxima.

	LATITUDE	ALT. (m)	RAINFALL (mm)
Mucubají	08° 48'N	3550	969
La Aguada	08° 35'N	3452	1811
Huancayo	12° 07'S	3380	724
Cuzco	13° 33'S	3312	750
La Paz	16° 30'S	3632	488
Oruro	17° 58'S	3708	282

northern South America. In the high valleys that deeply dissect the altiplano, such as the Mantaro Valley in the Huancayo area, winds may be important, particularly from September to November (Tosi, 1957). These winds have a daily pattern. From a light breeze in the morning, wind increases in the afternoon to average speeds of 5–12 km/hr, to die down later and end up in calm nights. The dessicating effects of wind necessitate the establishment of tree barriers around field crops.

To summarize and compare the environmental conditions prevailing in the Peruvian altiplano and those in the northern Andes (Figs. 2–16 to 2–19), I conclude that the moist eastern puna has a harsher climate induced both by the intensive drought of the midyear months and by the much lower temperatures of the dry season. At similar altitudes, puna localities have similar or higher means than páramo sites, but minima are many degrees lower. The dry season is much more severe in the puna than in the northern Andes and may well be called "winter," at least from the viewpoint of temperature, the puna being the sole tropical region in South America with a truly cold season. A complementary feature reinforcing the dry and cold character of the moist puna climate as compared with even the driest páramos is the higher unreliability of rainfall. Not unfrequently, in exceptionally dry and cold years temperatures reach the lowest values recorded in tropical mountains. It is clear that a major ecological gradient exists from the moist páramo of the Sierra Nevada de Mérida or of the eastern slope of the Colombian Cordillera Oriental, through the drier páramo, the moist puna, the dry puna, and finally to the desert puna of western Bolivia and northern Chile. The latter area lies outside the tropics and represents the most extreme type of highland environment in South America.

Pico de Orizaba, Mexico

The climate of the upper slopes of this great Mexican volcano (19°N, 5675 m) was analyzed by Lauer and Klaus (1975). They recorded several climatic elements at four elevations, from March 2 to 26 in 1974. Table 2–4 shows a typical daily cycle at each of the four sites for a sunny day and a rainy one, respectively. The altitudinal gradient in mean annual temperature is linear between 10° at 3000 m and 0° at 5000 m, whereas the number of frost days increases from 120 to 360 (Fig. 2–1). According to Lauer and Klaus (1975), a decrease with elevation in the maximum and minimum temperatures and in daily temperature range appears to be a valid generalization. It is interesting to notice that at timberline, formed by *Pinus hartwegii* forest at about 4000 m, there are about 200 frost days per year (Fig. 2–1). On the basis of data from the nearby Nevado de Toluca at 4120 m, these authors conclude that on these volcanoes freezing temperatures may occur throughout the year but with increased frequency during the dry winter months, whereas April and May are the months with fewer frost days. They also noticed the increase with elevation in the number

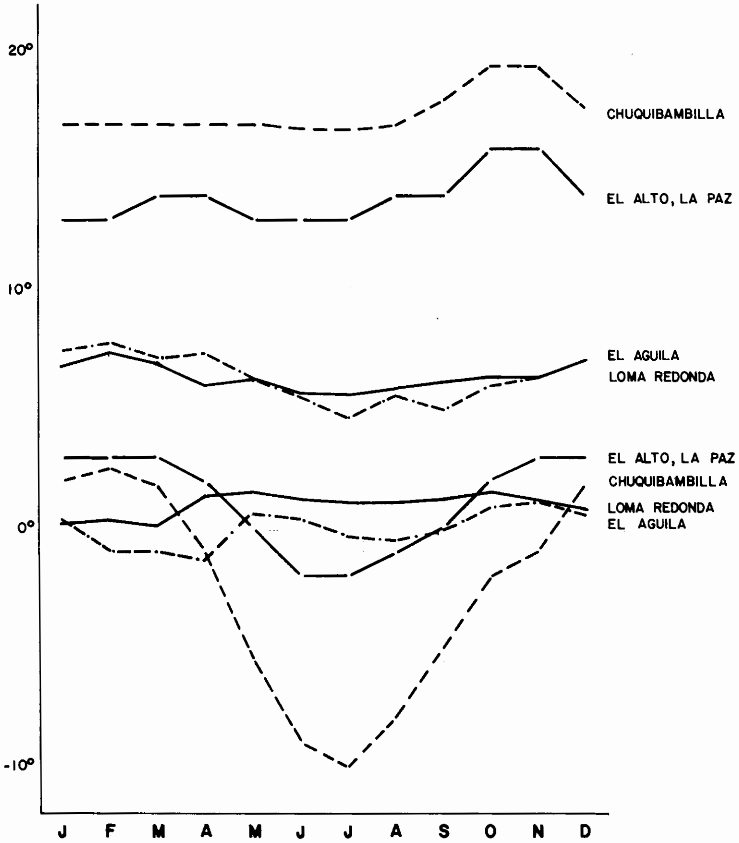

FIG. 2–18. Monthly maximum and minimum temperatures in four Andean localities at about the same elevation (about 4000 m) but differing in rainfall and latitude. The two sites in the Venezuelan páramo, El Aguila and Loma Redonda, have the lowest maxima and rather constant minima throughout the year. Chuquibambilla in the Peruvian puna and La Paz (El Alto) on the Bolivian altiplano, have higher maxima and a sharp decrease in the minima during the winter months.

