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HERAUSGEGEBEN VON WILHELM LAUER

BAND XVIII

Natural Environment and Man in Tropical Mountain Ecosystems

Natur und Mensch in Ökosystemen tropischer Hochgebirge

Herausgeber

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Proceedings of the Symposium of the Akademie der Wissenschaften und der Literatur, Mainz
– Kommission für Erdwissenschaftliche Forschung –
in Connection with the International Geographical Union
– Commission on Mountain Geoecology –
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Natural Potential and the Land-Use-System of the Kallawaya in the Upper Charazani Valley (Bolivia)

Wilhelm Lauer

With 22 Figures

1. Introduction

The Kallawaya are an Indian ethnic group living in an elevated valley of the northern East-Cordillera of Bolivia. Although their land is less than 300 km from the capital city of La Paz, it is located in a peripheral and comparatively isolated settlement area when applying todays standards of accessibility (see Fig. 1). There has been just one gravel road since the Seventies leading to this area and to a small market-town (Charazani), founded by the Spaniards, and also, in the meantime, to two further Indian communities. All other villages – there are 12 more – can only be reached via peripheral paths. However, this assessment of the accessibility of the area reflects to some extent ways of thinking in the automobile age, for the settlements communicate quite well with each other, having maintained since pre-colonial times a close-meshed network of exchange of goods within the population group itself and with the people living in the neighboring villages. Long-distance trade links are maintained down to the Amazon Valley via old Indian paths, to Peru and in the direction of the capital city of La Paz. In other words, this population group is well linked with the outside world, even when applying criteria of space and time different from ours.

The settlement area of the Kallawaya is located in the Muñecas Highlands, at the southern foot of the Apolobamba Cordillera in the system of valleys of the upper Rio Charazani, whose widely branched upper reaches are partly fed by the glacier creeks of the Apolobamba Cordillera and partly from the low ice-free tops of the Muñecas Highlands. The upper region of the Kallawaya settlement area was transformed by the glaciers in the glacial period and is partly characterized by wide valleys. On its further course, however, the Charazani River – in narrow valley sections interrupted by drier and wider valleys – dissects the Muñecas Highlands in the direction of the Rio Mapiri, which flows into the Rio Beni and thus unites with the Amazon River system.

Today, there are still approximately 8000–10 000 Kallawaya living in the Charazani Valley, their way of living largely based on the agro-ecological conditions established in pre-colonial and colonial times.

Today, the entire agrarian, Ketschua-speaking population, living in this area around the small district town of Charazani, is generally called Kallawaya. This term applies to the area occupied by 12–14 villages. In a stricter sense, however, the term actually refers only to a group of doctors and herb dealers. According to studies by W. Schoop (1982), there are about 150 whose leaders are still engaged in this highly important activity, but the question of whether their tradition goes all the way back to pre-colonial times is as yet unanswered. At any rate, a representation in the 16th century Chronicles of Poma de Ayala shows Kallawaya who were working as dignitaries at court in Cuzco and who were worthy of carrying the sedan-chair of the ruler and his wife. Today the Kallawaya doctors have a collection of approximately 20 medicinal herbs, which, by the way, are not from that area. Furthermore, as W. Schoop (1982) was able to determine, the Kallawaya doctors come particularly from the smaller villages of the area, where this activity was apparently performed as a secondary occupation due to the insufficiency of arable land.

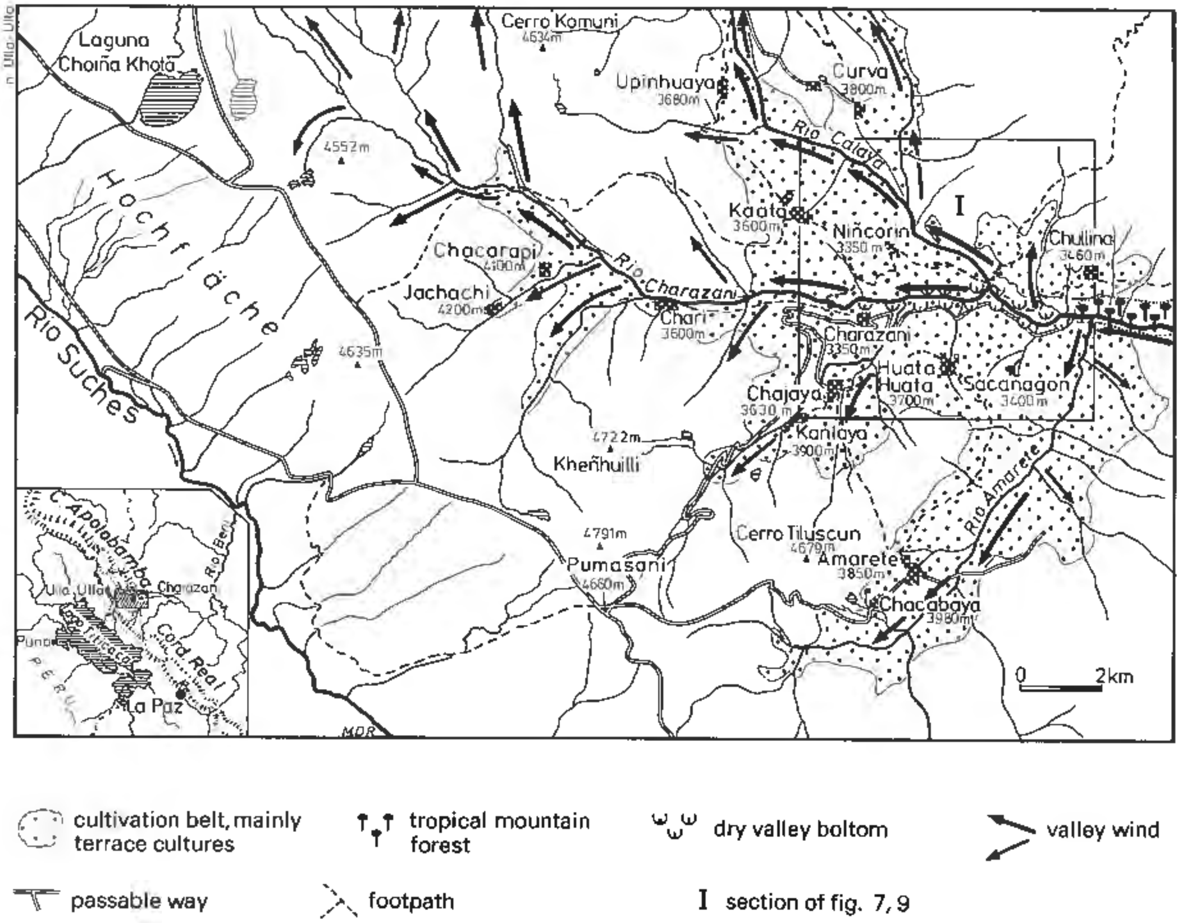


Fig. 1. Survey map of the study area.

While the Kallawaya undertook long trips throughout the Andes particularly in former times to exercise their profession, nowadays they travel mainly through the Ketschua-speaking highlands of Bolivia, so that they also work as doctors in southern Bolivia where Ketschua is spoken by the majority of the population.

The zones of settlement and agriculture of these Kallawaya people are located in the hygro-thermal altitudinal zone of the "tierra fría" above the forest line, between 2700 and 4300 m a.s.l., where the semi-humid climate with winter dryness still permits cultivation of land. The entire belt of cultivation shows a threefold vertical zonation. One can distinguish between a lower, a medium and an upper land-use belt, the characteristics of which are influenced by both eco-climatological and socio-economic factors. The large Kallawaya villages participate in all three land-use belts, each complementing the other and providing the Kallawaya with an almost self-sufficient economic system (compare Figs. 3 and 13).

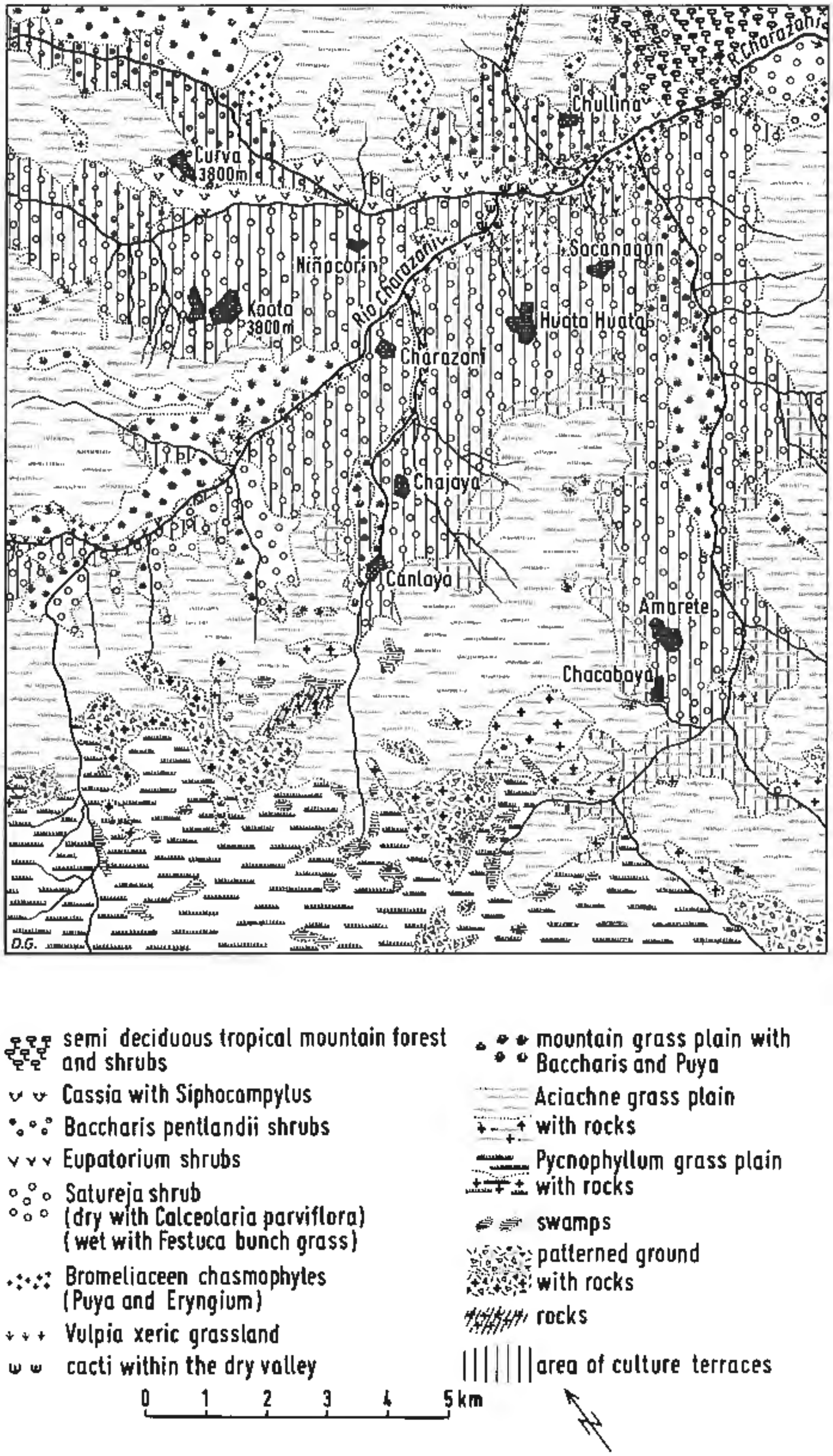


Fig. 2. Vegetation map of the inner Charazani region (part of the vegetation map of P. SEIBERT, 1982; revised form in preparation, 1984).

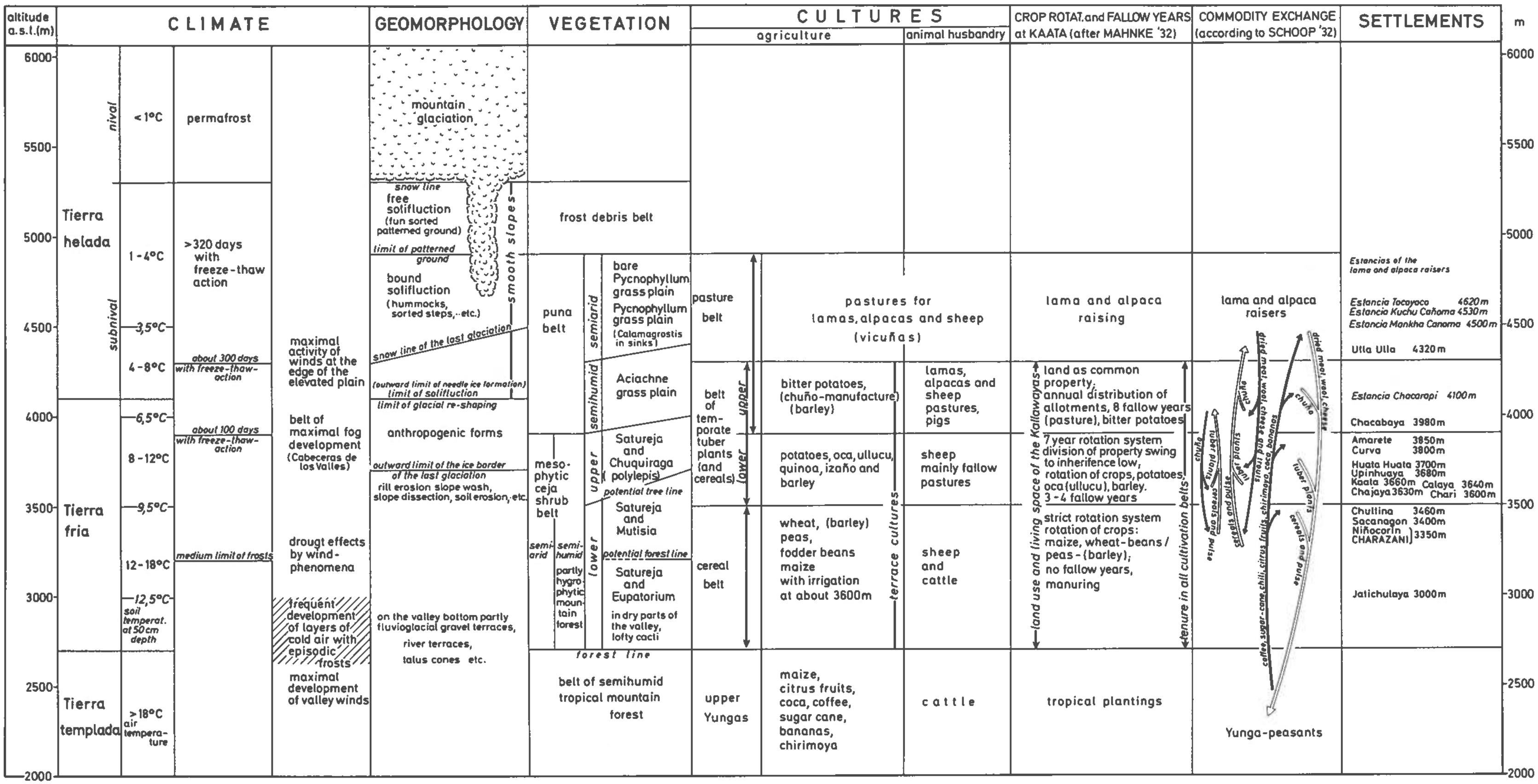


Fig. 3. Eco-climatic altitudinal belts of the Charazani region.

2. Geo-ecologial Conditions of the Agricultural Area

The altitudinal land-use zones may be described by means of climatic parameters, such as temperature, frost, precipitation and soil moisture, as well as by the potential natural vegetation.

Meanwhile, plant sociological surveys have been conducted and climatic parameters studied in the Kallawaya area. A group of botanists (P. SEIBERT and colleagues) has determined plant societies that are also suitable in the indication of ecological site conditions (Fig. 2).

On the basis of microclimatic studies in each altitudinal belts (W. LAUER and colleagues), it is possible to assign the plant communities to a three-dimensional temperature and humidity model, which provides an ecological description of the agricultural zone.

A survey (Fig. 3) shows the results of the studies carried out so far. It is a first attempt at a synopsis of the characteristics of the natural potential and of the Kallawaya land-use system.

The dependence of the arrangement of the plant sociological units on the adversely exposed slopes on both sides of the Charazani Valley is shown in a drawing (Fig. 4, compare also Fig. 2). The profile presents a picture of conditions in the valley area just above the present forest line. It reveals that during the winter-dry season, particularly when the sun is in its most distant position in the northern hemisphere, the northern and southern slopes differ greatly with regard to their thermal budget and thus in moisture conditions.

While the drier and warmer side of the valley between 3000 and 3900 m is characterized by an association of shrubs, the main species of which is *Satureja boliviana*, the opposite cooler and more humid slopes of the same altitudinal zone are distinguished by *Baccharis pentlandii* associations. Here then, the northern and southern exposures relative to the sun become clearly effective. On the lower slopes of the drier side of the valley, *Mutisia* shrubs predominate. In the driest positions (Fig. 5), cacti grow together with dry grass of *Vulpia spec.* These sites are exposed to an up-valley wind during the day. The strongly sunlit areas of *Satureja* shrubs at medium elevations are marked by *Calceolaria parviflora*. Only at higher elevations, where the up-slope winds condense and fog banks develop – mostly above 3600 m, does *Satureja* become physiognomically more prominent and dominate the vegetational picture more distinctly; here it is in association with *Chuquiraga*, representative of more humid locations. Islands of *Baccharis pentlandii* bushes can also be found.

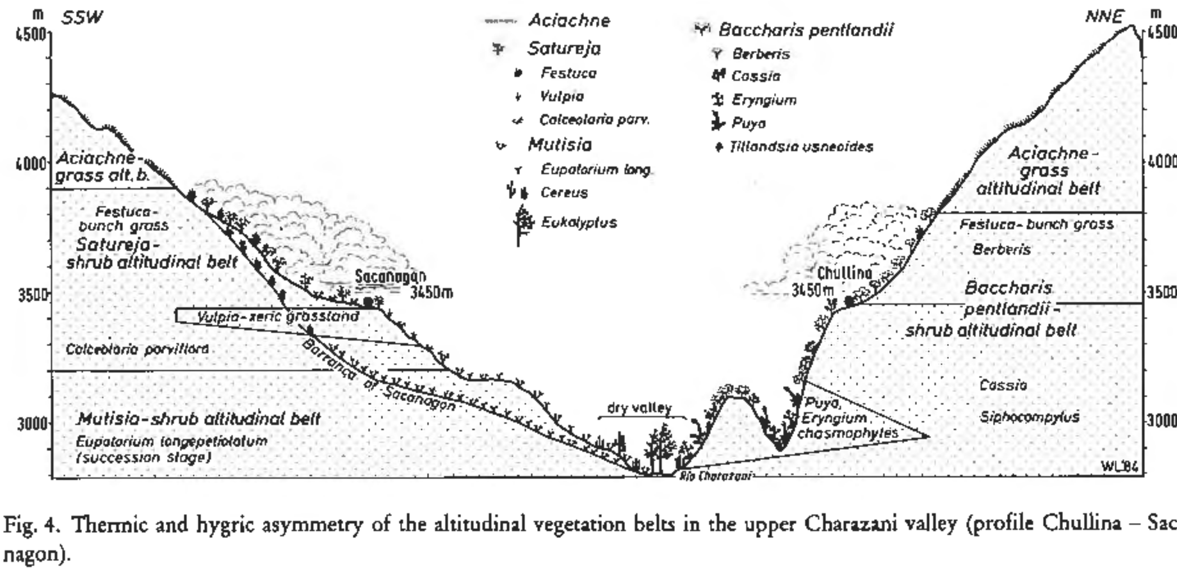


Fig. 4. Thermic and hygric asymmetry of the altitudinal vegetation belts in the upper Charazani valley (profile Chullina – Sacanagon).

Fig. 5. Dry part of a northerly exposed slope with cacti.

Likewise, on the opposite side of the valley with *Baccharis pentlandii* shrubs, which lies in shadow during the winter, the steep slopes are covered with grasses, especially the tall fascicle grass *Festuca dolichophylla*. Scattered within this area are *Eryngium* societies associated with *Puya* as the main species. *Puya* is found mainly on rocky sites, which, on these humid slopes exposed to the valley winds, are covered abundantly with terrestrial Bromeliaceas and *Tillandsia usneoides*.

Found particularly at the humid upper valley ends (Cabecera de Valle), remnants of *Polylepis* possibly mark a mesophytic bush-type forest line at an elevation between 3400 to 3600 m a.s.l. Other tree-like species, such as *Buddleya* and also *Fuchsia* and *Berberis* bushes, grow in the moist niches of the creeks.

The entire bush belt, on both exposures of the valley section described above, shows clear dependence on decreasing temperature with encreasing altitude, as well as on a moisture component, which makes itself felt in the greater dryness of the lower valley sections and greater humiditiy of the "Cabeceras".

Above 3900 m the bush belts of both slopes merge into the grass belt, where *Aciachne pulvinata* is dominant. This altitudinal belt corresponds to the upper belt of tuberous plant cultivation, as can be seen from Figs. 3 and 13. Here, steep rocky areas are covered with *Festuca* of medium height. The *Aciachne* grass is arranged in hexagonal patterns. The space between the grassy areas, seemingly bare from a distance, is actually densely covered with mosses and lichens. The most humid vegetational units of this altitudinal zone are *Plantago* and *Distichia* moors.

The gradiation of heat and humidity is not only reflected in the altitudinal zonation but also in the asymmetric arrangement of belts, depending on aspect and exposure. The contrast between slopes favoured and unfavoured by insolation is clearly marked. This contrast in insolation between slopes with different exposures plays an important role in the agricultural land-use of this altitudinal belt. The altitudinal boundaries of cultivation may vary between the sunny and shadowy slopes by up to 200 m.

3. Topoclimatic Bases

The climatic parameters were ascertained by several methods of measurement. By means of measuring journeys along the only road in the area at altitudes between 2700 and 4600 m, it was possible to determine three distinctive phenomena regarding air temperature and humidity in the hours of the early morning. A marked temperature and humidity inversion layer of differing thickness occurs between 3400 and 4100 m, depending on the meteorological conditions. Very often during the night cold air accumulates just at the bottom of the valley at an altitude of 2700 m and builds up to 3200 m.

During all measuring journeys in the dry season (Fig. 6), the daily frost limit was observed and measured, lying in most cases between 3600 and 4100 m. In this area, the ground freezes only on the surface and develops the so-called "needle-ice" phenomenon, while the snowfall boundary follows the frost limit.

The temperature and humidity inversion is mostly accompanied by a thick fog bank of differing vertical expansion. It disappears one hour after sunrise. At the same time, the temperature and humidity inversion remains measurable throughout the day. Only during the hours before and after the noonday position of the sun is it at a minimum though it disappears during the rain-producing weather types of the humid season.

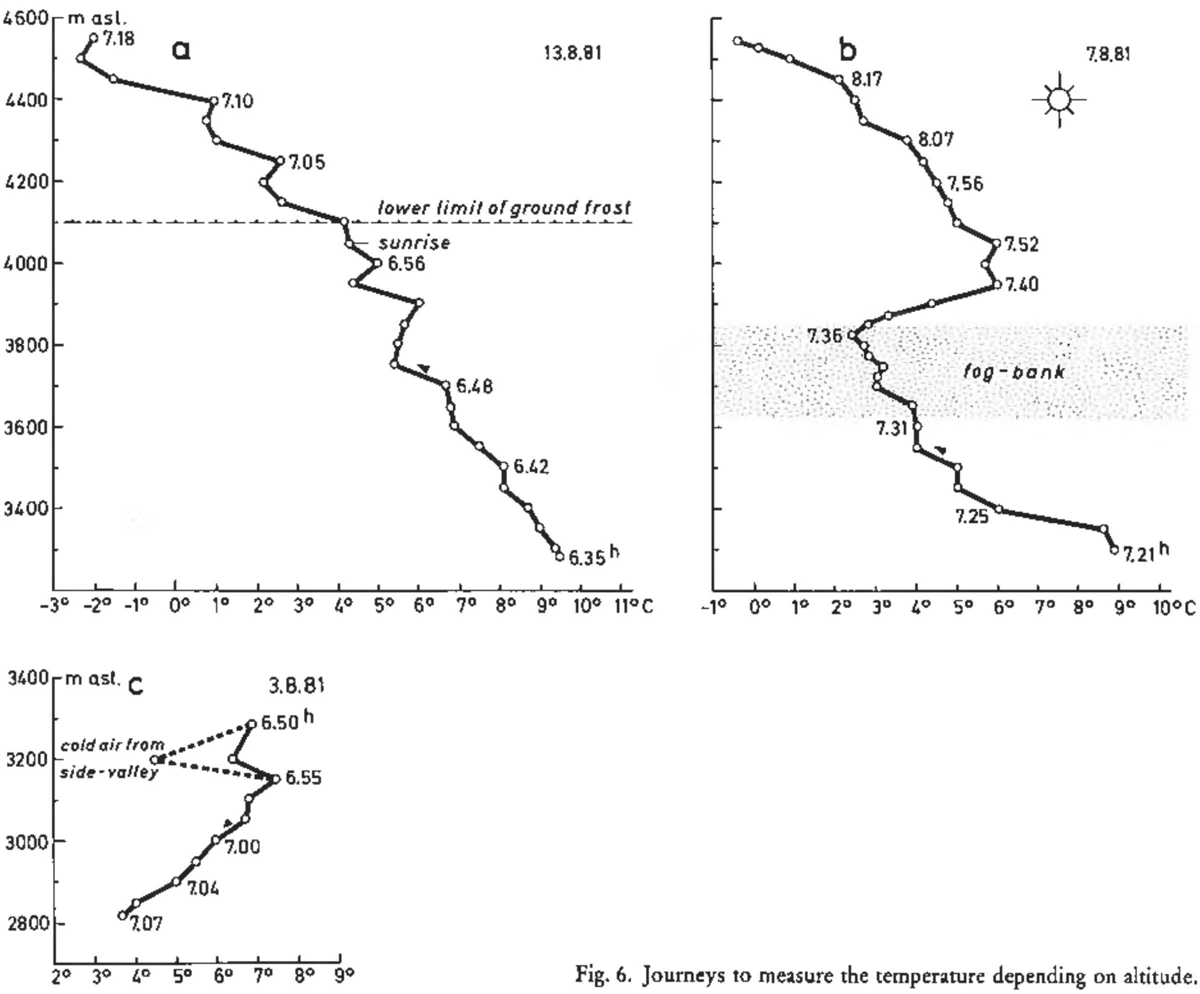


Fig. 6. Journeys to measure the temperature depending on altitude.

Fig. 7. Eucalyptus trees with wind shear features.

The altitudinal temperature and humidity zonation so far described is enhanced by a valley-mountain wind phenomenon, which is marked by intensive insolation, particularly during the dry season and on days with insolation during the rainy season. The valley wind flows up the valley and the slopes and promotes condensation and the formation of fog over the upper slopes. Over the middle section of the valley a downslope wind dries out the valley bottom.

Groups of cacti occur on the valley bottom and on the lower slopes as a result of dryness (see Fig. 5). The slope wind, which becomes more and more humid, favours the growth of *Bromelia* and *Tillandsia usneoides* already mentioned. The trees of the eucalyptus groups that have been planted everywhere show striking wind shear features (Fig. 7). Moreover, the transition from *Satureja-Chuquiraga* societies at higher elevations is attributable to the increased humidity with altitude, which is enhanced by the wind phenomenon.

The valley wind shows a daily cycle (Fig. 8). It sets in weakly between 9 and 10 hrs in the morning, reaches its maximum strength between 12 and 15 hrs – sometimes later – decreases sharply after 16–17 hrs and ceases to blow completely at approximately 19 hrs. The mean wind velocities range between 3 and 10 ms. Peak wind velocities over an average period of 3 minutes may be as high as 25 ms or more.

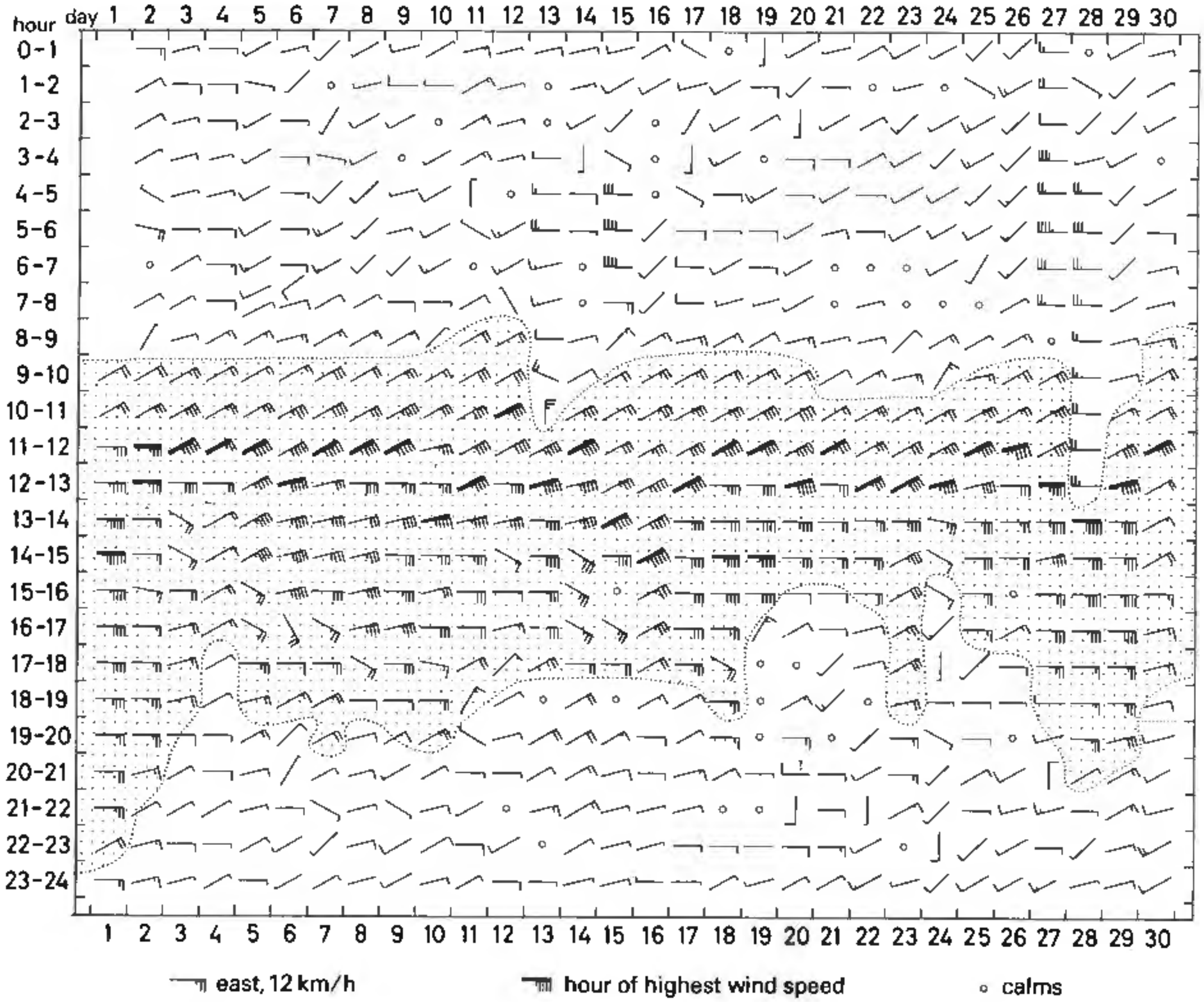
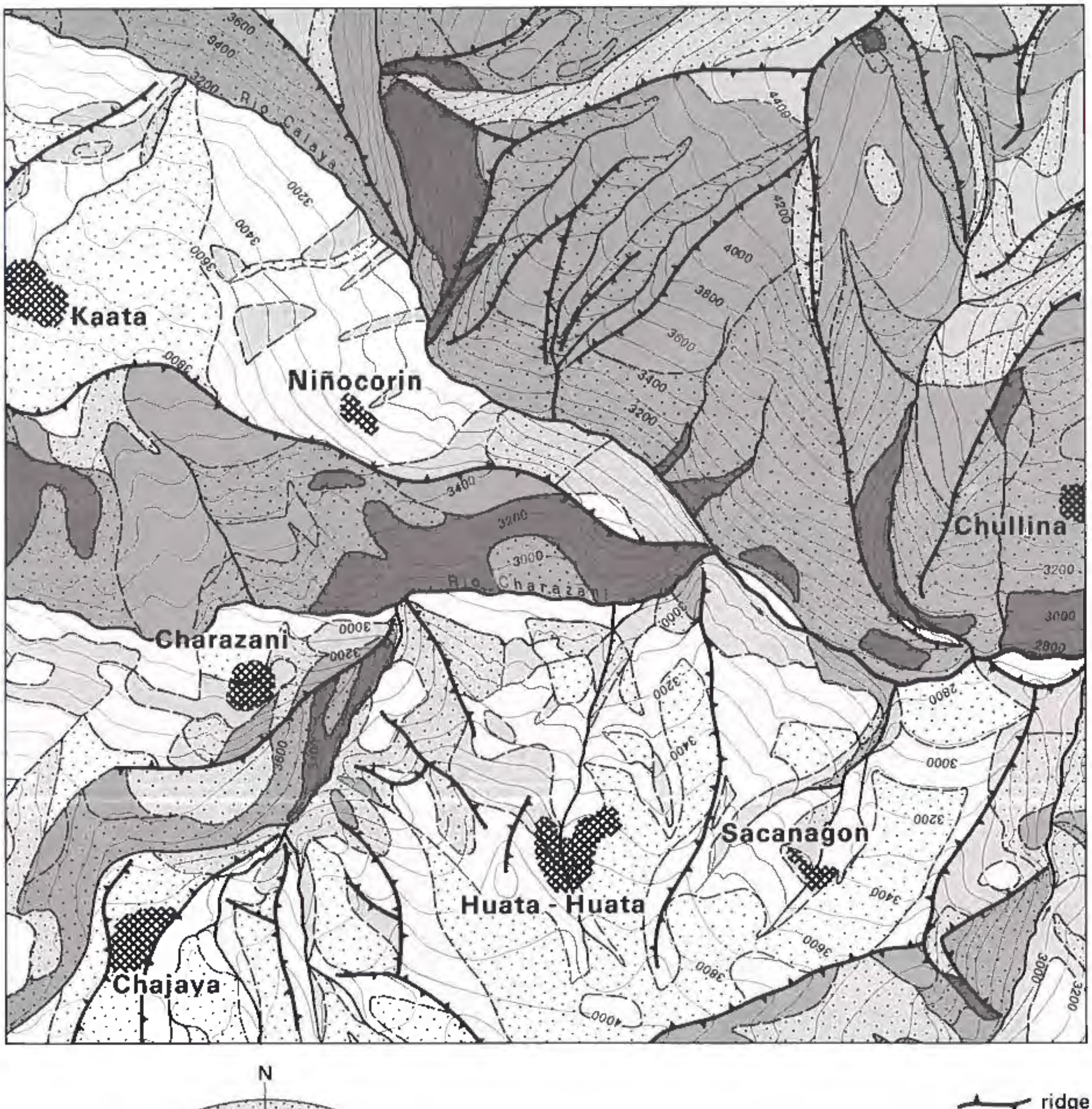


Fig. 8. Wind direction and wind speed during September 1981 in Charazani.

The valley wind phenomenon during the day has only a weak counterpart during the night. There may be considerable deviations, however, depending on the meteorological conditions. Normally, the velocity of the mountain wind ranges between 1 and 2 ms, but depending on the meteorological conditions, downslope gusts of 20 to 25 ms may occur and show bora-type features in the upper sections and on the valley bottom. Strangely enough, these gusts are often warmer on the slopes than the mean temperature of the season measured there. In such places they have foehn-like effects. Depending on the meteorological conditions, particularly in cases when cold air masses are present on the elevated plains and supported by katabatic winds from the nearby glaciers, they may occur extraordinarily strong bora-type downslope winds in the main section of the valley, which build up a pool of cold air just before the river reaches the narrow valley at an altitude between 2700 and 3200 m.

There is an extremely sharp contrast between the favoured and unfavoured slopes. This contrast in aspect plays an important role in the agricultural land use of the Charazani valley, and the altitudinal limits of cultivation may differ by up to 200 m between the sunny and shaded slopes.

The theoretical insolation (Fig. 9) of the area selected for investigation shows this spatial differentiation in the form of the possible insolation by the sun which shows how slopes with a northern aspect are favoured by insolation (Slope of Sacanagon) whereas slopes with a South-facing aspect receive the least insolation (Slope of Chullina) (Fig. 10).



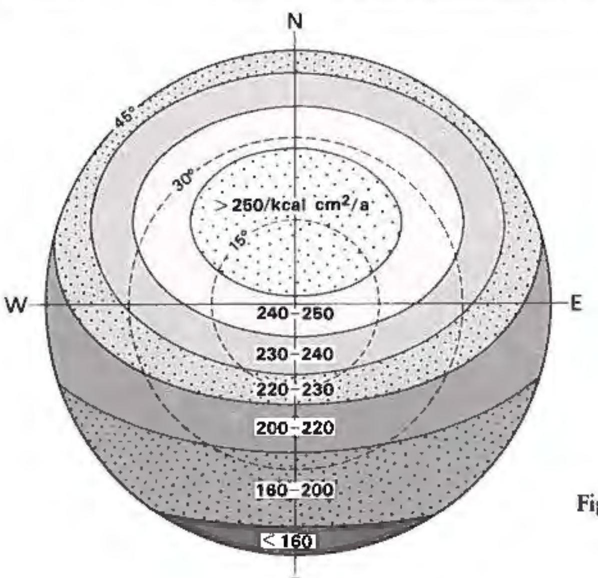


Fig. 9. Theoretical insolation (Calculation based on GESSLER, 1925).

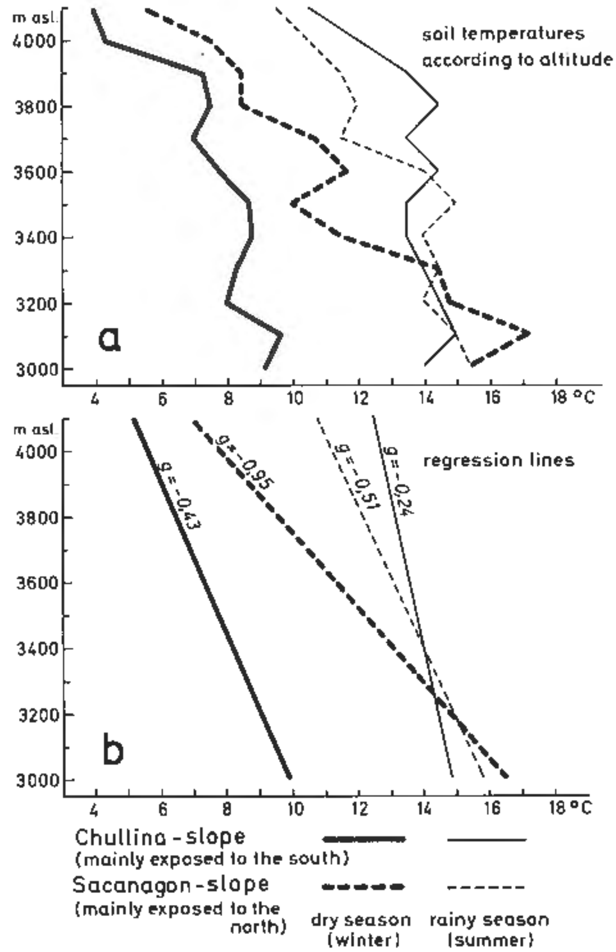


Fig. 10. Altitudinal variation of the 50cm-soil-temperatures on differently exposed slopes.

Since in the difficult terrain of the area under investigation it was impossible to install a climatological network of sophisticated equipment due to the lack of infrastructure, attempts were made to measure soil temperature as an ecological heat index at a minimum number of observation points. In this connection, the following methods were applied.

In the tropics, soil temperature, measured at a depth of 30–50 cm, at a shady location on an even surface, corresponds to the mean temperature in a meteorological screen. This fact is based on the observation that, under tropical thermal conditions, daily isothermic conditions occur at a depth of 20–30 cm.

In the area of investigation, located in the outer tropics, it is at all events possible to determine the monthly mean temperature by soil temperature measurements at this depth. By means of measurements at different sites with differing aspect and slope inclination, temperature patterns emerge that correspond with the terrain. An isothermal map of soil temperature at a depth of 50 cm (Fig. 11) thus reflects the thermal conditions of a selected area during a certain period of time. When averaged for the year, the measurements confirmed the thermal disadvantages of the south-facing slopes throughout the entire heat budget for the day. A heat surplus accumulates, particularly on the north-facing slopes at an inclination of 5 to 25°. South-facing slopes are generally cooler by up to 4 °C than the north-facing slopes in the lower valley sections. Positive deviations, i.e. heat surpluses, are experienced by the north-facing slopes almost throughout the year, except for the mid-summer months. A balance between these deviations naturally

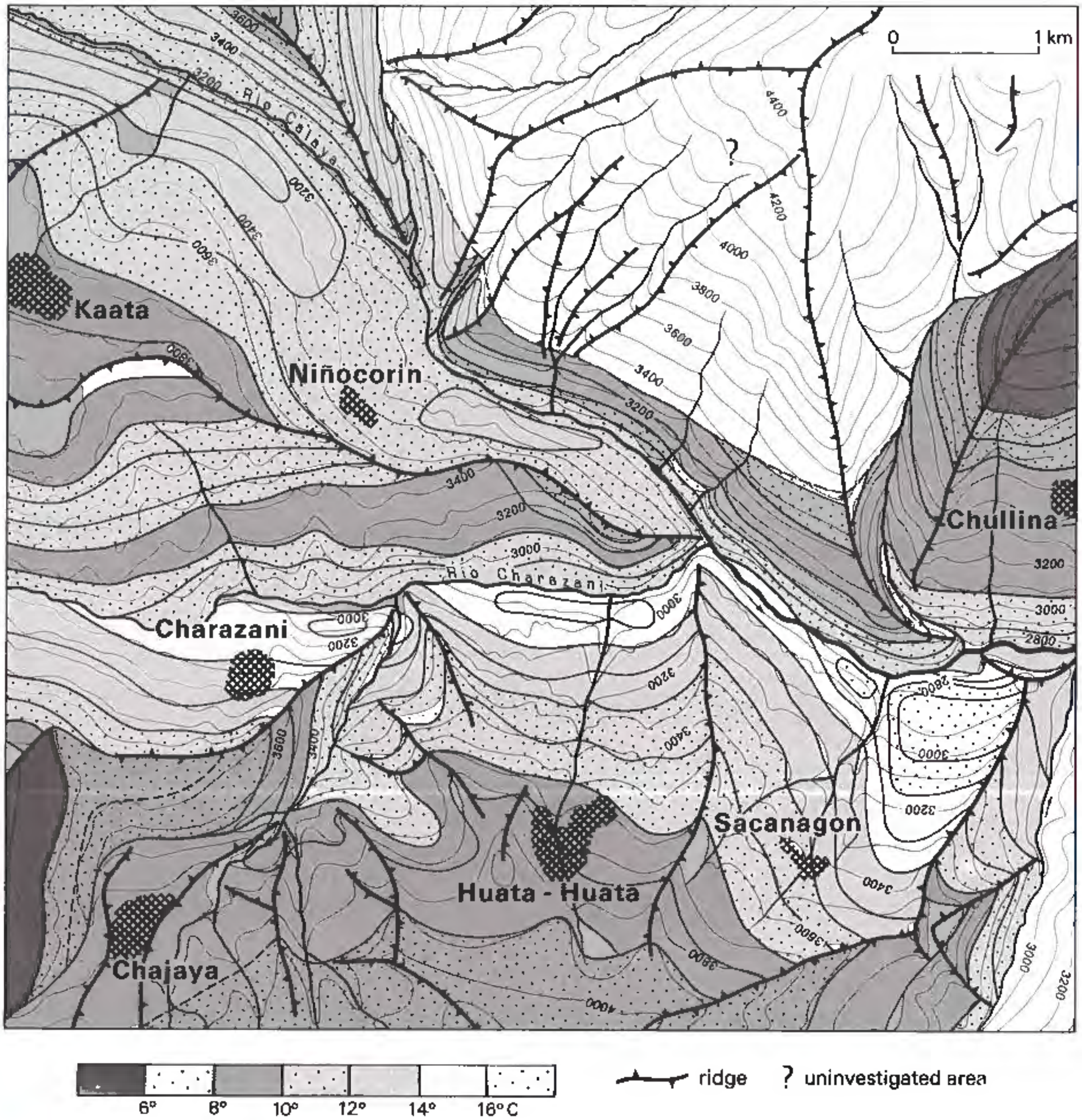


Fig. 11. Map of isotherms of the 50cm-soil-temperatures.

occurs briefly when sun is normal to the earth surface (Fig. 12). The different thermal conditions, with different aspect and inclination, are clearly reflected in the arrangement of the vegetational belts and the cultivation patterns of the crops. Together with measurement of the soil temperature, it was also possible to determine the altitudinal temperature gradient (approximately 0.6 °C/100 m between the lowest and highest points of the area under investigation).

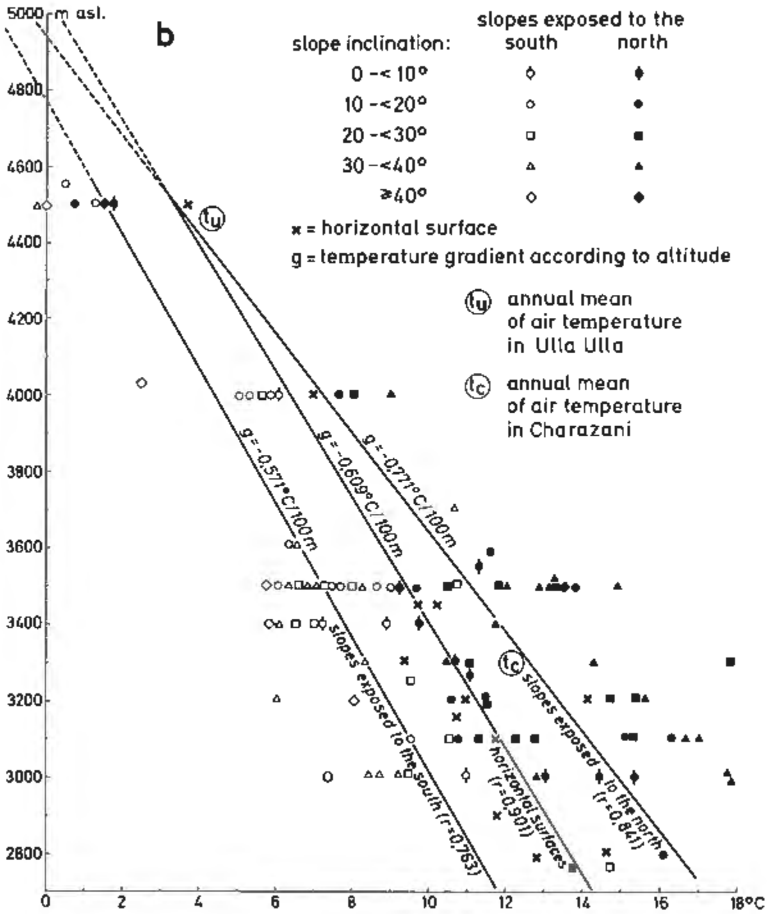


Fig. 12. Regression lines of the 50cm-soil-temperatures.

4. Cultivation Belts

In the lower cultivation belt (Fig. 13), below the central area of settlement, which is almost identical with the dry shrub belt of the valleys and the lower slopes, frost only occurs in valley basins and this only during the dry period of the winter months. Here, mainly grain is grown; since Indian times and, from the colonial era onward, wheat and also legumes, beans and peas (Fig. 14). Tillage is carried out by means of the hook plow which was introduced by the Spaniards. As a result of the gentle relief, particularly on the valley terraces themselves, damage caused by soil erosion is relatively small despite plowing. Breeding of sheep and cattle provides natural manuring in this belt, making a fallow period unnecessary in these warmer parts, where mean temperatures are between 12 and 18 °C. This holds true on the whole for the altitudinal belt up to 3600 m a.s.l. Here, available warmth is still sufficient for plowing under the dung quickly enough after the harvest to replace the nutrients that were extracted with the harvest. Metabolism still takes place in the soil. However, cultivation is not only restricted to the river terraces of the valley bottoms, but can also be found on artificial terraces that were built during early Indian times. By means of this practice the dangers of soil erosion are reduced considerably.