	LATITUDE	ALT. (m)	RAINFALL (mm)
El Aguila	08° 51'N	4118	860
Loma Redonda	08° 35'N	4045	1553
Chuquibambilla	14° 47'S	3910	830
La Paz (El Alto)	16° 30'S	4105	564

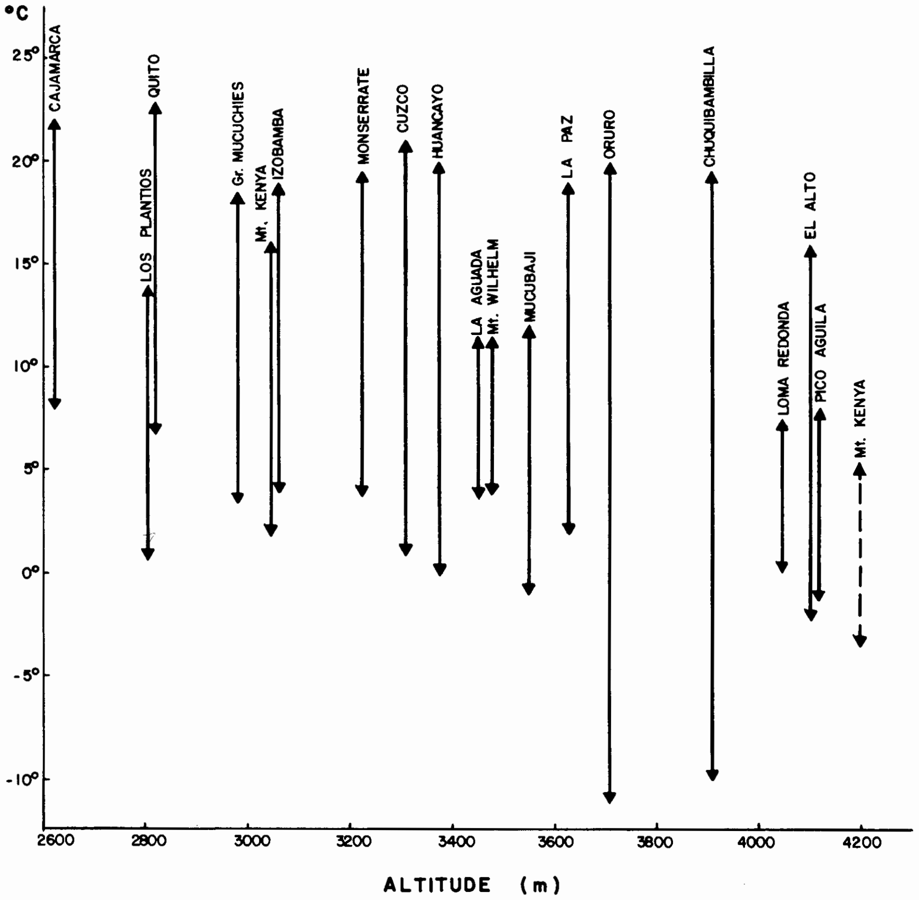

FIG. 2–19. Temperature range between the mean minimum of the coldest month and the mean maximum of the warmest month in various tropical highlands, arranged along an altitudinal gradient. Notice how the Venezuelan páramo sites, Los Plantíos, La Aguada, Mucubají, Loma Redonda, and Pico El Aguila, together with Mt. Kenya and Mt. Wilhelm, show the lowest maxima and the highest minima (i.e., the lowest annual ranges). By contrast, the puna sites, like Cuzco, Huancayo, Chuquibambilla, La Paz, Oruro, and El Alto, have the highest maxima and relatively lowest minima. The páramo sites in Colombia (Monserrate) and Ecuador (Izobamba) as well as the dry Venezuelan locality Granja Mucuchíes, show an intermediate pattern.

TABLE 2–4. Twenty-four-hour range in air temperature (°C) and relative humidity (%) along an elevational gradient on Pico de Orizaba, México.

Elevation	3480 m				3990 m				4250 m				4690 m			
	Temp.		RH		Temp.		RH		Temp.		RH		Temp.		RH	
	max	min	max	min	max	min	max	min	max	min	max	min	max	min	max	min
March 3	17°	−1°	30	15	16°	−5°	50	20	8°	−1°	30	15	5°	−6°	90	60
March 25	17°	5°	50	20	16°	3°	50	10	8°	0°	50	15	5°	−3°	90	30

Two days with contrasting weather have been taken as examples: March 3, a sunny day, and March 25, a cloudy and rainy day.

Data from Lauer and Klaus (1975).

of frost hours per day, from 1 hour or less at 3000 m to 24 hours at 5000 m in the glacial area.

As discussed in an earlier section, the climatic character of the Mexican highlands is transitional between that of tropical and that of temperate mountains. On Orizaba, the annual range of temperature between the warmest and coldest months is still low: 5.5° at 3000 m, decreasing to 2.5° above 4000 m (Lauer and Klaus, 1975). Thus, from the viewpoint of annual constancy, these mountains could be considered tropical. But the frequent incursions of cold air masses from North America, and the sharp decreases in temperature that accompany them, lead to sharp seasonal differentiation and particularly a dry and cold season during the winter months. The biota of the Mexican highlands show more affinities with boreal than with tropical floras and faunas. This may be seen either by the occurrence of conifers as the dominants of the upper forest belt, or by the dominance of boreal grasses in the mountain grasslands (*zacatonales*). A true páramo belt is lacking.

It would be enlightening to compare the Mexican volcanoes with Andean highlands at similar latitudes and elevations and with comparable annual rainfall. Unfortunately, a similar situation does not exist in South America, since at 19°S the Andes are much more arid than the mountains of southern Mexico. A comparable situation might be found in the eastern cordilleras of southern Peru and northern Bolivia between 14° and 17°S, but unfortunately these areas are not well known climatically. The only valid comparison that might be made, then, is between the respective plant formations. In both Mexico and Peru–Bolivia, hard tussock grasses predominate above the continuous forest, but in South America below this high-altitude ecological zone, tropical montane forest occurs. In Mexico and northern Central America, coniferous forest and mixed formations occupy the slopes between the timberline and 1800–1900 m, where a richer forest with more tropical elements appears.

This contrast in vegetation suggests a close correspondence with the different elevations where frost first occurs: near 3000 m in the Peruvian Andes, but less than 2000 m on the Mexican altiplano (Fig. 2–1). In southern Bolivia and northern Argentina, which lie outside the tropical climatic area, the eastern slopes of the mountains are moist enough to support a montane forest (though under a climate with frequent winter frosts). A coniferous forest belt, in this case a pure *Podocarpus* forest, is interposed between the subtropical rain forest on the lower slopes and the puna grassland on the summits, thus repeating the zonation on the Mexican volcanoes. One may suggest therefore, that the coniferous forest occupies an altitudinal zone where frost gradually increases from only a few frost days to more than half frost days per year. This ecoclimatic zone does not occur on mountains at low latitudes, where the frost gradient is abrupt. Thus this formation appears only at the two borders of the tropical altitude zone: in Mexico and Central America in the north, and in Bolivia and Argentina in the south.

Mt. Kenya, Kenya

The huge isolated massif of Mt. Kenya (5195 m), located on the equator, displays a variety of climates according to differences in altitude and exposure. The southeast slope is the rainiest, with a mean gradient of about 2 mm per meter of altitude between 1400 and 2200 m, where a maximum of 2500 mm is reached and maintained for another 1000 m, to decrease again at a rate of about 3 mm per meter, to the summit area, where the estimated amount is around 850 mm (Thompson, 1966). Northwesterly slopes have, in contrast, only about half this amount of rainfall. Figure 2–11 shows a rainfall profile adapted from Thompson (1966). On all sides of the mountain, the precipitation pattern is equatorial, but on the windward side the main dry season is June through August, and on the lee side and on the adjacent western plains, in the rainshadow of the massif, the driest months are January and February (Fig. 2–10).

Little is known about the temperature regime of Mt. Kenya. Coe (1967b) gave one-month records at three altitudes (Table 2–5). These figures show rather low absolute and mean minima, suggesting that the climate has a continental character. Furthermore, the decrease in temperature range with altitude clearly appears along this gradient. Coe (1967b) also remarked that one of the most conspicuous factors in the temperature regime is the great speed at which temperatures fluctuate near the ground. Under clear skies, the ground temperature rises sharply away from that of the air, but in a similar way, when the sky becomes clouded, it falls rapidly until air and ground temperatures are almost equal. This pattern is repeated constantly during the day. Hedberg (1964) also remarked on the rapid temperature changes frequent in the afroalpine climates, due largely to the thin atmosphere with low heat capacity and variable cloudiness. He noted that changes up to 10° in half an hour are not rare.

TABLE 2–5. Temperature data (in °C) on the slopes of Mt. Kenya, recorded between December 19, 1957, and January 17, 1958.

Altitude (m)	Mean	Mean max	Mean min	Average daily range	Max daily range	Min daily range	Absolute max	Absolute min
3048	7.4	16.2	1.7	14.5	20.5	7.8	19.5	−1.5
4191	2.0	5.5	−3.6	8.9	15.0	7.2	11.0	−6.7
4770	−1.9	1.2	−3.9	5.1	10.0	2.8	5.0	−8.3

From Coe (1967b).

In summary, Mt. Kenya is an equatorial mountain with rather wet, continental, highland climates, the dry seasons are short, and the number of humid months varies from 9.5 to 11 (Hedberg, 1964). The rainfall regime and amount of rainfall on this mountain closely resemble the environmental conditions of most of the Venezuelan Andes, as can be seen from the previous analysis of the climate of the páramos of Mucubají and Piedras Blancas.