The agrarian system is marked by a strict field system. Although the land is in private hands, it is severely parcelled out due to the proportionate distribution of land on succession. Tillage, harvest and

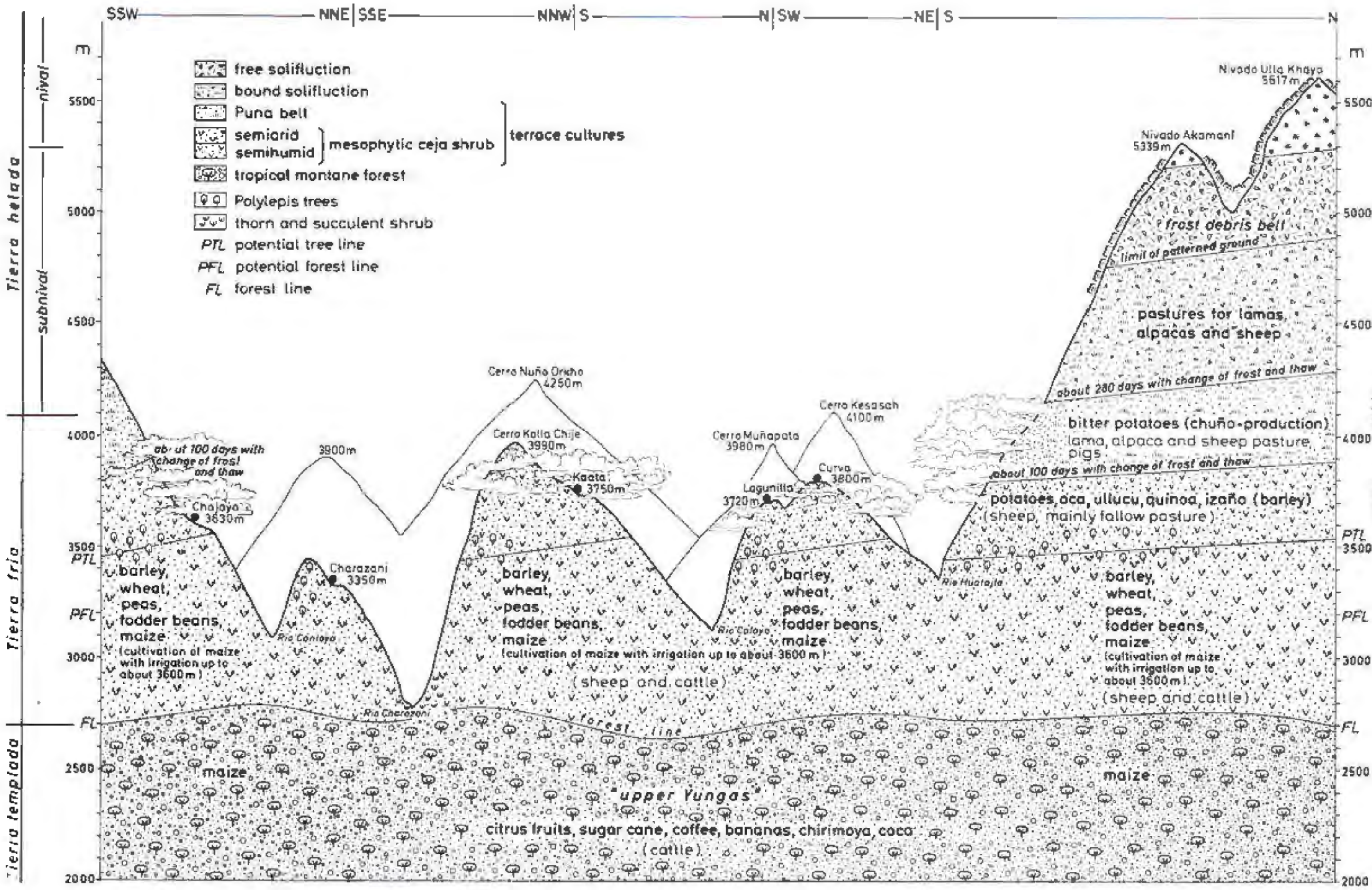


Fig. 13. Agro-ecologic altitudinal belts of the Charazani region.

Fig. 14. Lower cultivation belt with irrigable maize and wheat terraces and groups of eucalyptus trees.

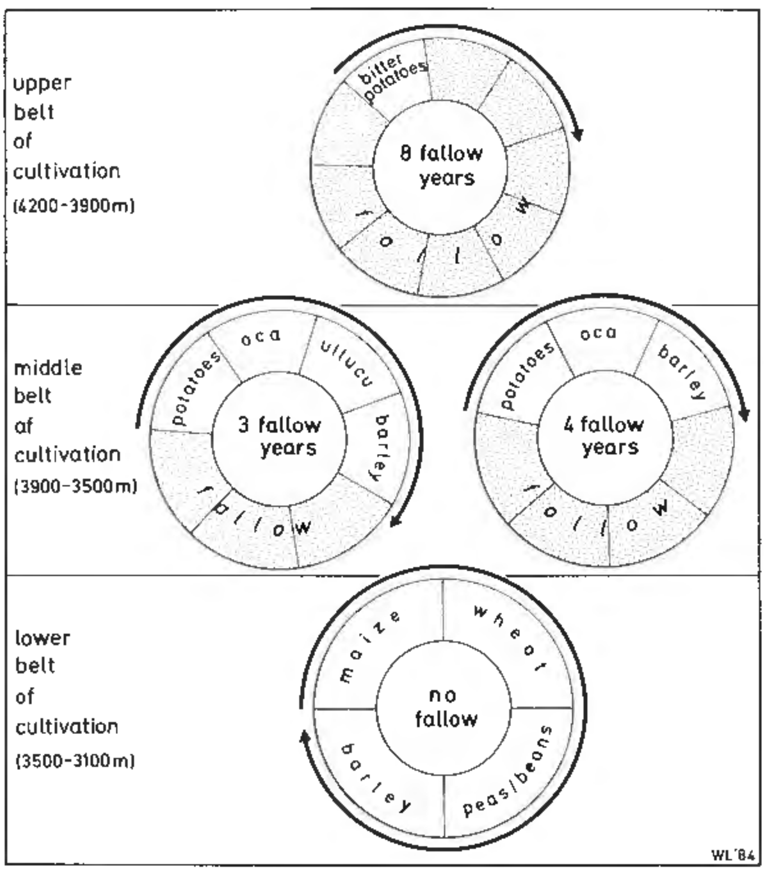


Fig. 15. Crop rotation and fallow times in the Kallawaya region as observed in the village of Kaata (based on MAHNKE, 1982).

Fig. 16. Village of Amarete, 3850 m a.s.l.

Fig. 17. Yard with weaving woman, also drying ground for potatoes.

Fig. 18. Terraced slope near the village of Amarete, tuber plant cultivation belt.

maintenance of the irrigation systems and terrace walls are largely carried out collectively in the form of assistance among neighbours, i.e. on a man-hour by man-hour basis. The field system dictates the rotation of crops: maize, wheat, beans or peas and possibly barley, which is only grown, however, in the drier areas (Fig. 15). Maize is partly irrigated, but does not appear in a purely dry-field cultivation pattern. Irrigation serves the purpose of compensating for precipitation fluctuations and increasing the yield as well as rendering the sowing date independent of the first rain.

In addition to maize, early potatoes and wheat are also included in this irrigated tillage system. Particularly in the areas where irrigated tillage is practiced, there are larger haciendas that were established in colonial times. Therefore, there is good reason for the assumption that the lower cultivation belt in its present form was not part of the old Kallawaya field system. A great portion of the area under cultivation is very likely to have been cleared only in colonial times and cultivated in hacienda operation. Thus one may proceed from the assumption that the established settlements are only partly of colonial origin, gradually developing later into villages. The present settlement structure in this area shows scattered settlements, haciendas and villages existing side by side. Many of the villages did not gain their independence until the agrarian reform on the Fifties, and have enlarged their acreage in order to build up farms of a more profitable size. However, even today, many campesinos are working on the haciendas of reduced size still existing today.

The central and original agrarian area of the Kallawaya Indians is located in the tuberous crop belt, which is identical with the somewhat more humid upper shrub belt of the vegetational zonation. This area is marked by a land-use system strictly adapted to the entire range of microclimatic conditions. This belt lies between 3600 and 3900 m, where the large agricultural villages of the Kallawaya are located (Figs. 16 and 17). Here, the Indian population has always grown the tuberous plants, potatoes, oka and ullucu, on artificially-terraced slopes (Fig. 18) in a strict crop and field rotation system, and also, since the Spanish era, barley as grain – particularly on the dry slope sections. The land is cultivated in a seven-part field

Fig. 19. Fields of bitter potatoes, near the upper limit of agriculture.

system (K'apanas). In each field, each family owns one parcel of land (Sayaña) (MAHNKE, 1982). Since the property can be transferred by way of proportionate distribution, the plots are often very small. Collective tillage and harvest are regulated by a strictly obligatory field system. For the example of the village of Kaata, MAHNKE (1982) has determined potatoes-oka-ullucu-barley as the dominating crop rotation (Fig. 15). This is followed by a three- to four-year fallow, depending only on whether ullucu is involved or not. The fallow areas are used for sheep. In unfavourable localities, permanent fallow areas can also be found, particularly on the steep slopes exposed to the south. The parcel-field-system probably dates back to the Inca agrarian system.

The fields are tilled with the traditional planting stick called taclla; this practice also represents a high degree of ecological adaptation to the existing terrain and climatic conditions. The small parcels of land hardly permit the use of plows. The parcels are determined by the size of the terraces: the steeper the slope, the smaller the terraces. The construction of terraces prevents the water from flowing down the gentle slopes and thus permits optimum utilization of rain water. Soil erosion is avoided to a great extent as well. The removal of the terrace walls and the introduction of plowing would only magnify soil erosion. The planting stick technique on artificial terraces – partly in conjunction with irrigation – constitutes a highly ecological adaptation to the natural conditions, causing only negligible damage to the system.

At an elevation of 3900 m a.s.l. the system of cultivation changes according to the natural vegetation. The grass belt which sets in at this altitude is marked by slightly increased precipitation (approximately 450 mm) and frequent fog. The grassy areas, characterized by *Aciachne pulvinata,* are arranged hexagonally, which is partly attributable to the effects of daily frost particularly during dry periods. The frost limit is clearly marked and is characterized by a sudden concentration of "Frostwechseltage" (days with temperatures alternating above and below zero) for a few days per year at 3900 m and 250 days from 4100 to 4300 m. In humid localities, so-called needle-ice is formed almost every day.

Fig. 20. Conservation of potatoes and oca: water is extracted from the tubers by trampling with bare feet, and potatoes are peeled.

In this area, particularly on sunny slopes, cultivation of bitter potatoes is still possible and even barley can be grown at some places. Potatoes are cultivated on plots owned by the community. Each year, individual plots are allocated to the heads of families (Fig. 19).

According to MAHNKE (1982), the cultivation of bitter potatoes is followed by a fallow period of eight years. This practice must also be regarded as an adaptation to the climatic conditions, particularly to the low temperatures which cause a reduction of the soil's regenerative capacity as a result of retarded soil processes. In this cultivation belt, a special agro-technical phenomenon has developed which is unique in cultural history and which is strictly confined to the marginal tropical highlands of Southern Peru and Bolivia, that is the preservation of tuberous plants with the aid of frost.

The Spanish chronicler CIEZA DE LEON described the so-called chuño production in 1550 only as a drying process. GARCILASSO DE LA VEGA provided a detailed description of the procedure and distinguished three stages of preservation: frosting, pressing out of the water and drying in the sun. Father COBO had differentiated earlier between the production of the common black chuño and the white chuño, which is called tunta in Bolivia. CARL TROLL (1931 and 1943 a) has described in detail the chuño production process which – except for minor differences – corresponds with practices in the Kallawaya area. The potatoes are spread out evenly for several nights on a flat surface with no or only a little vegetation cover, exposing them to frost during the night and to intensive insolation during the day. By means of the freezing process during the night and the thawing process during the day, water is extracted from the product; this process is expedited by trampling with bare feet (Fig. 20). The preservation product is blackened by intensive insolation which impairs its taste. During the production process of the white tunta, however, the potato is not exposed to the sun during the day soaked in water and frozen during the night. Thus, the tasty fruit stays white and is considered the better preservation product.

Apart from the potato, the thickened rhizomes of the wood sorrel species oka are also processed into the preserved product caya. Only seldom is this process carried out with aid of frost. The thick

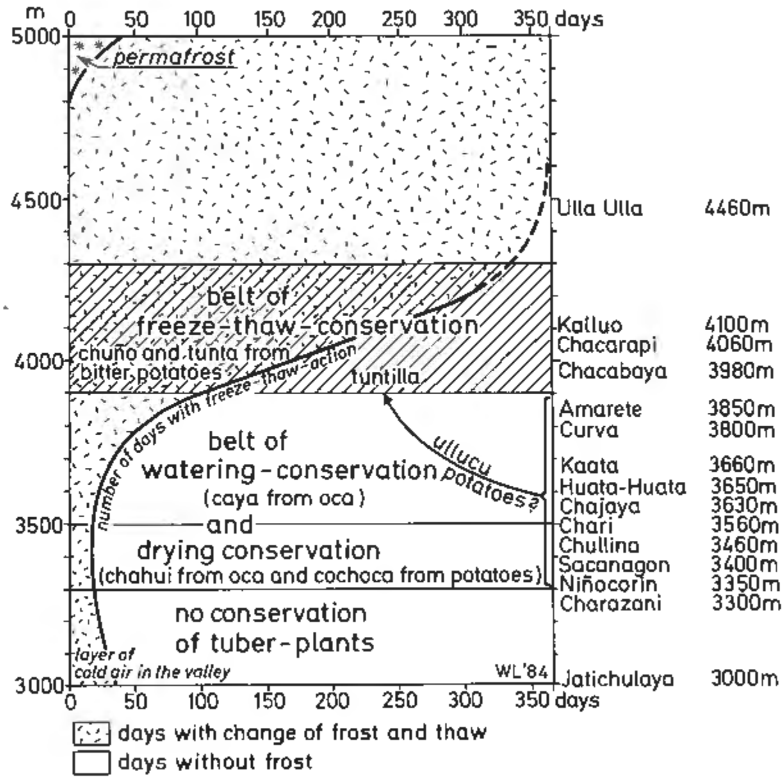


Fig. 21. Conservation of tuber plants and conditions of days with freeze-thaw-action ("Frostwechseltage") in the Kallawaya region.

rhizomes of the oka are generally subjected to a soaking process for several weeks in round basins near the village and then dried. From oka chahui also is produced by simple drying and the so-called tuntilla from papalisa by means of soaking and drying. Nevertheless, the most important preservation products are chuño and caya.

Preservation of the tuberous fruits permits stockpiling of food, which helps to bridge the dry season, but, on the other hand, promotes mobility, since the dried and lighter tuberous fruits may be used as food on trips particularly during the extensive caravan activities. According to TROLL (1931), chuño was also used as travel rations by the Inca during their expeditions. It is important to note that chuño production starts at an altitude of 3900 m because morning frost occurs daily between May and July after the harvest. Inhabitants of villages living below this climatic boundary of chuño production must carry out the preservation of the tuberous fruits grown by them in places above 3900 m. On the other hand, the inhabitants of villages located above 3900 m can preserve their tuberous fruits in the near vicinity of their homes (Fig. 21). It shows the relationship between the altitudinal location of the villages, the preservation methods and the occurrence of frost.

The fallow land in areas where bitter potatoes are grown serves as grazing grounds for lamas, alpacas and sheep and to some extent for pigs; driving of these animals to their grazing grounds is done centrally by each individual village.

A precondition for smooth functioning of the Kallawaya agricultural system is that the inhabitants of the villages have terraced slopes in all altitudinal belts between 3000 and 4300 m. In this way most of the communities can live relatively independently. This large vertical extent of the cultivation areas minimizes harvest risks, as it is quite improbable that the field produce of all altitudinal belts will be affected by negative harvest fluctuations simultaneously.

5. Exchange of Goods

Between the three-tier settlement area of the Kallawaya on the one hand and the higher area of the cattle breeders on the Puna high plateau as well as the lower altitudinal and mountain forest belt of the Yunga on the other, a vertical exchange of goods is practiced, which provides the inhabitants of all altitudinal belts with the vital supplementary goods (Fig. 22). Lama or mule caravans shuttle between the cattle breeders' belt of the Puna high plateau and the Kallawaya area. Caravans come into the Kallawaya region from the Yunga, i.e. from the tropical area. The products are sold on the individual markets and partly also on open fields. W. SCHOOP (1982) has described these activities in detail: the cattle breeders bring down dried meet, fish, wool, cheese and trout; the inhabitants of the tropical mountain forest belt provide citrus fruits, coca, sugar cane, bananas and chirimoya. In the markets of the Kallawaya area, these goods are exchanged by the inhabitants of the cattle breeders' belt and the tropical mountain forest belt for tuberous fruits, legumes and grain from the Kallawaya belt. Money plays only a minor role. Apart from the vertical exchange of goods, long-distance trade connections have in the meantime been established by means of trucks using the only road in the area, thus linking La Paz and also Peru with Charazani. There is a limited amount of traffic across the border to Peru where a much visited market is held every week.

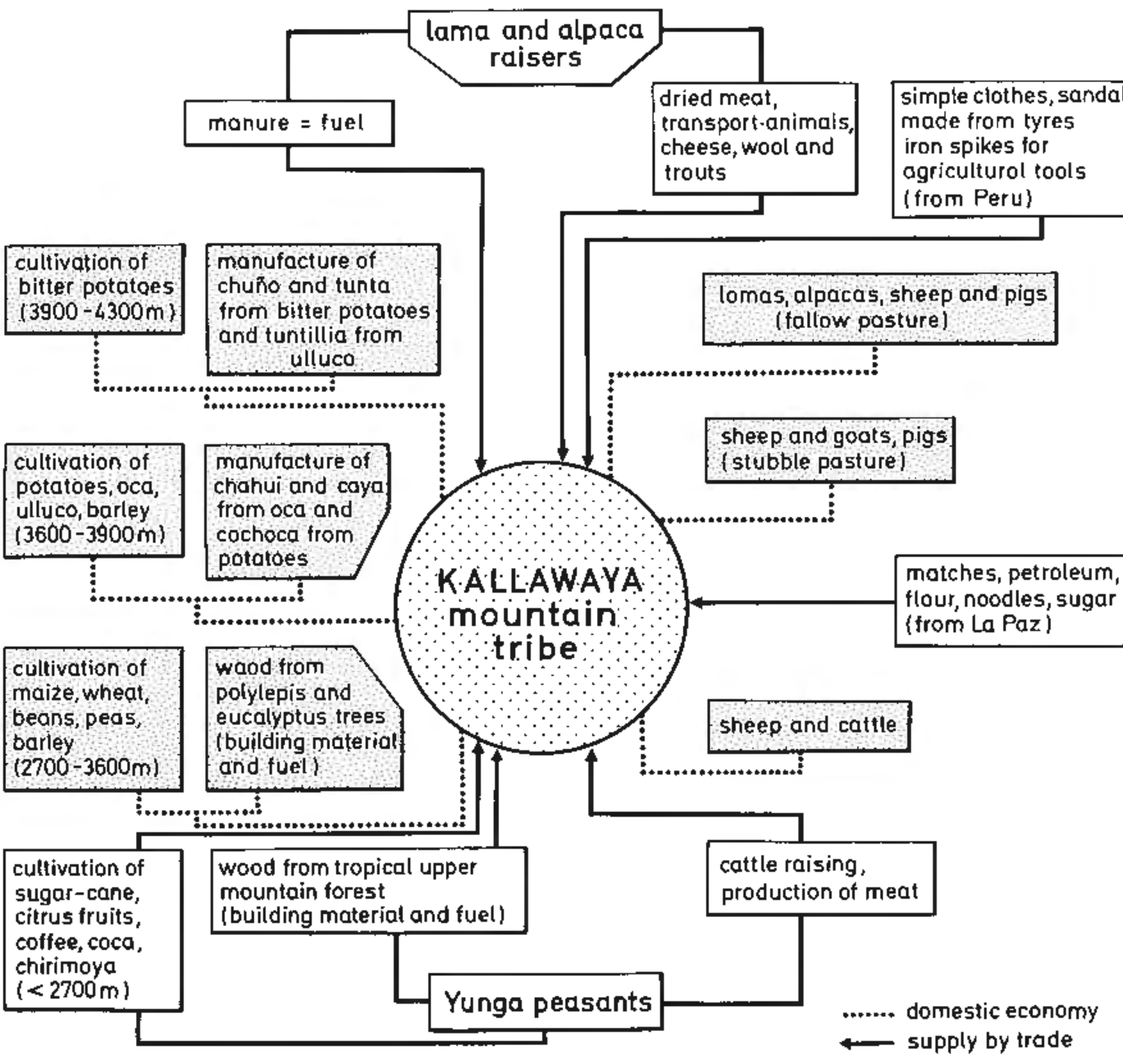


Fig. 22. Providing-system of the Kallawaya people.

6. Summary

The agrarian area occupied by the Kallawaya today still functions as a closed system. Up to the present, the Ketschua-speaking ethnic group in this region has succeeded in maintaining a system of vertical control (MURRA, 1975) deriving advantage from all innovations and amalgamating them as well as subordinating such innovations to their own system. Therefore, the land-use system and the natural potential in this area are still in an approximate state of equilibrium. The imprints of colonial influence are certainly remarkable and relate to the introduction of both large and small livestock from the Old World, i.e. cows, sheep and goats. This also holds for useful plants, weeds and ruderal plant societies, as well as for new forms of farming such as the use of the Spanish hook plow.

Today, however, there is a danger that the socio-economic conditions will be subject to drastic change due to socio-cultural change. External influences on this ethnic group are too strong. Since, at present, the danger of overloading this land-use system – e.g. as a result of overpopulation – does not yet exist, the present system may still be regarded as optimally adapted to the natural potential. The capacity of this region is still sufficient for the present population, since some of the inhabitants are migrating into the larger cities, and the total population might have been even greater in former times. This only means, however, that there is a shift of problem to the larger cities.

7. Summarized Comments

The interaction between the individual factors within the Kallawaya system is shown in Fig. 3. The following phenomena contribute to the close adjustment of the land-use system to the natural potential.

1. The area of cultivation occupied by the Kallawaya – particularly as a result of the altitudinal temperature gradient – can be subdivided into two or three altitudinal belts.
2. The location of the fields and their utilization are closely related to insolation and thus to the thermal conditions on specific slopes, according to aspect as well as to the angle of inclination of the terrain.
3. The agrarian year is determined by the distribution of rainy and dry periods.
4. The location and arrangement of the fields are also governed by the humidity regime of the area. Particular exposures with greater humidity are specifically utilized by the Kallawaya (e.g. locations with fog or dry areas).
5. The different crop rotation and fallow systems in the three altitudinal zones are governed by the thermal and moisture conditions as well as by the resulting state of the soil.
6. The cultivation and preservation of tuberous plants are closely dependent on the altitudinal temperature zonation. The freeze-thaw action during the months of May to August is a precondition for the freeze-thaw method of preservation in the upper land-use belt. In the medium belt only the soaking-drying method of preservation can be applied.
7. The cultivation of grain and tuberous fruits on artificial terraces represents an ecological adaptation to the relief of the terrain. Terraces provide protection against soil erosion and preserve rainwater. The size and form of the terraces are adjusted to the topographic conditions.
8. Tillage with the planting stick and/or the hook plow corresponds to careful cultivation of the thin soils.
9. Irrigation mainly serves the purpose of off-setting fluctuations in the rainy periods – particularly at the time of sowing.
10. The breeding of domestic animals is complementary to the agrarian system.
11. Supplementary goods are procured from other altitudinal belts with the aid of caravans – including protein-rich foods from the cattle-breeders' belt and vitamin-rich foods from the warm tropical region. The Kallawaya land-use belt provides the other region with carbohydrates by exporting tuberous fruits and grain.

References

CIEZA DE LEON, P. (1553): Primera Parte de la Crónica del Perú. Sevilla.

COBO, Padre B. (1653): Historia del Nuevo Mundo. (Sevilla 1890–1895).

GARCILASSO DE LA VEGA (1609): Primera parte de los Comentarios Reales que trata del origen de los Incas etc. Lissabon.

GESSLER, R. (1925): Die Stärke der unmittelbaren Sonnenbestrahlung der Erde in ihrer Äbhängigkeit von der Auslage unter den verschiedenen Breiten und zu den verschiedenen Jahreszeiten. Veröff. d. Preuß. Meteorol. Inst. Nr. 330, Abh. Bd. VIII, Nr. 1. Berlin.

KAERGER, K. (1901): Landwirtschaft und Kolonisation im spanischen Amerika. II. Bd. Leipzig.

LAUER, W. (1976): Klimatische Grundzüge der Höhenstufung tropischer Gebirge. Tagungsber. u. wiss. Abh. 40. Dtsch. Geographentag Innsbruck 1975. Wiesbaden, 76–90.

– (1979): Im Vorland der Apolobamba-Kordillere. Physisch-geographische Beobachtungen auf einer kurzen Studienreise nach Bolivien. In: HARTMANN, R. u. U. OBEREM (Eds.): Estudios Americanistas II. Homenaje a H. Trimborn. Coll. Inst. Anthr. 21. St. Augustin, 9–15.

– (1982): Zur Ökoklimatologie der Kallawaya-Region (Bolivien). Erdkunde, Bd. 36, H. 4, 223–247.

MAHNKE, L. (1982): Zur indianischen Landwirtschaft im Siedlungsgebiet der Kallawaya (Bolivien). Erdkunde, Bd. 36, H. 4, 247–254.

MONHEIM, F. (1959): Die indianische Landwirtschaft im Titicacabecken. Geogr. Rdsch. 11, 9–15.

MURRA, J. V. (1975): Formaciones económicas y políticas del mundo andino. Inst. de Estudios Peruanos, Lima.

POMA DE AYALA, F. G. (um 1613): Nueva Corónica y Buen Gobierno. (Traveaux et Mêmoires de l'Institut d'Ethnologie XXIII. Paris 1936.)

SAPPER, K. (1934): Geographie der alt-indianischen Landwirtschaft. Pet. Geogr. Mitt. 80, 41–45.

SCHOOP, W. (1982): Güteraustausch und regionale Mobilität im Kallawaya-Tal (Bolivien). Erdkunde, Bd. 36, H. 4, 254–266.

SEIBERT, P. (1982): Ökosystemforschung in den bolivianischen Anden. Naturwiss. Rdsch., 35. Jg., H. 4, 147–157.

TROLL, C. (1931): Die geographischen Grundlagen der andinen Kulturen und des Inkareiches. Ibero-Amerik. Archiv, Bd. 5, H. 3, 258–294.

– (1943 a): Die Stellung der Indianer-Hochkulturen im Landschaftsaufbau der tropischen Anden. Z. d. Ges. f. Erdkunde zu Berlin, Nr. 3/4, 93–128.

– (1943 b): Die Frostwechselhäufigkeit in den Luft- und Bodenklimaten der Erde. Met. Z., 60, 161–171.

– (1952): Die Lokalwinde der Tropengebirge und ihr Einfluß auf Niederschlag und Vegetation. In: Studien zur Klima- und Vegetationskunde der Tropen. Bonner Geogr. Abh., H. 9, 124–182.

WALTER, H. und E. MEDINA (1969): Die Bodentemperatur als ausschlaggebender Faktor für die Gliederung der subalpinen und alpinen Stufe in den Anden Venezuelas. Ber. d. Dtsch. Bot. Ges. 82, 275–281.

WINIGER, M. (1979): Bodentemperaturen und Niederschlag als Indikatoren einer klimatisch-ökologischen Gliederung tropischer Gebirgsräume. Methodische Aspekte und Anwendbarkeit dargelegt am Beispiel des Mt. Kenya. Geomethodica 4, 121–150.

Discussion to the Paper Lauer

Prof. Dr. A. Kessler:

Is not the foggy zone an unfit area for human settlement, because it is unhealthy?

Prof. Dr. W. Lauer:

On the dry slopes of the study area it is only in the fog belt that the water supply is relatively secure. Most of the river sources are situated here. Sometimes water is also collected in cisterns. The site of the villages is partly determined by the relief in the area of glacial mountain terraces and at the lower limit of the glacial frost-débris-belt ("Frostschuttzone") with marked solifluctional humps. Today, this mountain zone is identical with the belt of tuber plant cultivation.

Prof. Dr. W. Haffner:

1. What is the amount of rainfall in the foggy, densely-settled zone?
2. The humidity conditions, or rather the frequency of fogs, may be similar on the slope down to the Red Sea in the densely-settled Yemenite highlands.

Prof. Dr. W. Lauer:

According to the first, still incomplete measurements, with rain-gauges installed for that very purpose, we estimate the annual rainfall at 450 to 550 mm.

Prof. Dr. W. Eriksen:

Since the study area is north of the Tropic of Capricorn, slopes exposed to the south should be more strongly insolated and heated at least during the summer. Is this true, and what consequences can be observed for the agricultural utilization and the altitudinal zonation of these slopes?

Prof. Dr. W. Lauer:

A slight southern position of the sun is recorded between November 3rd and February 8th in the Kallawaya region. These are the days with a vertical position of the sun. During this period the slopes are evenly insolated, but slopes exposed from SE to SW are always steeper because of periglacial denudations within the study area, so that they still show temperature deficiencies even during this season.

Prof. Dr. W. Weischet:

The settlements are almost exclusively found somewhat below the Ceja de la Montaña. Mr. Kessler indicated that the living space just below and within the foggy zone might be unhealthy. Is it not possible that the selection of settlement sites was determined by the existence of reliable sources of water supply in the following context: the Ceja is a climatic altitudinal limit – it possibly has a correlation with pleistocene altitudinal belts of solifluction and slope formation. Solifluction leads to accumulations of loose material on flat slopes. Because of infiltration, ground-water and river sources, the bodies of loose material supply good preconditions for settlements in the concerned semi-arid area. Thus we see today the spatial coincidence of Ceja and settlements; the causes, however, may well be due to other factors dependent on climatology. Mapping of the geomorphological altitudinal zonation is therefore advisable.

Prof. Dr. W. Lauer:

The geomorphology of the area is largely mapped. It can be seen that the villages are situated on flat parts of the slopes at the lower end of late-pleistocene, periglacial débris-streams, which are remarkably rich in sources. The fact that today the belt of tuber-plant cultivation and the fog-belt of the Ceja, for the most part, coincide at these elevations is connected with the post-glacial shift of altitudinal belts, which in this area shows a superposition of the above mentioned phenomena. This is not a single case, however, for in other mountain areas of Latin America similar conditions can be observed, e.g. in Mexico, in Guatemala and in Peru.

Prof. Dr. J. Martens:

From the biological point of view, your study area looks completely degraded, lacking any natural plant cover. Are there actually any larger areas which are covered with original plant societies?

Prof. Dr. W. Lauer:

Within the map section presented, the area has largely been transformed into a terraced agricultural landscape (between 2800 and 3900 m a.s.l.). A secondary vegetation of agricultural weeds has appeared in the fields, which partly originates from the reservoir of the surrounding natural vegetation. Fallows and field balks mostly bear remnants of the natural flora. Permanent fallows and many extremely steep slope sections are largely covered by climax vegetation. Within the mapped transects the last-named areas occupy up to about 20–30% of the area.

Prof. Dr. B. Messerli:

1. Referring to the theoretical insolation: Is this the calculated, effectively possible, or the measured relative length of insolation?
2. Can an increase in soil erosion caused by man be indicated? Have there been negative tendencies in recent times?

Prof. Dr. W. Lauer:

1. The potential insolation for the study area was calculated after GESSLER (1925).
2. Hazard events, especially natural ones, and the ones caused by man, have been partially mapped. However, we cannot yet guess their full scope, especially in recent times, but following the recent slight depopulation of the area, damage should have increased somewhat by natural erosion, since not all areas are still used.

Dr. Yu Xiao-Gan:

Is there any potential for reforestation below 3900 m a.s.l.? If so, by what methods and with what kind of trees?

Prof. Dr. W. Lauer:

Systematic afforestation has not yet taken place. Planting of trees has happened, however, and still happens on a small scale, since the introduction of eucalyptus, cypresses, and pines.

Erdwissenschaftliche Forschung, Bd. XVIII, 197–209
Franz Steiner Verlag Wiesbaden GmbH · Stuttgart (1984)

Eco-Climatological Aspects of the Bolivian Puna with Special Reference to Frost Frequency and Moisture Conditions

Wolfgang Eriksen

With 10 Figures

For some decades the altitudinal belts of the paramo and puna regions in the tropical Andes of South America have given rise to intense scientific studies in various fields. Within the natural sciences most attention has been paid to the climatic and biogeographical conditions of these tropical mountain areas because they differ fundamentally from comparable belts in extratropical mountain systems. Moreover they are the basis for the development of well-populated and, at least in parts, highly developed cultural and economic regions.

Early studies made clear that this tropical mountain area cannot be regarded as a homogeneously structured region as far as its climate and vegetation is concerned, but that there is a marked change from equatorial latitudes to the southern margins of the altitudinal belts. This change is characterized on the one hand, in the central tropics, by a negligible annual range of temperature and all-year precipitation and on the other hand, towards the marginal tropics, by a progressively distinctive annual range of temperature and an increasingly seasonal precipitation regime. In addition, there is a decrease of precipitation towards the south and southwest, so that the puna region can be subdivided, from the point of view of moisture and of biogeography, into the "humid puna", the "dry puna" and the "thorn and desert puna" (TROLL, 1968).

Undoubtedly this differentiation finds its clearest expression in the Bolivian Andes, particularly in the Altiplano area. A distinct alternation of dry and humid seasons with a small and spatially differentiated amount of precipitation, a significant annual range of temperature, which decreases however with increasing altitude, and the frequent occurrence of frosts represent the most important macro-climatic characteristics of the comparatively populous puna belt at an altitude between 3300 m and 4500 m[1]. The winter cold period with frequent frosts coincides with the dry season, whereas the moderately warm summer with increased insolation coincides with the rainy season.

From the point of view of plant physiology and distribution, both the natural vegetation (montane grass or shrub semi-desert) and the cultivated plants of this altitudinal belt are highly adapted to the climatic conditions which have been mentioned. As LAUER (1982) expressed it more generally, the identification of the thermal and moisture variations within the puna belt is a basic requirement for ecological differentiation in space and time. The frequency of frosts, the distinctive dry period, the irregular setting in of the rains, as well as their variability in quantity, prove to be the eco-climatic factors which limit the growth of cultivated plants and natural vegetation. In recent years these relationships have been illustrated in several regional studies (e.g. TROLL, 1931, 1943; BECK and ELLENBERG, 1977; SCHRÖDER, 1981; LAUER, 1982; MAHNKE, 1982; BRUSH, 1982).

It is the purpose of the following remarks to examine from regionally limited case studies, what general eco-climatic rules are deducible for the area of the Bolivian "humid" and "dry puna" (in the sense of TROLL) with regard to the frequency of frosts and:

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[1] The altitudinal data refer to different authors: 3300 m: RUTHSATZ (1977); 4500 m: HERZOG (1923). As yet no generally accepted upper or lower limits to the puna belt have been defined.

1. its dependence on altitude together with spatial and temporal variation in this;
2. its interaction with the spatially and temporally structured moisture zones;
3. its relevance for the character and the altitudinal structure of agricultural activities.

Fundamental to this study are the long-period meteorological data (esp. FRERE et al., 1975), to which the results of the regional case studies can be related.

The research area extends from Lake Titicaca in the north to the Bolivian-Argentine border in the south and encloses the altitudinal belt between 3300 m and 4500 m (see above), which is occupied by a montane grass or shrub semi-desert.

1. Frost in the Puna Belt of Bolivia

The climatic map "Carta climática de la región andina boliviana" by SHERIFF (1979) shows that one can expect regionally severe winter frosts throughout the Bolivian puna. The mean minimum temperature of the coldest month in the dry-, thorn- and desert puna falls well below − 5 °C, at several stations even below − 10 °C and is thus evidently lower than at the high-Andean station of Chacaltaya (5280 m), where

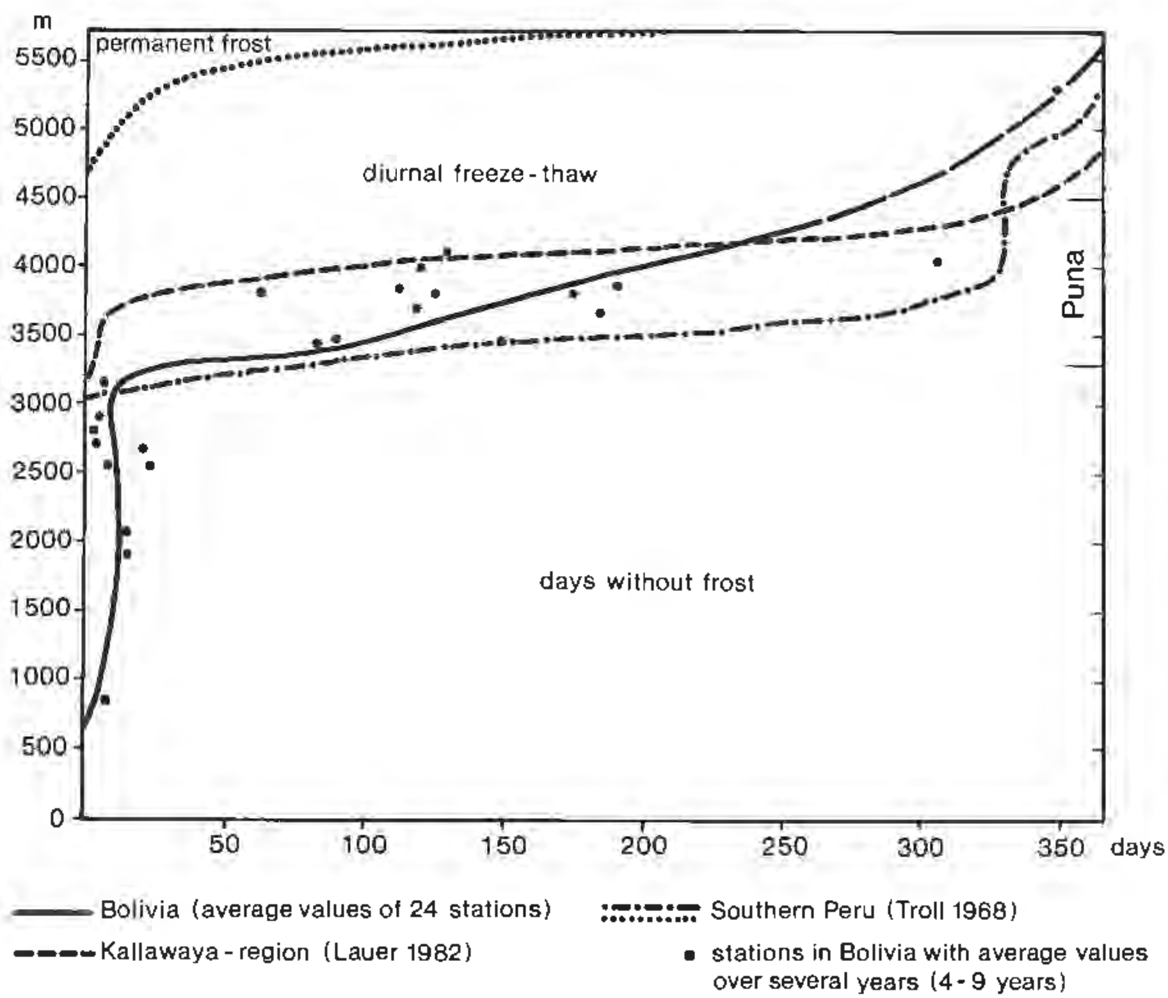


Fig. 1. The dependence of the frequency of diurnal freeze – thaw on altitude.

it reaches only $-6\,°C$. In the humid puna the winter frost intensity, with temperatures between $0\,°C$ and $-5\,°C$, is comparatively less severe. Only in the immediate periphery of Lake Titicaca do the mean minima of the coldest month remain above freezing point, correspondingly roughly to conditions in the upper yungas- and valle-region on the eastern flank of the Andes.

Data on frost intensity during the mid-winter season do not indicate much about the ecology, since they do not apply to the vegetative period. On the contrary information on the frequency of night frosts and on the frost-free period during the summer season is of far greater importance for agriculture, particularly since in the puna marked spatial and temporal variations are indicated (BECK and ELLENBERG, 1977).

Since TROLL's investigations in the tropical Andes it has been well known that the occurrence of frost and the frequency of diurnal freeze and thaw primarily depend on the altitude. Corresponding to the high temperatures in the lower regions of the Andes, regular frost – measured at 2 m above the ground – does not occur below an altitude of 3000 m. Above that level, in the "tierra helada", it increases rapidly in frequency, reflecting the seasonal regime of temperature at the fringe of the tropical zone, so that at altitudes of 4000 m nearly half the days of the year experience night frost. Finally at altitudes around 5000 m there are no longer frost-free days as permanent frost sets in (Fig. 1). Thus the puna between about 3300 m and 4500 m is characterized by the extremely wide range from about 25 nights with frost at the lowest to about 300 at the highest altitudes.

To a certain extent these data differ considerably from the findings of TROLL (1968) in southern Peru and of LAUER (1982) in the Kallawaya-region north of Lake Titicaca, although the general trends are similar (Fig. 1). The curve developed by the author is based on 24 Bolivian mountain stations, for which many years' meteorological records are available. It was determined by mean values for different altitudinal belts. It relates also to the occurrence of night frost in several cold-air basins of the southeastern Cordillera (above 700 m) and is dependent at altitudes above 5000 m on the data for the station at Chacaltaya.

The discrepancies between it and the curves of TROLL and LAUER might be caused by the smaller number of stations considered, by some very short periods of measurement (in some cases less than 2 years) and by the local conditions of the relief in the research areas (some measurements being taken on

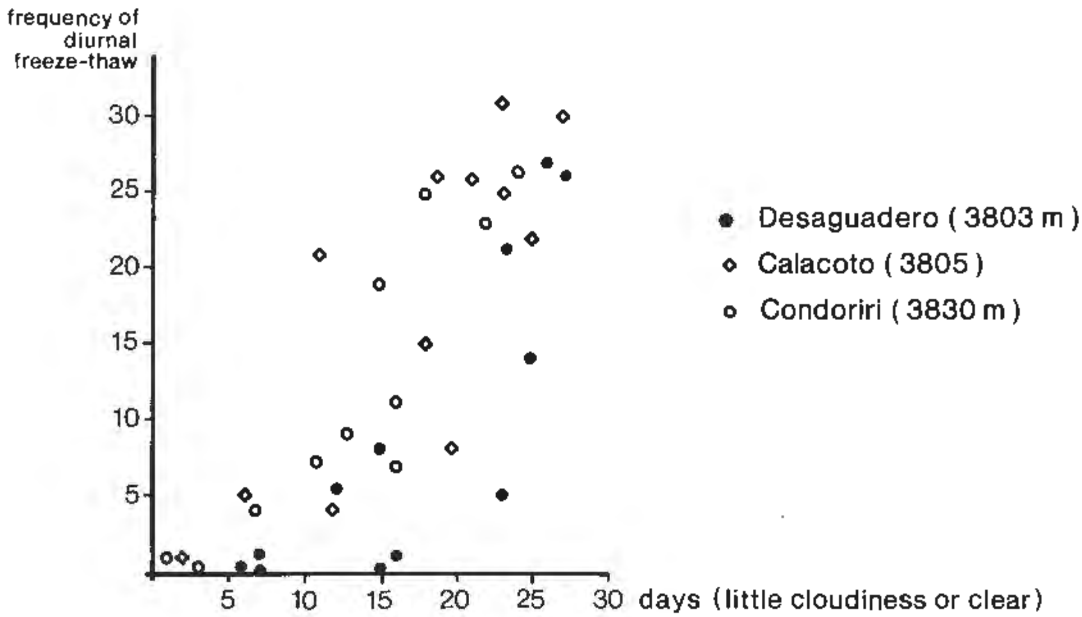


Fig. 2. The relationship between the frequency of diurnal freeze – thaw and cloudiness on the Altiplano (1973).

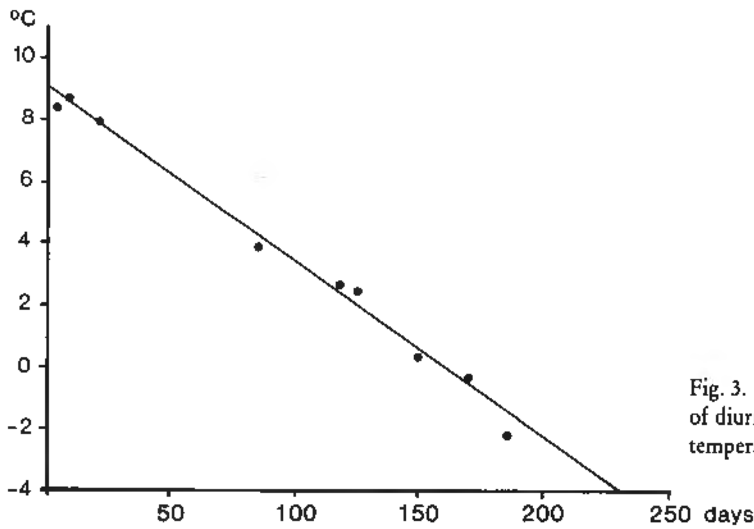


Fig. 3. The relationship between the annual frequency of diurnal freeze – thaw and the mean annual minimum temperature (Bolivia).

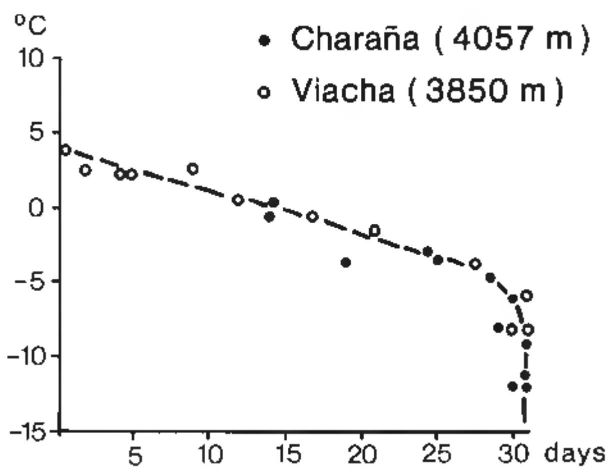


Fig. 4. The dependence of the mean monthly frequency of diurnal freeze – thaw on the mean monthly minimum temperature (Bolivia).

isolated mountain or steep valley sites). Moreover TROLL's curve should reflect the greater dryness (a dry variant) and LAUER's the greater humidity (a humid variant) of the particular research areas concerned.

The curve for the average values is influenced especially by the data for numerous stations on the Altiplano (between 3500 m and 4100 m). With respect to the frequency of frost, it is these data which show that the greatest regional differences can occur at comparable altitudinal levels. Charaña (4057 m) for example has 307 nights with frost, whereas La Paz–El Alto (4105 m) has only 129. These findings illustrate on the one hand the limited usefulness of average values, while on the other hand they prove that the number of nights with frost does not depend solely on the altitude of the station[1].

Besides local influences at the meteorological stations (e.g. the dispersal or accumulation of cold air determined by relief, that is by katabatic slope and mountain winds at night) it is the spatially and temporally variable degree of cloudiness that most influences the frequency of night frosts in the puna

[1] JORDAN (1983) stresses the considerable difference between extremes of temperature measured in and out of the screen in a mountain climate with intense solar radiation.

regions. Indeed the number of days with alternating freeze and thaw evidently increases with the number of days with little cloud, which thus experience more intense radiation loss (Fig. 2). This emphasizes the findings of Bolivian meteorologists who say that 80% of all frosts are caused by radiation loss at night (so-called "heladas blancas") (c.f. FRERE et al., 1975). At the same time this indicates a possible explanation for the extremely high frequency of alternate freezing and thawing (more than 250 days per annum) in the western and southwestern puna, which is very dry and has little cloud, compared with only about 150 days in the humid puna.

It is the radiation loss at night that predominantly determines the diurnal minimum temperature and thus the occurrence of frost. In this connection the close relationship between the occurrence of frost and the mean annual minimum temperature is significant (Fig. 3), so that the latter can be used at least roughly to determine the number of days with alternate freezing and thawing, if direct observations are not available. The same applies to the mean monthly minima (Fig. 4). Only at mean minima of + 4 °C to + 5 °C can frosts in the puna level be expected. With a mean monthly minimum temperature of − 5 °C, frost usually occurs every night.

It is clear that the frost intensity as well as the monthly frequency of frost primarily depends on the mean monthly minumum temperature. Since we are concerned in the marginal tropics with a marked annual range of temperature, there must be, in this connection, a distinct annual variation in the frequency of frost at stations in the Bolivian puna and also a marked contrast between periods during which frosts are frequent and those which have few frosts.

Here again the puna turns out to be a clear transition belt between altitudes above 5000 m with frosts almost daily and altitudes below 3000 m with very few days with frost (Fig. 5). With a decrease in altitude the frequency of frost diminishes and is increasingly restricted to the winter months. At the same time, the frost-free period extends from 0 months at higher altitudes of the puna to about 7 months at pre-puna levels.

The same picture emerges from the mean values for 24 stations for which observations have been collected over many years. Figure 6 shows clearly the rapid vertical increase in the frequency of night frost on the puna as well as the short period of frost risk at altitudes below 3000 m (particularly in frost hollows). In response to the increase in radiation and the consequent overheating of the mountain region (the climatic effect of mass elevation), isolines are raised by about 1500 m during the summer, so that a frost-free "bell" develops, which reaches upwards just into the puna level (up to about 3800 m). This "bell" is ultimately responsible for the fact that at this altitude, especially on the Altiplano, cultivation can still be practised. Nevertheless, the frost-free period is limited to a few (4–5) months and to the lower

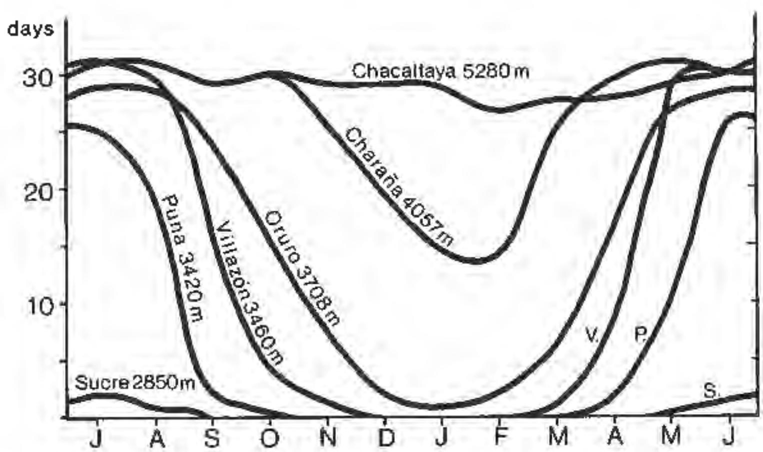


Fig. 5. The monthly frequency of diurnal freeze – thaw at selected stations at different altitudes (Bolivia).