Mt. Kilimanjaro, Tanzania

Mt. Kilimanjaro (3°S, 5899 m) is another imposing isolated volcano. At its highest elevations it displays ecological conditions that contrast sharply with those found on neighboring Mt. Kenya. Rainfall, for instance, decreases rapidly with altitude, resulting in such a barren landscape that the uppermost belt on this mountain has been considered an alpine desert (Salt, 1954). Mt. Kilimanjaro is one of the best known African mountains with regard to precipitation, because nine rain gauges have been in operation in the upper areas since the 1950s, allowing one to distinguish its striking climatic contrasts.

The rainfall regime is equatorial throughout, with the lowest monthly minima during the Southern Hemisphere winter, while the rainiest months are March and April (Fig. 2–10). Hedberg (1964), using the information available up to that time, showed the altitudinal variation in annual precipitation on the two contrasting slopes, the windward southeast one and the leeward west side (Fig. 2–20). On the southeastern slope, rainfall decreases from a maximum amount at 2200 m to a minimum at 4250 m, where just 203 mm has been recorded. Precipitation increases again to more than 500 mm to decrease finally to an estimated annual amount of 15 mm at the summit. On the west slope, precipitation decreases with a still steeper gradient from 935 mm at 4000 m to 84 mm at 4750 m. In accordance with the extreme dryness of the summit, the snow line is reported to be at 5400 m, about 800 m higher than on Mt. Kenya. The glaciers descend to 4500 m along the moister southeast slope, but they occur only at 5700 m on the drier northeast slope (Hedberg, 1964).

Although at 300 m there are eight to ten humid months, at high altitudes only two months, March and April, could be considered humid. But in spite of the rainless nature of the summits, Salt (1954) remarked that precipitation does occur in the form of dew and no doubt contributes to the maintenance of a favorable water budget in high-altitude plants. One may infer from Hedberg (1964) that plant formations on Kilimanjaro resemble more closely the puna of the drier eastern Peruvian altiplano than the páramos of the moister northern Andes, or than neighboring Mt. Kenya. Thus, the characteristic woodlands of giant rosette trees are quite reduced and localized in wet alluvial soils of the high valleys of Kilimanjaro, whereas, as in the puna, the slopes are covered by hard tussock grasses and dwarf shrubs.

As is normally the case in dry climates, inter-

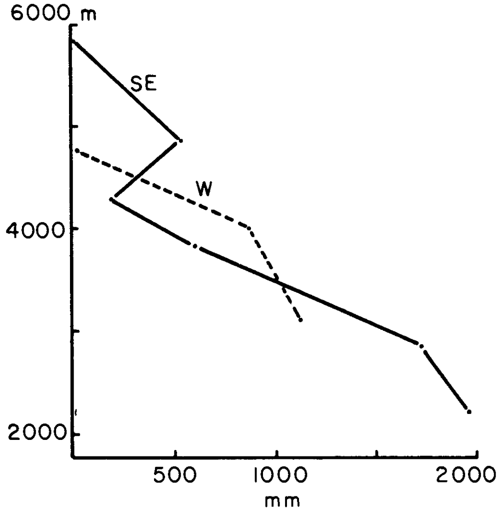

FIG. 2–20. Altitudinal variation in precipitation on the two opposite slopes of Mt. Kilimanjaro: the SE windward slope and the W rainshadow slope. Data from Hedberg (1964).

annual variability in precipitation is quite conspicuous on Mt. Kilimanjaro. On the basis of 6–12 years of records, the ratio between maximum and minimum rainfall attained the extreme value of 40 at 4750 m, thus indicating a tremendous unreliability that can be compared with that found in the Bolivian puna.

Very few data are available on temperature conditions at high altitudes. Klute (1920), as reported by Coe (1967a), recorded temperature at 4160 m during 46 consecutive days. Mean temperature was 1.8° with a daily amplitude of 10.1°. These few figures seem to confirm the rather extreme nature of the Kilimanjaro highlands, with wide daily ranges characteristic of climates with clear skies, low cloudiness, and high sunshine and radiation.

In spite of the much reduced extension of the afroalpine belt as compared with the páramo and puna of the South American Andes, a remarkable diversity of high-altitude environments and their corresponding biota is also apparent in Africa. This diversity constitutes an insular replica of the temperature and humidity gradients fully expressed in the Andes from the wettest and mildest páramos of Venezuela and Colombia, to the driest and most continental puna landscapes of the Peruvian and Bolivian Andes.

Mt. Wilhelm, New Guinea

Mt. Wilhelm (5°45′S, 4510 m) is one of the highest peaks in New Guinea. Hnatiuk, Smith, and McVean (1976) discussed the climate of Mt. Wilhelm on the basis of several years of records at the Australian National University Research Station at 3480 m, together with a few additional measurements at several other sites from 3215 m to 4400 m. A first singularity of this mountain is that the upper limit of natural forest is found at 3800–3900 m (Smith, 1975), that is, at least 600–700 m higher than in most other wet tropical mountains. Such a high timberline has been correlated with the rainy climate of this mountain: more than 3400 mm of rainfall at 3480 m and around 2900 mm at 4380 m. This factor may also cause the low upper altitudinal limit of agriculture, at about 2500 m.