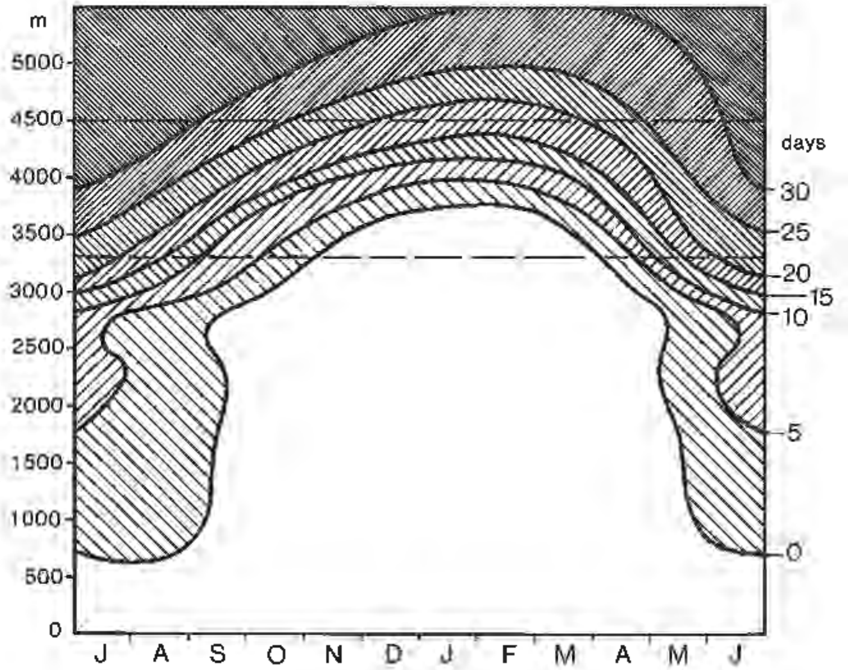


Fig. 6. The dependence of the mean monthly frequency of diurnal freeze – thaw on altitude (Bolivia).

altitudinal levels. It can be extended at most to 6–7 months, provided that the category "1–5 days of freeze and thaw" is included, the "bell" in this case reaching up to 4000 m. The inclusion of the period with a frequency of frost of 1–5 days per month is justified in so far as in such cases it is mostly a matter of relatively moderate night radiation frosts which are recorded only a few hours before sunrise, as the thermoisopleth diagram for Oruro (3706 m) reveals (TROLL, 1959)[1]. From the studies of FURRER and GRAF (1978), at the nearby station Patacamaya (3789 m), it is known that even during the winter (with mean minimum temperatures of approximately − 4.5 °C) frosts up to − 2 °C are registered only in the top layers of the soil (between 5 and 10 cm deep). LAUER (1982) refers particularly to the importance of soil temperature as an ecological factor.

It must be emphasized that the data given so far refer only to air temperature measured at the level of the meteorological screen (1.5–2.0 m above the ground). According to the findings of RUTHSATZ (1977) in the Argentine Puna, over flat terrain an average of 1–2 °C lower minima and thus a correspondingly greater number of days with frost and thaw can be expected in the air layer close to the ground (5 cm) compared with screen values. According to Fig. 4 a reduction of − 2 °C of the mean monthly minimum, measured at 2 m above the ground, would correspond to a rise in the monthly frequency of frost to about 6–7 days.

It stands to reason that the average frost conditions of the puna which have been taken into consideration can not take sufficient heed of the regional and local peculiarities such as inclination, aspect, type of soil and plant cover, and thus the katabatic flow and down-slope accumulation of cold air during the night and the differential insolation and heating of the ground during the day. Concerning this question much research remains to be done, as has been emphasized by BECK and ELLENBERG (1977). Nevertheless the information which has been given so far outlines the thermal conditions and the eco-climatic limits in the puna belt of Bolivia with sufficient exactness.

[1] The discrepancy between TROLL, 1959 (Oruro without night frost during the summer) and Fig. 5 (Oruro with night frost occurring throughout the year) results from the differing lengths of the periods of observations for the climatic data used. In Fig. 5 the mean values of long-period observations have been used.

2. Moisture Conditions in the Puna Belt of Bolivia

As already mentioned, the average precipitation in the puna region decreases from the east to the west and southwest, from more than 500 mm in the humid puna to 300–400 mm in the dry puna and less than 200 mm in the thorn- and desert puna.

All stations have in common a seasonal distribution of precipitation typical of the margins of the tropics, with maxima during the summer and minima during the winter. The summer rainy season begins at most stations with a pronounced increase in the amount of precipitation per month.

Within the puna, however, there are marked differences in the length of the rains (4–5 months in the humid puna, 3–4 months in the dry puna) as well as in the beginning and the end of the rainy season (Nov. or Dec., resp. Feb. or March) (Figs. 7 and 8).

In recent years numerous studies concerning the aridity or humidity of selected areas have shown that the distribution and amount of precipitation are undoubtedly the basis of the moisture status of a region. At the same time it is apparent that only the amount of precipitation not lost by evapotranspiration can be regarded as a water surplus (LAUER and FRANKENBERG, 1978, 1981; SCHMIEDECKEN, 1978). „Zur Bestimmung der Humidität bzw. Aridität eines Raumes kann nur die potentielle Verdunstung herangezogen und dem Niederschlag gegenübergestellt werden" (LAUER and FRANKENBERG, 1978). Without trying to enter into a discussion about different circumstances of evaporation and transpiration and the problems of their measurement and estimation (c.f. ERIKSEN, 1983), potential evapotranspiration in the present study (Fig. 7 and Fig. 8) has been calculated according to the formula by PENMAN (1956), which is generally regarded as satisfactory. The difference between precipitation and potential evapotranspiration determines the water balance, described by LAUER and FRANKENBERG (1981) as the "eco-climatic water balance".

Applying the potential evapotranspiration values (after PENMAN), published by FRERE et al. (1975), the following picture emerges for the moisture conditions of the Bolivian puna. Except for a single month, recorded for the station of El Belén, no fully humid month can be indicated for any station in the puna. Only if the evapotranspiration values are halved do semi-humid and semi-arid months emerge, which without exception coincide with the time of the summer rains. Thus in the humid puna March is still semi-arid, whereas in the dry puna it is already arid. On the whole the relatively humid period in the puna is confined to a few months (2–5) during the summer. Thus the preconditions for cultivation are decisively limited, all the more since the amount and the start of the summer rains vary markedly from year to year (FRERE et al., 1975).

If the moisture conditions of the puna belt are compared with the thermal conditions which have been analysed above, especially with the occurrence of frost, remarkable parallels appear concerning the annual distribution. The time without any or only few frosts (0–1 days with night frost per month) largely coincides with the relatively humid period of the year (Fig. 7 and Fig. 8). It is sometimes shorter and sometimes longer than the rainy season, the shorter humid period in the dry puna coinciding with a shorter period with few frosts on average. In the thorn puna with one semi-arid month, if any, no frost-free month is likely.

The period of October and November proves to be an especially crucial period with regard to the setting-in of the rainy season and the occurrence of late frosts. As for the end of the rains and the occurrence of early frosts, the crucial period is in March and April. Also in this respect the enormous variability of the annual course of the weather and its variability from year to year has to be taken into consideration. Only December, January and February seem to be comparatively safe regarding the availability of water and heat.

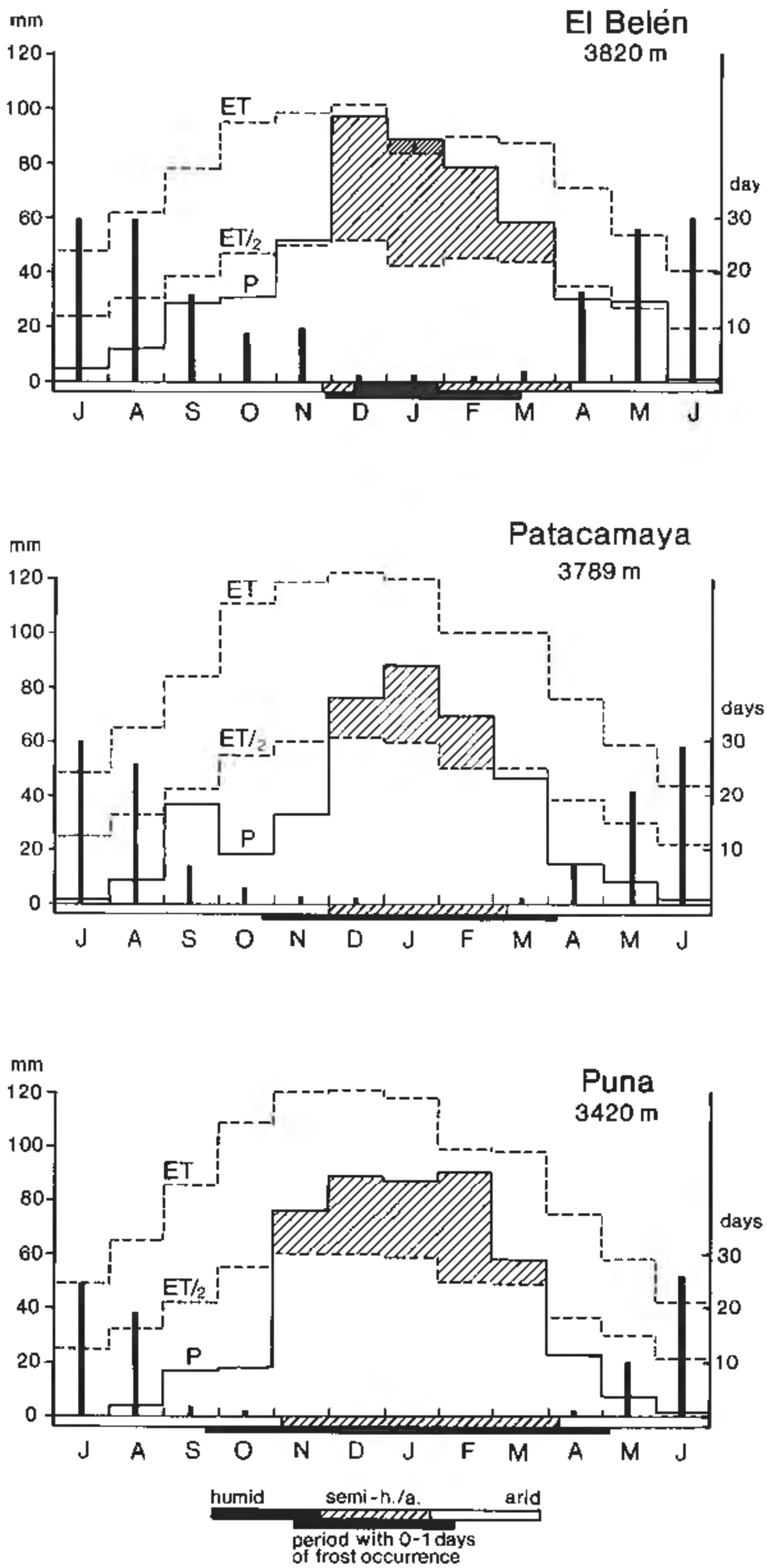


Fig. 7. Monthly precipitation (P), evapotranspiration (ET) and frequency of diurnal freeze – thaw at selected stations in the humid puna (Bolivia).

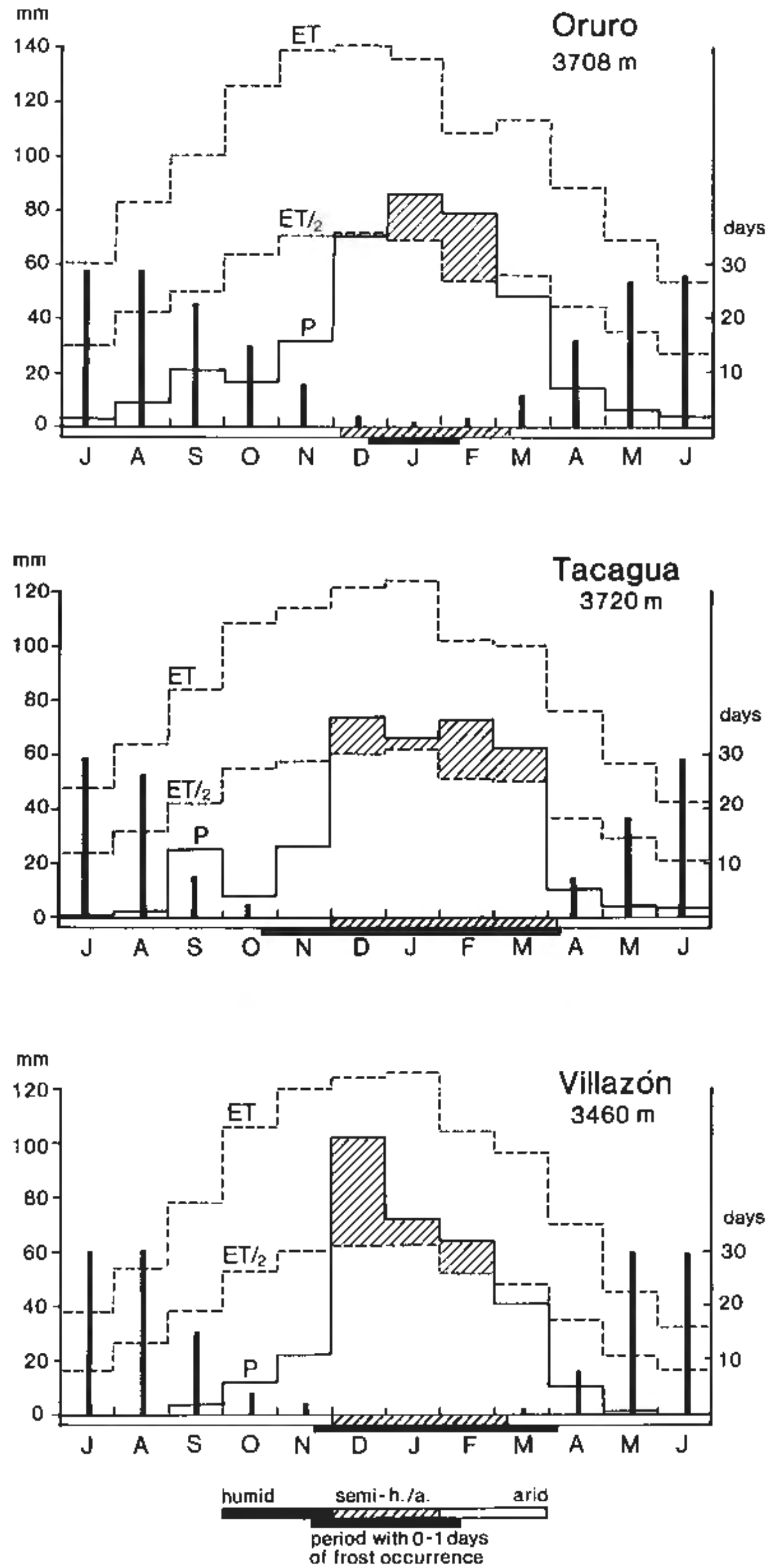


Fig. 8. Monthly precipitation (P), evapotranspiration (ET) and frequency of diurnal freeze – thaw at selected stations in the dry puna (Bolivia).

3. Agricultural Land-Use – the Dependence on the Thermal and Moisture Conditions of the Puna Belt

How is cultivation possible under the limiting eco-climatic conditions in the puna, which have been outlined above? This question – especially in the light of the development of well-populated and advanced civilizations in the Andes – has been widely analysed and discussed (c.f. TROLL, 1931; MONHEIM, 1959; SCHOOP, 1975; SCHRÖDER, 1981; MAHNKE, 1982; LAUER, 1982).

It has long been recognized that over the centuries the Indians of the puna belt have developed pronounced forms of adjustment by which an optimal utilisation of the limited thermal and moisture potential, that is a lessening of the risk of crop failure or financial loss, could be obtained. The most important adjustments to the climatic conditions will be mentioned briefly as follows:

1. In the humid puna intensive cultivation (compared with that in the dry puna), especially in the thermally favourable area close to Lake Titicaca.
2. The distribution of cultivated areas and field crops at different altitudes with different risks.
3. The utilisation of slopes with little danger of frost and with aspects favoured by insolation.
4. The intensification of cultivation by irrigation.
5. Cultivation on terraces which preserve the soils, collect the rain water and make irrigation possible even on steep terrain.
6. The development of a well contrived system of crop rotation and fallow periods.
7. The utilisation of the climatic conditions (frost occurrence) for special methods of preserving tuberous plants (e.g. production of chuño).
8. The cultivation of largely frost-resistant plants which have a short vegetative period.

These different methods of adjustment have frequently been described in the relevant literature (see above) and are widely known. With regard to the eco-climatic explanations which have been made so far only the last point (8) will be dealt with here.

A synopsis of all obtainable data on the distribution of the most important tuberous plants and cereals in the altitudinal belts of the Bolivian Andes (Fig. 9) shows that agriculture can indeed make use of a great variety of cultivated plants, several endemic species being confined to the puna level (Oca, Tarwi, Ulluco).

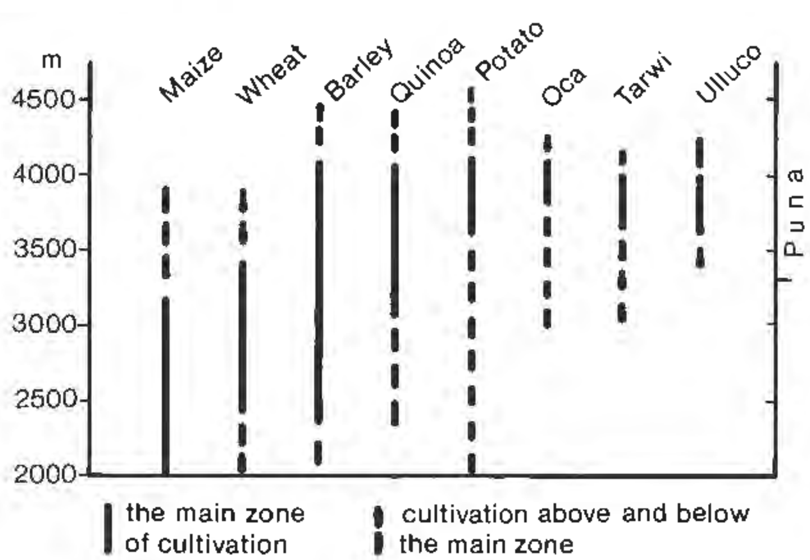


Fig. 9. The altitudinal distribution of important cultivated plants in the Bolivian Cordilleras.

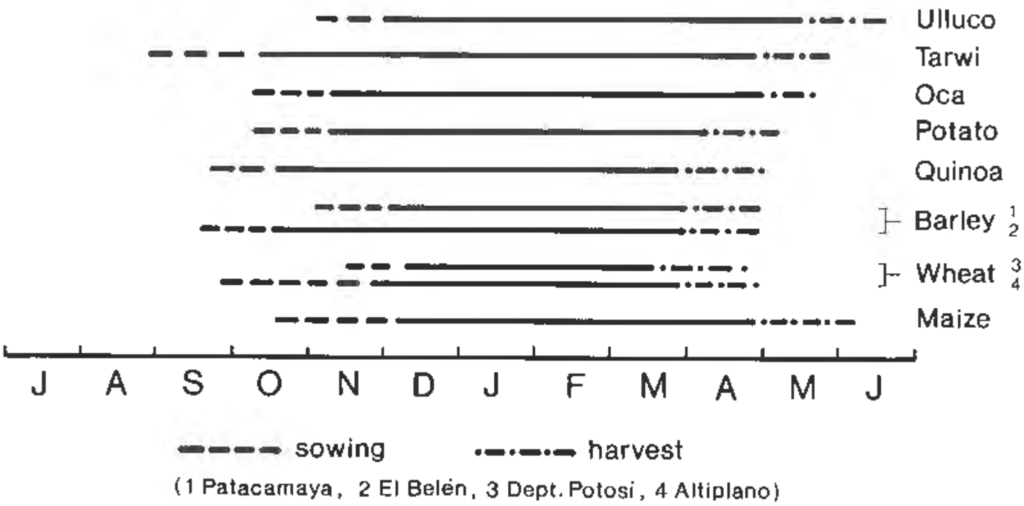


Fig. 10. The times of sowing and harvest for important cultivated plants in the Bolivian puna.

The altitudinal limit of the main cultivation belt is found at 4000 m, an altitude which has previously been regarded as the upper limit to the region without any or with only few frosts in summer. Only by means of an optimal adaptation to local relief (the use of slopes with few frosts, exposed to the sun) and by choosing cultivated plants which are little susceptible to frost (esp. Quinoa, potatoes and barley) can this altitudinal limit be transcended in certain areas (up to 4400–4500 m) (Fig. 9).

Moreover it is important that the comparatively frost resistant species of the high altitudes are sown on an average of 1–2 months earlier in the year and reaped about a month later compared with other species, so that they have a longer growing season with a smaller amount of heat at their disposal (Fig. 10). Nevertheless, both seedtime and harvest are crucial also for these plants, because they coincide with the period of October and November which has been recognized as being eco-climatically precarious (irregular setting-in of the rains with the occurrence of late frosts) and with March and April (rapid increase in night frosts).

Thus cultivation in the Bolivian puna belt remains precarious despite ingenious forms of adjustment to the eco-climatic conditions – including heavy rains and hailstorms during the summer. Unfavourable weather situations at the beginning and at the end of the growing season again and again result in disastrous crop failures or decreases in productivity so that life, which is already hard in this high altitude region, is exposed to further burdens.

References

BECK, S. und H. ELLENBERG (1977): Entwicklungsmöglichkeiten im Andenhochland in ökologischer Sicht. Göttingen.

BRUSH, S. B. (1982): The Natural and Human Environment of the Central Andes. In: Mountain Research and Development, Vol. 2, 1, 19–38.

ERIKSEN, W. (1983): Aridität und Trockengrenzen in Argentinien. Ein Beitrag zur Klimageographie der Trockendiagonale Südamerikas. In: ERIKSEN, W. (Hrsg.): Studia Geographica. Festschrift für W. Lauer. Coll. Geogr., Bd. 16, Bonn, 43–68.

FRERE, M. et al. (1975): Estudio agroclimatológico de la zona andina. (Informe técnico). FAO, Rom.

FURRER, G. und K. GRAF (1978): Die subnivale Höhenstufe am Kilimandjaro und in den Anden Boliviens und Ecuadors. In: Erdwiss. Forsch. 11. Wiesbaden, 441–457.

HERZOG, T. (1923): Die Pflanzenwelt der bolivianischen Anden und ihres östlichen Vorlandes. In: ENGLER, A., DRUDE, O.: Die Vegetation der Erde. Leipzig.

JORDAN, E. (1980): Das durch Wärmemangel und Trockenheit begrenzte Auftreten von Polylepis am Sajama Boliviens mit den höchsten Polylepisgebüschvorkommen der Erde. In: Tag.-ber. u. wiss. Abh. 42. Dt. Geographentag Göttingen. Wiesbaden, 303–305.

– (1983): Die Verbreitung von Polylepis-Beständen in der Westkordillere Boliviens. In: Tuexenia. Mitt. d. Florist.-soziol. Arb.-Gem., Neue Serie, Bd. 3 (Ellenberg-Festschrift). Göttingen, 101–116.

LAUER, W. (1982): Zur Ökoklimatologie der Kallawaya-Region (Bolivien). In: Erdkunde. 36, 4, 223–247.

– und P. FRANKENBERG (1978): Untersuchungen zur Ökoklimatologie des östlichen Mexico. Erläuterungen zu einer Klimakarte 1:500000. In: LAUER, W. (Hrsg.): Klimatologische Studien in Mexico und Nigeria. Beiträge zum Problem der Humidität und Aridität. Coll. Geogr., Bd. 13, Bonn, 1–134.

–, – (1981): Untersuchungen zur Humidität und Aridität von Afrika. Bonner Geogr. Abh. 66.

MAHNKE, L. (1982): Zur indianischen Landwirtschaft im Siedlungsgebiet der Kallawayas (Bolivien). In: Erdkunde 36, 4, 247–254.

MINISTERIO DE TRANSPORTES Y COMUNICACIONES (1973): Anuario Meteorológico 1973. La Paz.

MONHEIM, F. (1959): Die indianische Landwirtschaft im Titicacabecken. In: Geogr. Rdsch. 11, 9–15.

PENMAN, H. L. (1948): Natural evaporation from open water, bare soil and grass. In: Proc. Roy. Soc. London A. 193, 120–145.

– (1956): Estimating evaporation. In: Transac. Ann. Geoph. Union 37.

RICHTER, M. (1981): Klimagegensätze in Südperu und ihre Auswirkungen auf die Vegetation. In: Erdkunde 35, 12–30.

RUTHSATZ, B. (1977): Pflanzengesellschaften und ihre Lebensbedingungen in den Andinen Halbwüsten Nordwest-Argentiniens. Diss. Botan. Bd. 39. Vaduz.

SCHMIEDECKEN, W. (1978): Die Bestimmung der Humidität und ihrer Abstufungen mit Hilfe von Wasserhaushaltsberechnungen – ein Modell. In: Coll. Geogr. 13, Bonn, 136–159.

SCHOOP, W. (1971): Probleme und Möglichkeiten der Landwirtschaft Boliviens 1971. Auszug aus „Länderanalyse Bolivien – Dez. 1971", im Auftrage des BMZ, 1–41.

– (1975): The Potential and Limits of Bolivian Agriculture. In: Economics, 12, 34–62.

SCHRÖDER, R. (1981): Niederschlagsverhältnisse und agrarmeteorologische Bedingungen für die Landwirtschaft im Einzugsgebiet des Titicacasees. In: Erdkunde 35, 1, 30–42.

SEIBERT, P. (1978): Hochgebirgsvegetation der Anden und ihre Beziehungen zur Landnutzung im Inkareich. In: R. TÜXEN (Hrsg.): Ber. d. Int. Symp. der Int. Ver. für Vegetationskunde. Assoziationskomplexe (Sigmeten) und ihre praktische Anwendung. Vaduz, 515–521.

SHERIFF, F. (1979): Cartografía climática de región andina boliviana. In: Revista Geogr. Nr. 89, 45–68.

TROLL, C. (1931): Die geographischen Grundlagen der andinen Kulturen und des Inkareiches. In: Ibero-Amerikan. Archiv, V, 3, 1–37.

– (1943): Die Stellung der Indianerhochkulturen im Landschaftsaufbau der tropischen Anden. In: Zeitschr. d. Ges. f. Erdk., 3/4, 93–128.

– (1959): Die tropischen Gebirge. Bonner Geogr. Abh., H. 25.

– (1968): The Cordilleras of the Tropical Americas. Aspects of climatic, phytogeographical and agrarian ecology. In: Coll. Geogr. 9, Bonn, 15–56.

Discussion to the Paper Eriksen

Prof. Dr. W. Lauer:

Have the data, which you used to show the dependence of frequency of frosts on altitude (Fig. 1), been measured in the screen or close to the ground? The difference of both data might have a great influence on the course of the curve in the diagram.

Prof. Dr. W. Eriksen:

The data refer only to air temperature measured at the level of meteorological screens.

Priv.-Doz. Dr. P. Frankenberg:

Is it possible to differentiate the number of days with frost according to the frost intensity?

Prof. Dr. W. Eriksen:

Of course it would be useful to be able to do so. But the necessary data (observations for the various meteorological stations) were not obtainable.

Miss. J. M. Kenworthy M.A.:

Can you tell me whether you have studied the variability of the frost-free period?

Prof. Dr. W. Eriksen:

This was not possible, again because original data for the meteorological stations were not obtainable to illustrate variability, except for precipitation, for which FRERE et al. (1975) give mean monthly and annual values with 80% probability.

Dr. M. Winiger:

a) Is there any correlation between the frequency of frost and reduction in the density of plant cover? Is there any information about the degree of plant cover in the vicinity of the various stations?
b) From which altitude upwards does the frequency of repeated freezing and thawing decrease?

Prof. Dr. W. Eriksen:

a) Only a relatively rough assignment of stations to "humid", "dry" and "thorn and desert puna" is possible.
b) From about 5000 m upwards permanent frost sets in so that the frequency of freezing and thawing is reduced correspondingly.

Prof. Dr. B. Ruthsatz:

In the Aguilar region (NW-Argentina), the boundary between the high-Cordilleran and the subnival belt lies at about 4800/4900 m and corresponds to a mean annual temperature of 0 °C, i.e. regular night frosts and some days with continual frost. Here Cordilleran grassland gives way to tufted grassland.

W. Erlenbach:

You mentioned two crucial periods for agriculture. Let me add a third crucial period for plant growth (grass-cover) and thus for livestock production. From the diagram for Patacamaya (Fig. 7) it can be seen that at this station the month of September (climatologically) ought almost to be regarded as sub-humid. This applies to the long period mean value. We can proceed from the fact that sufficient precipitation falls in some Septembers to initiate growth of the grass. Yet this humid period in September lasts for 2–4 weeks only. After that October, and to some extent November, are definitely drier on average and are thus far more likely to show a deficit. The grass dries up after sprouting and taking root (this is confirmed by personal information from the director of the agricultural experimental station at Patacamaya). In such years the regular growth of the grass during the rainy season sets in markedly later, causing considerable hardship for stock farmers on the Altiplano, which is overstocked anyway.

Prof. Dr. W. Eriksen:

These are very interesting remarks which bring out the necessity for more precise analysis of mean monthly values as well as the importance of investigations into the environmental conditions at each locality.

Prof. Dr. W. Weischet:

a) In the diagrams showing annual variation of precipitation and evapotranspiration (Figs. 7 and 8), months with 80–100 mm precipitation are regarded as semi-humid. How has evapotranspiration amount been determined?
b) In the eco-climate of the Bolivian Altiplano, wind, with its characteristic diurnal range, must be an important influencing factor. How has wind been taken into account as a factor in evapotranspiration?

Prof. Dr. W. Eriksen:

Evapotranspiration was determined according to the formula of PENMAN (cf. FRERE et al., 1975). It takes into account the mean wind speed (m/sec) at 2 m above the ground during the period of analysis.

Erdwissenschaftliche Forschung, Bd. XVIII, 211–234
Franz Steiner Verlag Wiesbaden GmbH · Stuttgart (1984)

The Utilization of Natural Resources by a Small Community on the Highlands of Bolivia and Its Effects on Vegetation Cover and Site Conditions

Barbara Ruthsatz and **Ursel Fisel**

With 14 Figures and 3 Tables

1. Introduction

The Highlands of Bolivia have been exploited by man in a variety of ways for thousands of years. They were first settled by hunting tribes around the end of the last glacial period 10 to 12 thousand years ago. The transition to farming and animal domestication may have begun between 4000 and 3000 B.C., culminating between 200 and 800 A.D. in the Tiahuanaco Culture of the Aymara tribes – a stage of development in which the natural resources were being used both cautiously and effectively (LUMBRERAS, 1967; TROLL, 1968; NUÑEZ, 1970; for a detailed bibliography see RUTHSATZ, 1983). The influence of the Inca Empire, developed by the Quechua tribes, was not very intense in southern parts of the Andean Highlands. This was a result of the limited amount of time during which the area was under Inca rule (ca. 1438–1470 A.D.), as well as the apparently similar life-styles of the neighbouring tribes. A much stronger influence with regard to land-use practices resulted from the Spanish conquest of the Highlands. The Spaniards brought in new types of domesticated plants and animals as well as techniques of cultivation which probably spread rapidly throughout the Highlands as a result of their labor-decreasing/yield-increasing effects. But these improvements may not have lasted for long.

It is nevertheless astonishing to see how many of the old practices and customs have been maintained through the centuries.

It is frequently difficult to ascribe their origin to one culture or another. Under similar living conditions in parts of Spain and the Andean Highlands similar farming practices probably evolved: for example the "Zelgen"-system of land-use, grazing of fallow land, and transhumance. After the sharp population decrease at the beginning of the Spanish rule in the Lake Titicaca area (as much as 60%, according to SMITH, 1970, and SÁNCHEZ-ALBORNOZ, 1973), the number of inhabitants in the Highlands gradually began to increase again, and the present-day population density in the Lake Titicaca region presumably corresponds to approximately that existing shortly before the Spanish conquest.

The Andean Highlands stretch from southern Peru to northern Argentina over about 10 degrees of latitude. In Bolivia they reach a width of more than 300 km between the bordering East and West Cordillera. Individual peaks and mountain chains rise up to 5000 m above the 3500–4100 m high plains, subdividing them into several basins, most of which having an internal drainage system.

A marked dry-winter/wet-summer climate, corresponding to the highlands' location in the sub-tropical belt, predominates. Precipitation ranges from over 800 to less than 50 mm per year in a NE-SW-direction. Therefore, all levels of humidity exist, ranging from the subhumid Lake Titicaca area to the permanently arid Atacama Desert. The temperature regime is influenced by both the elevation and the precipitation characteristics. With increasing aridity we find increasing continentality with corresponding higher daily temperature variations as well as the danger of night frost.

Still nowadays, the basis for human life in the Highlands is, apart from a few mining locations the productivity of the plant cover (ELLENBERG, 1979; GUILLET, 1981; BRUSH, 1982), which decreases from northeast to southwest with the aforementioned increasing aridity. Parallel with this goes a decrease in human population density. In all of the zones the subsistence economy is based on farming and animal husbandry. The importance given to each activity varies, and in some areas there is a spatial separation between pastures and farm land. Only in the extremely humid upper elevations of the north and in the semiarid regions of the south it is probable that the population has subsisted entirely upon animal products, which nevertheless were used in trade with neighbouring agricultural communities for other types of food (eg. NACHTIGALL, 1965; WEBSTER, 1973; BROWMAN, 1974).

The long-lasting and ecologically variable land-use practices in the Andean Highlands have led to extensive alterations of the original plant cover as well as its habitats. Because of this, a reconstruction of the natural or original landscape – meaning a landscape without man's influence – is scarcely possible today. Likewise, the historical development of man's influence on the vegetation of the Highlands can only be considered in hypothetical stages (PRESTON, 1974; WENNERGREN and WHITAKER, 1965; RUTHSATZ, 1983). Within the contemporary landscape we can certainly recognize in many places evidence and consequences of past agricultural techniques; e.g. lichen-covered piles of gathered stones, narrow terraces, protecting stone walls, collapsed irrigation canals, vegetation mosaics due to differing land-use pattern in the past. We cannot with certainty, however, put these indicators into a chronological sequence. Without question, soil erosion, which is everywhere, has been caused or at least intensified by overgrazing and farming practices. One can only guess at the size of the area which has irreversibly been degraded this way (TERRAZAS, 1973; DOLLFUS, 1981). It is rather astonishing that the soils in many parts of the Highlands still produce yields without the application of fertilizer or special care. Fields have become larger, terraces are being neglected, steep slopes are planted, heavy soils are plowed with tractors, and the entire landscape is intensively grazed year around (LEBARON et al., 1979).

The investigation of the effects of current agricultural practices on ecosystems is part of the research carried out at the Ecological Institute of the University of La Paz. The Institute was founded as a partner-project with the University of Göttingen in 1978 by the GTZ. The research focuses on the following questions:

1. Will the present land-use pattern led to a gradual decline in production, or is it more or less in equilibrium with the habitat potentials?
2. In case the present system is not in equilibrium with the habitat: what long-term solutions could be recommended?

Until now, investigations with similar goals have only been carried out very rarely in the Andean Highlands (MACEWAN, 1969; PRESTON, 1973; BAKER and LITTLE, 1976).

The Ecological Institute selected the small Highland community of Huaraco on the road from La Paz to Oruro southeast from Sica Sica (ca. 17°22′ S, 67°38′ W) as an examplary region for investigation, because an agricultural project of "Bread for the World" had been carried out there for some time, facilitating good contact with the local population*.

The work started by the Ecological Institute concerns the care for a weather station as well as ongoing plant-ecological, zoological and pedological questions. For the most part these are being investigated in sample areas fenced in for long-term research and corresponding to pasture land currently in use.

In the following, we would like to deal in some detail with the general character of the Huaraco-area vegetation, its habitat conditions, and suitable uses of the village region and the connecting plains to the South.

*Institute members and graduate students carried out a very comprehensive study of the Huaraco ecosystems (HANAGARTH and FISEL, 1983). The authors wanted to contribute results based upon botanical-ecological analysis techniques. The research was financially supported by the GTZ and DAAD. Our thanks go especially to J. EWERT from Huaraco for his hospitality and the wealth of information he provided; it also goes to all of the village inhabitants, and to the Ecological Institute, especially Drs. E. GEYGER, S. BECK and W. HANAGARTH. Professor Dr. D. SCHRÖDER, University of Trier, helped to interprete the soil analysis data with respect to long-term fertility improvement measures.

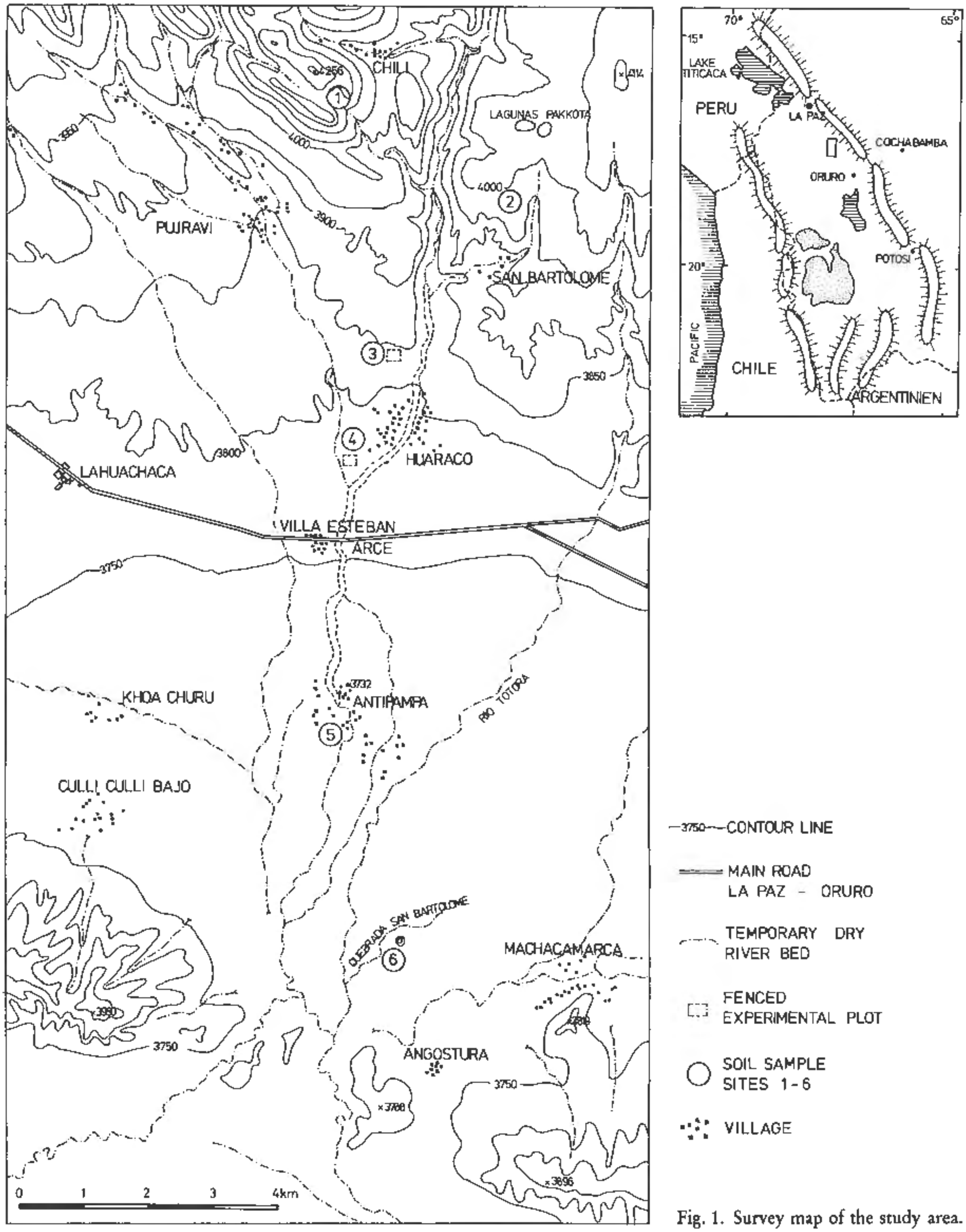


Fig. 1. Survey map of the study area.

2. General Features of the Huaraco Area

The community of Huaraco lies in the semi-arid portion of the Highlands at the foot hills of the East Cordillera. The latter consists at this location chiefly of quartzites, sandstones, arkoses and other palaeozoic strata (Devonian and Silurian). The bordering mountain chains in the north exceed 4500 m only with a few peaks, and descend over hills, small plateaus and gentle slopes of the plains which begin at approx. 3800 m. The more gentle hills are to a great extent covered with tertiary debris of varying thickness. The Huaraco river and some of its tributaries have in some places cut gullies into these sediments. The plains incline gradually towards the broad basin of the Desaguadero and are divided into different old sedimentary terraces, alluvial fans and recent floodplains. Although these are cultivated by the neighbouring communities, they have been drawn into the study area for purposes of comparison (Fig. 1).

The soils on the mountain slopes and in the hill zone are in part very poorly developed or at least rich in unweathered stone material. In some places hard quartzite ridges and sandstone benches have been carved out by erosion. The sandy-stony soils in the debris-covered hill zone become finer on the foot slopes and upper terraces, changing to sandy-silty or clay-rich soils in the plains and finally assuming the character of solonchak near the base of the basin.

The Huaraco river and some springs which appear in the lower part of the plain have water year around, at least in the underground. This fact and the semi-arid climate (Fig. 2), which is still favourable for farming without irrigation, certainly made it possible to settle this landscape quite some time ago. Archaeological investigations in similar regions located nearby (MÉTRAUX 1935/36; IBARRA GRASSO, 1955; PONCE SANGINÉS, 1970) and own discoveries of stone tools, pot sherds, agricultural implements made from stone as well as remains of pre-Inca grave towers ("chulpas") in the community area indicate that an early settlement is very likely. The community of Huaraco together with the bordering plains may therefore be considered as a typical example of the semi-arid portion of the eastern Bolivian Highlands.

The center of Huaraco lies on a terrace of the Huaraco river where the river flows out into the plains. It is a scattered settlement with many individual farms lying at some distance from each other. The presence of the asphalt road from La Paz to Oruro cutting through the area led some time ago to the foundation of the settlement of Villa Esteban Arce along its edge. The inhabitants of Huaraco bought their freedom from the former landowner around 1875 and split the land among themselves. Today about 80 families live here. Altogether there are some 300 people. They live predominantly on farming and livestock, the main trade products being potatoes and sheep meat. Only a few families produce some surplus. A subsistence economy is by and large the rule. Family members who work outside of the community contribute to the support of some families.

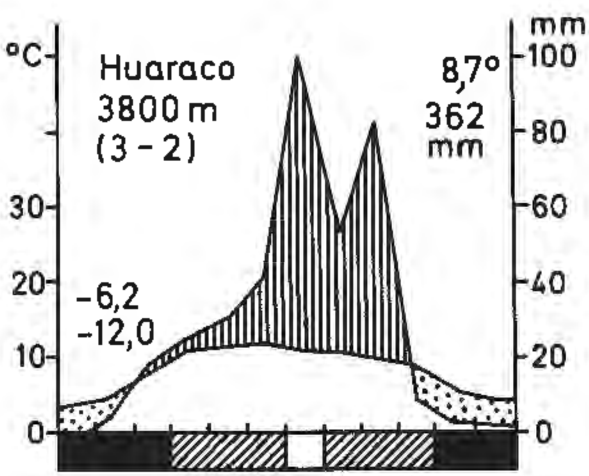


Fig. 2. Diagram of the mean monthly temperature and precipitation values of Huaraco from 1980 to 1982. Source: Ecological Institute, La Paz.

3. Agricultural Practices in the Huaraco Area

3.1. Farming

Many agricultural practices have been maintained by most of the communities of the Highlands which are characteristic for the Aymara people (SORIA LENS, 1954; LOZA BALSA, 1972; PRESTON, 1973; RUBIO Y DURÁN, 1980). Potatoes, barley, and the Andean cereal "Quinoa", are the principal crops.

The potato, today as always, constitutes the major human foodstaple, "sweet" potatoes and the frost-resistant "bitter" potatoes have to be distinguished from each another. 25 different kinds with varying growing requirements, sensitivity to frost, drought, and disease are well-known and put to good use in the study area. Each family converts a portion of the potato harvest into "chuño", meaning that during the coldest months the potatoes are put through a freeze-dry process. In this stage they can be preserved many years.

Potatoes are best grown on light, sandy soils. Heavy clayey soils are apt to mudding and in dry years do not guarantee the necessary water requirements. A good supply of nutrients is important: consequently, potatoes are always planted as the first crop in a newly started crop rotation sequence and manured with sheep dung from the corrals. Above 4000 m only the frost resistant bitter potatoes thrive, which for the most part are converted to chuño.

The largest portion of the cultivated barley serves as feed for cattle. Of the five usable varieties one type without awns is cultivated, the roasted grains of which are eaten. Barley requires more water than potatoes, but is planted at elevations as high as 4200 m.

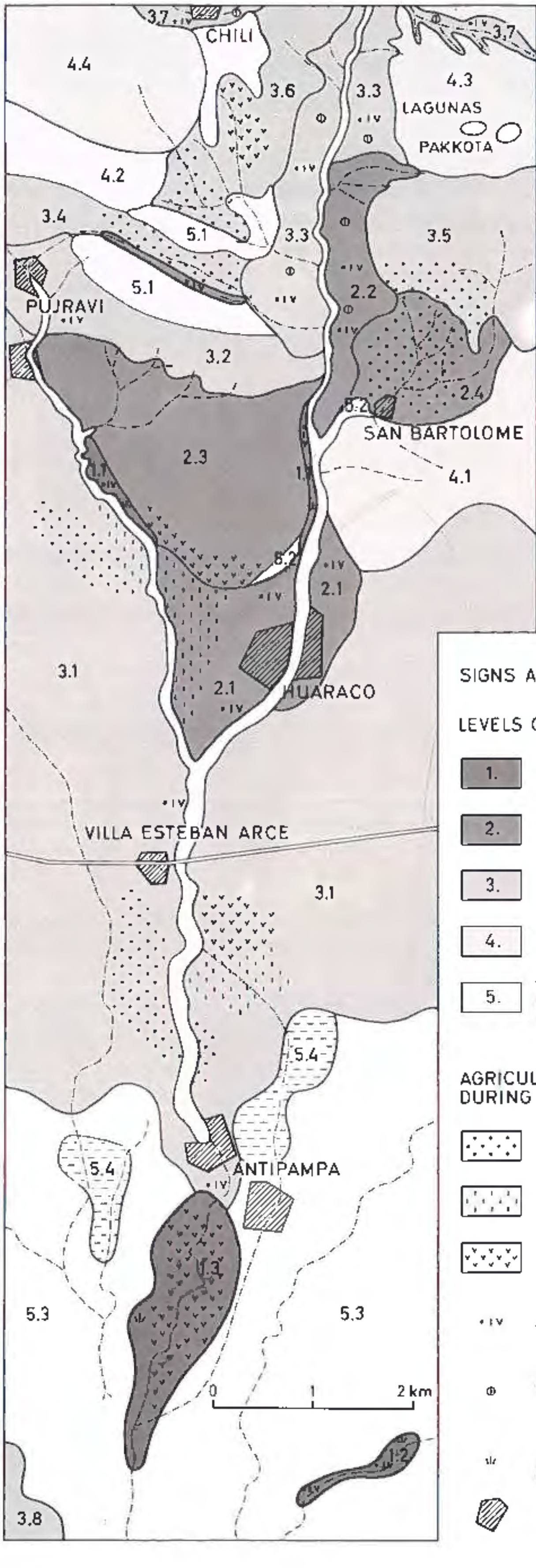
The traditional Andean cereal "Quinoa" (*Chenopodium quinoa;* six varieties) which is characterized by a special resistance to drought and a moderate salt tolerance, is declining because a much better profit can be gained from potatoes in the local markets.