Rainfall shows a pronounced single maximum during the Southern Hemisphere summer, but the two driest winter months each have more than 70 mm rainfall (Fig. 2–10). Snowfalls are frequent above 4000 m and may occur at all times of the year. Although there is a permanent water surplus, there may be short periods of water deficit during the dry season when up to 22 consecutive dry days have been recorded. Relative humidity is high, with minimum values between 40% and 80%.

Hnatiuk, Smith, and McVean (1976) distinguished three basic types of daily weather pattern whose distribution throughout the year reflects the seasonal cycle of rainfall. During the wet season, most days have fairly steady rain, thick fog, and little if any clear sky during the whole 24-hour cycle. Radiant energy input during such days may attain only 13% of total possible solar radiation. In the dry season, days tend to have clear sky either at night or during the day, with no or only light showers. On sunny days, up to 94% of total possible solar radiation may reach the land surface. A third weather pattern may occur at any time of year, when the day begins with a clear sky and often with ground frost or heavy dew. Cloud formation begins from the early morning on, and by about noon or in the early afternoon intermittent mist and showers occur. By sunset, clearing begins and in a couple of hours the sky again becomes cloudless.

Screen temperatures recorded at the research station give a yearly range of only 2.0°C, a mean maximum of 11.6°C, mean minimum of 4.0°C, with recorded extremes of 16.7° and −0.8°C. It is interesting to compare these figures with the extreme temperatures recorded over nine years at Mucubají, in the Venezuelan Andes, at similar elevation: 22.2°C and −8.6°C. The range is almost twice that of Mt. Wilhelm, suggesting what Hnatiuk, Smith, and McVean (1976) termed a quasi-oceanic climate. But as usual, the ground surface has a much more severe temperature regime than that shown by screen records. Thus, for instance, at 10 cm above a short grass turf, shielded from direct sunlight, mean maximum and mean minimum recorded during one year were 19.7°C and −1.1°C, respectively, with extremes of 29.4°C and −9.4°C. In correspondence with this temperature gradient upward from ground level, very few days with freezing temperatures have been recorded in the Stevenson screen at 1.5 m aboveground at 3480 m, but ground-level freezing temperatures appear to be quite common. Ground frost was recorded during more than 50% of nights in a year. It can occur any night of the year when skies remain clear. The number of frost days was not recorded. However, freezing temperatures seem to be common at ground level but rare at 1.5 m. Topography has an important influence on frost days, producing significant site-to-site variation during one year. There also appears to be great variability from year to year.

In summary, Mt. Wilhelm seems to have one of the rainiest and wettest tropical high-altitude climates, with more than 3000 mm rainfall, ten rainy months, and two somewhat less rainy months, the driest one with 75 mm rainfall. As a consequence, the temperature climate is comparatively mild, with low maxima and high minima, reflected in the scarcity of freezing temperatures and frost days at elevations where these events are much more frequent in tropical mountains of South America or Africa. Both humidity and temperature constancy and narrow range impart a definite oceanic character to this island mountain, a situation that contrasts sharply with the continental mountains of East Africa and the South American Andes.

According to Smith (1980b), the major climatic limitation to life at high altitudes does not derive from low minimum temperatures but possibly from low daylight temperatures together with the very reduced solar radiation due to cloudiness, fog, and mist. These characteristics seem to favor montane forest over páramo-like formations and to disadvantage the growth of any type of crop.

TOPOCLIMATES AND MICROCLIMATES

The Influence of Aspect and Topography

In mountain systems with abrupt and irregular relief, horizontal surfaces are either reduced to small areas or are nearly inexistent. Under such circumstances, the concept of regional climate loses most of its value, since the weather conditions recorded at any given site represent, at best, a small area around that site. Several dozen meters away from the recording station, differences in elevation, in slope, or in topography may induce significant changes in climatic conditions. In this way, topoclimates become ecologically more meaningful than regional climates. Geiger (1966, 1969) and Barry and Van Wie (1974) review this subject in mountain areas in general, stressing the effects of three key factors: slope angle, slope aspect, and relative topographic position. The first two modify diurnal temperature and humidity through their action on insolation, while topography influences night climate through its action on downward cold air movement and the daily cycle of slope and valley winds.

The role of slope aspect is fairly different in tropical and in temperate situations. The orientation of mountain slopes with respect to the movement of air masses leads to a sharp contrast in the amount of precipitation at regional level between lee- and windward slope. At low latitudes slope aspect produces more contrasting topoclimatic differences between east and west slopes than between north- and south, as is normally the case at higher latitudes. Within the tropics, direct sunshine reaches either the north or the south-facing slopes, depending on the period of the year, thus erasing most of the differences between these two slopes. In contrast, the particular conditions of local air circulation in tropical mountains are responsible for differences in insolation between east and west-facing surfaces. The subsequent differences in temperature and humidity are often reflected in the structure and composition of biotic communities as well as in land use.

In many tropical mountains, the daily weather pattern determines that insolation on west-facing slopes be significantly reduced by cloudiness or fog during the afternoon, in contrast with east-facing slopes receiving early morning sunshine. Sites of easterly aspect receive greater direct insolation and are therefore drier, having higher maxima and lower minima. This pattern has been shown for instance on Mt. Wilhelm (Hnatiuk, Smith, and McVean, 1976; Smith, 1977a) and in the Venezuelan páramo (Azócar and Monasterio, 1979, 1980b).