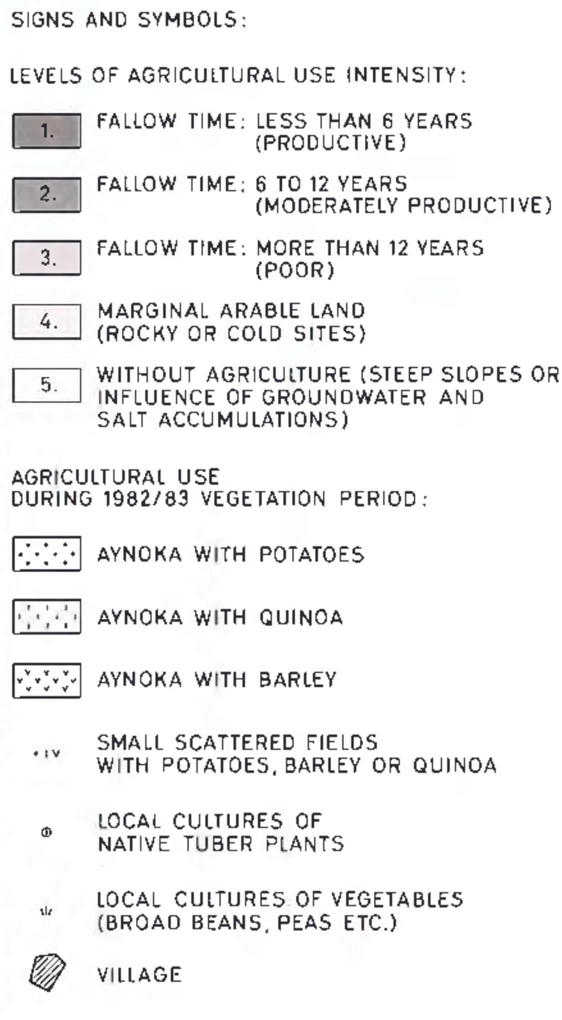
It is essential for the inhabitants of the area to harvest enough every year, even under adverse weather conditions. The families must have enough food-supply until the next harvest, and enough seeds must remain for the following spring. Cash income for purchases of food-stuffs and seeds usually cannot be earned. For personal consumption, the native tuber plants "Oca"*(Oxalis tuberosus),* "Ullucu" *(Ullucus tuberosus)* and "Isañu" *(Tropaeolum tuberosum)* are frequently cultivated in small quantities. One generally finds all three species growing together in frost-protected slope niches on small fields having good soils. Because of the characteristics of such locations, they cannot be used in a large-scale manner for a common purpose. The cultivation of tuber plants is reported to have sharply declined in the last few years. It is, nevertheless, still of great importance in the fields of the community of Chili, which is located at some distance to the north. Along with Quinoa *(Chenopodium quinoa),* a few rows are occasionally seeded with "Cañihua" *(Chenopodium pallidicaule).* Its fruits are prepared for various foods and a drink. The native lupine *(Lupinus mutabilis),* called "Tarhui", although thriving throughout the Andean Highlands, is not found here, possibly because of the exceptionally rough climate. On the floodplains with their silty-clayey soils, the broad bean, "Haba" *(Vicia faba),* is frequently cultivated on soils with a very low salt content. Peas, onions and other vegetables appear now and then in small frost-protected valleys, on especially good soils, or in a few walled-in house gardens.

Information regarding yields of cultivated plants is very difficult to obtain because of the variable habitat characteristics as well as the highly variable field sizes. For potatoes, yields between 1500 and 4000 kg/ha have been quoted, and for quinoa between 200 and 400 kg/ha. The yields for barley, including the straw, seem to lie between 1500 and 3000 kg/ha, the beans yield about 250–300 kg/ha (FISEL and HANAGARTH, 1983).

The most common sequence of crop rotation usually starts with potato cultivation in the first year, followed by 1–2 years of barley, and a growth period with quinoa. On especially nutrient-rich, sandy soils potatoes will sometimes be cultivated for 2 years. Occasionally quinoa will be seeded in the second year and then followed by barley. At 5 to 10 years – sometimes even longer – fallow period follows, which

Fig. 3. Map of the present day land-use in the Huaraco region. Bases: Topographical maps in 1:50000. Aerial photographs in 1:50000 in black and white. The ground survey has been carried out with the assistance of M. Libermann.





Legend of Figure 3

Land-use categories:

1. Very intensive use. Fallow period shorter than 6 years.
The farming areas put together in this category present the shortest fallow periods in the entire study area. They concern the lower terraces and sometimes inundated parts of the valleys with fertile soils, poor in stones, where, by individual family-use the highest yields can be obtained.

1.1 Fertile, sandy lower terraces along the Huaraco river and Pujravi river (Figs. 4 and 10), slightly inclinated and partly irrigated through canals, 3780 m. Intensely cultivated by single families. Field sizes up to 0.25 ha. Crops: Potatoes, quinoa, barley, broad beans, peas, onions.

1.2 Ground along the San Bartolomé river with profound, silty to clayey soils, where the salt content of the soil is reduced every year in the rainy season by inundations (Fig. 6), 3720 m. Field sizes up to 0.5 ha. Crops: Barley, broad beans, quinoa, cañihua.

1.3 Sandy sediments of the Huaraco river, to some extent influenced by salty groundwater but with profound fertile soils, 3730 m. Intensely used by single families. Field sizes up to 0.5 ha. Crops: Broad beans, potatoes, quinoa, barley.

2. Intensive use. Fallow period between 6 and 12 years.
Relatively productive farmland can be found on the alluvial sedimentation fan of the Huaraco river, which because of this reason has become the center of the Huaraco village. Parts of the slopes of the corresponding valley are similarly fertile. Normally they are not grazed. The extremely little danger that frosts may occur, permits the cultivation of the native tuber plants on small fields with quite reliable yields up to 3960 m above sea level.

2.1 Sandy stone-rich alluvial fan of the Huaraco river, slightly inclinated to the south (Fig. 7), 3780 to 3810 m. Individually used "sayana"-fields, field sizes up to 0.5 ha. Crops: Barley, potatoes, quinoa.

2.2 West-orientated, dissected slopes of the Huaraco valley (Fig. 10) with 10–15% inclination, including small rock formations, 3840 to 3960 m. Scattered, individually cultivated fields up to 0.5 ha with sandy-silty, often shallow soils. Crops: Barley, native tuber plants, potatoes, quinoa.

2.3 Spurs of the cordillera mountains to the north, covered with tertiary debris. 3820 to 3900 m. Slightly dissected slopes with 5–20% inclination (Figs. 8 and 10). Sandy-silty, stone-rich, often shallow soils. Field sizes up to 0.5 ha. Crops: Productive ground for potatoes; quinoa, barley.

2.4 South orientated slopes, intensively dissected by erosion gullies. 3860 to 3960 m. Profound sandy-silty soils with moderate stone content. Settlement area of the community section of San Bartolomé. The gully formation is probably initiated by human activities. Field sizes up to 1 ha. Crops: Productive ground for potatoes; quinoa.

3. Fallow periods more than 12 years.
Very long-lasting fallow periods are typical for large areas of the community land. Stony soils and frost damage on level plains are the main reasons for the extremely extensive land-use. This also holds true for many shallow sites with rocky outcrops. The continuous overgrazing does not permit here a permanent regeneration of soil fertility.

3.1 Extensive gravel plains and old sedimentation terraces of the Huaraco river, inclinated to the south up to 3%. 3730 to 3840 m. Sandy-silty, mostly profound but stone-rich soils with a southward decreasing amount of skeletic material. Fallow land to some extent older than 20 years, with scattered stonemounds and walls. Field sizes up to 1 ha. Crops: Potatoes, quinoa, barley.

3.2 Moderately steep, southwest-orientated mountain spurs (inclination: 15 to 25%), interrupted by narrow rock ledges, 3850 to 3920 m. Stony shallow soils, which permit only local farming on small fields up to 0.25 ha. Crops: Potatoes, quinoa, barley.

3.3 East- and west-orientated slopes of the Huaraco river in the northern part of the community area. 3860 to 4000 m. Large parts of rocky, extremely shallow or steep sites limit the farming possibilities to few, scattered fields of up to 0.25 ha. Crops: native tuber plants, potatoes, quinoa, barley.

3.4 Southwest-orientated slopes with 5 to 10% inclination at the base of the Janthaloma mountains (Fig. 12) and the neighboring ridge, 3950 to 4050 m. Stony, but profound, sandy-silty soils. Field sizes up to 0.5 ha. Crops: Bitter potatoes, barley.

3.5 Slightly inclinated plain in 3960 to 4000 m. Profound silty to clayey soils with moderate stone content. Field sizes up to 0.5 ha. Because of frequent frost damages only cultivation of bitter potatoes possible.

3.6 Intensively dissected slopes with variable inclination rates (5–30%). 3950 to 4100 m. Rock outcrops and mostly very shallow stony sites are limiting the farming activities to the foot parts of the slopes. Field sizes up to 0.25 ha. Crops: Potatoes, quinoa, barley.

3.7 North- and south-orientated, 10 to 35% inclinated slopes along the tributaries of the Huaraco river. 3950 to 4100 m. Profound, stone-rich, sandy-silty soils. Field sizes up to 0.25 ha. Crops: Potatoes, native tuber plants, quinoa, barley.

3.8 North-orientated spur of the mountain ridge bordering the study area to the south (Figs. 6 and 13), 3750 to 3850 m. North orientated slopes with 15 to 25% inclination. Farmland of the predominantly animal breeding communities of Culli Culli and Antipampa. Stone-rich, shallow, sandy-silty soils. Field sizes up to 0.5 ha. Crops: Potatoes, barley, quinoa.

4. Marginal farming sites.
Shallow and stony soils as well as climatically unfavorable highlands are limiting the farming activities in this land-use category very strongly. But nearly everywhere one can observe stone walls and mounds in decay, which give evidence of former agricultural habits.

4.1 Spurs of the northern mountain chains between 3800 m and 3920 m. Weakly dissected slopes with stony, silty and to some extent clayey soils, which hardly permit any crop cultivation because of their poor nutrient content and water deficiencies. Field sizes up to 0.5 ha with fallow periods of almost 30 years. Crops: Potatoes and dry-resistent quinoa.

4.2 Lower and central slopes of the Janthaloma mountain between 4050 and 4120 m (Fig. 12). Southwest-orientated slopes with 10 to 20% inclination. Stony, but profound soils with silty texture. The small fields of 100 to 200 m^2 size are surrounded by decaying stone walls. They have been mostly abandoned because they are too small and too steep for the usage of the wooden plough pulled by animals. The Andean foot plough is not any more in use at Huaraco.

4.3 Slightly inclinated plain at 4000 m. Two small lakes are situated in a shallow depression, which serve as watering place for the herds during the rainy season. Consequently the whole area shows intensive grazing damage.

4.4 Top crest and upper slopes of the Janthaloma mountain (Fig. 12) with 15–30% inclination, 4120 to 4250 m. Apart from rocky outcrops the soils rich in stones but to some extent of silty texture. Remnants of decaying field terraces indicate former crop cultivation. The change in the farming methods have led to the abandoning of these fields.

5. Pasture land
The areas put together in this land-use category cannot be used for crop production. Rocky outcrops, steep slopes, wet and salt-rich clayey sites permit only the use as grazing land. The moist surroundings of spring areas, however, give raise to very productive grass stands.

5.1 Intensively dissected steep slopes, 3920 to 4000 m. Outcrops of rocks and very shallow soils permit only occasional grazing.

5.2 Short, shallow and stony steep slopes with 30 to 45% inclination along the Huaraco river and one of its tributaries. 3820 to 3940 m. Striking erosion gullies occuring locally might be attributed to heavy grazing activities.

5.3 Vast alluvial plain, exclusively used for grazing, covering the entire southern part of the study area (Fig. 14). 3720 to 3750 m. Silt and clay soils, influenced by salt-rich groundwater. The vegetation cover is composed of short grass and salt plant formations, interrupted by extensive bare ground.

5.4 Productive grazing land on moist spring areas ("canchones") with clayey marsh soils, fenced in by decaying walls of mud bricks.

in good soils near the village is shortened, and lengthened on poor soils at distant locations. Figure 3 represents and explains the different land-use categories of the whole study area. From these categories the suitability of the agricultural land in use can be estimated with regard to its climatic and habitat conditions. The best soils are found on the terraces of the larger rivers or in especially protected niches and slope locations ("k'uchu"). The most frequent and best yields of corresponding cultivated plants, such as the native tuber plants and introduced vegetable types, are obtained here. The required fallow time is usually only 2–4 years. The heavy sandy-loamy soils ("l'aka"), which cover the entire plains of Huaraco, permit especially in dry years very poor yields. They lie fallow 10-20 years on the average. On high altitudes over 4000 m ("k'ollu") only the cultivation of bitter potatoes and barley is possible and, since the fields are relatively far removed, fallow periods of over 20 years are typical.

The most productive grounds are mostly those fields which surround the farms and are designated as "sayanas". These have belonged to the families since time immemorial as indisputable private possessions. Since every family owns "sayanas" between 2 and 6 ha in size, the farms are situated on the best soils, and the villages take on the form of a scattered settlement (SORIA LENS, 1954).

The illustration of the current land use during a vegetation period (Fig. 3) indicated that the potato, barley and quinoa fields mapped lie together in more or less closed blocks. For ages the land-use has been in the form of "Zelge" farming, i.e. with „Flurzwang". Every year the community assembly decides in what part of the community area the fallow ground should be broken for potato cultivation the following year. Since the farmland – as opposed to the pasture land – has remained in private ownership ever since the community bought it up, all the land parcels must be divided up in such a manner that each family in every "Zelge", called "aynoka", possesses a sufficiently large plot. Where this is not the case, there are various possibilities for farmers with little land of their own to farm within the „aynoka". The farmer without much land can, for example, lease a field for the duration of an entire crop rotation (3–4 years) for the price of one sheep. Another possibility is share-farming. The non-owner must undertake the work-intensive preparations for the seeding, i.e. removing the weeds and stones, as well as the plowing. Afterwards, the field is cut in two. The landowner and the leaser do the seeding, farming and harvesting separately. At least 2 "Zelgen" in different parts of the community area are newly farmed each year in order to decrease the risk of an insufficient potato yield.

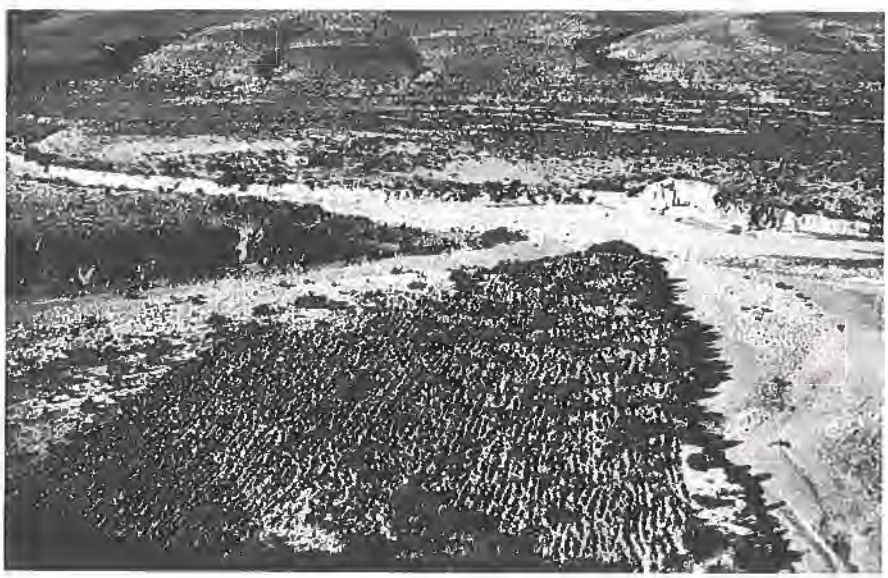


Fig. 4. Recently plowed fallow field (May 1980) in the valley of the Pujravi river, still with some scattered *Baccharis incarum*-shrubs (land-use category 1.1).

Altogether, only about 5% of the entire agriculturally suitable land can be cultivated during one year. Of this, 55% is potatoes, 25% is barley and 20% is quinoa. Whenever the population increases, a decrease in the number of fallow years is usually experienced although the usable land is limited (PRESTON, 1973). Nevertheless, in contrast to many other communities, Huaraco possesses enough land, and frequently 10–15 or more years of fallow can be counted on. The breaking of fallow land occurs in the fall, when the still somewhat moist soils can be worked more easily. A wooden hook-plow, strengthened with an iron tip and pulled by a team of bulls, has been used for plowing since the introduction by the Spaniards. By such a method, the soil is only broken to a depth of about 15 cm and not turned, which certainly has a soil-preserving and erosion-decreasing effect. The original working techniques of the Aymara farmers using shovels or digging sticks is no longer customary in Huaraco. For this reason, the narrow strips of fields surrounded by stone-walls on the steep south-facing slopes on the Cerro Janthaloma have also fallen completely into disuse.

The larger shrubs which are removed during the breaking to fallow land are used as burning material (Fig. 4). Smaller bushes are burned off on the field before the seeding in spring. However, the ashes are only rarely spread over the surface. The seeding of the crops follows between September and December (Fig. 5) depending on the quality of the land, the type of crop and the weather conditions. Only with potatoes, some sheep dung is mixed in. Mineral fertilizers must be paid for in cash, something very few families have.

The field work starts in August with the sowing of broad beans in soils that provide a relatively good water supply during the summer. The quinoa needs also a long vegetation period but is much more resistent to drought, a serious problem in some years. The native tuber plants, including potato, can be planted only when enough moisture has accumulated in the soil after the last dry season, that means not before October or even November. The last to be sown is barley, probably because it has a relatively short vegetation period and is of less importance to the farmers. Thus, it often does not reach maturity. Still, as green plant it serves as good fodder for cows and sheep. Only ripe corn can be stored for a longer period

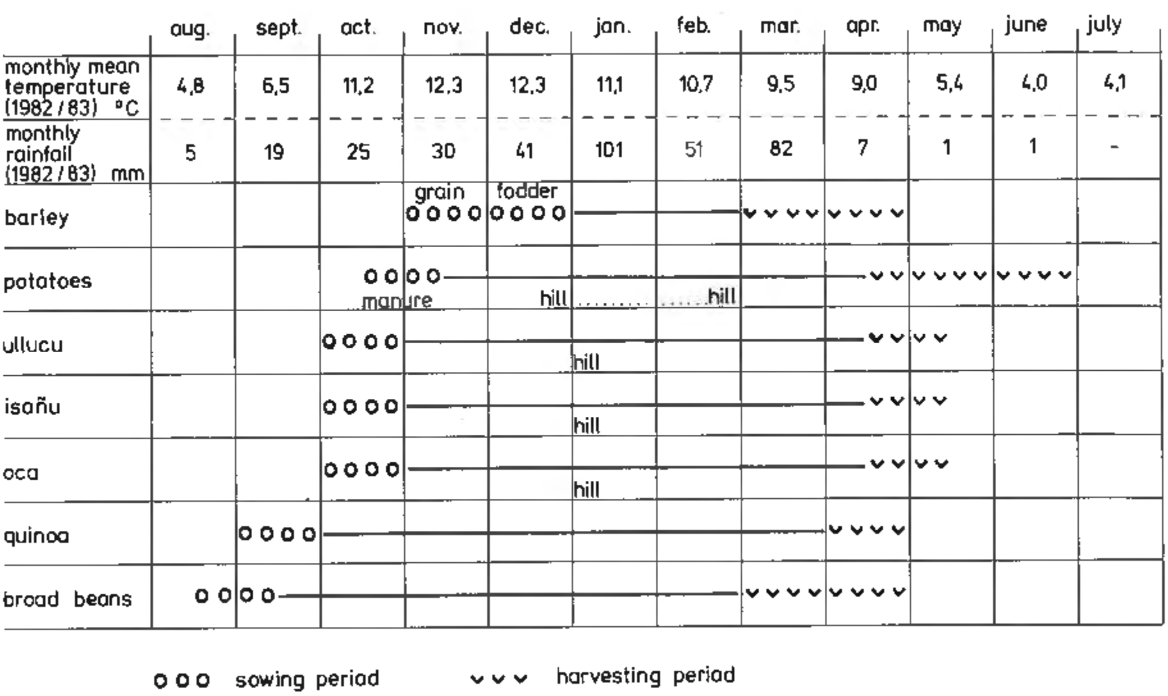


Fig. 5. Range of sowing and harvesting dates of the crop plants cultivated in the Huaraco region ("calendario agricola").

of time. Therefore, it is also needed. The harvest starts with broad beans and barley and ends with potatoes, because their collection requires much time but can be left to the end. Out of all crops the tuber plants need the greatest care since they have also to be hilled at least once during summer.

Fig. 6. Floodplain in the extreme south of the study area (March 1980). Productive farmland-islands along the San Bartolomé river (land-use category 1.2). In the background the Wacani mountain (detail on Fig. 13).

Fig. 7. Tillage of potatoes (November 1981) on the sedimentation terrace of the Huaraco river near the village (land-use category 2.1). In the background to the northeast some farms of Huaraco and the foot slopes of the hill-zone.

3.2. Pasture

Essential for the agricultural economy are sheep and llamas for meat and wool products, and cattle and donkeys as draught and pack animals. Moreover, the animals serve as "living saving accounts" for times of illness, poor yields and festivals. Each family in Huaraco owns 3–5 cows, about 20–50 sheep and a few donkeys. In addition many families have 10–15 llamas. Their importance as pack animals, however, has declined considerably in the vicinity of modern roads. Besides, the successful raising of llamas requires considerable skill and attention, and the community does not own any suitable pasture land for them (such as moist areas in valleys or extensive grasslands in the higher mountains). In the bordering community of Antipampa, however, grazing of domestic animals is much more important on the extensive plains with some moist spring areas. On the extensive short-grass pastures one finds herds of sheep up to 250 head and clearly more llamas than in Huaraco. The "canchones" are a pastureland speciality of this area. In very moist sites tall-grass stands are protected form constant grazing by walls made of mud bricks. They are used as pasture only from March to June. Unfortunately, an increasing number of walls are destroyed and a corresponding increase of unregulated grazing of the "canchones" is to be observed.

Sheep and llamas can be grazed freely, i.e. without rules concerning land-ownership or using-rights, with the exception of the areas designated during the summer to serve as farming "Zelgen". The herds are driven daily from the farmers' houses to the valley pastures and the fallow land and in the evening they return to be locked in corrals. This is usually the task of women and children. During the dry winter months, when fodder is lacking in the vicinity of the village, the herds are driven into farther and higher up grazing regions where small stone huts with nearby corrals are used by the shepherdesses and the herds during the night. Twice a year the sheep are desinfected and at the beginning of the rainy season they are shorn. Sheep are preferred to llamas since they, besides the wool, deliver 15–20 kg mutton per sheep. The mutton is then sold at the market of Lahuachaca, and with this money other foods such as noodles and sugar can be purchased.

The burning of the pasture land before the rainy season begins has not been customary in the community of Huaraco for a long time. The 24th of June is an exception because the burning at the time of solstice has a ritual meaning. Even on this day, however, it has decreased and burning is limited to small, steep slopes. One hardly finds, however, any place, where at the basis of the bunch grasses and scrubs charcoaled remains of plant parts cannot be observed, indicating earlier burnings.

The lack of fodder for the sheep and llama herds as well as the cattle and donkeys during the winter drought determines the condition and size of the herds. The animals must travel over long distances in order to find at this time of the year enough to feed on. Nevertheless, a system of stockpiling of fodder – as has been customary for quite some time in our country – has never been developed in the Andean Highlands. Quite often however the best moist areas generally serve as a reserve in times of emergencies.

4. Effects of Farming and Grazing on the Vegetation Cover and Its Habitats

All moderately suitable habitats, which are not too cold, frost-endangered, shallow, wet or containing too much salt are being cultivated or at least have been cultivated. Except for the river and brook valleys, the source marshes, salty clay-flats, steep slopes and alpine grasslands above 4200–4300 m, the vegetation corresponds more or less to fallow stages of varying ages, which moreover remain under the constant pressure of intense grazing by domestic animals. How the original plant cover may have been composed is not to be deduced from the present situation in the region. Whether or not an open forest of "quishuara" *(Buddleya* spec.) or "queñua" *(Polylepis* spec.) existed here a long time ago remains unknown. It is certainly possible for these trees to grow here today without additional water supply, but they must be protected from grazing animals as long as they are small.

The regularly repeated plowing of fallow land followed by a few years of use before another fallow period must, after hundreds to thousands of years, have led to a certain selection of plant types suited to these conditions. The most successful types of plants under such conditions are those which produce many, easily distributed seeds, which have a moderately long lifespan, which germinate under high light intensity and quickly develop an extensive root network. These characteristics may be found with all common herbs, grasses and even shrubs. On the fresh fallow, therefore, one regularly sees young plants of the predominant dwarf scrubs *Baccharis incarum* and *Tetraglochin strictum*. Since, however, only a small portion of the agricultural land is cultivated at one time and the fallow period can last several decades, other plant types with deviating characteristics can also survive in the region. The diversity of plant species of this landscape, which at first appears rather monotonous, can most likely be traced back more to the richness in micro-habitats, than to the differentiated use of the land.

Additional important selection-factors stem from the continuous and at times very intensive search for food by the domestic animals. The bite of the sheep, llamas and donkeys has predominantly allowed those plants to survive which can regenerate vegetatively, those which due to their chemical composition are poisonous or unpalatable for the animals, those which have developed stabbing shoots (*Adesmia* spec.) or pointy leaves (many grass copses), those that grow so close to the ground that they cannot be bitten (cushion and rosette plants), or those the seeds of which are especially prepared for successful germination having passed the digestive tracks of animals (possibly *Tarasa* spec.). During times of scarce food, nevertheless, almost all plants, even the hardly edible ones, are eaten. Only *Astragalus garbancillo* and other species of *Astragalus* as well as most of the ferns can be regarded as genuinely poisonous; and these alone are being avoided by the grazing animals even in emergencies. Since the herds only remain in the same area for a period of days or weeks, some good grazing grasses and herbs have been able to survive in the region, which then suddenly appear in large quantities on protected fallow land between fields which are actually being cultivated. Many of the better fodder plants can also be found thriving and bearing fruits under the protection of thick or thorny shrubs.

Fig. 8. Potato field with accumulation of eroded soil in the furrows of the lower part. The potato plants are partly damaged by frost (land-use category 2.3). In the background the Janthaloma mountain (detail on Fig. 12).

Besides the pressure or selection which farming and grazing directly exercise on the composition of the plant cover, the abiotic habitat conditions are also clearly influenced by these practices. During the years of cultivation the surface erosion on slope locations can be considerable. Despite the favourable infiltration rates on loose soils, the summer rainstorms lead to the sweeping of fine earths into the furrows and to the lower parts of the fields (Fig. 8), where former stone walls frequently hindered further movement. During the first two fallow years the soil is still not very effectively protected, as the redeveloping plant cover and its root system did not have enough time to become firmly established. The continual trodding of animals produces, on one hand, a compactation of the upper layers, and on the other it damages the soil surface by the sharp hooves of the sheep and donkeys (ELLENBERG, 1981). Llamas do not have the same effect because they are plantigrades. The compactation leads to the accumulation of water on the surface after heavy showers and with just a slight inclination of the slope it results in a quick run-off of the loose soil particels and organic material which has not been incorporated into the soil. The constant grazing of the whole area prevents the development of a complete cover of vegetation and dense rooting of the soil. Such a vegetation cover could be expected without question because of the annual rainfall between 300 and 400 mm. Indeed, it more or less quickly develops on surfaces protected from grazing as the fenced-in experimental plots are beginning to indicate.

Extensive farming and unregulated grazing of domestic animals on the fallow and community lands has led to intense soil erosion in Huaraco as well as everywhere else in the Highlands (LEBARON et al., 1979). The profound fine earth-alluvial soils of the lower plains are probably to a great extent anthropogenic, similar to the "Auen"-soils of Germany. Whether or not the erosion today is at all stronger or weaker than in former times remains unknown. The widely distributed stone heaps, mounds and walls permit the conclusion that soil erosion has been active for a long time. It even appears that the removal of stones is less customary or necessary today than before, as most of the stone piles are thickly covered with slowly growing lichen crusts.

The explanation of this mosaic of cultivated fields, fallow fields of varying ages, bare, stony islands of wasteland and grazing areas, in a way that the suitable uses of the habitats could be made clear by the respective plant covers, was one of the goals strived for by the botanical-ecological investigations around Huaraco. Phytosociological results according to the BRAUN-BLANQUET-method from fallow land as old as possible, from pasture land and from shallow rocky sites in the whole study area as well as from several series of succession stages on fallow fields are the basis for a simplified overview of the most important vegetation types in the Huaraco region (Table 1 and Fig. 9). A comprehensive cartographic representation of the vegetation cover is in preparation (FISEL und RUTHSATZ).

The analysis of the fallow vegetation of those sites more or less suitable for cultivation between the upper limit of farming at approx. 4200 m and the habitats which are too wet and/or salty provided a clearly differentiated mosaic of plant communities according to elevation, depth of soil and soil texture (Table 1). Most probably the difference between habitats would appear more clearly if older stages of fallow fields (more than 20 years) had been available for the phytosociologically analysed plots and if the succession stages would not have been influenced by the year-round intensive grazing. The plant species groups with very wide ecological amplitudes, as for example those of *Baccharis incarum, Stipa ichu* or *Parastrephia lepidophylla,* appear in almost the entire region and may be considered as indicators of the uniformation of the sites as a result of strong overgrazing. In Fig. 9 we have tried to make the vegetation and habitat gradients visible. The illustration includes, in addition to the farming sites, the vegetation types of the Andine grazing zone as well as azonal grazing communities at wet and/or salty habitats, distinguished by their characteristical species composition. The constant grazing has severely altered these areas. Most of the shrubs, many hard-leaved grasses as well as low-growing herbs and cushion plants (eg. *Anthobryum triandrum, Verbena minima* etc.) may therefore be favoured indirectly.

In order to obtain a general idea of soil nutrient supply of the main land-use categories and the way in which they are presently influenced by agriculture and grazing, soil samples were taken along an elevation gradient in 6 habitats on fallow land of varying ages. The fine earths (Ø less than 2 mm) were then

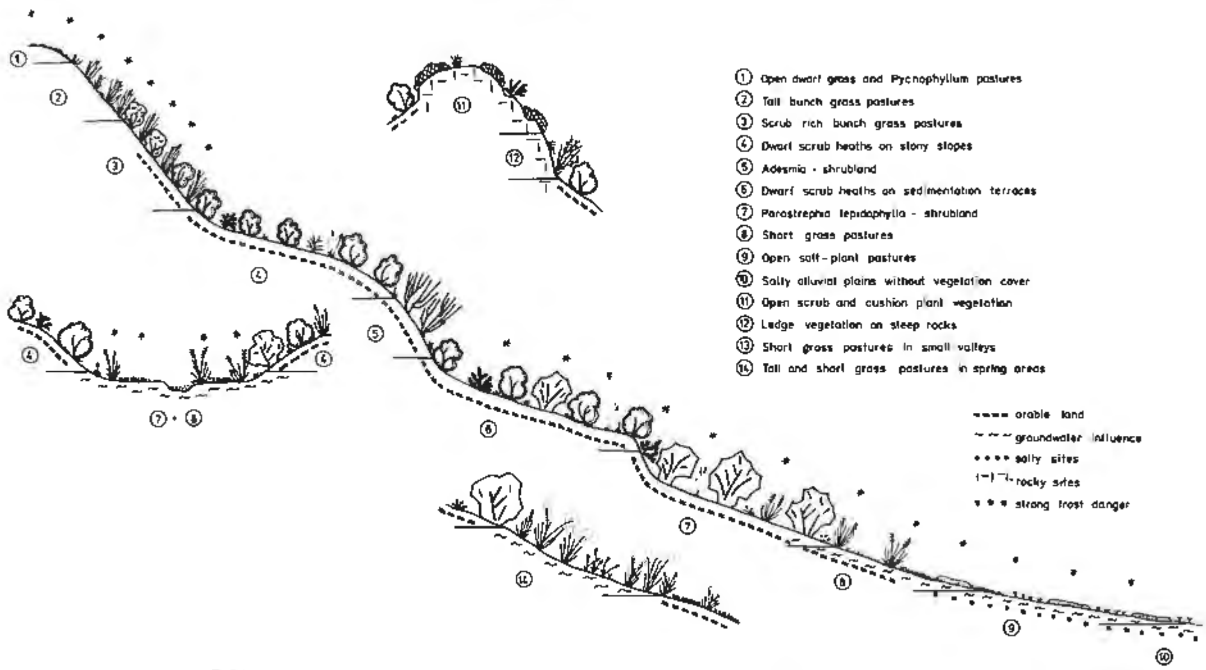


Fig. 9. Main plant communities in the Huaraco region, more or less influenced by agricultural and grazing activities. Common and typical plant species of the vegetation units:

1. Open dwarf grass and *Pycnophyllum*-pastures in the Andine belt. Outside the investigation area on hill tops and plains above 4500 m.

Pycnophyllum tetrastichum Remy	*Calamagrostis minima* (Pilger) Tovar
P. molle Remy	*Poa aequigluma* Tovar
Nototriche div. spec.	*Festuca magellanica* Lam.
Arenaria pycnophylloides Pax.	*Agrostis haenkiana* Hitchc.
Werneria denticulata Blake	and other

2. Tall bunch grass pastures in the Andine belt. Outside the investigation area above 4200 m.

Festuca humilior Nees et Meyen	*Luzula racemosa* Desv.
Poa asperifolia Hack.	*Lepidium meyeni* (Wedd.) Thell.
Stipa hans-meyeri Pilger	*Lupinus conicus* C.P. Sm.
Festuca andicola HBK.	*Werneria apiculata* Sch. Bip.
Scirpus rigidus Boeck.	*Englerocharis peruviana* Muschler a.o.

3. Scrub-rich bunch grass pastures in the sub-Andine belt. List of plant species: see Tab. 1, vegetation units A and B.

4. Dwarf scrub heaths in the foot hill zone. List of plant species: see Tab. 1, vegetation unit D.

5. *Adesmia*-shrubland on steep south-orientated slopes. List of plant species: see Tab. 1, vegetation unit C.

6. Dwarf scrub heaths on old stony sedimentation terraces. List of plant species: see Tab. 1, vegetation unit E.

7. *Parastrephia lepidophylla*-shrubland on young sedimentation terraces and alluvial plains. List of plant species: see Tab. 1, vegetation units F and G.

8. Short grass pastures on the alluvial plain (compare Tab. 1, vegetation units H and I).

Festuca dolichophylla Presl	*Hypochoeris taraxacoides* (Meyen et Walp.) Ball.
Muhlenbergia fastigiata (Presl) Henr.	*Conyza artemisiaefolia* Meyen et Walp.
Azorella diapensioides A. Gray	*C. obtusa* HBK.
Senecio humillimus Sch. Bip.	*Hordeum muticum* Presl
Trifolium amabile HBK.	*Ophioglossum nudicaule* L.
Astragalus micranthellus Wedd.	*Spergularia andina* Rohrb.
Plantago orbignyana Steinh. ex Decne	*Tarasa tenella* (Cav.) Krap.

9. Open salt-plant pastures on the alluvial plain.

Distichlis humilis Phil.	*Baccharis acaulis* (Wedd.) Cabr.
Anthobryum triandrum (Remy) Surgis	*B. juncea* Desf.
Atriplex herzogii Standl.	*Lepidium* spec.
Salicornia pulvinata R.E.Fr.	*Plantago* spec.

cont. Fig. 9.

10. Salty alluvial clay plains, nearly without vegetation cover.

11. Open scrub and cushion plant vegetation on shallow rocky sites.
Azorella compacta Phil.
Stipa hans-meyeri Pilg.
Muehlenbeckia vulcanica (Benth.) Endl.
Hieracium cfr. *eriospaerophorum* Zahn
Silene mandonii (Rohrb.) Bocq.
Stebia spec.
Oreomyrrhis andicola (Lag.) Hook. f.
Belloa cfr. *argentea* (Wedd.) Cabr.
Lobivia spec.
Ephedra americana var. *rupestris* (Benth.) Stapf

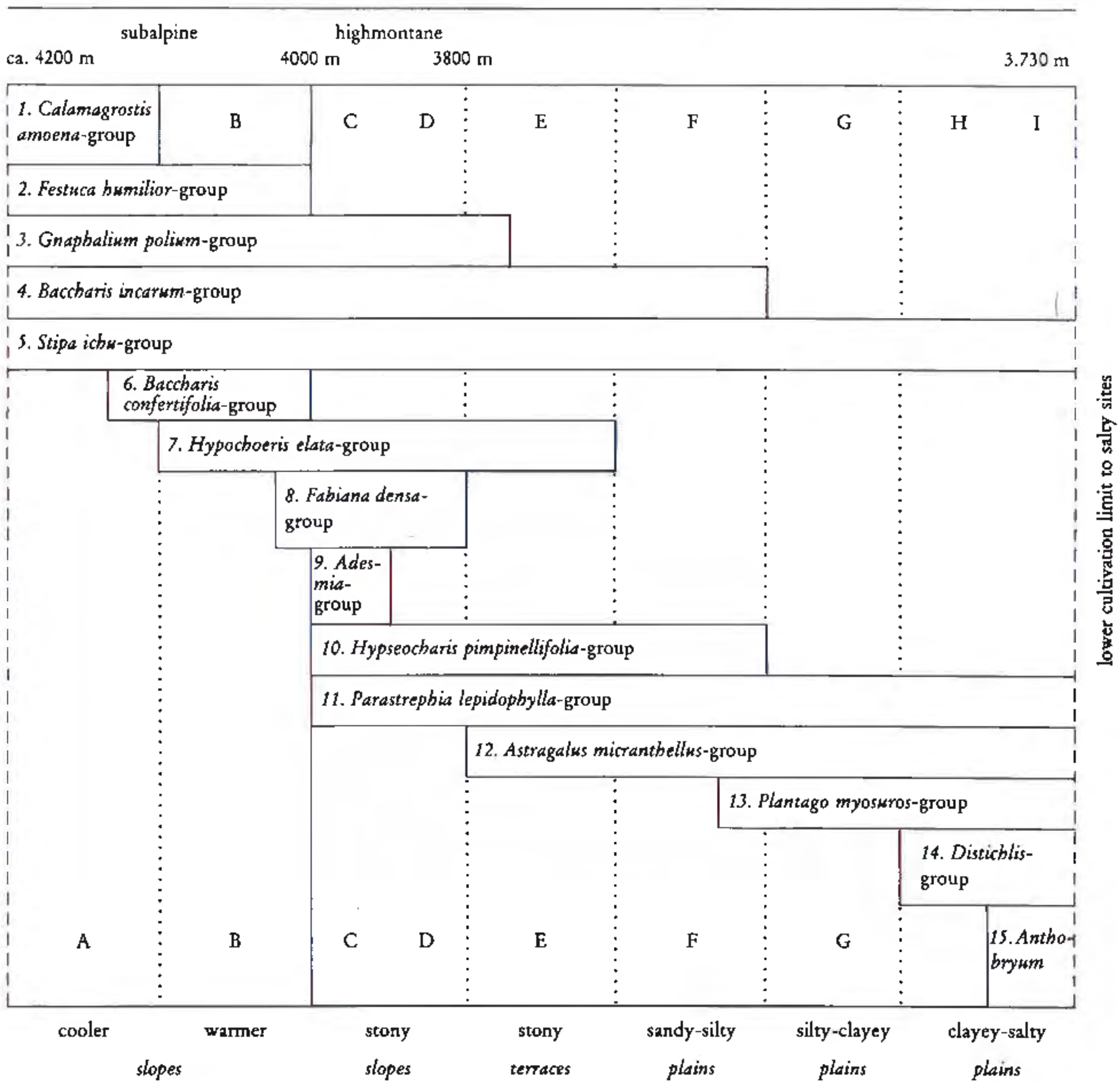
12. Ledge vegetation on steep rocks.
Calceolaria parvifolia Wedd.
Achyrocline ramosissima Britton ex Rusby
Eupatorium azangaroense Sch. Bip. ex Wedd.
Gerardia spec.
Chersodoma candida Phil.
Hedeoma mandoniana Wedd.
Asplenium fragile Presl
Pellaea ternifolia (Cav.) Link
Thelypteris spec.
Woodsia montevidensis (Spreng.) Hieron.
Notholaena nivea (Poir.) Desv.
Wahlenbergia linarioides (Lam.) A.DC.
Bartsia meyeniana Benth.
Bowlesia tropaeolifolia Gill. et Hook.
Crocopsis fulgens Pax.
Peperomia peruviana (Miq.) Dahlst.

13. Short grass pastures in small valleys of the foot hill zone.
Festuca dolichophylla Presl
Muhlenbergia fastigiata (Presl) Henr.
Hordeum muticum Presl
Hypochoeris taraxacoides (Meyen et Walp.) Baker
Lachemilla pinnata (R. et P.) Rothm.
Trifolium amabile HBK.
Plantago tomentosa Lam.

14. Tall and short grass pastures of percolated spring areas ("canchones").
Festuca dolichophylla Presl
Calamagrostis orbignyana (Wedd.) Pilg.
Carex spec.
Hordeum muticum Presl
Muhlenbergia fastigiata (Presl) Henr.
Trifolium amabile HBK.
Azorella diapensioides A. Gray
Lachemilla pinnata (R. et P.) Rothm.
Hypochoeris echegaray Hieron.
Taraxacum officinale Wiggers s. l.
Geranium sessiliflorum Cav.
Eleocharis spec.
Hypsela reniformis (HBK.) Presl
Ranunculus cymbalaria Pursh
Castilleja fissifolia L.f.
Poa glaberrima Tovar
Cotula mexicana (DC.) Cabr.

Fig. 10. Valley of the Huaraco river, looking southward (March 1983), with fertile grounds on the bottom (land-use category 1.1) and relatively productive fields protected from strong frosts on both slopes (land-use categories 2.2 and 2.3). In the background to the right vast flood plains.

Table 1. Characteristic groups of plant species on grazed fallow fields between 4200 and 3700 m in the Highland community of Huaraco and the adjacent plain to the south. A–I: Vegetation and site types. 1–15: Typical species groups.



1. *Calamagrostis amoena* (Pilg.) Pilg., *Parastrephia phyllicaeformis* (Meyen) Cabr., *Werneria apiculata* Sch. Bip., *Scirpus rigidus* Boeck, *Arenaria pycnophylloides* Pax., *Gentiana gayi* Griseb., *Lepidium meyeni* (Wedd.) Thell., *Nototriche* spec., *Perezia pygmaea* Wedd., *Crocopsis fulgens* Pax u. a.

2. *Festuca humilior* Nees et Meyen, *Wahlenbergia peruviana* A. Gray, *Relbunium hirsutum* (R. et P.) K. Schum., *Sisyrinchium* spec., *Luzula racemosa* Desv., *Poa gymnantha* Pilg., *Calamagrostis recta* (HBK.) Trin. ex Steud., *Stipa hans-meyeri* Pilg., *Luzilia violacea* Wedd., *Baccharis alpina* HBK., *Stipa brachyphylla* Hitchc., *Belloa virescens* (Wedd.) Cabr., *Gomphrena meyeniana* Walp., *Englerocharis peruviana* Muschler u. a.

3. *Hypochoeris meyeniana* (Walp.) Griseb., *Gnaphalium polium* Wedd., *Relbunium croceum* (R. et P.) Schum., *Cerastium subspicatum* Wedd., *Quinchamalium chilense* Lam., *Paronychia* div. spec., *Silene mandonii* (Rohrb.) Bocq., *Bartsia meyeniana* Benth., *Belloa subspicata* Wedd., *Bidens andicola* HBK., *Senecio spinosus?*, *Calceolaria parvifolia* Wedd. u. a.

4. *Pentacaena polycnemoides* (Schlecht.) Walp. non Bartl., *Baccharis incarum* Wedd., *Tetraglochin strictum* Poepp., *Conyza deserticola* Phil., *Muhlenbergia peruviana* (Beauv.) Steud., *Plantago sericea* R. et P., *Galinsoga calva* Rusby, *Tagetes multiflora* HBK.

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Land-Use Kathmandu - Kakani Area, Nepal

Geomorphic Damages

HYDROGRAPHY

A) CLASSIFICATION OF NATURAL STREAMS
- small or for other reasons not classifiable
- bed with latent erosion (bed in strong bedrock)
- bed in balance (balanced alternation of erosion and accumulation)
- bed with erosion
- bed with accumulation or rearrangements
- presumed bed condition (in inaccessible areas)

B) ARTIFICIAL STREAMS
- irrigation canal causing recent erosion
- canal diverting water into a damaged area

C) OTHER HYDROGRAPHIC ELEMENTS
- spring
- wet area
- lake, pond
- well
- reservoir

DEPOSITION

A) DEPOSITIONS OF SLIDES
- a) as a compact mass
- b) as boulders:
  - fresh
  - partially weathered
  - partially overgrown
- c) as a debris flow:
  - fresh
  - partially overgrown

B) OTHER ELEMENTS OF DEPOSITION

boulders, weathered in situ:
- fresh
- partially weathered
- partially overgrown

MAN-MADE ELEMENTS

A) DESTRUCTIONS

slope cutting
- a) in clastic material
- b) in highly weathered bedrock
- c) in hardly weathered bedrock
- d) in a, b or c with vegetation

man-made badland (intended terrace construction)

- cattle steps
- defile, sunken path
- gravel pit

B) CONSTRUCTIONS
- check dam
- lateral construction

constructions in rivers

- construction on terraces or roads
- Trisuli Road

EROSION

A) RILL AND GULLY EROSION
- rillwash
- gully active
- badland active (gullying, slope failure etc.)
- badland less than 5 meter deep
- area with rillwash
- gully inactive
- badland inactive
- badland more than 5 meter deep

B) MASS MOVEMENT ALONG CREEKS AND RIVERS

scarp of a slide or a slump caused by lateral corrasion
- a) in clastic material
- b) in highly weathered bedrock
- c) in hardly weathered bedrock
- d) in a, b or c with vegetation

scarp of a slide or a slump caused by vertical cutting
- a) in clastic material
- b) in highly weathered bedrock
- c) in hardly weathered bedrock
- d) in a, b or c with vegetation

C) MASS MOVEMENT ON OPEN SLOPES

scarp of a slide or a slump
- a) in clastic material
- b) in highly weathered bedrock
- c) in hardly weathered bedrock
- d) in a, b or c with vegetation

scarp of a planar slide
- a) in clastic material without vegetation
- b) in clastic material partially with vegetation
- c) in clastic material with vegetation
- d) on bedrock

groups of planar slides
- a) in clastic material without vegetation
- b) in clastic material partially with vegetation
- c) in clastic material with vegetation
- d) on bedrock

confirmed slow mass movement
- a) undefined
- b) shallow (less than 2 m)
- c) deep (more than 2 m)

presumed slow mass movement
- a) undefined
- b) shallow (less than 2 m)
- c) deep (more than 2 m)

rock wall
- a) fresh and continuous
- b) interrupted by slopes covered with vegetation

D) OTHER ELEMENTS OF EROSION
- tensile crack
- damaged irrigable terrace
- damaged non-irrigable terrace
- damaged vegetal cover

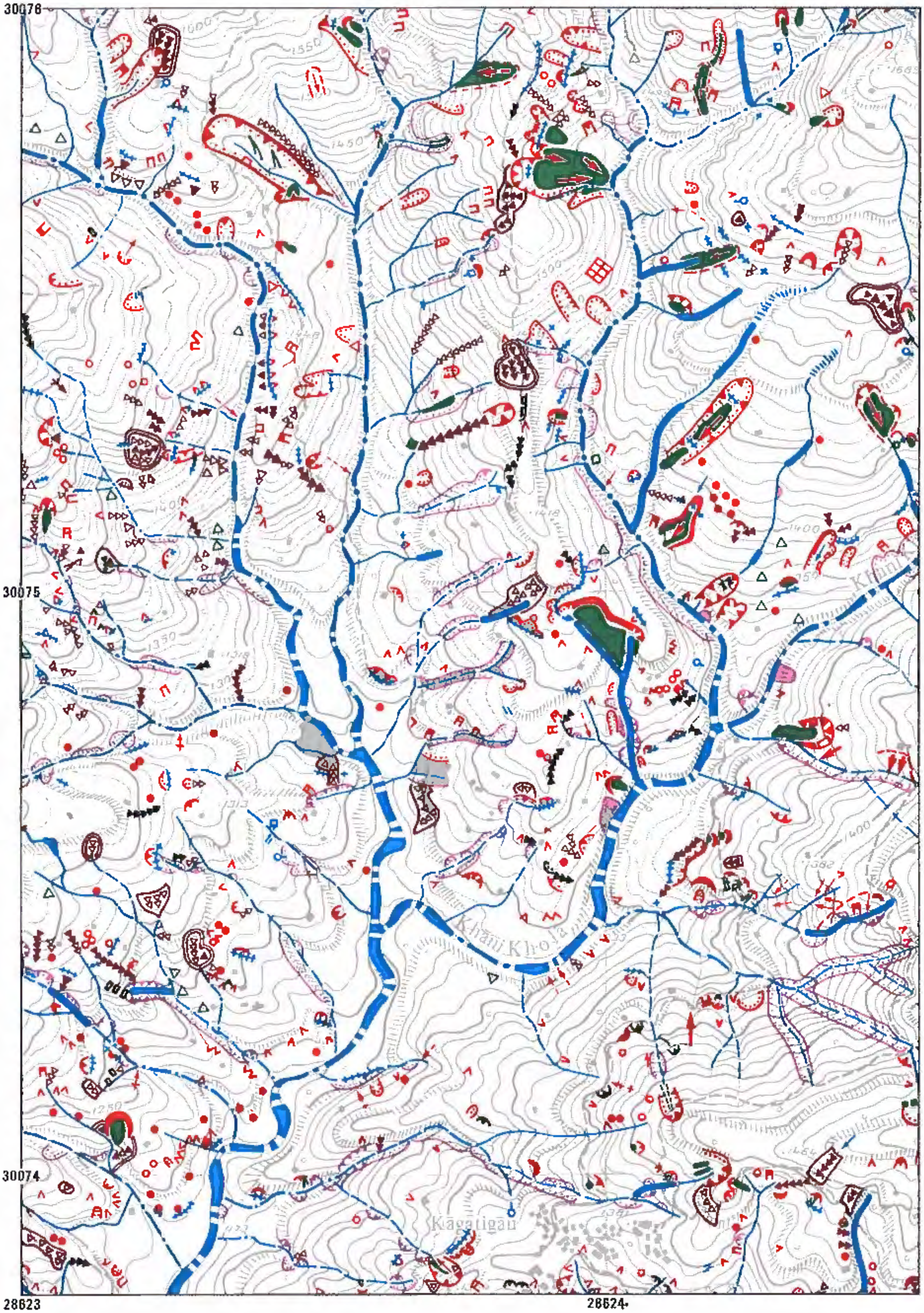
0 200 400 m

Land-Use

Terraced land:
- Irrigable terraces
- Non–irrigable terraces
- Idle terraces

Woodland:
- Shrubland (heigh less than 3 m)
- Deciduous or coniferous forest

- Pasture and grassland
- Barren land
- Mosaic of different land-use types
- Streams ,roads and industrial area



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Geomorphic Damages Kathmandu–Kakani Area, Nepal

Fig. 11. 7 to 10 year old fallow field with *Stipa ichu* and *Baccharis incarum* plants, north of the main road from La Paz to Oruro (land-use category 2.3). The former furrows of the field are still perceptible. In the background the Cielo Pata mountain south of Sica Sica.

cont. Table 1.

5. *Stipa ichu* (R. et P.) Kunth, *Stipa imconspicua* Presl, *Trifolium amabile* HBK., *Agrostis gelida* Trin., *Stipa depauperata* Pilg., *Heterosperma nana* Nutt. et Sherff, *Gamochaeta erythractis* (Wedd.) Cabr., *Facelis plumosa* (Wedd.) Sch. Bip., *Gnaphalium* cf. *calviceps*, *Cyperus andinus* Palla ex Kükenth., *Oenothera punae* O. Ktze., *Festuca orthophylla* Pilg.
6. *Baccharis papillosa* Rusby, *Hieracium* cf. *eriosphaerophorum* Zahn, *Azorella compacta* Phil., *Cheilanthus pruinata* Kaulf., *Poa asperiflora* Hack., *Hedeoma mandoniana* Wedd., *Silene* aff. *genovevae* Bocq., *Eupatorium azangaroense* Sch. Bip. ex Wedd., *Calandrinia acaulis* HBK., *Gerardia* spec.
7. *Adesmia vicina* MacBride, *Bromus unioloides* HBK., *Hypochoeris elata* (Wedd.) Griseb., *Bidens pseudocosmos* Sherff, *Sisyrinchium* spec., *Verbena microphylla* HBK. u. a.
8. *Fabiana densa* Remy, *Poa buchtienii* Hack., *Eragrostis* cf. *lugens* Nees, *Stipa mucronata* HBK., *Mutisia orbignyana* Wedd., *M. ledifolia* Decne. ex Wedd., *Zephyranthes* spec., *Lobivia* div. spec.
9. *Adesmia miraflorensis* Remy, *Opuntia* spec., *Clematis millifoliata* Eichl., *Chaptalia similis* R. E. Fries.
10. *Erodium cicutarium* (L.) L'Hérit. ex Ait., *Hypseocharis pimpinellifolia* Remy, *Baccharis incarum*-Verjüngung, *Aristida asplundii* Henrard, *Crassula* spec.
11. *Parastrephia lepidophylla* (Wedd.) Cabr., *Oxalis bisfracta* Turcz, *Bouteloua simplex* Lag., *Schkuhria multiflora* Hook. et Arn., *Astragalus garbancillo* Cav., *Conyza artemisiaefolia* Meyen et Walp., *Tarasa* cf. *tenella* (Cav.) Krapovickas, *Festuca dolichophylla* Presl.
12. *Gnaphalium badium* Wedd., *Junellia minima* (Meyen) Moldenke, *Astragalus micranthellus* Wedd., *Muhlenbergia fastigiata* (Presl) Henr., *Ophioglossum nudicaule* (Metf.) Clausen, *Gilia laciniata* R. et P.
13. *Plantago myosuros* Lam., *Plagiobotrys congestus* (Wedd.) J. M. Johnst., *Spergularia andina* Rohrb.
14. *Distichlis humilis* Phil.
15. *Atriplex herzogii* Standl., *Anthobryum triandrum* (Remy) Surgis.

Table 2. Chemical soil characteristics* of six agricultural sites in the Huaraco area between 4200 m and 3700 m above sea level. The figures are mean values of four different old fallow stages. The chemical analysis have been carried out according to standard methods by the "Landes-Lehr- und Versuchsanstalt, Trier", under the direction of Dr. Walter. Site locations: Fig. 1.

sample sites m above sea level		depth cm	C %	N %	C/N	pH (KCl)	P_2O_5 **	K_2O **	Mg **	Na **	Cl **	SO_4 **	Bor ppm
1	*Chili:* andine	0–15	1.40	0.09	22.6	5.1	3	11	8	3.2	1.8	0.1	0.4
	grass belt (4180m)	15–30	1.60	0.10	18.1	5.1	2	6	8	2.7	1.5	0.1	0.8
2	*Pakkota:* plateau	0–15	1.17	0.11	11.0	5.2	3	35	10	1.4	1.2	2.0	0.9
	of the hills (4000 m)	15–30	0.69	0.09	5.5	5.5	2	22	13	1.7	0.6	2.1	0.9
3a	*Huaraco:*	0–15	0.68	0.10	7.2	5.6	3	26	17	0.5	1.8	0.2	1.3
	hill tops (3850 m)	15–30	0.38	0.06	7.0	5.6	2	19	18	0.8	1.8	0.1	1.0
3b	*Huaraco:* depression	0–15	1.05	0.15	7.3	5.6	2	30	31	1.2	1.8	0.2	1.7
	between hills (3850 m)	15–30	0.75	0.11	7.2	5.5	1	30	40	3.7	1.8	0.1	2.1
4	*Huaraco:* stony	0–15	1.27	0.11	11.4	5.3	4	38	18	0.9	1.8	0.3	0.7
	sediment-plain (3800 m)	15–30	0.54	0.07	7.8	5.7	2	18	23	1.4	1.3	0.2	0.8
5	*Antipampa:*	0–15	0.51	0.06	8.9	7.1	7	27	28	27.0	7.1	15.5	4.4
	alluvial plain (3750 m)	15–30	0.52	0.05	10.7	7.7	9	18	36	40.4	9.7	13.5	8.7
6	*Antipampa:*	0–15	0.57	0.07	8.6	7.5	9	32	28	27.7	7.1	16.7	4.9
	alluvial plain (3720 m)	15–30	0.46	0.05	8.7	7.6	16	26	29	116.6	13.0	16.8	20.4

* Analytical methods: Total C = Wet oxydation with $K_2Cr_2O_7$ followed by a colorimetric determination. Total N = Kjeldahl. pH = in n/10 KCl. Exchangeable P and K = Extraction with Ca-lactate and colorimetric determination as molybdate/vanadate-P complex. Exchangable Mg = Extraction with $CaCl_2$ and colorimetric determination as Mg-titane yellow complex. Exchangable Na = Extraction with n/10 HCl and determination of the Na-content in a flame-photometer. Cl = Extraction with water and titration with $AgNO_3$ against K_2CrO_4 as an indicator. SO_4 = Extraction with 1% NaCl, precipitation with 10% $BaCl_2$ and determination of the turbidness with a photometer or by weighting the precipitate. Bor = Extraction with hot water and colorimetric determination with carmine.

** mg/100 g.

analysed with regard to their nutrient content. The average values drawn from two to four samples are compiled in Tables 2 and 3.

Apart from the soils of the lower floodplains (sites 5 and 6), which are influenced by salty groundwater, the pH-values in the hill soils and those at their bases are between 5 and 6, or relatively favourable. With the exception of the Andean grass belt at 4180 m above sea level, where the breakdown of the organic substance is limited by climatic factors, the carbon and nitrogen content is extremely low and the C/N-ratios are usually very narrow. The nitrogen level could therefore certainly be an important minimum factor. At least as deficient is phosphorus, a fact which is generally known (COCHRANE, 1973; SALM, 1983). On the other hand, the base content of the soils is relatively favourable with the exception of Calcium. This fact is in connection with the potassium of great meaning for the cultivation of potatoes. All in all, the portion of exchangeable bases is altogether not very high (40 to 60%).

The question pertaining to the effectiveness of the fallow years in regard to the lasting production capacity of the farm soils remains unanswered. Usually the following advantages have been ascribed to the fallow periods:

Table 3. Exchangeable bases* of six agricultural sites in the Huaraco study area. The figures are mean values of four different old fallow stages. Location of the sample sites: Fig. 1.

sample sites m above sea level		depth cm	K	mval/100 g dry soil: Na	Ca	Mg	T-value	S-value	% V-value
1	*Chili:* andine grass belt (4180 m)	0–15	0.16	0.50	1.88	0.49	12.40	3.03	24.2
		15–30	0.01	0.95	1.67	0.69	16.06	3.32	22.5
2	*Pakkota:* plateau of the hills (4000 m)	0–15	0.94	0.76	2.46	0.80	8.40	4.97	59.5
		15–30	0.61	0.69	3.44	1.06	8.15	5.80	72.8
3 a	*Huaraco:* hill tops (3850 m)	0–15	0.50	0.88	3.37	2.36	17.70	7.10	40.5
		15–30	0.46	0.57	4.85	2.98	21.55	8.85	42.1
3 b	*Huaraco:* depression between hills (3850 m)	0–15	0.62	0.53	2.74	1.34	9.13	5.23	56.9
		15–30	0.36	0.64	3.42	1.69	10.59	6.10	57.5
4	*Huaraco:* stony sediment-plain (3800 m)	0–15	0.82	0.67	2.87	1.37	12.50	5.72	47.1
		15–30	0.32	0.75	4.38	1.90	13.60	7.35	55.9
5	*Antipampa:* alluvial plain (3750 m)	0–15	0.63	2.02	4.57	2.19	12.41	9.42	81.2
		15–30	0.33	2.64	4.95	2.95	14.78	10.86	77.5
6	*Antipampa:* alluvial plain (3720 m)	0–15	0.69	2.24	9.04	2.55	31.75	14.53	47.5
		15–30	0.53	8.40	6.89	1.81	29.70	17.64	54.3

* Analytical methods: Extraction with 5% $BaCl_2$. Determination of K, Na and Ca in the extract with a flame-photometer and of Mg with an AAS. T-value = Total exchange capacity of cations in mval. S-value = Sum of the analyzed cations in mval. V-value = % of S-value from the T-value.

1. Enrichment of organic material in the soil, and consequently the improvement of water-holding capacity and soil structure, as well as enhanced supply of mineral nitrogen.
2. Storing of precipitation in the soil profile.
3. Mobilization of mineral nutrients from deeper soil layers by deep-rooted plants and weathering processes.
4. Dying-out of the long-lived stages of plant pathogens.

All of these processes are conceivable; however, none of them has actually been proven. Comparative soil analyses of fallow lands of varying ages (RUTHSATZ, unpublished) indicate a tendency towards a certain degree of enrichment with organic material and therefore a possibility of short-term improvement in the N-supply in freshly broken ground. Since the fallow lands are, however, continuously and intensively grazed, the plant cover can neither above nor below ground strongly develop, so that the nitrogen replenishing effect cannot be too great and, above all, cannot be effective over a long-term period.

The storage of precipitation input during the fallow years likewise could not be too effective, since the constant grazing and damage to the vegetation subsequently leads to instinct compactation and, after heavy rain storms, to the loss of topsoil, such that the overland flow is considerable (SALM, 1983). Moreover, only one or two rainy seasons would be necessary to fill the soil to its maximum water-holding capacity, as most of the soils can only take up and maintain small amounts through the dry season. Regarding long-lived stages of parasites, e.g. Nematodes, up until now no positive evidences have been recorded. Nevertheless, the farmers of the Highlands consider the fallow a soil-fertility measure.

Fig. 12. Southeast facing slopes of the Janthaloma mountain (March 1980). The trend to abandon the farmland with increasing hight and inclination of the slope is obvious (land-use categories from below to above: 3.4; 4.2; 4.4). On the upper slope very old field terraces are still visible.

5. Suggestions for the Improvement of the Land-Use

The greatest problem for the long-lasting productivity of the soils on the semi-arid Highlands is the intense soil-erosion as a consequence of the present land-use methods. To limit these, while guaranteeing the growing population better yields without large investments is not a simple task. A number of scientists have already tried to come to terms with this (PRESTON, 1973, 1974; BECK und ELLENBERG, 1977; LEBARON et al., 1979; ELLENBERG, 1981; TAPIA, 1982). Above all, it would not be easy to motivate the extremely tradition-bound Highland peoples to change their life-styles, since they have already had less than encouraging experiences with similar proposals. For the community of Huaraco and comparable regions in the semi-arid portion of the Highlands, the following reforms may promise some success:

5.1. Separation of Intensely Used Farmland and Public, Unregulated Pasture Land

Grazing should be regulated according to the various habitats in the community area in order to achieve a lasting performance as well as to reduce soil erosion. If the fallow years are to have a soil-improving effect, then the resting fields should not be overgrazed year round. Grazing compacts the upper layers of the soil, it makes it difficult for the water to infiltrate, it regularly wounds the soil surface and consequently creates starting points for water erosion, and it hinders the vegetation from covering the soil surface and densely rooting the soil. Overgrazing can limit the enrichment of organic material and the improvement of living conditions for the soil organisms. The unhampered grazing of all community lands including the fallow areas is one of the principal causes for the ubiquitous soil erosion and the deficient production capabilities of the pasture lands. The herd sizes and grazing rights were regulated by the old Aymara and Inca cultures as well as under the government of the Spanish land owners (MURRA, 1965; MONHEIM, 1966). At that time there was already erosion damage, but probably not to the degree observed today.

Fig. 13. Southeast facing slope of the Wacani mountain (October 1982) in the very south of the study area with 5 to 7 and more than 15 year old fallow land. The walls and mounds of gathered stones are defining the property limits (land-use category 3.8).

To compensate for the necessary restriction of the grazing on fallow land, especially during the dry season, new solutions must be found. Conceivable enhancement efforts could include:

1. Cultivation of alfalfa on the better farmland during the fallow period.
2. Preservation of the more productive grassland for dry-season grazing or fodder harvesting.
3. If possible, irrigation of alfalfa and productive grassland.
4. Selection, breeding and cultivation of indigenous fodder plants on the fallow land instead of unregulated succession development.

5.2. Improvement of Farming Techniques

A community which does not possess extensive and productive pasture land, but, on the other hand, owns relatively frost-protected, moderately fertile agricultural ground should concentrate on improving the latter. Ways in which this can be done include the following:

1. Increasing the organic fertilization (manuring) and moderate mineral fertilization, especially with phosphorus.
2. Including the cultivation of legumes (e.g. Lupine) with the usual crop rotation sequence.
3. In as much as it is possible, occasional watering of the fields in the valley grounds.
4. Construction or repair of agricultural terraces and supporting walls on slope locations.
5. No expanding or combining of fields.
6. Maintenance of habitat-specific plant varieties within crop plants.
7. Maintenance of the traditional soil-preserving ploughing method.
8. Consistent measures against the most important plant diseases and pathogens.

The most important goal of all these measures should be the lasting improvement of the fertility of the farmland through reduction of erosion and favouring of the humus accumulation of the soils. Suitable

Fig. 14. Vast flood plain near Antipampa with short grass pastures for sheep and llamas (land-use category 5.3). The small cushions of *Anthobryum triandrum* indicate the influence of salt-rich groundwater (March 1980).

rotation crops ("Zwischenfrüchte") and sufficient mineral fertilization to compensate for losses could eventually lead to a sharp decrease in the number of fallow years required, or even render them superfluous as well as allow the farming to be limited to the most favourable habitats.

Summary

The Highlands of Bolivia have been exploited by man in a variety of ways for thousands of years. The chosen community of Huaraco is situated south to Sica Sica near the main road from La Paz to Oruro. It makes a good example for the semi-arid portion of the Highland. The study area ranges from high mountains of 4500 m in elevation down to the vast flood plain in the central valley of the Desaguadero river at 3730 m above sea level. As many others, the village of Huaraco is located just where the first hills rise from the plain beside a small temporary dry river. The summer rains (350 to 400 mm/year) are quite irregular but still allow farming without irrigation. The people live on potatoes, barley and the Andean cereal "quinoa" as well as some native tuber plants. The farming methods are still based on old Aymara traditions, to some extent modified by the Spaniards. Their characteristics are: Cultivation in common "Zelgen", crop rotation of 3 to 4 years, followed by 7 to 15 and more years of fallow, and tilling of the fields with primitive wooden, hooked plows, pulled by bulls. Besides farming the breeding of sheep and some llamas is necessary. The herds are grazing without any restriction on native pastures and fallow land all the year round.

The objectives of the investigation were to analyse the interrelations between site conditions, vegetation cover, the aptitude for usage alternatives and actual land-use as well as their reactions on soils and plants. For that purpose the following measurements were carried out:

1. Description and classification of the more frequent plant communities.
2. Analysis of the interdependency between vegetation mosaics and site conditions.
3. Investigation of the farming and breeding customs of the local population.
4. Compilation of the usual "calendario agricola" of the crop plants.
5. Chemical analysis of soil samples from typical farming areas with respect to their nutrient content.
6. Mapping of the actual land-use categories and their interpretation for the use-aptitudes of the different sites.

The results demonstrate that, besides dry and frost periods, especially P- and N-deficiencies in the soil are a main minimum-factor for crop yields. The unregulated and year-round intensive grazing of fallow and pasture land blocks a sufficient regeneration of the vegetation cover and of soil fertility. As a consequence many sites are degraded in a probably irreversal way by heavy soil erosion.

This process could be at least restrained by some changes in the farming and grazing habits. To that end a list of proposals is presented.

References

BAKER, P. T. and M. A. LITTLE (Eds., 1976): Man in the Andes. A multidisciplinary study of high-altitude Quechua. US/IBP Synthesis Series 1. Stroudsburg, Pennsylvania.

BECK, S. und H. ELLENBERG (1977): Entwicklungsmöglichkeiten im Andenhochland in ökologischer Sicht. Studie im Auftrag d. BMZ. Göttingen.

BROWMAN, D. L. (1974): Pastoral nomadism in the Andes. Current Anthrop., 15, 188–196.

BRUSH, S. B. (1982): The natural and human environment of the Central Andes. Mountain Research and Development, 2, 1, 19–28.

COCHRANE, T. T. (1973): El potencial agrícola del uso de la tierra de Bolivia: Un mapa de sistemas de tierra. La Paz.

DOLLFUS, O. (1981): El reto del espacio andino. Peru problema, 20. Instituto de Estudios Peruanos, Lima.

ELLENBERG, H. (1979): Man's influence on tropical mountain ecosystems in South America. J. of Ecology, 67, 401–416.

– (1981): Desarrollar sin destruir. Respuestas de Agrónomos y Planificadores Bolivianos. Inst. de Ecología, UMSA, La Paz.

FISEL U. y W. HANAGARTH (1983): Estudio ecológico en una communidad del Altiplano boliviano. Descripción de las interrelaciones físico- y económico-geográficas. Revista del Instituto de Ecología, UMSA, La Paz, No. 4, 1–17.

– und B. RUTHSATZ: Die Vegetationsdecke einer bolivianischen Hochlandgemeinde und ihre Nutzung durch den Menschen (in preparation).

GUILLET, D. (1981): Agrarian Ecology and Peasant Production in the Central Andes. Mountain Research and Development, 1 (1), 19–28.

HANAGARTH, W. und U. FISEL (1983): Ökologische Forschung in der Puna des bolivianischen Altiplano – Ein Überblick. Verh. d. Ges. f. Ökologie, XI, 185–193.

IBARRA GRASSO, D. E. (1955): Esquema de la arqueología boliviana. Zeitschrift f. Ethnologie, Bd. 80–81, H. 2, 192–199.

LEBARON, A., L. K. BOND, S. P. AITKEN and L. MICHAEL sen. (1979): An explanation of the Bolivian highlands grazing-erosion syndrome. J. of Range Management, 32 (3), 201–208.

LOZA BALSA, G. (1972): Acerca de la Agricultura aymara. Pumapunku, 4, La Paz, 71–76.

LUMBRERAS, L. G. (1967): La Alimentación vegetal en los origines de la civilización andina. Peru indigena, 26, Lima, 254–273.

MACEWAN, W. J. (1969): Changing rural Bolivia. A Study of Social and Political Organization and the Potential for Development in Six Contrasting Communities. (Peace Corps Rism Bolivia Project) Research Institute for the Study of Man.

MÉTRAUX, A. (1935–36): Les Indiens Uro-Chipaya de Carangas. Journal de la Société des Américanistes, 27, 111–128; 28, 155–207.

MONHEIM, F. (1966): Studien zur Haziendawirtschaft des Titicaca-Beckens. Heidelberger Studien zur Kulturgeographie, H. 15, Wiesbaden, 133–163.

MURRA, J. V. (1965): Herds and herders in the Inca State. In: LEEDS, A. and A. P. VAYDA (Eds.): Man, Culture and Animals. AAAS. Washington, D.C., 185–215.

NACHTIGALL, H. (1965): Beiträge zur Kultur der indianischen Lama-Züchter der Puna de Atacama (Nordwest-Argentinien). Zeitschr. f. Ethnologie, 90, 184–218.

NUÑEZ, L. (1970): La agricultura prehistórica en los Andes meridionales. Edición Universidad del Norte, Chile.

PONCE SANGINÉS, C. (1970): Las culturas Wankarani y Chiripa y su relación con Tiwanacu. Acad. Nac. de Cienc. de Bolivia, No. 25, La Paz, 1–78.

PRESTON, D.-A. (1973): L'agriculture dans un désert d'altitude: l'Altiplano central de Bolivie. Les Cahiers d'Outre-Mer, 102, 26. Année, 113–128.

– (1974): Land Tenure and Agricultural Development in the Central Altiplano, Bolivia. In: HOYLE, B. S. (Ed.): Spatial Aspects of Development. London.

RUBIO PINILLOS, G. y J. DURÁN BEJERANO (1980): Tecnología apropiada para la muyer campesina de comunidades del Altiplano, Valle y Yungas paceños. La Paz.

RUTHSATZ, B. (1983): Der Einfluß des Menschen auf die Vegetation und Standorte arider tropischer Hochgebirge am Beispiel der Hochanden. Ber. dt. Botan. Ges., 96, 535–576.

SALM, H. (1983): Estudio preliminar de suelos del altiplano central de Bolivia. Revista del Instituto de Ecología, UMSA, La Paz, No. 4, 43–57.

SÁNCHEZ-ALBORNOZ, N. (1973): La población de América Latina desde los tiempos precolombinos al año 2000. Madrid.

SMITH, C. T. (1970): Depopulation of the Central Andes in the 16th century. Current Anthropology, 11, 453–464.

SORIA LENS, L. (1954): La ciencia agricola de los antiguos Aymaras. Boletin de la Sociedad Geográfica de La Paz, Jg. 64, 85–99.

TAPIA, M. (1982): El medio, los cultivos y los sistemas agrícolas en los Andes del sur del Peru. Cusco.

TERRAZAS URQUIDI, W. (1973): Bolivia, País saqueado. La Paz.

TROLL, C. (1968): The Cordilleras of the Tropical Americas. Aspects of climatic, phytogeographical and agrarian ecology. Coll. Geographicum, Bd. 9, Bonn, 15–56.

WEBSTER, St. (1973): Native Pastoralism in the South Andes. Ethnology, 12, 2, Pittsburgh, 115–133.

WENNERGREN, B. and M. D. WHITAKER (1975): The status of Bolivian Agriculture. New York, Washington, London.

Discussion to the Paper Ruthsatz

Prof. Dr. W. Lauer:

Which are the areas of origin of the secondary vegetation mapped out by you?

Prof. Dr. B. Ruthsatz:

Most of the plant species now frequent on fields and fallow land are indigenous of the Bolivian highlands. The few neophytic species from other continents, such as *Brassica rapa, Poa annua, Capsella bursa-pastoris* etc. from Europe are restricted to disturbed or cultivated areas. Many of the weeds from arable fields are natives of temporary dry river beds and flat plains, inundated during the summer, when erosion especially by water and sometimes by wind disturbs the vegetation cover. These weeds disappear more or less rapidly after cultivation stops. We neither know how the original vegetauon was composed, nor can we estimate the pasture pressure by the wild camelids and rodents. But one can observe some phenomena, which perhaps in oue way or another are informative:

1. Plants and plant communities on mountain slopes climb several ten meters higher on old fallow land than on undisturbed sites. This means that plants of the actual vegetation may be native to similar sites but at 50–100 m lower in altitude.
2. From vegetation changes in areas which have occasionally been protected from grazing and browsing by domestic animals during several years, one can deduce that especially grasses and herbs are suffering from pasture activities favouring indirectly dwarf shrubs and cushion plants. The invasion of herbaceous vegetation in nonpastured areas is the more obvious the more fertile – in terms of nutrients and water – the sites are. This is correct at least for the first succession stages (15–30 years). Perhaps several of the woody pasture-resistant species are natives from shallow and dry slope sites and invaded the heavily browsed plains only at the expense of the better fodder plants.

Prof. Dr. E. Löffler:

What is the origin of soil oversalting, and is it connected with the groundwater level? If so, would the irrigation of the valley floors lead to a rising of the groundwater level and thus to an increasing danger of soil oversalting?

Prof. Dr. B. Ruthsatz:

The salt content of the soils on the lower flood plain in the surroundings of Antipampa is the result of the contact to salty groundwater ascending in the clayey material. During rainy summers the salt content in the upper layers declines, but during the dry season salt crusts can be formed on the surface.

The Huaraco river carries too little water to be used for the irrigation of large areas. But some probably pre-Spanish canals prove the restricted application of field watering for yield improvement. The upper part of the valley has water without high salt concentrations, that can be used to some extent.

Prof. Dr. P. Höllermann:

Which are the criteria for distinguishing between high montane and sub-Andean in the study area?

Prof. Dr. B. Ruthsatz:

The limit between the oreal (high montane) and the sub-Andean vegetation belt ranges from about 4000 m to 4200 m. It corresponds more or less to the upper limit of the agricultural activities and can be clearly defined floristically (see Table 1). Several shrub species just end here at their upper distribution limit, as f.e. *Fabiana densa.* Others reach here their lower limit like some bunch grasses, f.e. *Festuca humilior.*

Dr. C. Schubert:

In this paper, as in others presented during the past 2 days, I have heard repeatedly workers use the terms "winter" and "summer" for tropical regions. I would like to propose that we finally refrain from using these terms in the tropics because they make no sense. There are no seasons in the sense of the temperature regions in the tropics.

Prof. Dr. B. Ruthsatz:

"Winter" in the extra-tropics refers to a cold and less sunny season, when most of the plant species interrupt their growing period. „Summer", on the contrary, means the season with optimal vegetative and generative development for most of the plants because of high temperatures and light intensities as well as good water supply. In the Andean Highlands of Bolivia very marked wet and dry seasons exist from November to April and May to October, respectively. Although the dry period is the more sunny one, it is also the colder one because of regularly occuring intense night frosts. The rhythm of plant growth is in great part regulated by mean and threshold temperatures. With very few exceptions all plant species of the highlands interrupt their growing period during the dry and cold season. Many of them do so before the soil is really dry only reacting to temperature. Therefore, I think it reasonable to use the terms „summer" for the growing and "winter" for the resting period as well in the subtropical Andean Highlands south to the Titicaca Lake.

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Tropical Glacier and Climate Variations

Stefan Hastenrath

With 10 Figures

Abstract

The glaciers in the high mountain regions of the tropics are extremely sensitive, albeit complex indicators of long-term climatic change. Historical evidence of glacier variations is limited to the four most recent decades for New Guinea; sources extend to the end of the last century for East Africa and the Northern Andes; but for the equatorial Andes documentation covers half a millenium. A monotonic recession since the beginning of records is borne out for New Guinea, East Africa, and the Northern Andes; for the equatorial Andes there are indications for the ice retreat to have started in the first half of the 19th century.

A central task in climate reconstruction is the inference of the climatic forcing which has brought about the glacier response. A sensitivity analysis shows that glaciers are particularly responsive even to small changes in surface albedo and cloudiness, less to temperature variations, and least to changes in solid precipitation.

The following two independent approaches are being used to construct climatic history from field observations on tropical glaciers:

a) Analyses of microparticle content, oxygen isotope ratios, and gross beta activity performed on ice cores retrieved from the Quelccaya Ice Cap, Peru, and Lewis Glacier, Mount Kenya, offer the prospect of a net balance chronology.

b) For Lewis Glacier, Mount Kenya, measurements of current net balance, kinematics, and morphology, serve as input to numerical modelling of the ice dynamics, geared at simulating the observed long-term glacier behavior. An abrupt precipitation decrease in the latter part of the 19th, and temperature change in the course of the 20th century are identified as the climatic forcings of the continuing glacier recession.

1. Introduction

An abundance of geomorphic evidence attests to a formerly much larger ice extent in various mountain regions of the tropics, including some that are presently not glaciated, such as the Central American Cordilleras, the Ethiopian highlands, Borneo, and Hawaii. The Pleistocene to early Holocene glaciations are the subject of other contributions to this symposium. At present, glaciers near the Equator still exist in three regions of the World: East Africa, New Guinea, and the South American Andes. Tropical glaciers are extremely sensitive – albeit complex – indicators of climate variations. The translations of glacier observations into climatic history remains a fundamental task.

In the following, I will first review the recent glacier variations in the tropics, and then I will sketch two independent approaches that are being developed to infer a climatic history from glacier observations. The present written version of the symposium lecture is intended as a source of reference. It draws on the numerous original publications listed in the bibliography.

2. Tropical Glacier Inventory and Recent Glacier Variations

International efforts directed at global environmental monitoring and the physical causes of long-term climatic change have recognized the study of glaciers as a task of high priority (UNESCO, 1970; World Meteorological Organization, 1980; World Meteorological Organization-ICSU, 1975, pp. 7, 11, 60; International Association of Hydrological Sciences – UNESCO, 1977; Temporary Technical Secretariat for World Glacier Inventory of IUGG-ICSI-UNESCO, 1977; United Nations Environment Programme, 1979; United Nations Environment Programme – World Meteorological Organization, 1982). For the low latitudes, inventories of existing glaciers and systematic compilations of fluctuations in ice extent are just being initiated (International Association of Hydrological Sciences-UNESCO, 1977; Temporary Technical Secretariat for World Glacier Inventory of IUGG-ICSI-UNESCO, 1977; United Nations Environment Programme – World Meteorological Organization, 1982; HOPE et al., 1976).

The modern ice distribution in the Ecuadorian Andes and on Kilimanjaro, Mount Kenya, and in the Ruwenzori in East Africa has been assessed from field observations and the evaluation of air photographs and topographic maps. On this basis, I provided the Ecuador, Tanzania, Kenya, Uganda, and Zaire contributions to the World Glacier Inventory, at the request of the Temporary Technical Secretariat for World Glacier Inventory of IUGG-ICSI-UNESCO. Based on a variety of historical sources and observations in the terrain I reconstructed the secular glacier variations since the 1500's for the Ecuadorian Andes, and since the latter part of the 19th century for East Africa. In accordance with a request by the Permanent Secretariat for Glacier Fluctuations of IUGG-ICSI-UNESCO, I contributed pertinent results for publication (HASTENRATH, 1977). For the Ecuadorian Andes, the modern ice extent, glacier variations in historical times, and evidence on pleistocene and early holocene glaciations are presented in a recent book (HASTENRATH, 1981 a). A monograph on the glaciers of equatorial East Africa is in preparation (HASTENRATH, 1983). Recent ice extent and glacier variations in New Guinea are described in HOPE et al. (1976). Glacier inventories for various regions of the tropical Andes are also being compiled under the auspices of the Temporary Technical Secretariat for World Glacier Inventory of IUGG-ICSI-UNESCO.

At the three presently glaciated mountains of East Africa, Kilimanjaro, Ruwenzori, and Mount Kenya, a drastic and monotonic ice recession is documented from the earliest observations in the latter part of the 19th century to the present (HASTENRATH, 1975, 1983). A detailed reconstruction of terminus history was possible for Mount Kenya, where a relatively abundant historical documentation is available, as well as an excellent topographic base map at scale 1 : 5 000 (Forschungsunternehmen Nepal-Himalaya, 1967). Lewis Glacier in particular is now the ice body with the most complete historical documentation in all of the tropics.

The ice-capped Mount Carstensz (Jaya) in Western New Guinea (HOPE et al., 1976) was first sighted in 1623, but this report was disbelieved until around 1900. The peak region was first reached in 1912, and visits since then have remained rare (HOPE et al., 1976). A drastic and monotonic ice retreat is borne out from the 1930's to the 1970's.

The existence of snow and ice in the equatorial Andes was known since the 1500's and historical accounts extend over more than four centuries (HASTENRATH, 1981 a). The earliest sources are the municipal and church records from the era of Spanish colonization. These indicate a much larger ice extent than at present. The French Academicians BOUGUER and LA CONDAMINE worked in Ecuador in the mid 1700's, with the aim of measuring the first three degrees of the meridian. Their books are not only classics in geodesy, but they also contain useful observations on ice conditions, indicating a much lower ice equilibrium line than at present. Alexander VON HUMBOLDT visited the country at the beginning of the

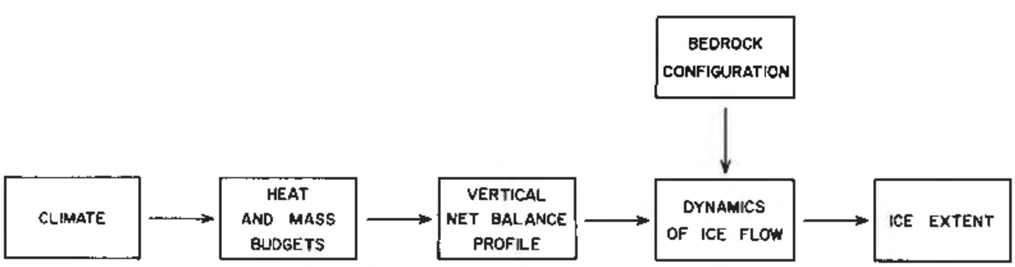

Fig. 1. Causality chain of climatic forcing and glacier response.

19th century. His observations also indicate an abundance of snow and ice. It is not until the middle of the 19th century that a drastic upward shift of the ice equilibrium level sets in; the recession continuing to the present.

In summary, a drastic and monotonic ice retreat continuing from the 19th century to the present is documented for East Africa and the Ecuadorian Andes, while observations for New Guinea only start in the 1930's. The reconstruction of a climate history from glacier observations is the task that lies ahead.

3. Climatic Forcing and Terminus Response

One approach to inferring the (unknown) climatic variations from the (well documented) glacier behavior is through computer simulation of climate, net balance, and ice dynamics. A causality chain is illustrated in Fig. 1. Climate controls the mass and heat budgets, which are reflected in the vertical net balance profile. The vertical net balance profile and the bedrock configuration in essence determine the ice dynamics, which lead to variations in ice extent. The intent is to reconstruct the climatic forcing from the glacier response. The regional input to the computer simulation includes

(a) the record of terminus positions;
(b) bedrock configuration;
(c) modern mass budget conditions.

From this information, the climatic variations are to be reconstructed that caused the observed terminus behavior. A glacier of maximum extent is created, as indicated by moraines. Then a retreat is simulated in such a way that the various observed terminus positions are reproduced. This then allows quantitative inference on the history of the climatic forcing.

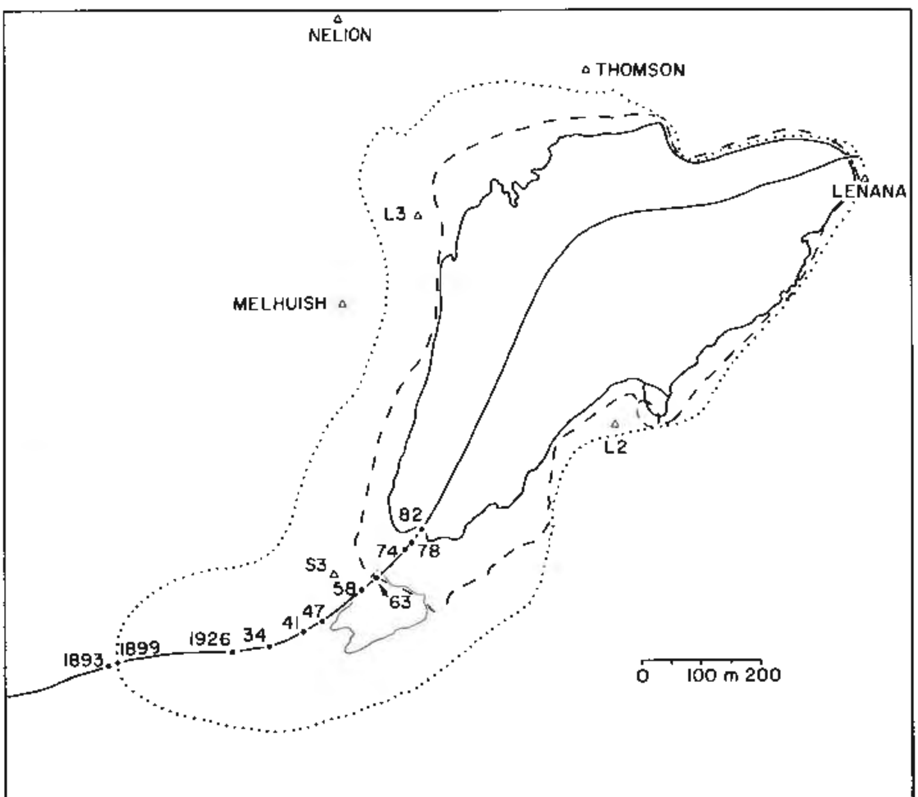

Fig. 2. Map of the terminus and area variations of Lewis Glacier since the turn of the century. Scale 1 : 12 500.

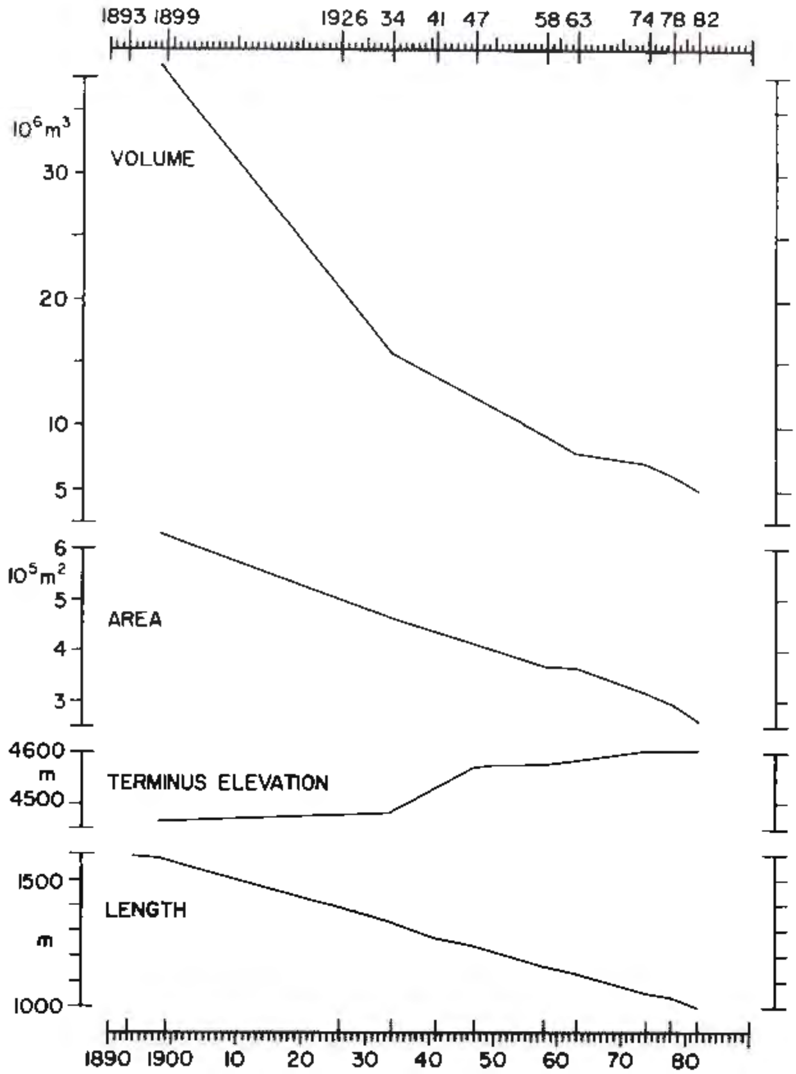

Fig. 3. Secular variation of Lewis Glacier 1899–1982. Volume in 10^6 m^3; area in 10^5 m^2; length of the glacier and elevation of terminus in m.

Lewis Glacier on Mount Kenya is the glacier with the most comprehensive historical documentation of long-term variations in all of the tropics. My reconstruction of Lewis Glacier variations since the turn of the century based on a variety of historical sources (TROLL und WIEN, 1949; CHARNLEY, 1959; Forschungsunternehmen Nepal-Himalaya, 1967; HASTENRATH, 1975, 1981 b, 1983) is illustrated in Figs. 2 and 3. It is the largest ice body on Mount Kenya, its catchment is well defined, and it is comparatively accessible. Based on these considerations, Lewis Glacier was chosen for a study of cryosphere-climate relations including the quantitative reconstruction of the climatic forcing from the observed glacier response. Basic to this effort is a multi-annual field investigation of glacier morphology, kinematics, and heat and mass budgets. A pilot project was undertaken during my affiliation with the University of Nairobi in 1973–74. A more comprehensive and continuous field program materialized since December 1977. This encompassed observations throughout the year and intensive field expeditions. The tasks of this field program are as follows.

Aero-photogrammetric mappings of the glacier at scale 1 : 2 500 were accomplished in February 1974 (CAUKWELL and HASTENRATH, 1977), in February 1978 (HASTENRATH and CAUKWELL, 1979), and in

February and March 1982 (CAUKWELL and HASTENRATH, 1982). These mappings document a glacier average decrease in ice thickness over the four year interval 1974–78 of about 4 m, which corresponds to a volume loss of the order of 11 × 10^3 m^3. Over the four year interval 1978–82, the ice thickness decreased further by 3.6 m and the volume by 1.067 × 10^3 m^3. These mappings further reveal changes in the crevasse pattern: while longitudinal crevasse orientation prevails in the lower, and transverse alignment in the upper glacier, the transition between these two regimes is gradually being displaced glacier upward (HASTENRATH and KRUSS, 1979, 1982; KRUSS and HASTENRATH, 1983). Ice thickness and bedrock topography were determined by the seismic and gravimetric techniques and through numerical modelling (BHATT, HASTENRATH and KRUSS, 1980). On this basis, the total ice volume for the February 1978 datum is estimated at about 10^7 m^3.

An array of stakes was installed on the glacier for purposes of net balance measurements and determination of surface ice flow velocity through repeated surveys of these poles. The stations in the lower glacier consist of various 2 m long wooden stakes that are linked together, while single 4 m long bamboo poles are used in the upper glacier. The network was repeatedly refurbished since 1978 with a major overhaul during the 1981/82 expedition.

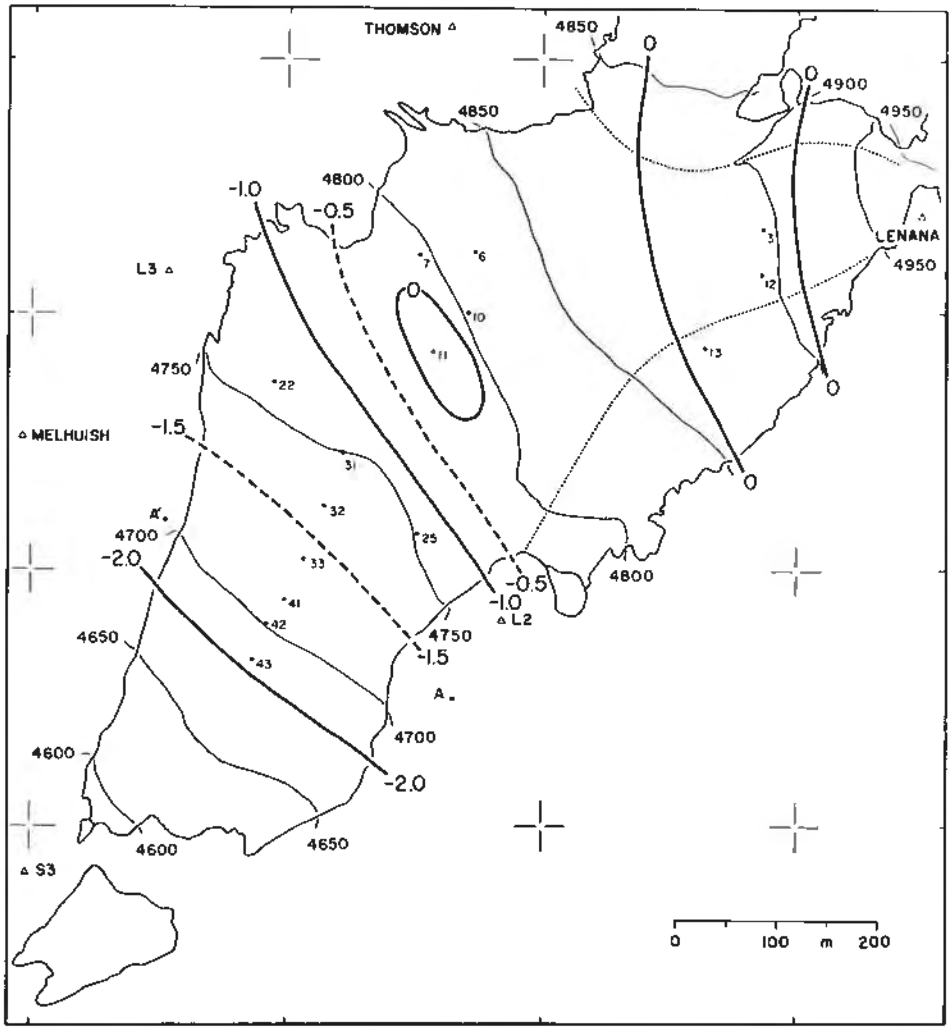

Fig. 4. Map of net balance averaged for the budget years 1978/79, 1979/80, 1980/81, and 1981/82, in m of liquid water equivalent.

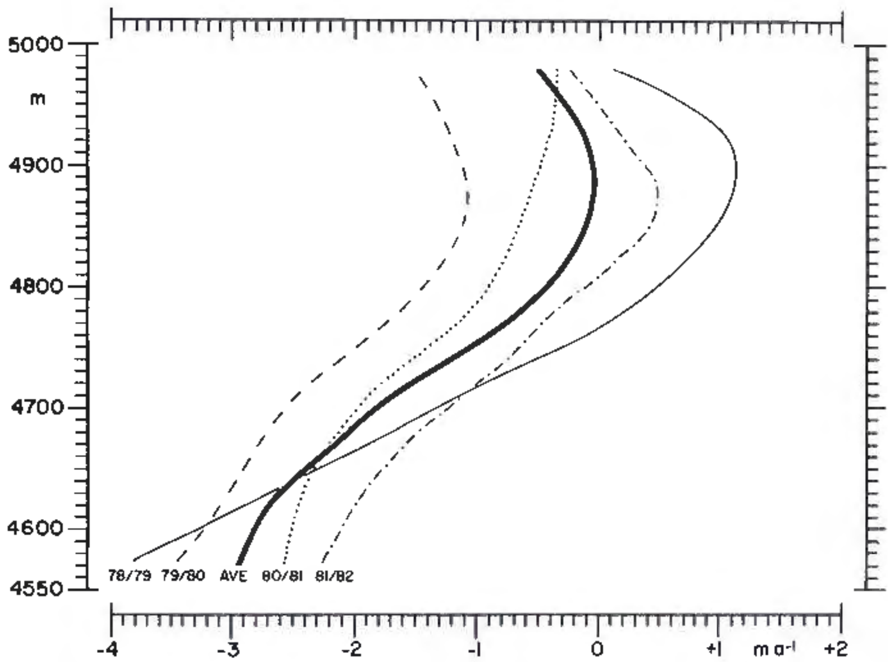

Fig. 5. Vertical net balance profiles, in m of liquid water equivalent, for the budget years 1978/79 (thin solid), 1979/80 (broken), 1980/81 (dotted), 1981/82 (dash-dotted), and the four-years combined (heavy solid line).

Readings at the stake network are converted into liquid water equivalent net balance under consideration of densities representative of various portions of the glacier, as obtained from ice pit investigations. The latter are complemented by climatic ice core studies (THOMPSON and HASTENRATH, 1981). The net balance pattern for the four year period 1978–1982 is shown in the map Fig. 4. Small positive values are found in the upper glacier, while large negative values are characteristic of the ablation zone in the lower glacier. Planimetering of the map yields for the glacier as a whole a deficit of 1.007×10^3 m^3 of liquid water equivalent over the four year period 1978–82. Based on individual annual maps comparable to the four-year map Fig. 4, vertical net balance profiles are constructed such as displayed in Fig. 5. The profiles reveal pronounced interannual variations in the net balance conditions, which parallel those of precipitation, as monitored by the gauges we installed in January 1978. Thus the abundant precipitation year 1978/79 shows the largest positive net balance in the upper glacier, and for the glacier as a whole mass equilibrium is almost reached. By contrast, during the extreme drought year 1979/80 net balance was negative everywhere, that is the entire glacier behaved as ablation area; the mass deficit for the glacier as a whole was accordingly large. The budget years 1980/81 and 1981/82 show intermediate conditions. The four-year average profile is also plotted in Fig. 5 for comparison.

Our observations show that the interannual variability of net balance is considerably larger than that of precipitation. It is realized that precipitation variations are typically associated with changes in cloudiness and in albedo of the glacier surface. The latter two factors strongly affect net radiation and thus the surface heat budget, which is in turn intimately linked with the mass budget. Thus precipitation changes appear greatly magnified in the net balance conditions. Quantitative relationships are being developed empirically and through heat and mass budget calculations. In conjunction with our radiation measurements (HASTENRATH and PATNAIK, 1980), the intended installation of a sunshine counter would be useful in this effort.