On Mt. Wilhelm, Hnatiuk, Smith and McVean (1976) placed max–min thermometers 10 cm aboveground at 3480 m, 4020 m, and 4380 m, on slopes of opposing aspect but with similar plant cover and slope angle. The results of several weeks of recording show that minimum temperatures were generally lower, and maximum temperatures higher, on the east-facing slope. The differences between maximum temperatures may attain 10° or more. Hnatiuk et al. (1976) attribute higher maxima on east-facing slopes to a longer period of insolation due to a lower frequency of clouds in the morning than in the afternoon. Lower minimum temperatures may be due to drier soils, possibly because of greater evaporation under conditions of greater insolation. The differences may be confined, however, to the air layer below 20 cm and to the uppermost soil layers. Barry (1978b) measured soil temperatures on a 35° east-facing slope, and on a 25° west-facing slope about 30 m apart. Plant cover at both sites was tussock grass up to 30 cm high and sparse shrubs. The easterly slope averaged up to 10° warmer at 1 cm, in the morning before cloud had built up. But in the afternoon, the west-facing slope was just a few degrees warmer because cloud cover reduced the warming effect of direct sunshine. These results support the view that differences in east–west aspect could be

TABLE 2–6. The effect of slope aspect, topographic position, and vegetation on air temperature (in °C) at 10 cm and 150 cm aboveground in the Páramo de Mucubají (3700 m), Venezuela.

Slope	West-facing	East-facing	East-facing	Valley bottom
Vegetation	Páramo	Páramo	*Polylepis* forest	Páramo
10 cm				
Annual mean	3.2	6.1	5.4	4.9
Mean max	13.7	19.1	15.0	17.9
Mean min	−4.4	−2.3	0.3	−5.8
Frost days	230	115	39	235
150 cm				
Annual mean	3.0	5.4	5.3	3.8
Mean max	17.0	18.1	16.7	16.7
Mean min	−3.4	−1.2	−2.0	−3.4

Data from Azócar and Monasterio (1980b).

important ecological factors in many tropical mountains.

During one year Azócar and Monasterio (1980b) recorded air temperatures on slopes of contrasting aspect at the Páramo de Mucubají (3700 m) in the Venezuelan Andes. Both east- and west-facing slopes in this area have páramo vegetation with only minor floristic differences. Temperature was recorded at 10 cm and 150 cm above ground. The effect of aspect on air temperature is more evident at 10 cm, where the difference between annual means of east- and west-facing slopes reaches almost 3° (Table 2–6). Notice also how this warmer character of the easterly slope appears clearly reflected in the annual number of frost days. Frost is in fact half as frequent on the east-facing slope. That these differences in temperature were mainly due to differential insolation was shown by the fact that on days with clear mornings, the eastern aspect may receive up to 15% more sunshine than the opposite slope. Table 2–5 also indicates the influence of topographic position on site climate. The recording site in the valley bottom, at 3600 m, even though located 100 m lower than the two slope stations, does appear to be the coldest, as indicated by the lower mean minimum. Furthermore, the valley has three times more frost days than the average number of frost days recorded under screen at 150 cm in the nearby recording station at Mucubají, at the same altitude. The topoclimate of the valley is the coldest of the whole area probably because of the night inversion in temperatures due to downward flow of valley and slope winds.

The topoclimatic effect of slope angle has not been analyzed in tropical mountains, although it could be expected to have a significant influence. In contrast to the situation prevailing at middle latitudes (Geiger, 1966), in the tropics gently sloping surfaces ought to receive more direct sunshine than either horizontal or steeper slopes. However, no data are available to verify this suggestion.

The preceding examples illustrate the crucial importance of topoclimates as generators of particular microhabitats where living beings may escape from the full impact of adverse atmospheric conditions in high tropical mountains. All highland environments are therefore patchy and are differentiated into a rich and complex mosaic of microhabitats that often exhibit sharply contrasting patterns of temperature and humidity. This mosaic of environmental patterns must not only be studied from a static viewpoint. One must also remember that they may suffer astonishingly rapid changes in just a few minutes, leading to sudden alterations in radiation, humidity, wind, and temperature. The ecological consequences of this dynamism cannot be overemphasized.

The Microclimates of Plants and Plant Formations

Plant cover modifies the heat budget of a land surface by its influence on incoming and outgoing radiation, as well as by its direct modification of humidity and temperature below the canopy. These microclimatic influences have been well documented in tropical high mountains, and are particularly noticeable when different plant formations are compared with each other. This is the case, for instance, when forest and páramo formations growing at the same altitude in nearby sites are simultaneously monitored for weather variables.

Table 2–6 compares data on air temperature under the canopy of a *Polylepis sericea* grove at 3700 m in the Venezuelan Andes with the surrounding páramo dominated by rosettes of *Espeletia*, low shrubs, and herbs. Mean and maximum air temperatures are lower under the forest canopy than under the sparse cover of páramo plants, on a similar slope and at a similar elevation, but minimum temperatures are higher in the forest 10 cm above the ground. Notice also how the number of days of frost is greatly reduced inside the forest as compared to the sites with páramo vegetation. The forest canopy, even if it is low and light as at Mucubají, operates effectively as a screen for short- and and long-wave radiation. Temperature fluctuations are thus dampened and the daily climatic cycle is less contrasted.