The annual mean heat and mass budgets of Lewis Glacier are schematically summarized in Figs. 6 and 7. In Fig. 6 the downward directed shortwave radiation SW↓ results from the radiation geometry and a representative cloudiness of 6 tenths. The upward directed shortwave flux SW↑ is then commensurate with a representative surface albedo of 57 percent. Cloudiness, temperature, and humidity control the net longwave radiation LW↑↓. The sensible heat flux Q_s amounts to a heat input to the glacier. The resultant heat gain allows large melting rates, but a substantial portion of the heat input is spent on the energetically more expensive sublimation. In the mass budget scheme Fig. 7, solid precipitation is available from gauge measurements. Melting and sublimation rates are consistent with the energy budget scheme Fig. 6, as well

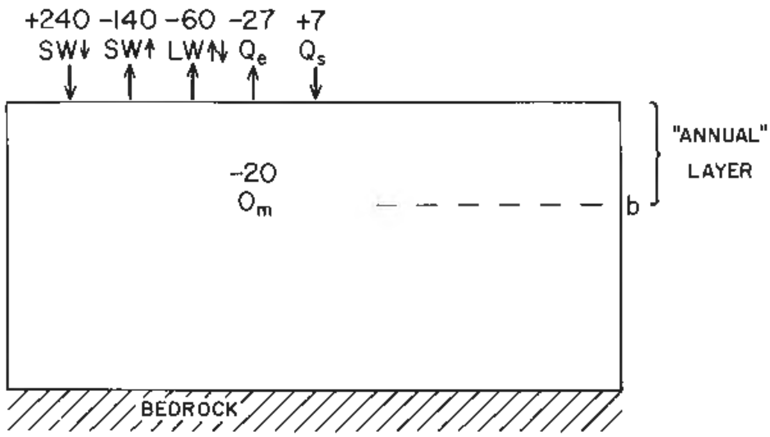

Fig. 6. Scheme of average annual heat budget of Lewis Glacier.
SW↓ downward directed shortwave radiation
SW↑ upward directed shortwave radiation
LW↑↓ net longwave radiation
Q_e latent heat flux at glacier-air interface
Q_s sensible heat flux at glacier-air interface
Q_m heat used in melting throughout a column except at base
(A glacier average albedo of 57 percent, and cloudiness of about 6 tenths are adopted. Numbers are in $W \cdot m^{-2}$.)

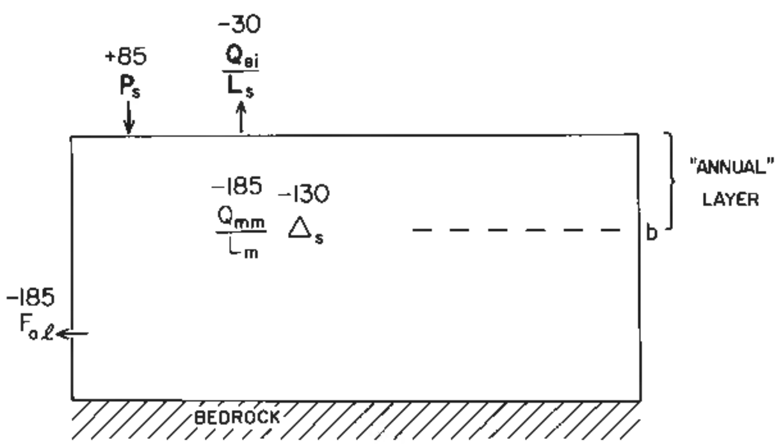

Fig. 7. Scheme of average annual mass budget of Lewis Glacier, commensurate with heat budget illustrated in Fig. 6.
P_s solid precipitation
Q_{ei}/L_s sublimation
Q_{ei}/L_e melting
Δ_s net balance
F_0 water discharge
(Numbers are in cm of liquid water equivalent or g $H_2O \cdot cm^{-2} = 10$ kg $\cdot m^{-2}$)
($F_{0\ell} = 1.850$ kg $\cdot m^{-2}$ corresponds to 17 $\ell \cdot s^{-1}$.)

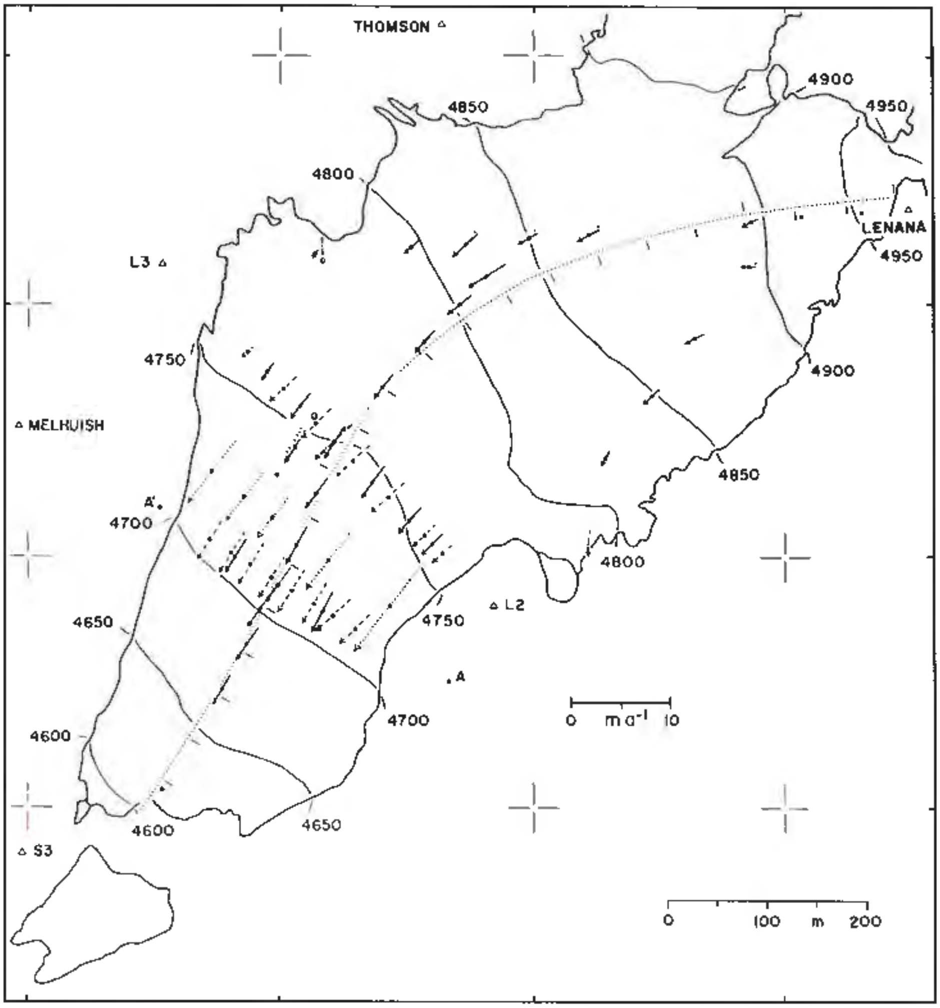

Fig. 8. Surface velocities measured at various epochs during the 20th century. Dots indicate the location of targets, and arrows the direction and magnitude of motion. Velocity scale in $m \cdot a^{-1}$ is ten times the horizontal scale in m (i.e. $10\ m \cdot a^{-1}$ would be represented as a 100 m arrow). Dotted, dash-dotted, broken, and solid arrows refer to measurements in 1934 (TROLL und WIEN, 1949), in 1957 (CHARNLEY, 1959), in 1973–74, and during 1978–80, respectively. Solid arrows with small dot at right-hand side of tail denote measurements limited to January-February 1978. Open circle and dot indicate the 1958 and 1974 locations of a meteorological shelter and its remnants. The corresponding motion vector, shown by solid line shaft with perpendicular short barbs to the right, is plotted at the midpoint of this distance. The dotted line represents the modeled central line, with tick marks at 50 m intervals indicating longitudinal distance. 1978 height contours in m are entered as thin solid lines. Scale 1 : 7500. (From HASTENRATH and KRUSS, 1982.)

as with the water discharge measured at the exit of Lewis Tarn. Losses through melting and sublimation far exceed the mass gain by solid precipitation. The deficit is manifested in the continuing mass decrease of the glacier, as borne out by the repeated aero-photogrammetric mappings and the net balance stake network discussed above.

Repeated surveys of the aforementioned stakes yield estimates of surface ice flow velocity. Values obtained for the 1978–80 interval are plotted in the map Fig. 8, along with measurements for various earlier epochs. The observations from various epochs are consistent in both spatial pattern and general magnitude, although a gradual slowdown of surface flow is indicated. The secular variation of ice flow velocity along the central line is illustrated in Fig. 9, which combines field observations with the results of

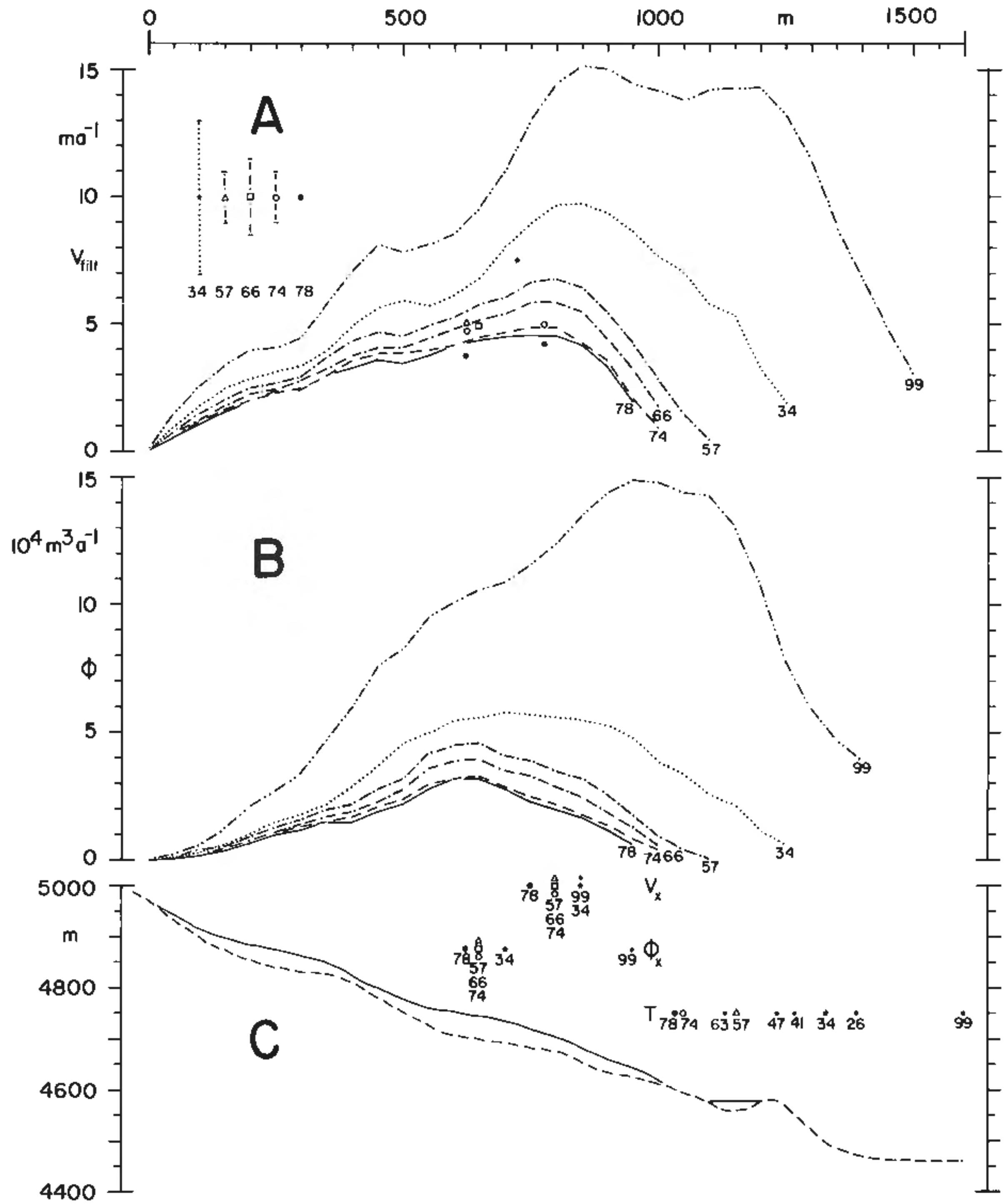

Fig. 9. Secular variation of surface velocity and mass flux along central line. Modeled longitudinal profiles are shown of filtered velocity V_{filt}, and filtered mass flux ϕ, for various epochs as follows: 1899 (double dot-dashed), 1934 (dotted), 1957 (dash-dotted), 1966 (double dash-dotted), 1974 (broken), 1978 (solid line). In the graph of V_{filt}, observed velocities are entered as asterisk for 1934, triangle for 1957, square for 1958 to 1974 mean displacement rate (labelled 1966), open circle for 1974, and large dot for 1978–80 (labelled 1978). Vertical lines to the left indicate the estimated uncertainties of measurements. In the bottom part, bedrock topography is depicted as broken, and tarn and 1978 ice surface topography by solid line. Modeled maxima of surface velocity V_x and mass flux ϕ_x are denoted by the aforementioned symbols for the 1899, 1934, 1957, 1966, 1974, and 1978 epochs. The observed terminus positions T are furthermore indicated by small dots for the additional epochs 1926, 1941, 1947, and 1963. (From HASTENRATH and KRUSS, 1982.)

numerical modelling. Figure 9 shows a monotonic decrease of velocity and a gradual displacement of the velocity maximum glacier upward, since the beginning of the century.

The reconstruction of terminus positions for various epochs since the end of the 19th century along with study of recent morphology, mass and heat budget, and kinematics, serve as a basis for the quantitative reconstruction of climate variations through numerical modelling (KRUSS, 1981, 1983, 1984). On this basis the following major forcings emerge as causes of the continued glacier recession since the 19th century: (i) a precipitation decrease of the order of 150 mm a^{-1}, concomitant with a small decrease of cloudiness and surface albedo, during the last two decades of the 19th century; and (ii) a temperature increase of a few tenths of °C during the 20th century, concentrated in the 1920's. The drastic precipitation decrease in the latter part of the last century is also reflected in a drastic drop of the water level of East African lakes.

The climatic forcings responsible for the conspicuous and well documented glacier response are as a rule too small to be ascertained by conventional sensing techniques. The Lewis Glacier study thus points the way for the quantitative assessment of climate variations from glacier observations. The Lewis Glacier field program is now being continued in the mode of long-term monitoring of net balance, precipitation, and kinematics.

4. Ice Cores

Extraordinary climatic records have been reconstructed from ice cores in the polar regions. Indicators evaluated include microparticle concentration, total beta radioactivity, and oxygen isotope ratios. Application of climatic ice core techniques to the tropics is novel. In the tropics, particular difficulties must be considered, that are not encountered in the well-established polar glaciology. Aside from logistic considerations, the following criteria guide the choice of an ice body for coring and paleoclimatic studies in the tropics:

(i) the ice cap should be at very high elevations and thus low temperature to preclude significant melting and percolation;
(ii) for an extended ice plateau with gentle topography, the effects of flow dynamics on stratigraphy are summarized;
(iii) location in the outer tropics allows same seasonality in the stratigraphy;
(iv) the thickness and net balance are limiting factors for the length of the climatic record to be expected.

These conditions are ideally met for the Quelccaya Ice Cap. This vast ice plateau in the Eastern Andes of Peru (Fig. 10) is the object of a multi-annual field program conducted since 1974. The central objective is the retrieval of ice cores for microparticle and isotope analysis and climate reconstruction. The study of the present climate, heat and mass budget is an important component of the project, inasmuch as this should put paleoclimatic interpretations on a firm footing. Reference is made to the various publications stemming from this project (MERCER et al., 1975; THOMPSON and DANSGAARD, 1975; HASTENRATH, 1978; THOMPSON et al., 1979; HASTENRATH and KOCI, 1981).

The ice stratigraphy at Quelccaya is characterized by a conspicuous annual layering, the June/July dry season being marked by an ice horizon and concentration of microparticles and total beta radioactivity. The annual net balance is obtained from the mass contained between annual horizons. On the Quelccaya summit plateau net balance is essentially equal to precipitation, because virtually no energy is available for ablation. This is a direct consequence of the large surface albedo (HASTENRATH, 1978). The few years' net balance series obtained for the Quelccaya summit compares well with precipitation at stations outside the ice cap. Thus, the microparticle and beta profiles offer a good prospect for establishing a net balance or precipitation chronology for Quelccaya.

Regarding the oxygen isotope ratios, the Quelccaya cores offer a surprise when compared to the classical records from the Arctic and Antarctic, where they were interpreted in terms of a temperature

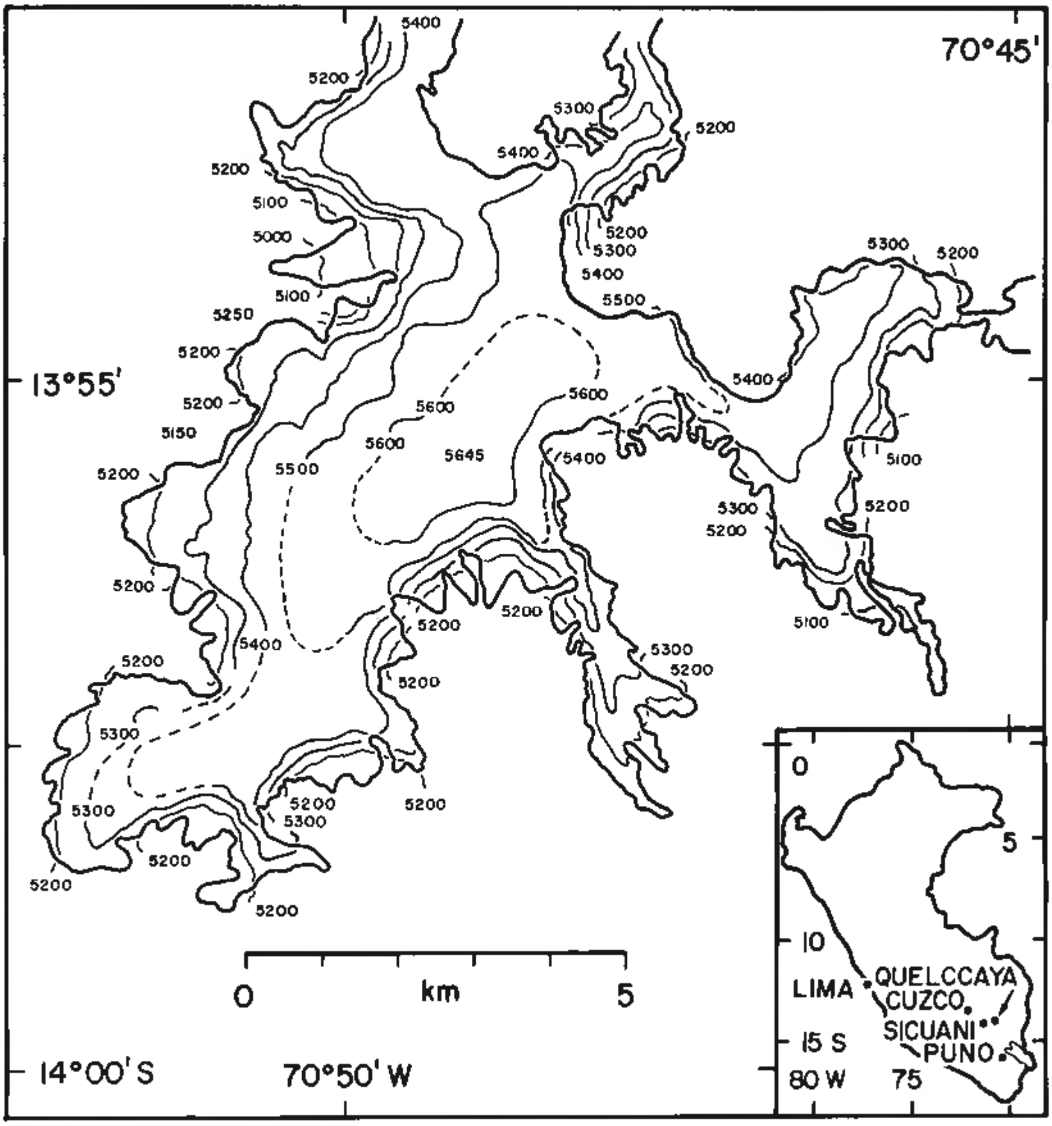

Fig. 10. Map of Quelccaya Ice Cap and orientation map of Peru.

history. Thus at Quelccaya the annual range of δ-values is as large as that in the polar regions from the last ice age to the present; and the least negative values occur at the coldest time of year – again contrary to the polar experience. The results indicate the need for a revision of isotope "thermometry" for application in the tropics.

In brief, the Quelccaya cores show the potential for a net balance and precipitation chronology based on the identification of annual horizons from ice layers, microparticle concentration, and total beta radioactivity. A temperature history similar to the polar regions is unlikely, but this may be of subordinate importance for the tropics. The theoretical foundation still needs to be created for the evaluation of oxygen isotope ratios in terms of climate. A drilling to bedrock as intended for the near future is expected to yield a record of about half a millenium or more for the Eastern Peruvian Andes.

Elsewhere in the tropics, the prospects for climatic ice core studies appear more limited, as melting and percolation at lower elevations contaminate the ice profile. These complications were also recognized at Lewis Glacier on Mount Kenya (THOMPSON and HASTENRATH, 1981). The summit ice fields of Kilimanjaro appear most nearly suitable for climatic ice core studies in East Africa.

5. Concluding Remarks

In all three glaciated high mountain regions under the Equator, ice has been receding monotonically since the 19th century. The onset of the glacier recession differs between the three regions, being around the middle of the 1800's in the Ecuadorian Andes and around 1880 in East Africa. The inferred onset of retreat of the New Guinea glaciers is around the mid 1800's (ALLISON and KRUSS, 1977). In all three regions the ice retreat is continuing to the present.

While the glacier retreat is drastic and generally well observed, the climatic changes that caused it are not known. Two independent approaches are being developed to quantitatively infer a climate history from glacier observations. The application of ice core techniques is novel for the tropics, but offers good prospects for a few locations at very high elevations. The numerical simulation of the causality chain climate – net balance – ice dynamcis terminus translates the observed glacier response into the unknown climatic forcing. A detailed terminus history is essential. Inasmuch as the climatic forcings responsible for the conspicuous and well documented glacier response are as a rule too small to be ascertained from conventional sensing techniques, this methodology merits attention for long-term environmental monitoring.

References

ALLISON, I. and P. KRUSS (1977): Estimation of recent climatic change in Irian Jaya by numerical modelling of its tropical glaciers. Artic and Alpine Research, 9, 49–60.

BHATT, N. V., S. HASTENRATH and P. KRUSS (1980): Ice thickness determination on Lewis Glacier, Mount Kenya: seismology, gravimetry, dynamics. Zeitschrift für Gletscherkunde und Glazialgeologie, 16, 213–228.

CAUKWELL, R. A. and S. HASTENRATH (1977): A new map of Lewis Glacier, Mount Kenya. Erdkunde, 31, 85–87.

–, – (1982): Variations of Lewis Glacier, Mount Kenya, 1978–82. Erdkunde, 36, 299–303.

CHARNLEY, F. (1959): Some observations on the glaciers of Mount Kenya. J. Glaciol., 3, 483–492.

Forschungsunternehmen Nepal-Himalaya (1967): Mount Kenya 1 : 5 000. Wien.

HASTENRATH, S. (1975): Glacier recession in East Africa. In: WMO-IAMAP Symposium on long-term climatic variations. Aug., 1975, Norwich, England. WMO-No. 421, Geneva, 135–142.

– (1977): Fluctuations of Mount Kenya glaciers. In: IUGG-ICSI-UNESCO, Permanent Service on the Fluctuations of Glaciers, 1970–75, vol. 3, UNESCO, Paris, pp. 14, 80, 105, 119.

– (1978): Heat budget measurements on the Quelccaya Ice Cap, Peruvian Andes. J. Glaciol., 20, 85–97.

– (1981 a): The glaciation of the Ecuadorian Andes. Rotterdam.

– (1981 b): The glaciers of Mount Kenya and Kilimanjaro, and: The climate of Mount Kenya and Kilimanjaro. In: ALLAN, I. (Ed.): Guide to Mount Kenya and Kilimanjaro. Mountain Club of Kenya, Nairobi, 25–35 and 36–38.

– (1983): The glaciers of equatorial East Africa (in preparation).

– and R. A. CAUKWELL (1979): Variations of Lewis Glacier, Mount Kenya, 1974–78. Erdkunde, 33, 292–297.

– and B. KOCI (1981): Micro-morphology of the snow surface at the Quelccaya Ice Cap, Peru. J. Glaciol., 27, 423–428.

– and P. D. KRUSS (1979): Dynamics of crevasse pattern at Lewis Glacier, Mount Kenya. Zeitschrift für Gletscherkunde und Glazialgeologie, 15, 201–207.

–, – (1982): On the secular variation of ice flow velocity at Lewis Glacier, Mount Kenya. J. Glaciol., 28, 333–339.

– and J. K. PATNAIK (1980): Radiation measurements on Lewis Glacier, Mount Kenya. J. Glacial., 25, 439–444.

HOPE, G. S., J. A. PETERSON, I. ALLISON and U. RADOK (Eds., 1976): The equatorial glaciers of New Guinea. Rotterdam.

International Association of Hydrological Sciences – UNESCO (1977): Fluctuations of glaciers, 1970–75. Paris.

KRUSS, P. D. (1981): Numerical modelling of climatic change from the terminus record of Lewis Glacier, Mount Kenya. Ph.D. Dissertation, Department of Meteorology, University of Wisconsin, Madison.

– (1983): Climatic change in East Africa: numerical modelling from the 100 years of terminus record of Lewis Glacier, Mount Kenya (submitted for publication).

– (1984): Terminus response of Lewis Glacier, Mount Kenya, to sinusoidal net balance forcing. J. Glaciol. (in press).

– and S. HASTENRATH (1983): Variation of ice velocity at Lewis Glacier, Mount Kenya, Kenya: verification midway into a forecast. J. Glaciol., vol. 29, no. 101, 48–54.

MERCER, J., L. G. THOMPSON, C. MARANGUNIC and J. RICKER (1975): Peru's Quelccaya Ice Cap, 1975: glaciological and glacial geological studies. Antarctic J. of the U.S., 10, 19–24.

Temporary Technical Secretariat for World Glacier Inventory of IUGG-ICSI-UNESCO (1977): Instructions for compilation and assemblage of data for a World Glacier Inventory. ETH, Zürich.

THOMPSON, L. G. and W. DANSGAARD (1975): Oxygen isotope and microparticle studies of snow samples from Quelccaya Ice Cap, Peru. Antarctic J. of the U.S., 10, 24–26.

– and S. HASTENRATH (1981): Climatic ice core studies at Lewis Glacier, Mount Kenya. Zeitschrift für Gletscherkunde und Glazialgeologie, 17, 115–123.

–, – and B. MORALES ARNAO (1979): Climatic ice core records from the tropical Quelccaya Ice Cap. Science, 203, 1240–1243.

TROLL, C. und K. WIEN (1949): Der Lewisgletscher am Mount Kenya. Geografiska Annaler, 31, 257–274.

United Nations Environment Programme (1979): The Environment Programme, report of the Executive Director. UNEP Na 79–0075, Nairobi.

–, World Meteorological Organization (1982): Climate-related monitoring, a review of GEMS achievements and future activities. March 1982, Geneva.

UNESCO (1970): Perennial ice and snow masses. A guide for compilation and assemblage of data for a World inventory. Technical Papers in Hydrology No. 1.

World Meteorological Organization (1980): Outline plan and basis for the World Climate Programme 1980–83. WMO-No. 540, Geneva.

–, ICSU (1975): The physical basis of climate and climate modelling. GARP Publication Series, No. 16.

Discussion to the Paper Hastenrath

Prof. Dr. A. Kessler:

How much is the annual mean of the net allwave radiation (Gesamtstrahlungsbilanz)?

Prof. Dr. S. Hastenrath:

1. For the highest part of the Quelccaya ice plateau in South Peru SWLW↑↓ is about zero.
2. For the Lewis Glacier of Mount Kenya the annual mean of SWLW↑↓ is about 40 Wm^{-2}.

Miss J. M. Kenworthy M.A.:

Have you found it possible, from the model you have developed, to estimate how long it would take for the Lewis Glacier to disappear, given that the present range of climatic conditions continue?

Prof. Dr. S. Hastenrath:

We have modelled the past history of the Lewis Glacier, and have predicted velocity (and men's) changes for the *near* future only. From the smaller and higher residual glacier, man economy becomes increasingly more favourable. Our monitoring shows a decrease in volume of about 12 percent over the four-year-interval 1978–82. Accordingly I am looking foreward to a walk on the ice of Lewis Glacier at the beginning of the next millenium.

Prof. Dr. W. Weischet:

1. How high is the mean accumulation of snow-cover on the Quelccaya ice-plateau?
2. With all reservations concerning the transferability of results from Peru to East-Africa, the deeper layers of the Quelccaya-ice could give direct hints at the drastic diminuation of annual precipitation during the last two decades of the 19th century, which till now had to be calculated from the lowering of the lake-level.

Prof. Dr. S. Hastenrath:

1. About 3 m of snow.
2. No. The drastic decline of precipitation from 1880 to 1900 concerns East-Africa in particular, and possibly the east coasts of the lower latitudes.
   Reference: KRAUS, E. B. (1955): Secular changes of east-coast rainfall regimes. Quat. J. Roy. Met. Soc., Vol. 81, No. 349, 430–439.

Dra. M. L. Salgado-Labouriau:

The retreat of glaciers that you have observed in the tropical zone occurs also in higher latitudes, including arctic and antarctic ice?

Prof. Dr. S. Hastenrath:

During much of this century the recession of tropical glaciers was paralleled by ice retreat in the mid-latitudes. However, since the 1970's there are indications for glacier advance in the mid-latitudes (Alps, Himalayas), while the glaciers of East-Africa and South America continue to retreat. For New Guinea ice recession is indicated at least for the early 1970's, the most recent observations available for that area.

Dr. H. Kienholz:

You have shown the velocity-distribution for the surface of the Lewis Glacier. What about the vertical velocity-distribution?

Prof. Dr. S. Hastenrath:

The theory of glacier dynamics makes it possible to calculate the velocity of flow within the interior of a glacier from observations at the surface. The velocity rises from the middle of a glacier to its sides, but declines approaching its ground. The vertical component is directed downward in the upper glacier, upward in the glacier-tongue. For the Lewis Glacier the internal velocity-distribution is shown in a longitudinal section (compare: KRUSS and HASTENRATH, 1983).

M. D. Rafiqpoor:

1. In his Book "Geologie von Ecuador" Mr. SAUER reports moraine-levels at 800 m above sea-level and explains them tectonically. Do you share his opinion and do you know similar examples from Peru and Bolivia?
   Reference: SAUER, W. (1971): Geologie von Ecuador. Beiträge zur regionalen Geologie der Erde, Bd. 11. Berlin/Stuttgart.
2. How do you explain the asymmetric construction of the glacier-tongues (lower on the eastern slope, higher on the western slope) at the Ecuadorian vulcanoes?

Prof. Dr. S. Hastenrath:

1. SAUER's interpretations are entirely based on stratigraphy, but not on surface-morphology, and his observations are confined to lower regions. He doesn't attempt to compare his scheme with the older-one of MEYER. Revision is indispensable!
2. Humidity was supplied from the Amazone-Region.

Erdwissenschaftliche Forschung, Bd. XVIII, 249–259
Franz Steiner Verlag Wiesbaden GmbH · Stuttgart (1984)

Pleistocene and Present Day Glaciations in the High Mountains of New Guinea

Ernst Löffler

With 6 Figures

Summary

The Pleistocene glacial history of New Guinea may date back to about 700 000 ± 100 000 yrs. BP when lava erupted under ice on Mt. Giluwe. At 290 000–300 000 yrs. BP Mt Giluwe was again covered by ice and this glacial event may have been synchronous with glaciations in other parts of the world.

The onset of the last glaciation is not known but the maximum extent of glaciation was reached between 18 500 and 16 000 yrs. BP when nearly 2000 km² were covered by ice and the snowline lay at approximately 3600 m with only minor variations due to local climatic conditions or as in one case due to tectonic uplift.

From 15 000 yrs. BP the glaciers retreated rather rapidly to completely disappear by about 9000 yrs. BP. These dates are consistent over the entire island and also with evidence of climatic change in Australia where conditions changed from arid to less arid.

The reconstruction of the climate during the last glaciation is complicated by conflicting geomorphological and palynological evidence. While the extent of the glaciation indicates a lowering of the snowline by some 1000 m corresponding to a temperature depression in the order of 5–6 °C the depression of the forest/grassland boundary seems to have been nearly twice as much. It is argued that this extraordinarily large depression in the forest boundary could be due to local conditions and not to a general temperature depression of 10 °C.

From about 5000 yrs. BP some glaciers in the highest areas formed again and survived to the present day where some 7–8 km² are covered by glacial ice. The ice retreat in recent times is broadly synchronous with world wide glacier fluctuations.

Although neither Pleistocene nor present day glaciations are of any direct consequence to man in New Guinea the glaciation has created topographic and resulting edaphic and ecological conditions for the occurrence of valley floor grasslands well below the timber line and through burning man has extended these grasslands to cover large areas of formerly forested terrain.

1. Introduction

Although the presence of glacial ice on the island of New Guinea has been known since the 17th century when the ice capped summit of Mt. Carstensz was sighted by the great Dutch explorer, research into the glacial history started relatively late. Early this century a British exploring party reached the ice of the Carstensz glacier and in 1936 a Dutch expedition undertook the first scientific work on glacial geomorphology in the Carstensz Mts. DOZY, the geologist of the expedition, mapped the extent of the present and Pleistocene glaciation and claimed that valley glaciers descended to surprisingly low altitudes, in one case to 2000 m (DOZY, 1938). Recent glaciers were marked by cairns.

Despite of several other mountaineering expeditions it was not until the 1970's that a second scientific expedition visited the area and provided more detailed information not only about the Pleistocene and recent glaciations but also the associated vegetation changes (HOPE et al., 1976). Because of the great difficulties of access and for political reasons no further work has been possible.

In Papua New Guinea, the eastern part of the island, formerly under Australian administration and until the First World War partly under German rule, no work was done until the sixties when members of Australian Universities and Research Institutions such as CSIRO worked in the area. The time between 1965 and 1975 undoubtedly was the great time of research in Papua New Guinea as this work was generously supported by the Australian Administration and Universities.

The following account represents a review of the state of knowledge on Pleistocene and recent glaciations and some ideas on how Pleistocene glacial features have influenced man's access to the mountain areas and how man has modified the high mountain vegetation.

2. Pre-Würm Glaciations

Evidence for glaciations pre-dating the last are always difficult to find in areas where glaciation was restricted to cirque and valley glaciations, and New Guinea is no exception. So far only two areas have been discovered where there is clear evidence for older glaciations. In West Irian weathered moraine material was found outside the limits of the last glaciation by DOW (1968) and by HOPE and PETERSON (1975) on the Kemabu Plateau north of the Jaya Mountains, but no dating was possible.

My own work which was entirely restricted to the eastern part of the island has shown that on Mt. Giluwe eruptions of lava were intermittent with certainly one, possibly two periods of ice cover. Dating of lavas associated with palagonitic breccias has shown that at 290 000 yrs. BP much of the present summit area was covered by ice. This data is supported by another finding which shows moraine material sandwiched between two lava flows the one underlying the moraine being 319 000 years old, the one overlying the moraine having an age of 290 000 yrs. BP (LÖFFLER, 1976; LÖFFLER et al., 1980).

A second site with palagonitic breccia was found near the main peak but dating of the associated lavas has been poor and given a spread of ages between 750 000 and 880 000 years.

Therefore there can be no doubt that the New Guinea Mountains experienced earlier glaciations relatively early in the Pleistocene and consequently must have reached altitudes similar to the present ones. The 290 000 years date is synchronous with dates from other parts of the world such as Hawaii, Kilimanjaro, New Zealand and also agrees well with the oxygen isotope dates of SHACKLETON and OPDYKE (1973), and we can assume that the glaciation represents the third last glaciation.

3. Last Glaciation

No evidence for the second last glaciation has been found and it is not known how much the earlier glaciations had modified the mountain terrain, however the traces of the last glaciation are exceptionally well preserved and obvious even to the casual observer. Most striking is the sharp contrast in valley cross sections between the V shaped fluvially formed valleys below and the broad U shaped valleys above the limits of glaciation. Terminal and lateral moraines are up to 100 m, in the Carstensz area up to 200 m high and are exceptionally well preserved, a feature typical for tropical mountains and probably due to the diurnal regime of melting with relatively constant rates of discharge even during times of glacial retreat and the relatively minor effect of periglacial solifluction.

The total area covered by ice amounted to some 2000 km^2 of which nearly three quarters are situated in Irian Jaya (Fig. 1). In Irian Jaya there existed a nearly continuous ice field from Mts. Idenburg and Carstensz (Mt. Jaya) in the west to the Star Mountains (Jayawijaya Ranges) in the east (DOZY, 1938; VERSTAPPEN, 1964; HOPE and PETERSON, 1975). Most extensive was the glaciation in the Carstensz area where huge moraines, up to 200 m high were deposited on the Kemabu Plateau to the north at 3400 m altitude while on the southern fall the moraines descended down as far as 2300 m as already claimed by DOZY.

The Pleistocene snowline was at 3600–3700 m. This was slightly higher than on the mountains further east and may be due to the "continental" position of the Carstensz mountains during the low sea level stand when the Torres Strait and Arafura Sea were dry land.

While the western New Guinea Mountains contained the largest and most spectacular expressions of glaciation the eastern New Guinea Mountains being more accessible are better known and more intensi-

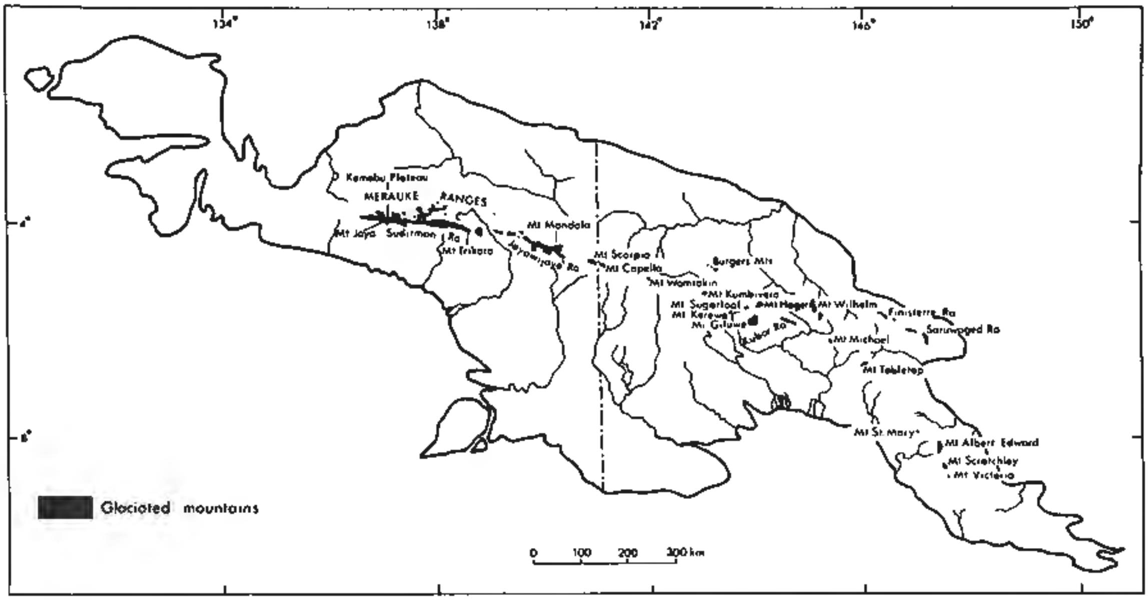

Fig. 1. Generalized map of the distribution of Pleistocene glaciers in New Guinea.

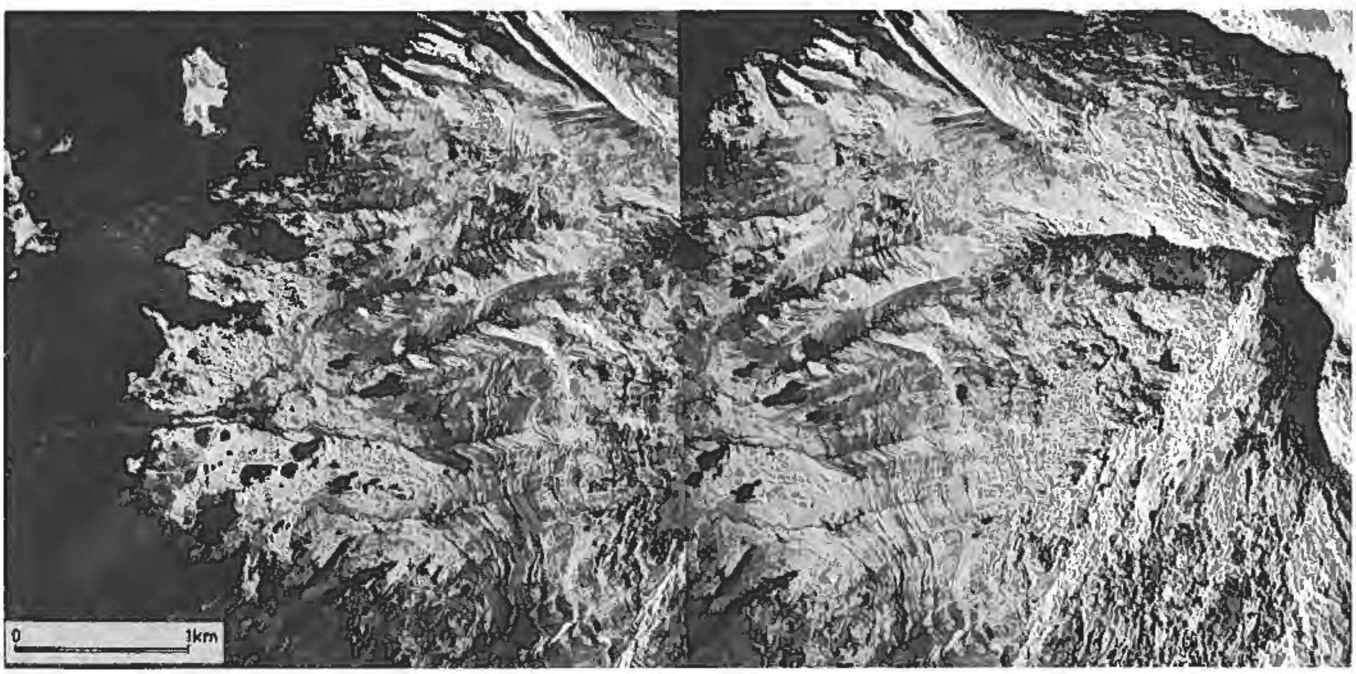

Fig. 2. Stereopair of western side of Mt. Giluwe, a Pleistocene volcano that was covered by an extensive ice cap during the last glaciation. The broad moraine of the main glaciation and the numerous recessional moraines are exceptionally well preserved. Some of the small recessional moraines overtop the moraine of the main glaciation.

vely studied. The two most interesting and best researched mountains are Mt. Wilhelm and Mt. Giluwe with 4509 and 4368 m the higest and second highest mountains in East New Guinea (Fig. 1).

Mt. Giluwe has already been mentioned as the site where evidence for older glaciations has been found. It is also the mountain most extensively glaciated with an ice cap type of glaciation covering some 190 km^2. Terminal moraines are again well preserved and form a nearly continuous belt around the summit area of the broad dome shaped volcano (Fig. 2) (LÖFFLER, 1972). They extend down to an altitude of 3100–3200 m with several tongues descending further down deeply incised valleys to about 2750 m. The snow line during the maximum extent was at 3550 m.

While Mt. Giluwe experienced an ice cap glaciation with a more or less continuous thick ice cap from which only short valley glaciers extended further down, Mt. Wilhelm being a much more dissected mountain was covered by an alpine type glaciation with long and thick valley glaciers emerging from deeply excavated cirques which today are filled with lakes and form a spectacular mountain scenery. Although some 200 m higher than Giluwe the area available for snow accumulation was smaller and the ice covered area only about half that of Mt. Giluwe.

There is a certain asymmetry in the distribution of cirques as already pointed out by REINER (1960) who undertook the first survey of the glacial morphology of the mountain. However this asymmetry is not restricted to the cirque distribution but is also apparent in slope profiles with smoother and gentler east-facing slopes and more irregular and steeper west facing slopes (Fig. 3).

This asymmetry is similar even though not as pronounced as the north-south asymmetry of mountains in subtropical latitudes where the difference in the sun insolation favours glacial action on north facing slopes and periglacial solifluction on south facing slopes. A similar explanation can be sought for the asymmetry of Mt. Wilhelm however the difference in sun insolation is caused by the daily changes in cloud cover whereby easterly facing slopes receive more insolation than westerly facing slopes due to the rapidly increasing cloud cover during the day, a phenomena already noticed by TROLL.

Fig. 3. Mt. Wilhelm, with asymmetric summit ridge. Smooth slope is facing east, irregular slope is facing west.

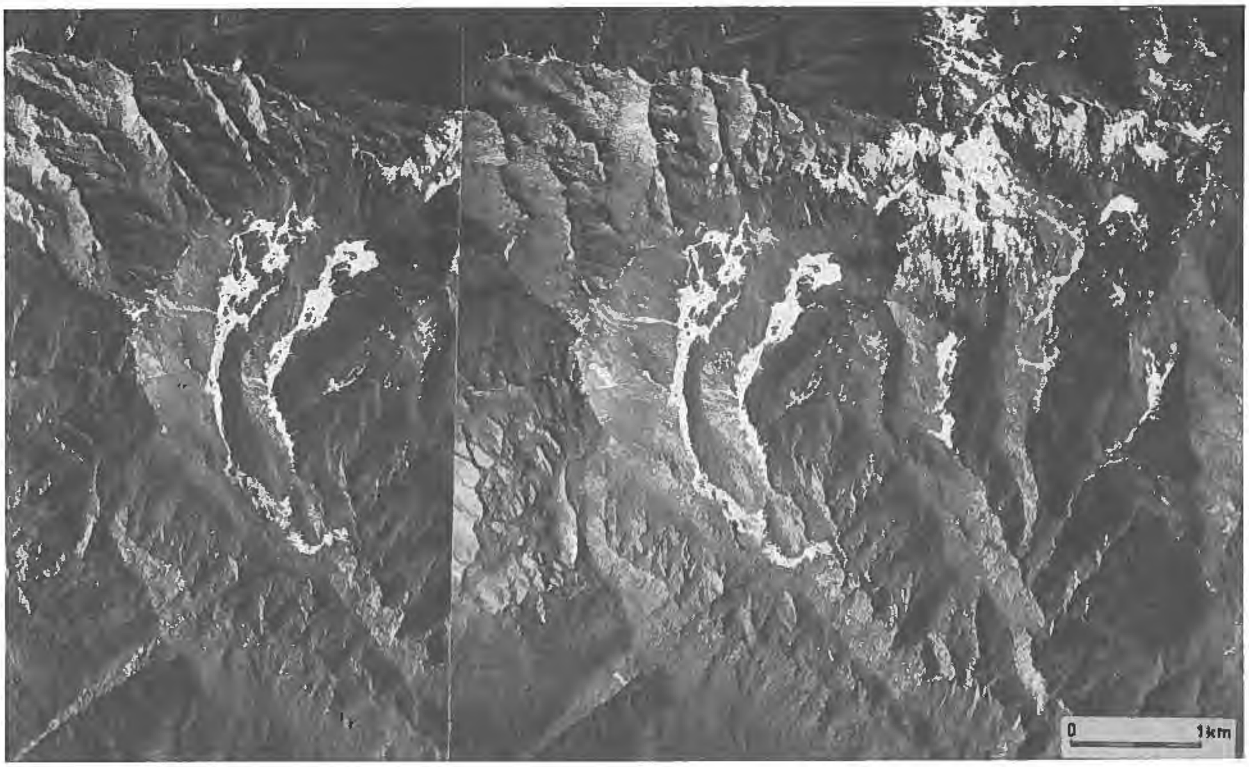

Fig. 4. Stereopair of Mt. Digini, Kubor Range. The contrast between the formerly glaciated and non glaciated terrain is particularly obvious in the valley cross sections. The contrast is further accentuated by the grassland covering the floors of the glaciated valleys.

One difficulty with this explanation for New Guinea is that this kind of asymmetry is only present on Mt. Wilhelm. Two factors could account for this. The asymmetry can only develop where a deeply dissected terrain is present and secondly no prominent rock structures such as bedding in limestone, layering in lavas or foliation in schist must be present otherwise they override the climatic geomorphic factors.

It is interesting to note that a certain asymmetry in the distribution of plants has been observed by SMITH (1977) with altitudinal limits being some 200 m higher on east facing slopes.

Apart from the two mountains there are several other isolated mountain areas that experienced glacial ice cover (LÖFFLER, 1972). The largest of these is Mt. Albert Edward, an extensive summit surface in the eastern part of the central ranges. Despite of the modest summit height of 3980 m the plateau area was extensively glaciated with some 90 km^2 being under ice. The oldest deglaciation date is 12 000 yrs. BP.

The other relatively large area of glaciation was on the Saruwaged Mountains on the northern coastal ranges where a limestone plateau was covered by an ice cap measuring some 80 km^2. Surprisingly the snow line on this mountain which at present is the wettest area is some 100 to 200 m higher than elsewhere in New Guinea and the reason for this must be sought in the extraordinarily high rates of uplift of these mountains. This is manifested in a series of raised coral terraces along the northern coast (CHAPPELL, 1974).