Monasterio (1979) presented data from still higher elevations in the Andes concerning the microclimate of plants growing at the Páramo de Piedras Blancas at 4200 m (the climate in this area was described earlier in this chapter). The desert páramo formation, characteristic at this altitude, leaves the soil almost entirely devoid of plant cover, the giant rosettes of *Espeletia* being the major living component of this ecosystem. Daily cycles of air, soil, and plant temperatures were followed in the dry and in the rainy season. Under the cloudy skies and foggy days of the rainy season, vertical profiles of air temperature tend to flatten out; thus temperatures 10 cm aboveground were persistently about 1° higher than at 150 cm. But under the clear skies prevailing during the dry season, air temperature at 150 cm was several degrees higher than at 10 cm, at least throughout the night and the morning, while the reverse was true in the afternoon. These slight differences along a vertical gradient upward from the ground surface may help to explain the vertical structure of this ecosystem, with its green biomass located mostly well above ground level, between 1 and 3 m.

Species of *Espeletia* living at this high altitude are able to maintain the same temperature as that of the air throughout the 24-hour cycle. In fact, the difference between leaf and air temperatures never exceeds a few degrees, the leaves being slightly warmer during the daylight hours and cooler by night. Leaves can control their temperature in some way, but this behavior appears even more striking at the apical bud of the rosette, where the whole process of renewal of the assimilatory structures rests. The apical bud lies well protected among the dense envelope of developing leaves, thus allowing its temperature to be maintained several degrees higher than that of the air. The exception to this pattern is during the hours of more intense sunshine, in the morning, when the apical bud is cooler than the air (Monasterio, 1979). These features suggest that morphophysiological mechanisms operate to maintain a favorable heat budget in these plants submitted to circadian cold stress in the periglacial zone in the high tropical Andes.

Other interesting microclimatic data come from the upper limit of the *Pinus hartwegii* forest on Orizaba at 3990 m. At this altitude an open pine woodland intermingles with the mountain grassland (Lauer and Klaus, 1975). These authors recorded temperatures at various soil and plant surfaces during one daily cycle. At 150 cm above the ground needles of *P. hartwegii* maintain their temperature between 2° and 17° when air temperature ranges between −2° and 15.5°. Moreover within a tufted grass cushion of *Festuca* temperature oscillated between 0.5° and 27°. Clearly, living plant surfaces are able to maintain their temperature higher than the atmosphere near the ground, a feature that may be particularly important during frosts.

Other examples of the influence of plant cover on temperature conditions above different vegetation canopies and in various plant and soil surfaces have been reported from several tropical highlands, such as Mt. Wilhelm (Smith, 1977a; Barry, 1978b), Mt. Kilimanjaro (Coe, 1967a), and the Colombian páramo (Schnetter et al., 1976). All of these studies emphasize the fact that biological surfaces create and maintain their own boundary conditions at their interfaces with the lower atmosphere and that these biologically conditioned microclimates tend to favor survival under the limiting conditions imposed by low temperatures.

SUMMARY AND CONCLUSIONS

On the basis of this review of climatic conditions of tropical highlands, I wish to make some generalizations about the features constantly found in these regions, the range of variation in the major climatic parameters, the main peculiarities of some especially interesting situations, and finally, about the crucial ecological characteristics of climate for the upper limits of life or for survival.

All high tropical mountains share many important climatic features that make them quite specific environments for the colonization and the maintenance of plant, animal, and human populations. They are part of the world's circumtropical belt, and hence they show the relative annual constancy in incoming radiation, daylength, and temperature that generally distinguishes low from high latitudes. In this respect, they contrast sharply with the highly seasonal rhythmicity of higher latitudes, where life must cope with an unfavorable winter season and must profit from a rather short growth season to accomplish most of its activities. But tropical mountains differ from adjacent lowlands too, principally by the lower temperatures prevailing throughout the annual cycle. The climate of high tropical mountains makes these areas peculiar environments that are ecologically apart from both extratropical mountains and from tropical lowlands.

In spite of the many climatic features that distinguish tropical highlands from any other type of environment, the first generalization to be made is that it does not seem possible to refer to a single type of tropical high-altitude climate. Indeed, the diversity of weather types and regimes makes it necessary to distinguish several climates within the upper belts of tropical mountains.

A first gradient is latitudinal: annual ranges increase as one proceeds farther and farther away from the equator. At a given point, annual oscillation in temperature becomes so important as to delimit the tropical or thermically constant zone. This transition may be analyzed either in the central Andes or in the Mexican highlands, since these are the only two areas with a continuous range of high mountains from tropical to temperate latitudes. In both cases, some common features appear. Thus, for example, the influence of polar air masses is felt periodically during the winter, drastically lowering the temperature for several days. This naturally contributes to amplify differences in mean monthly temperatures.