The ice cover on all other mountains of New Guinea was considerably smaller mostly extending only over a few square km. However with great regularity all mountains extending into the Pleistocene snowline which was at 3600 m ± 50 were glaciated and the contrast between the glaciated and non-glaciated terrain is always pronounced (Fig. 4). This contrast is further accentuated by a contrast in vegetation. The U shaped glacial valley floors are always covered with grassland while the V shaped valleys below are always forest covered. This close correlation between former ice cover and present day extent of grassland is not simply the result of climatically controlled altitudinal zonation since the lower limits of these grasslands vary considerably with the extent of the glaciers.

The presence of grasslands in these glacial valleys is probably primarily due to the high degree of wetness. Frost may be an additional factor but the sharp boundary between grassland and forest at the change of valley profile indicates that cold air drainage is not the main factor since it would also affect the V shaped valleys at least at their upper margin where they meet the U shaped valley section. The occurrence of these valley floor grasslands well below the natural timber line has undoubtedly permitted easier access to these mountains for primitive man and through burning and felling he has extended these grasslands from the valley floors to the adjacent slopes. Comparison between mountains with relatively easy access and close to populated areas and those of greater remoteness (Fig. 4) shows that man induced extension of the grasslands is much more advanced on the former (LÖFFLER, 1979).

The reconstruction of the climate during the last glaciation is complicated by conflicting geomorphological and palynological evidence (WALKER and FLENLEY, 1979; LÖFFLER, 1980). The Pleistocene snowline was at 3600 m ± 50 and the present snowline is some 1000 to 1100 m higher indicating a Pleistocene snowline depression of this magnitude. This would correspond to a temperature depression of 5–6 °C assuming precipitation was not drastically different to the present. There is no evidence for such a difference in precipitation at least as far as the mountain areas are concerned and the low snowline itself would not be explicable under low precipitation rates.

Palynological evidence from some sites especially from Sirunki (WALKER and FLENLEY, 1979; FLENLEY, 1984) however suggest that the temperature depression was of the order of 10 °C calculated from a depression of the timber line of over 1500 m.

My own work in the Lake Trist area, however, shows that there was no dramatic change in vegetation around a small lake basin at 2000 m altitude. Although the pollen data do not permit such a fine resolution as the Sirunki data they indicate that during the last 32 000 years the vegetation around the lake was dominated by *Nothofagus* forest. There is some change in sedimentation from strongly organic to less organic, and there is also some change in the pollen spectrum with an increase in pollen from aquatic plants up the sequence, reflecting a change in the hydrological regime of the small karst basin. This change may have been caused by a change in precipitation, however the continued presence of *Nothofagus* montane forest around the small basin indicates continuously high rates of precipitation. The total absence of pollen of "alpine" and "subalpine" plants, however, clearly shows that in this area the altitudinal vegetation zones were not depressed by the same amount as at Sirunki. The exceptionally large depression of the forest/grassland boundary at Sirunki may reflect the basin position of Sirunki where excessive wetness and frost may have prevented forest growth. Similar basins exist today some 1000 m below the timber line as for instance the Neon Basin below Mt. Albert Edward (PAIJMANS and LÖFFLER, 1972).

4. Deglaciation

Although there is rough agreement in the dates of deglaciation across New Guinea there is considerable variation in detail.

From about 15 000 yrs. BP the glaciers retreated rather rapidly and by 11 000 yrs. BP most New Guinea mountains were ice free and by 9000 yrs. BP even those that have a present day ice cover. The recession did not proceed continuously but was interrupted by numerous readvances. The number of recessional moraines varies from mountain to mountain as a result of local orographic and climatic conditions. Most numerous are the recessional moraines on the eastern slopes of Mt. Giluwe where over 20 single moraines can be distinguished (Fig. 2). Dates of peat bogs behind these moraines have given minimum dates of 13 050 ± 750 yrs. BP for the second oldest group of moraines, 11 250 ± 550 yrs. BP for the second youngest group and 9980 ± 280 yrs. BP for a peat bog near the main peak at 4160 m. These dates show that by 13 000 yrs. BP the ice had already receeded considerably from its maximum extent and that by 10 000 yrs. BP the mountain was free of ice and no further ice developed. The rate of ice retreat was in the order of 1 m/yr.

The deglaciation dates from Mt. Wilhelm are in good agreement with the Giluwe dates. There are only few recessional moraines present and this may reflect the completely different nature of the glaciers. On Giluwe the broad exposed and probably not very thick ice cap reacted relatively quickly to small climatic changes while valley glaciers on Mt. Wilhelm were thick and partly protected from insolation by steep sided ridges towering above the ice and consequently were much less likely to react to small climatic oszillations. The retreat on Mt. Wilhelm was therefore more uniform reflecting the general change to warmer conditions. According to the palynological work of HOPE (1976) the glaciers retreated rapidly from about 14 000 yrs. BP and by 11 000 yrs. BP most of the mountain massif was free of ice except for a small glacier probably around the main summit above 4000 m. By 9000 yrs. BP the deglaciation was complete. This slight difference between Mt. Wilhelm and Mt. Giluwe is probably due to their difference in summit height and summit morphology.

The only deglaciation date not fitting into the general trend was reported by PETERSON and HOPE (1972) from the Carstensz area where a date of 10 300 yrs. BP was obtained for moraine material at the surprisingly low altitude of 1750 m. The initial interpretation was that this extraordinary glacial advance was caused by sudden influx of moist air following the flooding of the Arafura Sea and Torres Strait during the post glacial rise in sea level. In view of the fact that in the humid tropics precipitation is usually not the limiting factor for glacial development this explanation is unlikely and it has not been upheld by the authors.

Fig. 5. Oblique aerial photograph of the Carstensz glaciers with Carstensz and Meren glaciers in the foreground and the Northwall Firn in the background. (Photograph by Australian Universities Expeditions to Irian Jaya).

Fig. 6. Mt. Wilhelm with periglacial scree at 4350–4450 m. Note the dense cover or tussock grass in the foreground indicating that periglacial activity can not be very efficient even at this altitude.

According to pollen-analytical work of HOPE (1976) the time between 7000 and 5000 yrs. BP was one of higher temperatures than today and all New Guinea mountains were free of ice. Ice redeveloped again after 5000 yrs. BP in the Carstensz Mts. and the other presently glaciated peaks and by 3500 yrs. BP a glacier advanced in the Carstensz area down to 4200 m. There were some further glacier oszillations at 3000–2400 yrs. BP, after 2400 yrs. BP and at 1500–1350 yrs. BP in the same area but the presently non glaciated mountains remained free of ice.

Present day glaciation is restricted to Mt. Carstensz where about 7 km^2 are under ice and to three isolated peaks Mt. Juliane, Mt. Wilhelmina and Idenburg Top (Fig. 5). Glaciers have been retreating rapidly over the last 35 years and the rates measured by PETERSON et al. (1973) are of the order of 33 m/yr. and 16 m/yr. for the two main glacier tongues of Carstensz. Air photo evidence shows that the ice on all other New Guinea mountains has also retreated and in two cases completely disappeared. The ice retreat in New Guinea is therefore broadly synchronous with world wide glacier fluctuations and is probably due to a slight rise in temperature since precipitation does not appear to be a limiting factor for glacier development in this area.

5. Periglacial Processes

The relative geomorphic stability of the high mountains of New Guinea is surprising in view of the generally high rate of processes in the lower altitudinal zones (LÖFFLER, 1977). There are several reasons for this. Most important are the diurnal regime of melting as already mentioned in connection with the well developed moraines, the relative insignificance of periglacial solifluction, and the protective cover of the dense root mat of the upper montane forest or peat layer of high altitude grasslands.

Despite systematic investigations no evidence for periglacial solifluction has been found outside the areas formerly covered by ice, and one must assume that periglacial solifluction did not have a significant erosional impact during and after the glaciation.

This fact, however, is hardly surprising if one studies the present day periglacial processes and their altitudinal distribution. Periglacial solifluction is an important process only above 4350 m (LÖFFLER, 1975), and even here it is only a surficial process affecting a soil horizon of some 10 cm (Fig. 6). With the present day snowline at 4600–4650 m this means that the periglacial altitudinal belt is compressed to a mere 250–300 m and the reason for this must be sought in the exceptionally uniform climate of the New Guinea mountains with a small range of diurnal temperature variations and the virtual absence of any seasonal temperature changes (HNATIUK et al., 1976).

During the Pleistocene the ice caps and glaciers extended well below the climatic snowline especially where larger ice masses were developed. If we assume a similar uniformity in climate and thus a similarly narrow altitudinal belt of periglacial activity then most of the terrain that was climatically suitable for periglacial activity, namely the belt of diurnal frost and thaw, was covered by glacial ice.

Once the ice retreated, the formerly glaciated terrain became subject to periglacial solifluction processes, however, since the temperature rose rather rapidly the period during which this occurred was too short to affect the low lying moraines to any significant degree. Once a vegetation cover had developed surface erosion was reduced even more since both the upper montane forest as well as the dense grass cover with its thick root mat stabilize the slopes.

References

CHAPPELL J. (1974): Geology of coral terraces, Huon Peninsula, New Guinea. Bull. Geol. Soc. Am., 85, 553–570.

DOW, D. B. (1968): A geological reconnaissance in the Nassau Range, West New Guinea. Geol. en. Mijnbouw, 47, 37–46

DOZY, J. J. (1938): Eine Gletscherwelt in niederländisch Neuguinea. Z. Gletscherkd. Glazialgeol., 26, 45–51.

FLENLEY, J. R. (1984): Late Quaternary Changes of Vegetation and Climate in the Malesian Mountains. Erdwiss. Forschung, XVIII, 261–267.

HNATIUK, R. J., J. M. B. SMITH and D. N. MCVEAN (1976): Mt. Wilhelm Studies 2: The climate of Mt. Wilhelm. Dept. Biogeogr. and Geom. Publ. BG/4, Aust. Natn. Univ., Canberra.

HOPE, G. S. (1976): The vegetational history of Mt. Wilhelm, Papua New Guinea. J. Ecol., 64, 627–664.

– and J. A. PETERSON (1975): Glaciation and vegetation in the high New Guinea mountains. Bull. Roy. Soc. N. Z., 13, 155–162.

–, –, U. RADOK and I. ALLISON (1976): The equatorial glaciers of New Guinea. Rotterdam.

LÖFFLER, E. (1972): Pleistocene glaciation of Papua New Guinea. Z. Geomorphol., N.F., Suppl. 13, 32–58.

– (1975): Beobachtungen zur periglazialen Höhenstufe in den Hochgebirgen von Papua New Guinea. Erdkunde, 28, 13–18.

– (1976): Potassium-argon dates and pre-Würm glaciations of Mount Giluwe volcano, Papua New Guinea. Z. Gletscherkd. Glazialgeol., 12, 55–62.

– (1977): Geomorphology of Papua New Guinea. Aust. Nat. Univ. Press.

– (1979): Ursprung und Verbreitung der Paramo-Grasländer in Ostneuguinea. Erdkunde, 33, 226–236.

– (1980): Neuester Stand der Quartärforschung in Neuguinea. Eiszeitalter und Gegenwart, 30, 109–123.

–, D. E. MACKENZIE and A. WEBB (1980): Potassium Argon dates from New Guinea highland volcanoes and their relevance to the geomorphic history. J. Geol. Soc. Aus., 26, 387–397.

PAIJMANS, K. and E. LÖFFLER (1972): High-altitude forests and grasslands of Mt. Albert Edward, New Guinea. J. Trop. Geogr., 34, 58–64.

PETERSON, J. A. and G. S. HOPE (1972): A lower limit and maximum age for the last major advance of the Carstensz glaciers, West Irian. Nature, 240, 36–37.

PETERSON, J. A., G. S. HOPE and R. MILTON (1973): Recession of snow and ice fields of Irian Jaya, Republic of Indonesia. Z. Gletscherkd. Glazialgeol., 9, 73–87.

PORTER, S. C., M. STUIVER and I. C. YANG (1977): Chronology of Hawaiian glaciation. Science, 195, 61–63.

REINER, E. (1960): The glaciation of Mt. Wilhelm, Australian New Guinea. Geogr. Rev., 50, 491–503.

SHACKLETON, N. J. and N. D. OPDYKE (1973): Oxygen isotope and paleomagnetic stratigraphy of equatorial Pacific core V 28–238, Oxygen isotope temperature and ice volume on a 10^5 year and 10^6 year scale. Quat. Res., 3, 39–55.

SMITH, J. M. B. (1977): Vegetation and microclimates of east-and-west facing slopes in the grasslands of Mt. Wilhelm, Papua New Guinea. J. Ecol., 65, 39–53.

VERSTAPPEN, H. T. (1964): Geomorphology of the Star Mountains, Nova Guinea. Geology, 5, 101–155.

WALKER, D. and J. R. FLENLEY (1979): Late Quaternary vegetational history of the Enga Province of upland Papua New Guinea. Phil. Trans. Roy. Soc. London., Biol. Ser., 286, 265–344.

Discussion to the Paper Löffler

Dr. C. Schubert

The asymmetry you mentioned on Mt. Wilhelm is very similar to the one found in the Sierra Nevada de Mérida. Here, the western side has a much better-developed glacial complex than the eastern side.

Prof. Dr. E. Löffler:

It is not surprising that the east-west asymmetry is found in other parts of the tropical high mountains for the same reasons as I explained and as in fact already noted by TROLL. However, compared to the marked north-south asymmetry of the subtropical high mountains it will always be a relatively minor feature and it will only develop where prominent rock structures are not interfering.

Prof. Dr. W. Klaer:

1. What is the reason for the moraine of the last glacial period below the field station on Mt. Wilhelm being still so incredibly well preserved, while in the Alps it would correspond more to the type of the 1850-moraine?
2. How did the snowline-depressions of the Pleistocene glacial period effect the lower sections of the mountain?
3. How can the "moraine steps" at Mt. Giluwe be explained?

Prof. Dr. E. Löffler:

1. The excellent preservation of the moraines of the last glacial period is mainly due to two factors. Firstly, to the daily rhythm of melting of the glaciers even in times of their retreat. For the same reason, fluvioglacial sediments are mostly lacking. Secondly, to the small effect of periglacial solifluction, which must be explained by the extreme uniformity of the climate and thus the extremely narrow altitudinal range of the zone of periglacial processes. In addition to this the areas suited for periglacial processes, i.e. the areas with daily freeze-thaw action, were largely covered with ice during the glacial period. A periglacial zone hardly existed during this period. Thus, no indications of older periglacial forms can be found outside the area which was once covered by glaciers. The thick mossy or upper montane forest, which mostly covers the moraines today, also contributes to their good preservation.
2. The snowline-depression of about 1000–1100 m first of all effected a depression of the vegetation belts in lower sections; there is, however, no agreement concerning its extent, as can be learnt from the paper of Dr. FLENLEY. I think that the amount for the grassland depression and the snowline depression is roughly the same while FLENLEY and also WALKER and HOPE report a substantially higher figure based on pollenanalytic results. It is still unknown how this depression effected the lower belts. From the geomorphological point of view, however, it can be stated with some certainty that the depression of altitudinal zones did not result in a considerable change of geomorphological processes.
   This is quite obvious, since even today a differentiation of geomorphological processes according to altitudinal zones does hardly exist, except for the periglacial and glacial zones.
3. I would not use the term "moraine steps". As can be seen from the aerial photograph (and even better from the stereopair, Fig. 2) the small moraines represent low ridges, 0.5–2.0 m high that follow the general shape of the broad plateau area like reversed contour lines bending downwards in valleys and depressions and upwards on ridges and spurs. For this reason alone they can not be related to the structure of the basalts as might seem from the aerial photo at first sight. Their moraine character is also obvious in the field. My explanation for the multitude of moraines on Mt. Giluwe lies in the particular topographic situation of the Mt. Giluwe volcano as compared to the other mountains of New Guinea in particular since these moraines are only present on this mountain. On Mt. Giluwe they occur mainly on the broad and open eastern and western slopes and are

largely lacking in the deeper glacial valleys that extend to the south and north. Therefore I think that the moraines are related to the ice cap situation. We do not know how thick the ice cap was but the glacier depositing the moraine of the main glaciation must have been considerably thicker than the glacier that was responsible for the small moraines. I assume that with the general warming up at the end of the last glacial period the ice cap first lost its thickness without much altitudinal retreat. It then reacted quite sensitively to small climatic oscillations and even managed to overtop the main moraine without causing much erosion. The valley glaciers being much thicker than the ice cap reacted much more slowly to small climatic changes and therefore reflect the general trend to warmer conditions.

Dr. C. Schubert:

Concerning the small moraines within the large end moraine, could they also be explained by rapid glacier retreat with very short stationary periods?

Prof. Dr. E. Löffler:

The small moraines within and partly overtopping the moraine of the main glaciation have intrigued me too and I have mentioned already that their development must be linked with the particular ice cap conditions on the broad western and eastern slopes of the volcano. Your suggestion that the small moraines could be explained by rapid glacier retreat with very short stationary periods does not account for the overtopping of the main moraine and the C^{14} dates indicate that retreat was not all that rapid.

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Late Quaternary Changes of Vegetation and Climate in the Malesian Mountains

John R. Flenley

With 4 Figures and 1 Table

The Malesian floristic region, as defined by GOOD (1947) consists mainly of South-east Asia and New Guinea. We shall be concerned here only with New Guinea, Borneo and Sumatra, since this is where most of the research has been carried out. Malesia differs from the other major equatorial regions, Africa and South America, in consisting of separate islands. During the Pleistocene, however, these would mostly have been amalgamated into two main land masses, the Sunda platform and the Sahul shelf.

Many, but not all, of the mountains of Malesia are volcanic. In New Guinea the mountains rise to over 5000 m. Research has chiefly been carried out on the lower mountains of eastern New Guinea, however. The main interest in New Guinea has been in fluctuations of the altitudinal forest limit. The mountains are generally forested today up to c. 3600 m, except where forest clearance by man has occurred. Above the forest is the "tropicalpine" vegetation, rich in taxa of temperate affinities. This gives way at c. 4500 m to bare ground, and permanent snow occurs above about 4700 m. There are also boundaries within the forest, especially that between the lower montane forests, dominated by Fagaceae, especially species of *Nothofagus*, *Lithocarpus* and *Castanopsis*, and the mixed mountain and subalpine forests, which tend to be dominated by Gymnosperms such as *Papuacedrus*, *Podocarpus*, *Phyllocladus*, *Dacrycarpus* (FLENLEY, 1969; WALKER and FLENLEY, 1979).

The palynological technique for vegetational reconstruction relies heavily on modern pollen rain studies. The pollen spectra collected on the New Guinea mountains (FLENLEY, 1973) suggest a fairly direct relationship between vegetation and modern pollen rain. For example, samples from "beech" *(Nothofagus)* forest are dominated by *Nothofagus* pollen; samples from "oak" forest by *Lithocarpus/Castanopsis* pollen. There is one exception to this; samples from above the forest limit contain significant quantities of forest pollen. They are recognisable, however, by the high values for Gramineae and/or the presence of "alpine" taxa. These include *Astelia*, *Drapetes*, *Oreomyrrhis* and some *Plantago* spp., none of which occur below 3000 m.

Lake Inim, in a tectonic basin at 2550 m, is about 1000 m below the forest limit (FLENLEY, 1972; WALKER and FLENLEY, 1979). It has a large surrounding swamp, but inflow streams are few and small. The surrounding *Nothofagus* forest is being actively cleared for cultivation of sweet potato. The pollen diagram from this site shows dominance by *Nothofagus* during the latter part of the time represented, until very recent forest clearance. The earlier phase represented, however, has high values for Gramineae and *Astelia*, and forest pollen drops to 50%. It is difficult to avoid the conclusion that the forest limit was depressed by at least 1000 m. The end of this phase is between 8000 and 12 000 B.P. The inversions in the radiocarbon dates here could result from various causes. One possibility is that a lowering of water level led to erosion and redeposition of sediment at this time.

The nearby Sirunki Swamp, at 2500 m, is a very much larger tectonic basin and has major inflow streams, so that pollen could be derived from a much greater range of altitudes. The site extends beyond the range of C^{14} dating, but the part so far published (WALKER and FLENLEY, 1979) covers the last c. 33 000 years. This is a pollen influx diagram (i.e. in grains/cm^2/annum). In the earlier half of this record there is a great abundance of *Astelia* and Gramineae pollen, but there is an interesting peak of forest pollen between 28 000 and 25 000 B.P. The forest revives between 14 000 and 13 000 B.P., but has disappeared again by 12 500 B.P. Forest development began again about 9000 B.P. and a closed forest resulted. From 5000 B.P. forest starts to decline, however. This decline is much earlier than at Inim, and is therefore diachronous. It is almost certainly the result of forest clearance by man. The decline in all pollen influx from c. 3000 B.P. is perhaps related to overgrowth of the lake by swamp, reducing inwash of material.

From Draepi at 1900 m we also have evidence of early forest clearance, from at least 5100 B.P. (POWELL et al., 1975).

Analogous results have been obtained from the group of sites on Mt. Wilhelm (HOPE, 1976). At Imbuka bog (3550 m) a replacement of unforested by forested conditions was dated at approximately 9000 B.P. By 8500 B.P. the forest limit had reached even to Brass Tarn at 3910 m, which is above its present level. It declined again about 5000 B.P., perhaps either as a result of climatic change or because of burning by hunting parties. There is no agriculture at this altitude. The tree line never reached the summit bog.

The overall sequence during the last 30 000 years in the New Guinea mountains may thus be summarized as shown in Fig. 1. The forest limit, apart from a brief excursion, was below 2500 m (perhaps around 2200 m) until 14 000 B.P. The chief rise in forest limit occurred about 9000 B.P. It is particularly interesting that there is no evidence for the existence of the mixed-mountain and sub-alpine forests until c. 9000 B.P. It has been suggested that these survived as rare individuals of the constituent taxa around the forest limit during the Pleistocene (WALKER and FLENLEY, 1979). Perhaps the Pleistocene climate was in some way less suitable for them: possibly too dry.

The mountains of Western Malesia are lower, and only from Mt. Kinabalu (4000 m), in Borneo, do we have evidence of glaciation. The summit plateau of this granite mountain is glacially smoothed and there are other glacial features (KOOPMANS and STAUFFER, 1968).

A small pool on the summit plateau is perhaps the result of glacial plucking adjacent to a fault. The basal organic sediment from this pool gave a radiocarbon date of 9186 ± 120 B.P. (FLENLEY and MORLEY,

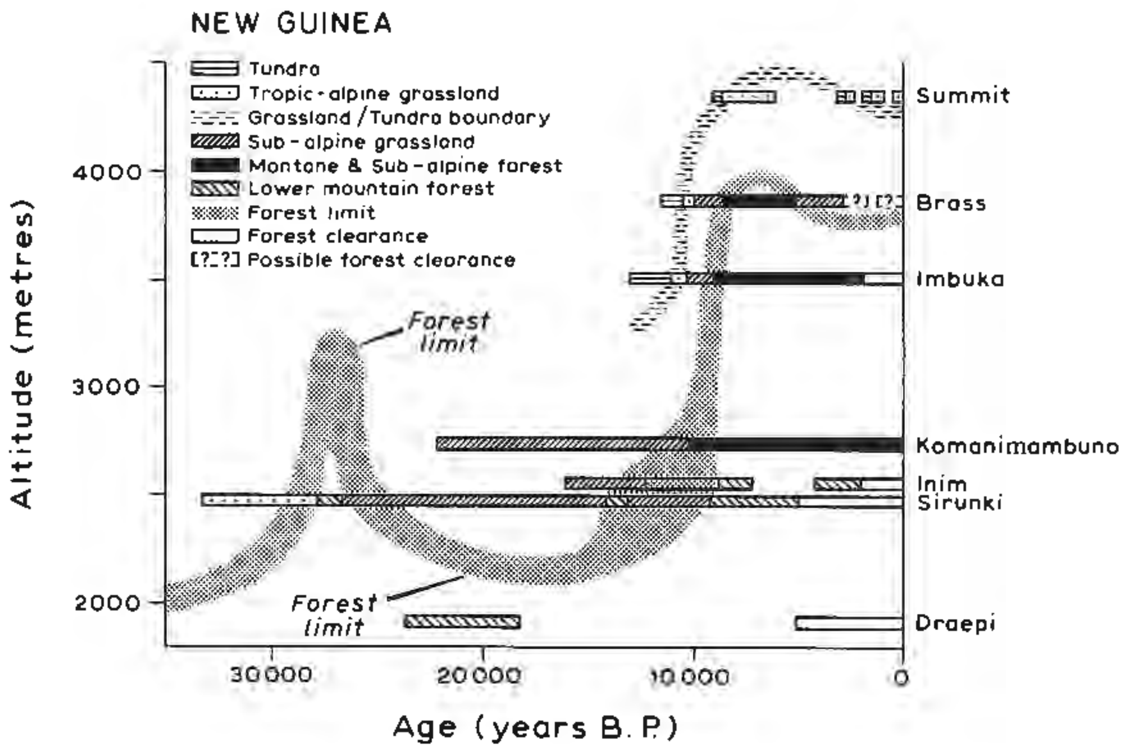

Fig. 1. Summary diagram of Late Quaternary vegetational changes in the New Guinea Highlands (after: FLENLEY, 1979).

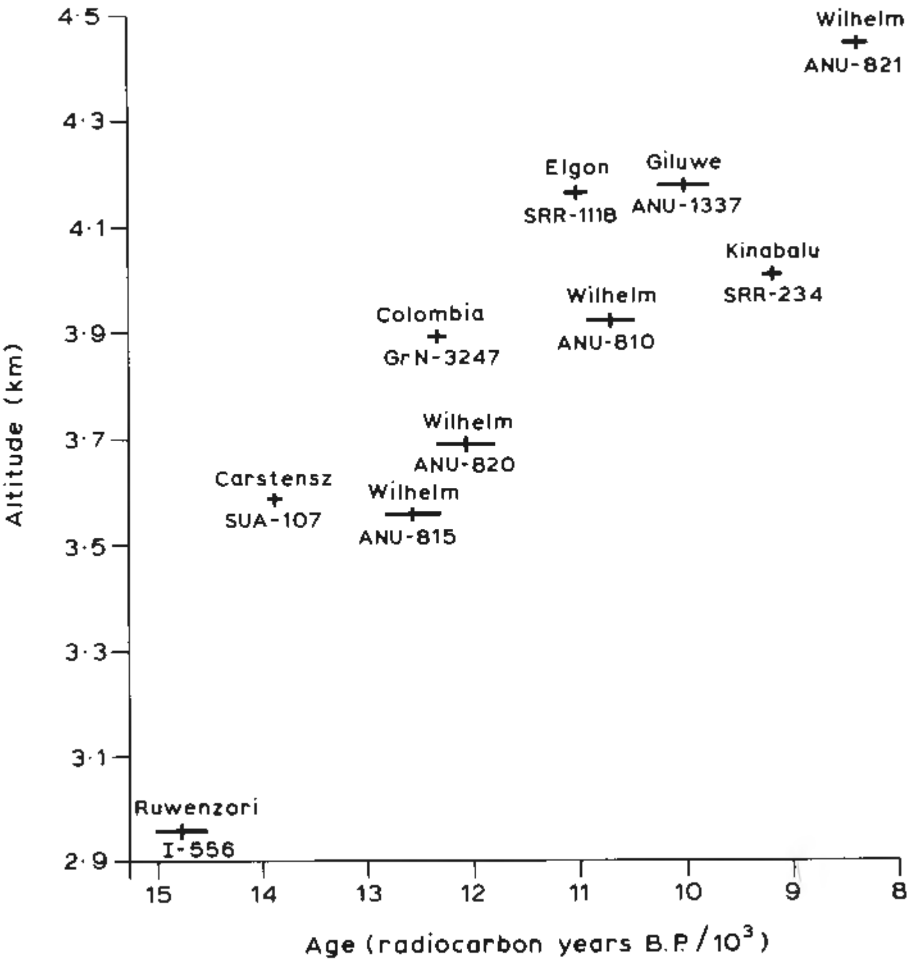

Fig. 2. Minimum ages for deglaciation of some equatorial mountains (after: FLENLEY and MORLEY, 1978).

1978). This provides a minimum age for deglaciation of the plateau. The date is not altogether out of line with some from other tropical mountains at various altitudes (Fig. 2). So far we have no pollen evidence from Borneo, although it seems an appropriate area for study.

The Sumatran mountains form a chain, chiefly volcanic, with a rift valley running longitudinally through it (VAN BEMMELEN, 1949; VERSTAPPEN, 1973). The result is that there are numerous sites suitable for pollen analysis (MORLEY, FLENLEY and KARDIN, 1973). The principal areas studied, by the group centred at Hull, U. K., are those near Mt. Kerinci and those near Lake Toba.

The Sumatran mountains bear a vegetation which, where undisturbed, may be zoned approximately as shown in Table 1 (MORLEY, 1982). The forest types of particular interest to us are the Sub-montane forest, c. 1000 – c. 1400 m, Montane forest I, c. 1400 – c. 1800 m, Montane forest II, c. 1800 – c. 2400 m and Ericoid forest, 2800–3000 m. Characteristic taxa include *Celtis* sp. for Sub-montane forest, and for Montane forest II, *Dacrycarpus imbricatus* and *Symingtonia*. There are no taxa absolutely characteristic of Montane forest I, but it tends to be rich in *Quercus* and *Lithocarpus* species.

A limited number of surface samples suggests that the modern pollen rain is rather similar in distribution to its parent vegetation types, although there is some tendency, as in New Guinea, for pollen types to be carried to higher altitudes (e.g. *Celtis*).

Table 1. Altitudinal Zonation of Vegetation in Sumatra (after MORLEY, 1982).

Vegetation type	Structural characteristics	Altitudinal range	Orographic Zone (VAN STEENIS, 1965, 1972)	Rain Forest Formation (GRUBB, 1974; WHITMORE, 1975)
Ericaceous scrub	low microphyll shrubs with herbs	3000 m – 3600 m	Sub-Alpine Zone	Upper Montane Rain Forest Formation
Ericoid forest	closed, low mossy microphyll forest	c. 2800 m – 3000 m		
Gleichenia scrub	Gleicheniaceae with low microphyll trees and shrubs	c. 2400 m – c. 2800 m		
Montane forest II	closed, high-stemmes floristically little-diverse mossy mesophyll forest, lianes rare, ground flora rich	c. 1800 m – c. 2400 m	Montane Zone	
Montane forest I	closed, high-stemmed, floristically diverse mesophyll forest, mosses and lianes common, buttresses and emergents rare, ground flora rich	c. 1400 m – c. 1800 m		Lower Montane Rain Forest Formation
Sub-montane forest	closed, high-stemmed, floristically diverse mesophyll forest, emergents and lianes common, buttresses present, little moss, poor ground flora	c. 1000 m – c. 1400 m	Sub-Montane Zone	

Lake Padang at 950 m is a small tectonic lake with a surrounding swamp about 300 m × 1 km (MORLEY, 1982). The site is surrounded by hills up to 1250 m. The pollen record extends back to about 10 000 B.P. and shows an early phase in which *Dacrycarpus imbricatus* and *Symingtonia populnea* occur in small quantities. It is not suggested that these were growing next to the lake, but they could have been on the surrounding hills. Sub-montane taxa are absent, so the vegetation around the lake was probably similar to Montane forest I. A change to present-day forest types occurred about 8600 B.P. From about 4000 B.P. there is evidence of forest disturbance, indicated especially by abundance of *Trema* pollen. According to MORLEY, an altitudinal shift of c. 350 m would explain the change at 8600 B.P.

The record is extended by studies at Lake di-Atas (1535 m). The site is a swamp in a narrow side-arm of this tectonic lake in the rift valley. The pollen record extends back to 31 000 B.P. The early part is all dominated by Gymnosperms, including *Dacrycarpus imbricatus*. There is even a peak of Gramineae and herbs at c. 21 000 to c. 18 000 B.P. Carbon dates in this part of the core are inverted, suggesting disturbance of the deposits. One possibility is a lowered water level, leading to erosion of marginal sediments. Perhaps the climate was drier and/or colder, either of which would be compatible with the peak of Gramineae. There is a gradual change to forest of modern type indicated from about 12 000 B.P., and the Gymnosperms disappear completely by about 7000 B.P. Disturbance is suggested (especially at another site in the same area) from c. 6000 B.P., by peaks of *Trema*, and, much later, Gramineae (J. C. NEWSOME, pers. comm.).

From the Lake Toba area we have evidence from two craters at 1400 m on the Toba plateau. Pea Sim-sim crater (MALONEY, 1980) has a record extending back to ca. 18 000 B.P. Before ca. 12 000 B.P. it shows presence of Gymnosperms (including *Dacrycarpus*), and *Symingtonia* in some quantity. About 17 000 B.P. there is a peak of herbs reminiscent of that found at Lake di-Atas during the Gymnosperm phase there. Forest disturbance is evidenced continuously from c. 7000 B.P. Sipinggan crater has a 12 000 year record which substantially confirms what is found in the same period at Pea Sim-sim (MALONEY, 1981).

The tentative conclusions to be drawn from this Sumatran work seem to be:

a) The Sub-montane/Montane forest boundary was depressed by c. 350 m (1400–1050 m) prior to 8600 B.P.
b) The Montane forest I/II boundary was depressed by c. 400 m (1800 m–1400 m) prior to c. 12 000 B.P.
c) The Sub-alpine/Alpine zone boundary was depressed by c. 1000 m (2400 m–1400 m) around 17 000 B.P. for a limited period.

If we combine these results with those for New Guinea (Fig. 3), we find a remarkably consistent series of events. Late Pleistocene vegetation zones were everywhere depressed and/or compressed. The gradual change to present vegetation took place everywhere between 14 000 and 8600 B.P., and especially between 12 000 and 9 000 B.P. The forests established by 8000 B.P. began to be disturbed as early as 7000 B.P., especially around 1400 m altitude. By 4000 B.P. forest clearance was common between 950 m and 2500 m.

The compression of zones in the Late Pleistocene is perhaps expressible in terms of mean annual temperature. The present lapse rate of c. 0.6 °C per 100 m conforms with the sea surface temperature,

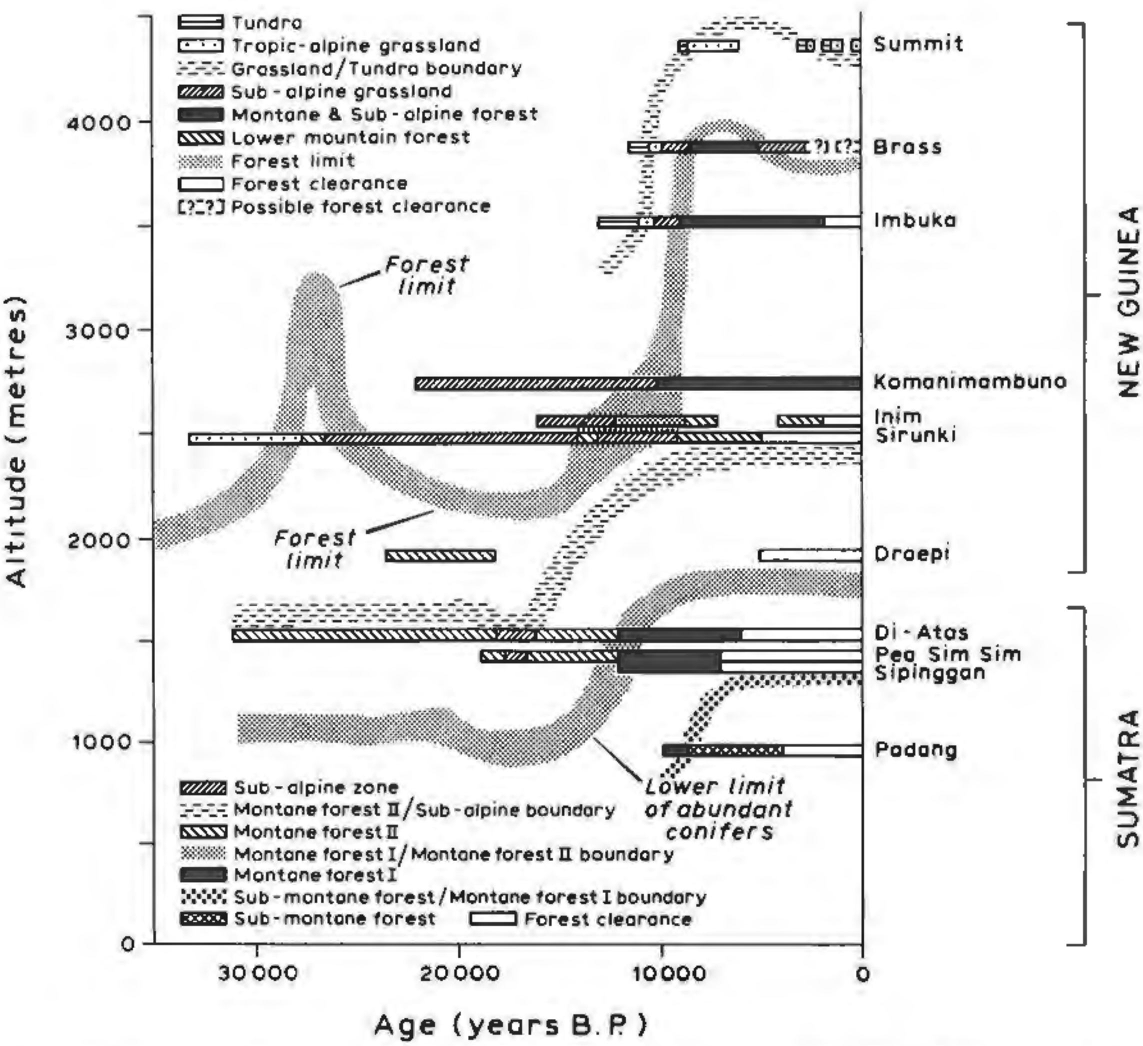

Fig. 3. Combined summary diagram showing Late Quaternary vegetational changes in the New Guinea Highlands and Sumatra.

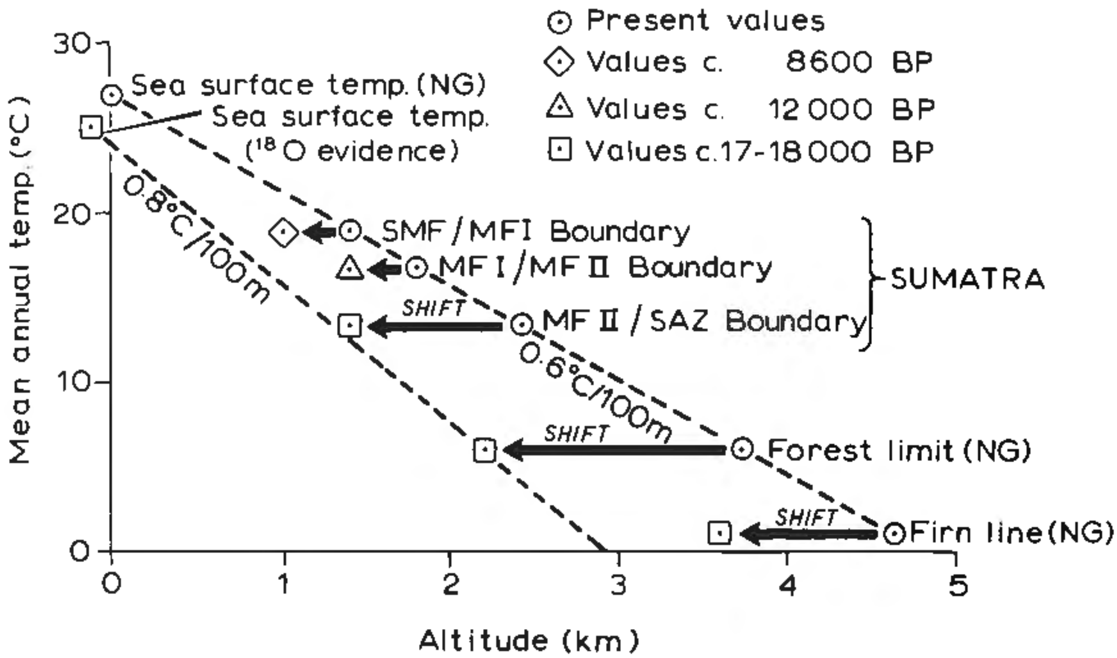

Fig. 4. The relationship between mean annual temperature and altitude in South-East Asia at present and in the Late Quaternary, the latter as judged from palynological evidence. Abbreviations refer to the altitudinal zonation given in Table 1 and Fig. 3.

vegetation zone boundaries and the snow line. At c. 18 000 B.P. the sea surface temperature of New Guinea and Sumatra was only c. 2 °C lower than at present (CLIMAP, 1976), and the surface perhaps 100 m lower. The depressions of the various vegetation zone boundaries are shown on Fig. 4, assuming that these are determined by mean annual temperature and that their temperature requirements remained the same in the past. Including also the marine temperatures, we now have three points for 17 000–18 000 B.P. These fall almost on a straight line which corresponds to a lapse rate of c. 0.8 °C per 100 m. This steeper lapse rate is nearer to the dry adiabatic lapse rate and therefore implies a drier atmosphere. This would be consistent with the relatively small depression of the snow line, which was perhaps kept high by low precipitation.

References

BEMMELEN, R. W. VAN (1949): The geology of Indonesia. Vols. I, II a and II b, Govt. Printing Office, The Hague.

CLIMAP PROJECT MEMBERS (1976): The surface of the Ice-Age Earth. Science, N.Y., 191, 1131–1137.

FLENLEY J. R. (1969): The vegetation of the Wabag region, New Guinea Highlands: a numerical study. J. Ecol. 57, 465–490.

– (1972): Evidence of Quaternary vegetational change in New Guinea. In: ASHTON, P. and M. (Eds.): The Quaternary Era in Malesia. Transactions of the Second Aberdeen-Hull Symposium on Malesian Ecology. Aberdeen 1971. University of Hull, Department of Geography, Miscellaneous Series No. 113, Hull, England, 99–109.

– (1973): The use of modern pollen rain samples in the study of the vegetational history of tropical regions. In: BIRKS, H. J. B. and R. G. WEST (Eds.): Quaternary Plant Ecology. The 14th Symposium of the British Ecological Society, Mar. 1972. Blackwell, Oxford, 131–141.

– (1979): The equatorial rain forest: a geological history. London.

– and R. J. MORLEY (1978): A minimum age for the deglaciation of Mt. Kinabalu, East Malaysia. Modern Quaternary Research in South-East Asia, 4, 57–61.

GOOD, R. (1947): The geography of the flowering plants. 1st edition, London.

GRUBB, P. J. (1974): Factors controlling the distribution of forest-types on tropical mountains: new facts and a new perspective. In: FLENLEY, J. R. (Ed.): Altitudinal Zonation in Malesia. Transactions of the Third Aberdeen-Hull Symposium on Malesian Ecology, Hull, 1973. University of Hull, Department of Geography, Miscellaneous Series No. 16, Hull, England, 13–46.

HOPE, G. S. (1976): The vegetational history of Mt. Wilhelm, Papua New Guinea. J. Ecol., 64, 627–663.

KOOPMANS, B. and P. H. STAUFFER (1968): Glacial phenomena on Mount Kinabalu, Sabah. Borneo Region, Malaysia, Geological Survey Bull., 8, 25–35.

MALONEY, B. K. (1980): Pollen analytical evidence for early forest clearance in North Sumatra. Nature, 287, 324–326.

– (1981): A pollen diagram from Tao Sipinggan, a lake site in the Batak Highlands of North Sumatra, Indonesia. Modern Quaternary Research in South-east Asia, 6, 57–66.

MORLEY, R. J. (1982): A palaeoecological interpretation of a 10000 year pollen record from Danau Padang, Central Sumatra, Indonesia. J. Biogeogr., 9, 151–190.

– , J. R. FLENLEY and M. K. KARDIN (1973): Preliminary notes on the stratigraphy and vegetation of the swamps and small lakes of the Central Sumatran Highlands. Sumatra Research Bulletin, 2 (2), 50–60.

POWELL, J. M., A. KULUNGA, R. MOGE, C. PONO, F. ZIMIKE and J. GOLSON (1975): Agricultural traditions of the Mount Hagen Area. University of Papua New Guinea, Department of Geography, Occasional Paper No. 12.

STEENIS, C. G. G. J. VAN (with A. F. SCHIPPERS-LAMMERTSE) (1965): Concise plant-geography of Java. In: BACKER, C. A. and R. C. BACKHUIZEN VAN DER BRINK (Eds): Flora of Java. Vol. 2, 1–72.

– (1972): The Mountain Flora of Java (Illustrated by Amir Hamzah and Moehamad Toha). Leiden.

VERSTAPPEN, H. T. (1973): A geomorphological reconnaissance of Sumatra and adjacent islands (Indonesia). Groningen.

WALKER D. and J. R. FLENLEY (1979): Late Quaternary vegetational history of the Enga District of Upland Papua New Guinea. Phil. Trans. R. Soc., B, 286, 265–344.

WHITMORE, T. C. (1975): Tropical Rain Forests of the Far East. Oxford.

Discussion to the Paper Flenley

Priv. Doz. Dr. P. Frankenberg:

You showed a synthetic diagram in which one saw a peak of the upper timberline at about 30000–28000 B.P. for New Guinea. This could mean the Stillfried B-Interglacial, documented by ice-core analysis in Greenland and the Antarctis by DANSGAARD et al. This did obviously not appear in Sumatra. What could be the reason for these differences of upper timberline development in New Guinea and Sumatra?

Prof. Dr. J. R. Flenley:

I think there are three possible reasons. Firstly, our Sumatra data is from a much lower altitude and concerns changes within the forest, rather than the timberline. At this altitude the changes could have been relatively minor.

Secondly, our pollen diagram is estimated to go back to c. 31000 B.P., but this is based on a single carbon date and the diagram could start only after 28000 B.P.

Thirdly, our pollen samples are widely spaced in this part of the core, so it is possible, if unlikely, that a 2000 year event could be missed.

Dr. C. Schubert:

I am very happy with the temperature gradient you derive from your palynological data (0.8 °C/100 m). We have found a very similar glacial gradient for the Dominican Republic, based on different data, namely CLIMAP sea-level tempeature estimates, elevation of glacial erosional and sedimentary features, and the "Massenerhebungseffekt".

Prof. Dr. J. R. Flenley:

Since preparing the paper I have heard that new estimates for the Pleistocene sea surface temperatures in the S.E. Asian region are somewhat lower. Thus the value of 0.8 °C per 100 m for the lapse rate may now be too high.

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Franz Steiner Verlag Wiesbaden GmbH · Stuttgart (1984)

The Pleistocene and Recent Extent of the Glaciers of the Sierra Nevada de Mérida, Venezuela

Carlos Schubert

With 5 Figures and 1 Table

Abstract

The Sierra Nevada de Mérida and its northern branch, the Sierra de Santo Domingo, were affected by the Mérida Glaciation during the Late Pleistocene; this glaciation culminated at about 18 000 years B.P. and ended at about 13 000 years B.P., based on radiocarbon dating and comparison with the Cordillera Oriental of Colombia. The Mérida Glaciation was characterized by at least two main glacial advances: a possible early one which reached 2600 to 2800 m elevation, and a well documented late advance, which reached 3000 to 3500 m. This glaciation gave rise to a typical Alpine glacial topography and large glacial sedimentary deposits in the form of morainic complexes. A reconstruction of the Pleistocene glaciers suggests that the great late glacier system of these two mountain ranges occupied an area of less than 197 km^2; at present, only remnants of this system remain in the Sierra Nevada de Mérida, occupying an area of less than 3 km^2. This implies an areal glacier retreat of 98.5% with respect to the Late Pleistocene. The Holocene glaciers probably experienced small neoglacial advances; during the last 100 years, a spectacular glacier retreat has been documented, based on photographs, maps, and paintings. In the Sierra de Santo Domingo, a small firn field existed at least until 1922. The Pico Espejo Glacier, inexistent today, still existed in 1936. It is estimated that between 1885 and 1972, the glaciers of Pico Bolívar (5002 m) retreated vertically at a rate of the order of 6 m/year.

Zusammenfassung

Die Sierra Nevada de Mérida und ihr nördlicher Ausläufer, die Sierra de Santo Domingo, wurden im Spätpleistozän von der Mérida-Vergletscherung modelliert; diese Vergletscherung erreichte ihren Höhepunkt um die 18 000 Jahre vor heute und endete um die 13 000 Jahre vor heute. Die Mérida-Vergletscherung kennzeichnete sich durch mindestens zwei Hauptgletschervorstöße: ein möglicher früherer, der bis zu 2600 bis 2800 m Höhe vorstieß, und ein gut belegter späterer, der bis zu 3000 bis 3500 m vorstieß. Diese Vergletscherung hat eine typische alpine Glazialmorphologie und mächtige glaziale Sedimentablagerungen erzeugt. Eine Rekonstruktion der pleistozänen Gletscher deutet auf eine Gesamtfläche des großen Spätglazialsystems, das in diesen beiden Sierras existierte, von weniger als 197 km^2; heute bleiben nur noch Reste dieses Systems in der Sierra Nevada de Mérida, mit einer Gesamtfläche von weniger als 3 km^2. Dieses deutet auf ein Gletscherrückgangsareal von 98,5% im Vergleich mit dem Spätpleistozän. Die holozänen Gletscher hatten wahrscheinlich kleine neoglaziale Vorstöße; in den letzten 100 Jahren ist ein spektakulärer Rückzug der Gletscher belegt worden, hauptsächlich durch Photographien, Karten und Gemälde. In der Sierra de Santo Domingo gab es ein kleines Firnfeld bis mindestens 1922. Der Pico Espejo Gletscher, der heute ganz verschwunden ist, war noch 1936 bekannt. Es ist angedeutet, daß die Gletscher des Pico Bolívar (5002 m) zwischen 1885 und 1972 eine vertikale Rückganggeschwindigkeit von ungefähr 6 m/Jahr hatten.