A second gradient arises from the geographic position of each mountain massif, either with reference to distance from the ocean or with respect to the position of the chain in connection with the circulation of the lower atmosphere. Distance from the sea induces a differentiation between predominantly oceanic highlands and rather continental massifs. The New Guinea highlands afford a clear example of oceanic influence while the interior volcanoes of East Africa or the Peruvian and Bolivian altiplano represent continentality. The orientation of a given chain is important to induce differentiation between windward and leeward slopes. Examples were given of this feature, such as Mt. Kenya, Mt. Kilimanjaro, the different Andean chains in Colombia, and the contrasting Amazonian and Pacific slopes of the Peruvian Andes.

A third gradient of environmental variation is altitude. Altitudinal gradients of temperature and precipitation play a major role in the zonation of tropical mountains. Some conspicuous ecological boundaries related to these gradients are the upper continuous forest line, the timberline, the lower limit of periglacial climate, and the nival limit. The case of the upper limit of the tropical montane forest or cloud forest was considered in various situations. The most valid generalization seems to be that on moist slopes this boundary is closely related to frost frequency, since apparently even a few frost days per year are sufficient to replace the forest by páramo. In the case of the coniferous forest of the Mexican volcanoes, the situation is completely different, since the frost line delimits mixed forest from pine forest, whereas the latter vegetation formation extends well into the frost climate.

Periglacial climates, characterized by the actual periglacial sculpture of the land (Tricart, 1970, Hastenrath, 1973, 1977; Schubert, 1979, 1980), permit one to define two types of high-altitude ecosystems in the Venezuelan Andes, which Monasterio (1980a) named the Andean and the high Andean zones. However, it is not yet possible to indicate precisely what climatic features are at the root of this sharp geomorphological and ecological boundary. Finally, the nival zone occurs at quite difference altitudes in various chains, being related either to total rainfall or to the temperature lapse rate. Along the humid slopes of the Andes, the nival belt begins very close to the line of permanent frost, where every day in the year is either a frost day or a frost-change day. Thus, in the Sierra Nevada de Mérida, the glaciers descend to 4700 m. But in very dry mountains, as on the peaks that emerge from the puna, or on volcanoes such as Kilimanjaro, this limit may be found as high as 5500 or even 6000 m.

One of the more complex and less understood altitudinal gradients in tropical mountains is the increase in number of frost days with elevation. It differs widely in various mountain chains, being related to several concurrent factors such as latitude, amount and annual distribution of rainfall, and intensity of drought periods. On moist slopes, with short and weak dry periods, frost begins higher than on dry slopes, well above 3000 m in the lowest latitudes; upwards, the number of frost change days increases slowly up to 4500 m or more, to change suddenly at the 4700 m level at the nival limit (Fig. 2–1). Under these circumstances, the periglacial zone does not exist, since the change from half to all days in the year with freezing temperatures is too abrupt, collapsing thus the periglacial area between the páramo and the nival zones. Quite the opposite situation is found on the Mexican meseta, where the frost gradient is rather smooth from the level of first frost occurrence, at about 1600 m, up to 4000 m. The gradient then becomes steeper above this level, which precisely constitutes the pine forest–mountain grassland boundary (Fig. 2–1). On dry slopes of the northern Andes, such as the upper Chama Valley in Venezuela, frost behavior appears to be similar to that of the Mexican altiplano, but the curve is displaced toward higher elevations. Finally, on the high peaks that tower over the Peruvian puna, such as El Misti volcano, the curve relating the number of frost days per year to altitude appears to be entirely different from all others, because frost increase is abrupt at lower elevations, changing from a few frost days to about 200 frost days in the narrow range between 3200 and 3400 m. Above this level, the increase becomes gradual up to 4700 m. This zone of gradual increase corresponds in this area to the moist puna belt.

I wish to end with a brief consideration of the ecological impact of high-altitude climates on plant and animal populations. In this respect, some similarities and many differences between tropical and temperate mountains must be emphasized. In tropical highlands, strong winds or a seasonal snow cover do not operate on biological processes as they do in most temperate mountain areas. Moreover a frost-free growth season does not exist at any altitude above the frost line, since seasons are absent, and frost may occur at any time of the year (within the limitations imposed by the rainfall patterns discussed here).

The two factors that most authors consider to be highly significant filtering agents for maintenance and survival of life in tropical mountains are freezing temperatures at night and insufficient radiation and suboptimal temperatures during daylight hours. Adaptations to permit survival with the erratic or the normal occurrence of freezing imply serious modifications in form, function, behavior, or all three, which rather few tropical species have been able to accomplish. Furthermore, adaptations should also allow a favorable performance during the day, when quite often heat and light may be limiting factors and when sudden and hazardous changes do occur from day to day or even from hour to hour. The lack of well-marked annual thermal seasons does not imply lack of response of biological populations to temperature changes. Quite the contrary. Responses not only have to exist, but have to be instantaneous, and each species must be prepared to withstand as drastic changes in radiation, temperature, or humidity in a few minutes, as other populations suffer in contrasting annual seasons. In this way, a combination of opportunistic responses to sudden changes of extremely short periods and high frequency must accompany in their life strategies the capacity to permanently support low-temperature stress as well as the ability to maintain a favorable heat-and-carbon balance under conditions of limited energy supply.

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