Resumen

La Sierra Nevada de Mérida y su ramal norte, la Sierra de Santo Domingo, fueron afectadas por la Glaciación Mérida durante el Pleistoceno Tardío; esta glaciación culminó hace aproximadamente 18 000 años A.P. y terminó hace aproximadamente 13 000 años A.P. basado en datos radiocarbónicos y comparaciones con la Cordillera Oriental de Colombia. La Glaciación Mérida se caracterizó por un posible avance glacial antiguo hasta elevaciones de 2600 a 2800 m y un avance final bien documentado hasta elevaciones de 3000 a 3500 m. Esta glaciación originó una topografía glacial alpina y grandes depósitos sedimentarios glaciales en forma de complejos morrénicos. Una reconstucción de los glaciares pleistocenos sugiere que el gran sistema glacial tardío de estas dos sierran ocupaba un área menor a 197 km^2; actualmente quedan remanentes de este sistema en la Sierra Nevada de Mérida, ocupando un área menor a 3 km^2. Esto implica un retroceso glacial holoceno del 98,5% en área con respecto al Pleistoceno Tardío. Los glaciares holocenos probablemente sufrieron pequeños avances neoglaciales; durante los últimos 100 años, se ha documentado un retroceso espectacular de los glaciares, con base en fotografías, mapas y pinturas. En la Sierra de Santo Domingo existía una pequeña capa de nieve perenne hasta por lo menos 1922. El glaciar de Pico Espejo, actualmente inexistente, todavía existía en 1936. Se estima que entre 1885 y 1972, los glaciares de Pico Bolívar (5002 m) retrocedieron verticalmente con una velocidad del orden de los 6 m/año.

1. Introduction

The Sierra Nevada de Mérida and the Sierra de Santo Domingo (Fig. 1) are the most important massifs of the Venezuelan Andes; they have an area above an elevation of 3000 m above sea level of approximately 850 km^2. The maximum elevation is 5002 m (Pico Bolívar) in the Sierra Nevada de Mérida and 4609 m (Pico Mucuñuque) in the Sierra de Santo Domingo.

Just as most of the high mountain systems, both in temperate and tropical regions, the Sierra Nevada de Mérida and the Sierra de Santo Domingo, and other ranges of the Venezuelan Andes, were affected by Quaternary glaciations. These have been described in detail in the northwestern flank of the Sierra de Santo Domingo, in the Pico Bolívar area, in Páramo de La Culata, in Páramo de Piedras Blancas, and in

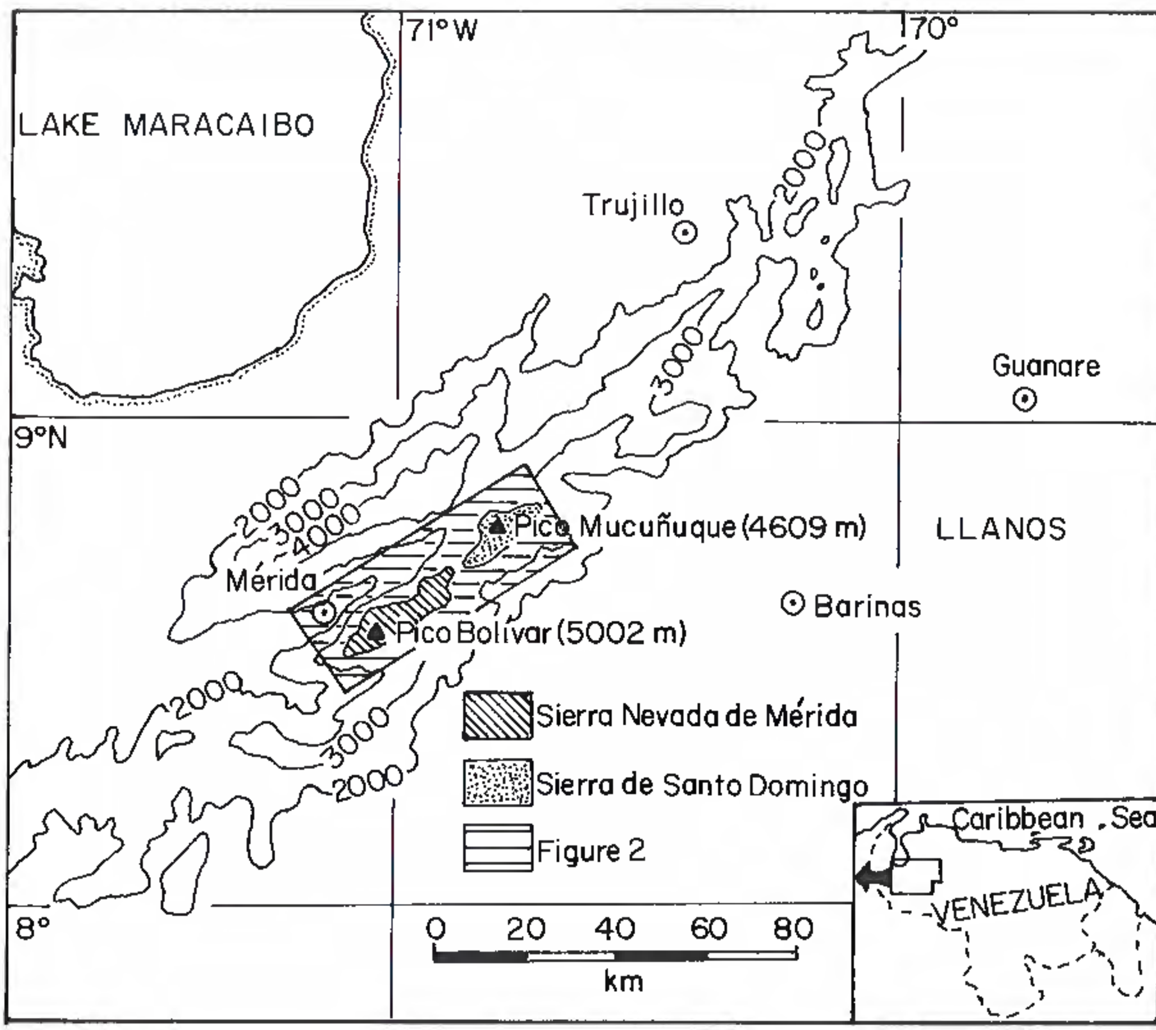

Fig. 1. Index map.

Páramo El Batallón (SCHUBERT, 1970, 1972, 1975, 1982; SCHUBERT and VALASTRO, 1974). Based on these studies, the Mérida Glaciation was defined (SCHUBERT, 1974), which comprises the last glacial advance of the Pleistocene. This advance has been approximately dated as Late Pleistocene (18 000 to 13 000 years B.P.), based on radiocarbon dating of organic-rich sediments, and stratigraphic and palynological comparisons with the Cordillera Oriental of Colombia (SALGADO-LABOURIAU et al., 1977; VAN DER HAMMEN, 1974; VAN DER HAMMEN et al., 1981). The Mérida Glaciation was characterized by a possible glacial advance to elevations of 2600 to 2800 m, and a well documented late advance to elevations of 3000 to 3500 m.

Only remnants of morainic sediments remain in some valleys from the older glacial advance (Chama, Mucujún, and Santo Domingo river valleys), in the form of isolated outcrops of a diamicton, a conglomerate without bedding, with grain-sizes ranging between sand and boulders. The latter show little fluvial action (poor rounding), are frequently faceted, and rarely striated. Another indirect evidence of the existence of this older glacial advance is the presence of possible fossil periglacial sediments (formed principally by solifluxion) in the Aracay river valley, at an elevation of 1600 to 1800 m, much below the present and Pleistocene elevation (3600 and 2400 m, respectively) at which this type of sediment forms and formed, due to the action of frequent daily freezing and thawing of the soil.

The final advance of the glaciers of the Mérida Glaciation is represented by spectacular morainic complexes above approximately 3000 m, by evidence of glacial erosion (glacial valleys, roche moutonnées, whaleback forms, rock steps, glacial channels). In addition, striae and grooves of glacial origin are frequently found on the outcrops of basement rocks in the glacial valleys. The moraines consist of long horse-shoe shaped ridges, which close the glacial valleys; several superimposed moraines are frequently found, which indicate multiple glacial advances. The morainic sediments contain all the classic evidence of Alpine glacial sedimentation (FLINT, 1971, p. 182): a great variety of grain-size (clay to boulders), little or no bedding (except in sediments left in open channels through the moraines by post-glacial streams), glacial abrasion of pebbles and boulders (facets, polygonal clasts, striae), and an oriented internal fabric which reflects the flow direction of the glaciers (SCHUBERT, 1979).

In the high parts of the glacial valleys, evidence of the Holocene glacier retreat and small re-advances is found in small recessional moraines. Of these glaciers, only remnants still exist in the Sierra Nevada de Mérida, with a total area of less than 3 km^2 (SCHUBERT, 1980). It has been estimated that the total area covered by glaciers during the final advance of the Mérida Glaciation, in the Venezuelan Andes, was approximately 600 km^2. This implies that the areal decrease during the Holocene was approximately of the order of 99%.

2. The Pleistocene Glaciers of the Sierra Nevada de Mérida

A detailed study of aerial photographs of Mission A-34 (Cartografía Nacional, Caracas, 1952, Nos. 176–190, 285A–299A, 317A–333A, 609A–626A, 969–982, and 995–999), and field study of some relevant regions (Sierra de Santo Domingo, Pico Bolívar, Mucuchíes-Mucubají region) revealed abundant evidence of former and present-day glacial activity, related to the Late Pleistocene Mérida Glaciation (Fig. 2), and permitted the reconstruction of the glacial geography during that glaciation.

Fig. 2 A shows the glacial morphology of the Sierra Nevada de Mérida and the Sierra de Santo Domingo. This morphology consists of erosional and sedimentary features. The glacial erosional features are located at the highest elevations and consist of arêtes, which form the crests of the ranges; cirques, which generally are round depressions with very steep walls and one or several rock steps below their outlet; roche moutonnés and whaleback forms, which indicate the direction of glacier flow; glacial valleys, which reach down to elevations of approximately 3500 m; and numerous striated and grooved rock surfaces on all of the former features. The sedimentary features consist of lateral and end moraines, which close the glacial valley outlets, in some cases damming the river which drains them; recessional

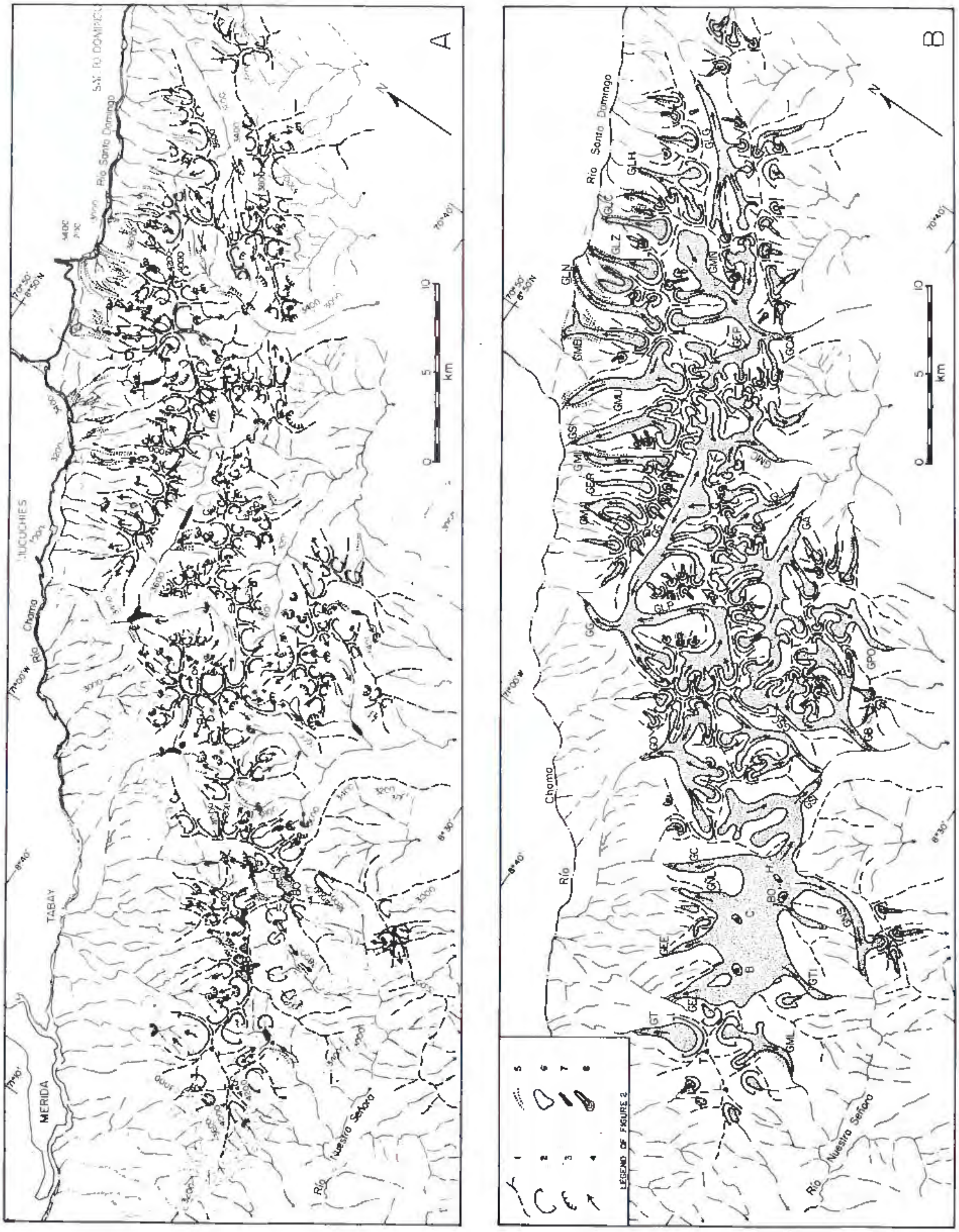

Fig. 2. *A:* Glacial geomorphological map of the Sierra Nevada de Mérida and the Sierra de Santo Domingo. Legend: 1. arête; 2. cirque; 3. rock step; 4. oriented feature (roche moutonnée, striae, grooves, whaleback form); 5. moraine; 6. glacier; 7. peat bog; 8. glacial lake; B. Pico Bolívar; BO: Pico Bonpland; C: Pico La Concha; H. Pico Humboldt; L. Pico El León; T. Pico El Toro.
B: Reconstruction of the Late Pleistocene glaciers of the last advance of the Mérida Glaciation in the Sierra Nevada de Mérida and the Sierra de Santo Domingo. The arrows indicate the direction of glacier flow. The glacier nomenclature corresponds to that of Table 1.

moraines within the glacial valleys and cirques; and peat bogs at different levels within the glacial and morainic valleys, in part produced by desiccation of former glacial lakes. Glacial lakes are found very frequently filling the bottoms of the cirques; the largest is Laguna Santo Cristo (1.5 km long and 0.75 km wide) in the Páramo of the same name, approximately 17.5 km south of Mucuchíes. The arrows in Fig. 2 A indicate the probable flow direction of the ancient glaciers, based principally on the presence of roche moutonnées and glacial striae and grooves on the walls and floors of the glacial valleys.

One of the most prominent features on Fig. 2 A is the concentration of moraines in the region situated between Mucuchíes and Santo Domingo, on the northwestern flank of the Sierra de Santo Domingo. In no other region of the map there are morainic complexes of equal magnitude, except the recessional moraines in the high parts of the glacial valleys. From the topography (Fig. 2 A), it can be deduced that the region between Mucuchíes and Santo Domingo is relatively flatter when compared with the other flanks of the Sierras, both to the northwest (Chama river valley) and to the southeast (Barinas piedmont). This region corresponds to the Páramos de Mucuchíes and Mucubají, a small *altiplano* on which great morainic sedimentary masses were deposited during the last advance of the Mérida Glaciation; later fluvial

Table 1. Nomenclature of the Pleistocene glaciers of the Sierra Nevada de Mérida and the Sierra de Santo Domingo.

Symbol (Fig. 2)	Name	Area (km^2)
GT	El Toro	5.7
GE	Espejo	
GEE	El Encierro	
GÑL	Ño León	
GC	Coromoto	49.3
GNS	Nuestra Señora	
GTI	Timoncito	
GSI	Sinigüis	
GML	Media Luna	
GG	Gavidia	
GLP	Las Piñuelas	32.6
GMC	Micarache	
GA	Arenoso	
GSC	Santo Cristo	26.4
GB	Bizcochito	
GCA	Canaguá	
GEP	El Potrero	17.3
GMÑ	Mucuñuque	
GM	Misteque	2.9
GEL	El Royal	
GMI	Michurao	1.7
GS	Saisay	4.8
GMU	Mucuchache	
GMB	Mucubají	3.4
GLN	La Negra	2.5
GLZ	Los Zerpa	
GLC	La Carbonera	
GLH	La Honda	2.9
GLG	Los Granates	6.0
GLL	Las Lajas	4.7
GPO	Los Pozones	3.4
GO	El Oro	6.9
Total area (minimum)		170.5

Area measured with planimeter

Fig. 3. Photographic evidence of glacier retreat during the last 60 years.
Above: The western Pico Bolívar glaciers in 1910 (left) and 1962 (right).
Middle: The western Pico Humboldt glaciers in 1910 (left) and 1972 (right).
Notice the possible neoglacial moraines below the glacier termini.

cont. Fig. 3.

Below: Southern Pico Bonpland glaciers in 1910 (left) and 1972 (right).
Sources of the photographs: JAHN (1912), HERRERA (1973), and the author.

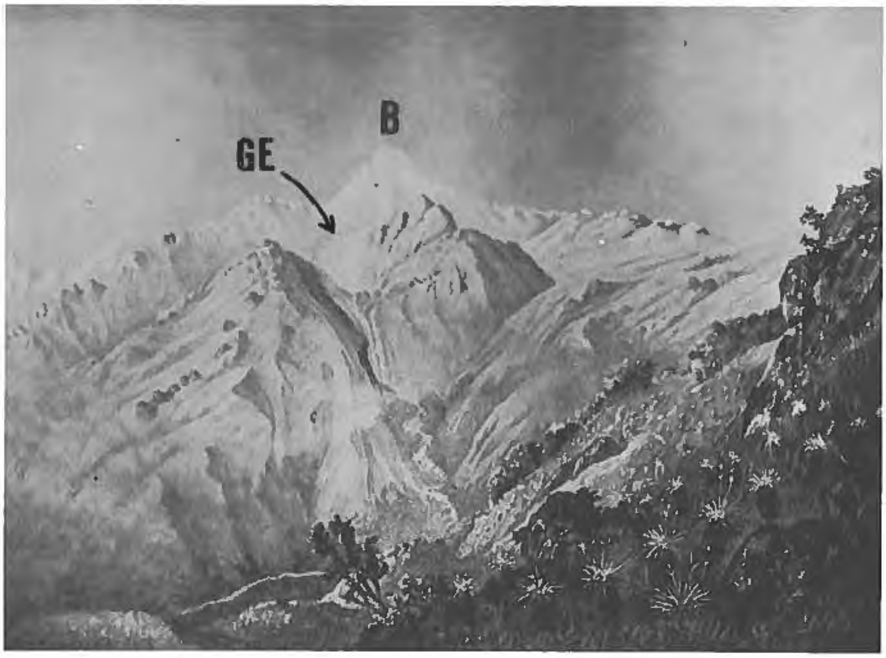

Fig. 4. Painting by Anton GOERING (1962), done between 1864 and 1874, clearly showing the Pico Espejo Glacier (GE) filling the western cirque below Pico Bolívar (B). This glacier is non-existent today.

and periglacial erosion during the Holocene has not been able to significantly remove these moraines, mainly due to the low slope values. At the same time, this region is situated in the transition zone between the humid climate of the Barinas piedmont (Santo Domingo river valley) and the dry climate of the high Chama river valley and the Páramo de Piedras Blancas (FLOHN, 1968; SCHUBERT, 1975), which suggests a slower weathering and erosion. On the rest of the flanks of the Sierras, erosion has been very effective, as indicated by the great erosional power of the rivers and the great alluvial accumulation on the Barinas piedmont.

An attempt to reconstruct the extent of the glaciers during the last important advance of the Mérida Glaciation (approximately between 18 000 and 13 000 years B.P.) is made in Fig. 2 B. This reconstruction is based on the data of Fig. 2 A. Table 1 shows the nomenclature of these glaciers and the area occupied by the most important of them. The arrows in this figure indicate the direction of glacier flow. The total area covered by the glaciers during this advance was approximately 197 km^2. Compared with the area occupied by glaciers at present (somewhat less than 3 km^2), it can be estimated that the Holocene glacier retreat in the Sierra Nevada de Mérida and Sierra de Santo Domingo was approximately 98.5%.

3. Contemporary Glacier Retreat

The Holocene glacier retreat documented in the preceding section continues today, as is suggested by photographic (Fig. 3) and pictographic (Fig. 4) comparison, and the observations made by different explorers during the last 100 years (SCHUBERT, 1980). In the Pico Bolívar massif, a vertical upward migration of the snowline, of approximately 100 to 150 m, has been observed since 1910. Timoncito Glacier has retreated in a spectacular manner during the last 20 years; the recently abandoned zone is characterized by outcrops of basement rocks, polished, striated, and covered by glacial debris. Retreat was so rapid that no moraines could accumulate. Vegetation, which is generally very sparse at this elevation (4700 m), has not been able to invade this zone yet, which testifies to its recent subaerial exposure. Another evidence of the rapid glacier retreat can be found in the reports by SIEVERS (1886; 1888, p. 188), BLUMENTHAL (1923), and JAHN (1925), who mention the existence, at least until 1922, of a small firn field below Pico Mucuñuque in the Sierra de Santo Domingo (significantly, at that time this mountain range was called Sierra Nevada de Santo Domingo). These authors also mention the existence of perpetual snow on Pico El Toro and Pico El León, of the Sierra Nevada de Mérida; at present, neither peak supports perpetual snow. The retreat of the snowline estimated by various authors is shown in Fig. 5. The accuracy of these data is probably quite variable, because the elevations were measured by different methods. However, the data suggest a clear and rapid retreat of the order of 6 m/year.

The Late Holocene glacier retreat documented here parallels a similar retreat observed elsewhere in northern South America. In the Sierra Nevada de Santa Marta (northern Columbia), WOOD (1970) documented that at least one third of the ice present in 1939 had disappeared by 1969, with glaciers on the southern flank being more affected by ablation (mean glacier termini in 1969 were at 4700 m on the north flank and 5000 m in the south flank). In the Sierra de Perijá, no glacier has survived the Holocene retreat due to its low elevation (3750 m; SCHUBERT, 1976). In the Sierra Nevada del Cocuy (Cordillera Oriental of Colombia), VAN DER HAMMEN et al. (1981) observed a marked glacier retreat from a possible neoglacial (or "Little Ice Age") moraine to the present glacier limit of about 4800 m. Similarly, in the Cordillera Central of Colombia, HERD (1977, p. 58) recorded a significant glacier retreat from a neoglacial moraine and an upward migration of the snowline by about 200 m in approximately the last 500 years. Finally, HASTENRATH (1981) documented in detail the spectacular glacier retreat in the Ecuadorian Andes during the last few centuries. The snowline retreated upward from about 4650 m in the late 18th century, to 4800 m in about 1900, to somewhat less than 5000 m in 1975. HASTENRATH (1981, Table 4) calculated an approximately 90% decrease in glacier-covered area between the probable last glacial maximum and present conditions.

In human terms, this spectacular glacier retreat means a progressive loss of one of the principal water sources of the high tropical mountains (see, for example, JORDAN, 1978). At the same time, the climatic-ecological belts progressively move upward and expand vertically, increasing the area of human exploitation and consequent environmental effects.

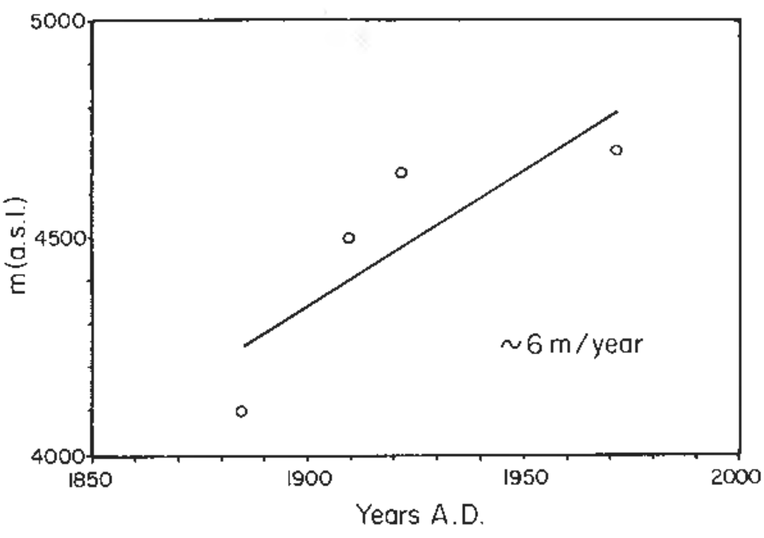

Fig. 5. Vertical retreat of the snowline in the Sierra Nevada de Mérida, after SIEVERS (1886), JAHN (1925), BLUMENTHAL (1923), and SCHUBERT (1980). A regression analysis ($r^2 = 0.69$) suggests a vertical retreat velocity of the order of 6 m/year.

4. Acknowledgments

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References

BLUMENTHAL, M. (1923): In der Längsrichtung durch die venezolanischen Anden. Jahrb. Schw. Alpenklub, v. 57, 213–240.
FLINT, R. F. (1971): Glacial and Quaternary Geology. New York.
FLOHN, H. (1968): Ein Klimaprofil durch die Sierra Nevada de Mérida (Venezuela). Wetter u. Leben, v. 20, 181–191.
GOERING, A. (1962): Venezuela, el más bello país tropical. Univ. de los Andes, Mérida.
HASTENRATH, S. (1981): The glaciation of the Ecuadorian Andes. Rotterdam.
HERD, D. G. (1977): Neoglaciation in the tropical Colombian Andes. Abstracts, X Inqua Congress, Birmingham, 202.
JAHN A. (1912): La cordillera venezolana de los Andes. Rev. Técnica Ministerio de Obras Públicas, Caracas.
– (1925): Observaciones glaciológicas en los Andes venezolanos. Cultura Venezolana, No. 64, 265–280.
JORDAN, E. (1978): Boliviens Gletscher als Wasser-Reserve. Umschau in Wissensch. u. Technik, v. 78, 190.
SALGADO-LABOURIAU, M. L., C. SCHUBERT and S. VALASTRO (1977): Paleoecologic analysis of a Late Quaternary terrace from Mucubají, Venezuelan Andes. Jour. of Biogeog., v. 4, 313–325.
SCHUBERT, C. (1970): Glaciation of the Sierra de Santo Domingo, Venezuelan Andes. Quaternaria, v. 13, 225–246.
– (1972): Geomorphology and glacier retreat in the Pico Bolívar area, Sierra Nevada de Mérida, Venezuela. Z. f. Gletscherk. u. Glazialgeol., v. 8, 189–202.
– (1974): Late Pleistocene Mérida Glaciation, Venezuelan Andes. Boreas, v. 3, 147–152.
– (1975): Glaciation and periglacial morphology in the northwestern Venezuelan Andes. Eiszeitalter u. Gegenwart, v. 26, 196–211.
– (1976): Evidence of former glaciation in the Sierra de Perijá, Western Venezuela. Erdkunde, v. 30, 222–224.
– (1979): Glacial sediments in the Venezuelan Andes. in: SCHLÜCHTER, C. (Editor): Moraines and varves, Rotterdam, 43–49.
– (1980): Contributión de Venezuela al inventario mundial de glaciares. Bol. Soc. Venez. Ciencias Naturales, v. 34, No. 137, 267–279.
– (1982): Geologica glacial del Páramo El Batallón, Estado Táchira, Venezuela Acta Cient. Venezolana, v. 33, 66–71.
– and S. VALASTRO (1974): Late Pleistocene glaciation of Páramo de La Culata, North-central Venezuelan Andes. Geol. Rundsch., v. 63, 516–538.
SIEVERS, W. (1886): Über Schneeverhältnisse in der Cordillere Venezuelas. Mitt. Geog. Ges. München, 1885, Heft 10, 54–57.
– (1888): Die Cordillere von Mérida nebst Bemerkungen über das karibische Gebirge. Geog. Abhandl., v. 3, No. 1.
VAN DER HAMMEN, T. (1974): The Pleistocene changes in vegetation and climate in tropical South America. Jour. of Biogeog., v. 1, 3–26.
–, J. BARELDS, H. DE JONG and A. A. DE VEER (1981): Glacial sequence and environmental history in the Sierra Nevada del Cocuy (Columbia). Palaeogeog., Palaeoclim., Palaeoecol., v. 32, 247–340.
WOOD, W. A. (1970): Recent glacier fluctuations in the Sierra Nevada de Santa Marta, Columbia. Geog. Rev., v. 60, 374–392.

Erdwissenschaftliche Forschung, Bd. XVIII, 279–293
Franz Steiner Verlag Wiesbaden GmbH · Stuttgart (1984)

Late-Quaternary Palynological Studies in the Venezuelan Andes

Maria Lea Salgado-Labouriau

With 12 Figures and 2 Tables

The high elevations of the Venezuelan Andes and the steepness of its mountains cause a number of altitudinal belts of vegetation that ranges from savannas and deciduous forests, at about 200 m elevation, to a sequence of montane forests and finally, to "páramo" vegetation. The páramo region, at elevations between 2800 and 4700 m, is covered by an open plant formation, generally formed by a low stratum of cushion-, rosette- and tussock-form herbs, mainly Gramineae, Compositae, Rosaceae. Scattered through this low stratum are small shrubs and tall rosettes of which the species of *Espeletia* (Compositae) are, to the human eye, the most conspicuous feature of the páramos. Rivers, creeks and small lakes are abundant and usually bordered by bogs. Peat formation is common and constitutes, together with the glacial lakes, good environments for pollen and spore accumulation and preservation.

At present glaciers are limited to the highest peaks (above 4700 m) but geological evidence has shown that the glaciation at the end of the Pleistocene reached elevations between 3000 and 3500 m (SCHUBERT, 1974 and 1984). The moraines of this glaciation are covered today by páramo vegetation and montane forest.

The Mérida Andes, where mountains reach their highest elevations in Venezuela, were chosen to start the palynological investigation (Fig. 1). It is based in the analysis of pollen grains, pteridophyte spores and algal remains. An outline of the results is presented here, including unpublished data.

1. Modern Pollen and Spore Deposition

The study of pollen, spores and algal remains that are being deposited at present in the páramo belt by modern vegetation (SALGADO-LABOURIAU, 1979) made possible the characterization of assemblages from the transition zone between páramo and forest, the páramo proper, and the superpáramo (subdivisions according to CUATRECASAS, 1957). It was also possible to determine the local, the regional and the long-distance types, as well as the dispersion power of the most abundant types. The results point out that:

1. Compositae and Gramineae are the main source of pollen in the páramos;
2. pollen of the Caryophyllaceae and the genera *Polylepis*, *Acaena*, *Geranium* and *Montia* also occur in modern sediments and are indicators of páramo condition in the past;
3. the pollen assemblages that are being deposited at present change according to the altitude making possible the distinction of subpáramo, páramo, páramo proper and superpáramo samples;
4. the long distance pollen types belong to the arboreal genera *Podocarpus*, *Alnus* and *Hedyosmum*, all from the humid montane forest; their pollen may reach the highest elevations in the superpáramo. Nevertheless, their frequency decreases with the increase in altitude. Also are long-distance types the spores of the forest Cyatheaceae.

These results and those from the Colombian Andes by GRABANDT (1980) enabled the intepretation of assemblages from old sediments.

2. Late-Pleistocene Gallery Forest

In the Motatán river basin there are several fluvial terraces (or mesas) that have been geologically described and radiocarbon dated (SCHUBERT and VALASTRO, 1980). A landslide occurred in one of them (at 2490 m elevation) displaying a stratigraphic section of about 200 m height (Fig. 2) in which organic layers were separated by layers of sandy conglomerate. Fragments of trees were embedded in these sediments allowing an accurate radiocarbon dating. A whole trunk was identified as a Myrtaceae, *Eugenia* or *Myrcia* (SCHUBERT and VALASTRO, 1980).

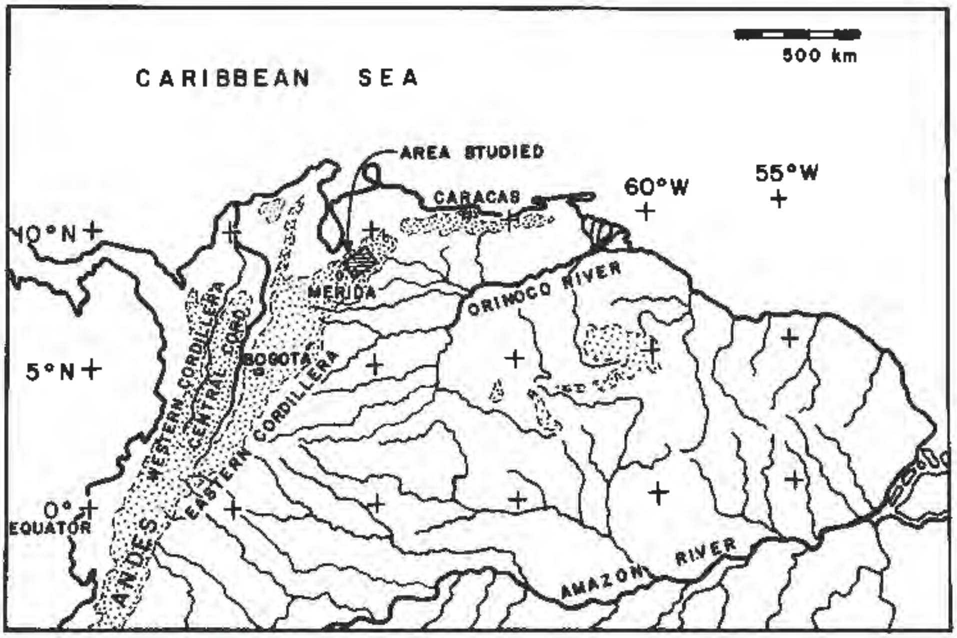

Fig. 1. Map of South America showing the Northern Andes and the area studied in this article.

Fig. 2. Landslide of the terrace in the Tuñame river, a tributaire of the Motatan river in the Mérida Andes (Venezuela).

The pollen analysis of the organic layers from this terrace (Tuñame river) is in progress. Due to problems in the identification of a few types the complete analysis is not yet concluded. Nevertheless, the preliminary results allow some conclusions (Fig. 3).

All the levels in the Tuñame deposits are dominated by pollen of *Alnus*, followed by a large frequency of pollen of *Podocarpus*. The presence of *Alnus* pollen dates the terrace as of Pleistocene age. It has been well established in the stratigraphy of Venezuela that the first occurence of this pollen type indicates the Lower Pleistocene. *Alnus*, a Northern temperate genus, is thought to have migrated to South America after the uplift of the Panamá isthmus in the Late Tertiary (VAN DER HAMMEN, 1974), and has reached Venezuela in the beginning of the Pleistocene.

Arboreal pollen, besides *Podocarpus* and *Alnus*, is not abundant but occurs throughout the Tuñame deposit. The most common taxa are *Ilex*, *Hedyosmum*, *Juglans*, *Alchornea*, *Myrica*, *Escalonia*, *Weinmania*, *Valea* and the families Myrtaceae and Melastomataceae. The low frequency of Myrtaceae pollen (below 2.5%) in levels where their macrofossils are found shows that Myrtaceae pollen is under-represented in sediments. The sum of the grains from the genera quoted above constitutes the majority of the pollen in all levels and points out the existence of a rain forest at that time. The Tuñame sediments also contain spores of humid forest ferns, such as *Lindsaea* and the tree-ferns *Alsophila* and *Cyathea*, that may reach a very large amount in some levels. The presence of rain forest ferns, together with arboreal pollen, reinforces the interpretation that the site was occupied by a humid gallery forest between > 50 000 and 33 700 B.P. This interval of time is included within the last glacial event, and the moraines formed by its glaciers are found at 3000–3300 m elevation in this region (SCHUBERT and VALASTRO, 1980). The altitudi-

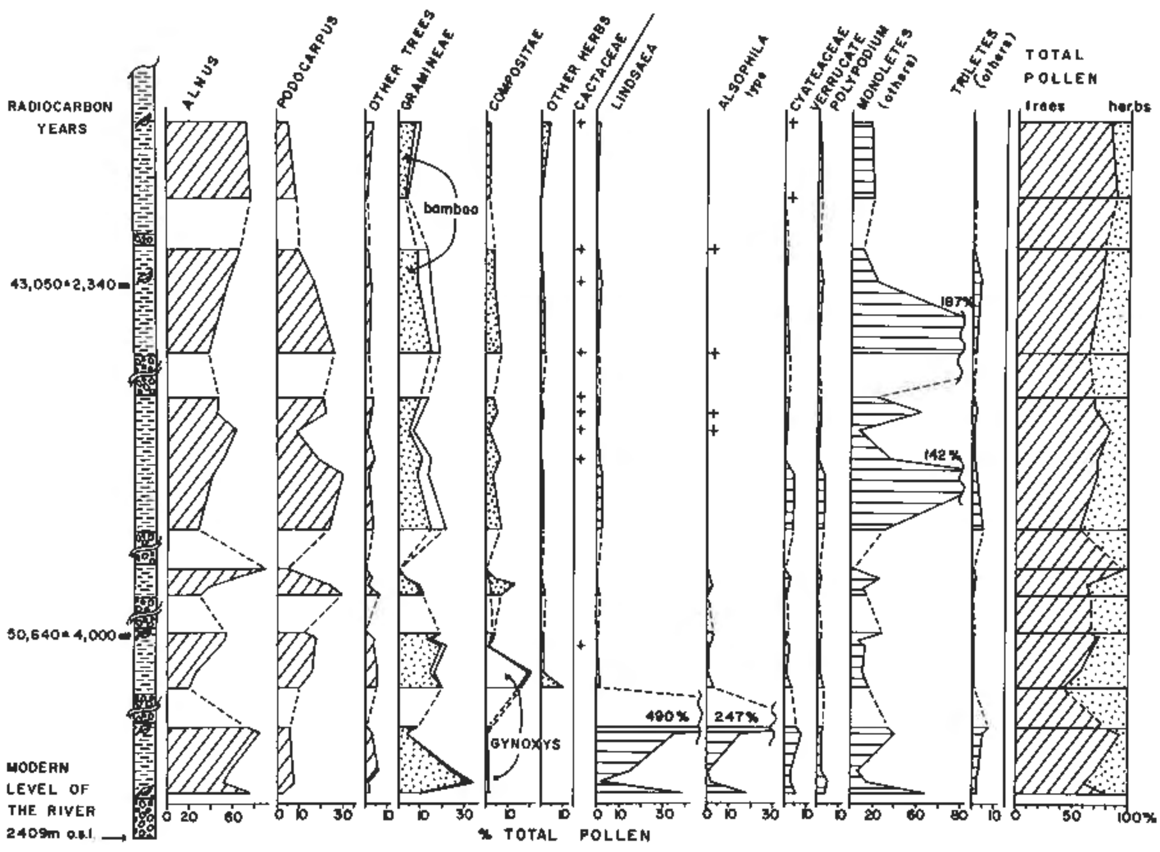

Fig. 3. Pollen und spore diagram of selected types from the Tuñame terrace, based on SALGADO-LABOURIAU, unpublished data.

nal position of the moraines indicates that the gallery forest, by modern standards, was too close to the snowline, and the páramo belt would have been altitudinally compressed in the 500 m between the snowline and the forest at that time.

The forest pollen and spore assemblages of Tuñame are associated in some levels with a large frequency of pollen of Compositae and/or Gramineae (Fig. 3). Since the plants of both these families grow mainly in open vegetation, it was necessary to study the pollen morphology of their Northern Andes species to verify which grasses and composites had grown in the Tuñame gallery forest.

The study of Compositae pollen (SALGADO-LABOURIAU, 1982) has shown that the Compositae maxima in the Tuñame deposits were due to the genus *Gynoxys*. It was probably *G. meridensis* (Fig. 4), a shrub or small tree that grows at present in the upper limit of the cloud forest and also in the *Polylepis* dwarf forest of the páramo. *Gynoxys* would therefore be part of the forest.

The genera of Gramineae cannot be identified by qualitative morphological features of their pollen. Nevertheless, size distribution of grass pollen from modern ecosystems follows a continuous sequence from very small (about 20 μm) to large grains (over 40 μm diameter). The species that are at the two tails of the size distribution are significantly different. This can be well seen, for example, for the Brazilian savanna grasses (CAMPOS and SALGADO-LABOURIAU, 1962) and North European grasses (ANDERSEN, 1978).

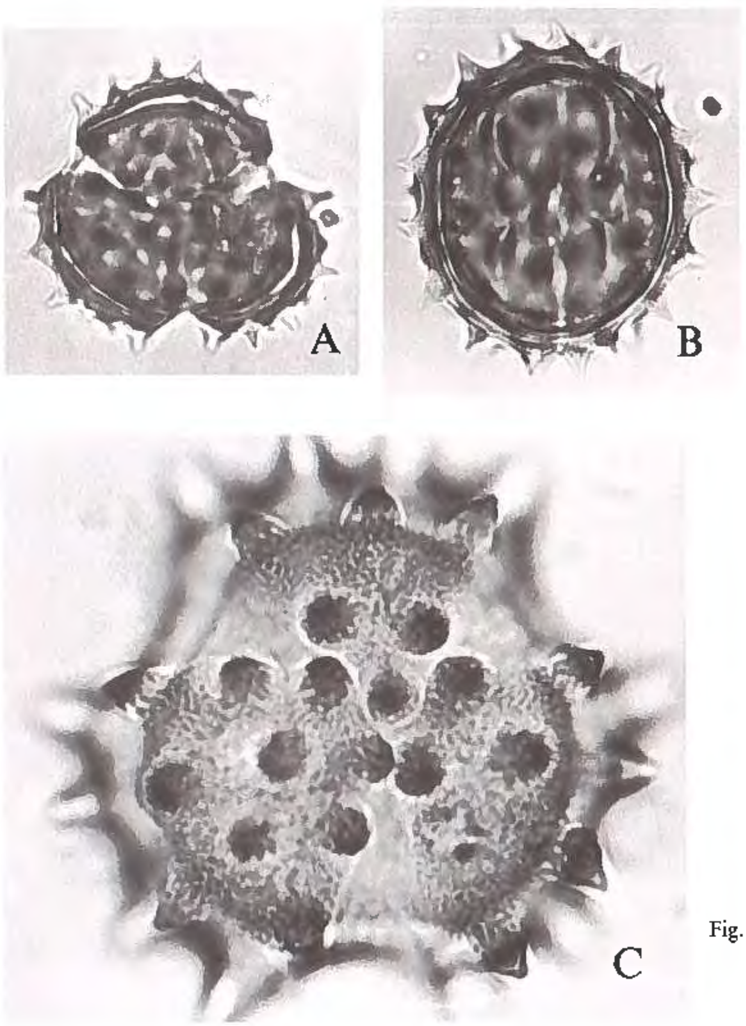

Fig. 4. Modern pollen grains, light microscope:
A – *Gynoxys meridana* Cuatr., in polar view;
B – idem, equatorial view;
C – *G. violacea* Sch. Bip., polar view.

Most of the grass pollen in the Tuñame sediments are over 40 µm in diameter and the grain surface is smooth. Therefore, a statistical study of the Andean grasses was undertaken to verify which are the montane grasses that have large grains with smooth surface. The results (Fig. 5) show that pollen grains above 40 µm in diameter belong to the genera *Bromus, Trisetum, Heleria, Festuca* and to the subfamily Bambusoideae, cultivated grasses not included (SALGADO-LABOURIAU and RINALDI, unpublished data). It

Fig. 5. Size distribution of grass pollen from the Northern Andes. An asterisk before the name of the species indicates introduced or cultivated grasses. *Rhipidocladum racemiflorum* and *Arthrostylidium racemiflorum* are two different specimens of the same species (*R. racemiflorum* McClure); *R. parviflorum* and *A. parviflorum* are specimens of *R. parviflorum* McClure. Observe that the grains with polar diameter below 37 µm do not include bamboos; all of them belong to species that occur in the páramo belt.

was also found that most of the bamboo pollen grains are psilate (smooth surface), whereas the other genera present coarsely granulated grains. These results indicate that the grass pollen found in the Tuñame sediment is most probably bamboo pollen. It is well known that bamboos are mainly forest elements; the herbaceous species flowering almost continuously throughout the year; the woody bamboos, although usually monocarpic or blooming at long and irregular year periods (CALDERÓN and SODERSTROM, 1980), always flower abundantly. This irregular blooming probably could explain the high frequency of grass pollen found in some levels of Tuñame that may reach more than 20% of the total pollen whereas it is scarce in levels immediately above or below them (Fig. 3).

The analysis of the pollen and spore assemblages from the Tuñame terrace points out that between 50 640 and 33 700 radiocarbon years B.P. the site was not occupied by páramo vegetation nor by a grassland of a cold tropical climate, even though it is only a few hundred meters below well preserved moraines. It had a humid gallery forest that could have been a forest refuge area during the Mérida glaciation.

3. Late-Quaternary Climatic Oscillations and Post-Glacial Vegetational Succession

The Páramo of Mucubaji (3500–3700 m elevation) was covered by glaciers during the Late-Pleistocene glaciation and high moraines were formed confining a deep glacial valley. Paleoecological data show that glaciers have retreated from the Mucubaji valley at 12 650 ± 130 B.P. (SALGADO-LABOURIAU, SCHUBERT and VALASTRO, 1977). Superpáramo vegetation started to establish at that time in the glacial valley. The first plants to reach the newly deglaciated soil belong to the families Gramineae, Portulaceae and Compositae (Fig. 6). In the beginning *Montia*-type pollen, probably *Montia (Mona) meridensis* (Fig. 7), was the most abundant, but it decreased shortly after. *M. meridensis* is a small unconspicuous herb of humid soils; at present it is more frequent in bogs above 4000 m elevation. It produces very little pollen which suggests the plants were very abundant at that time.

Gramineae and Compositae pollen is scarce in the beginning. At about 12 400 B.P. the Caryophyllaceae arrived at the site, followed by *Lycopodium* (foveolate type). Only at about 12 000 B.P. these taxa attained

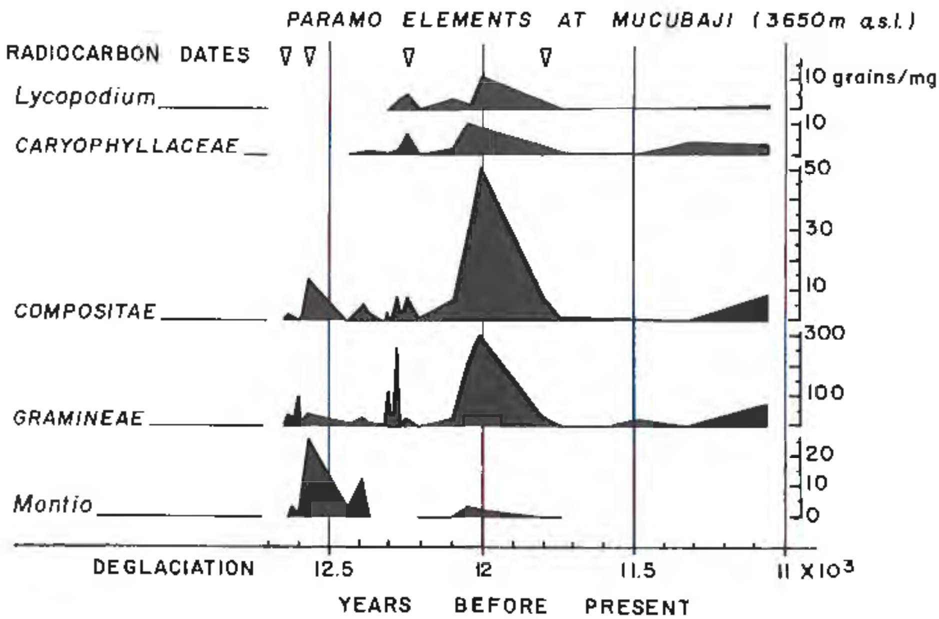

Fig. 6. Sequence of colonization of the newly deglaciated soil in the Páramo of Mucubaji, Venezuelan Andes.

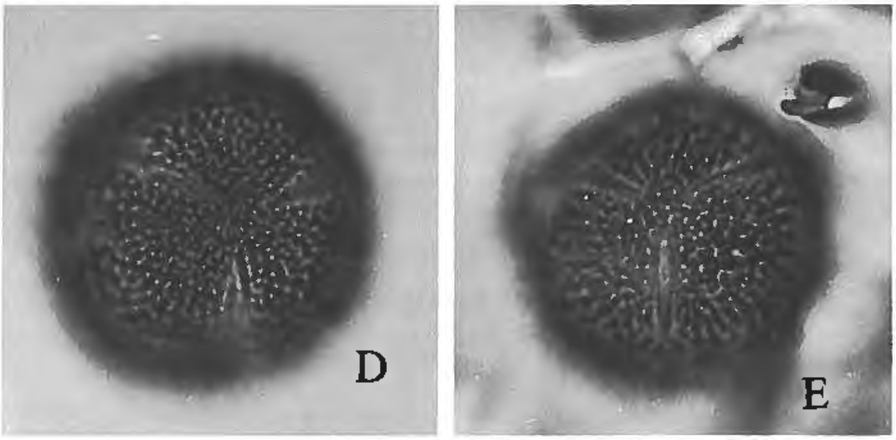

Fig. 7. Pollen grains of *Montia meridensis* Friedrich in polar view:
D – modern grain;
E – fossil grain from the Mucubaji terrace, level SD-42, about 12500 years before present.

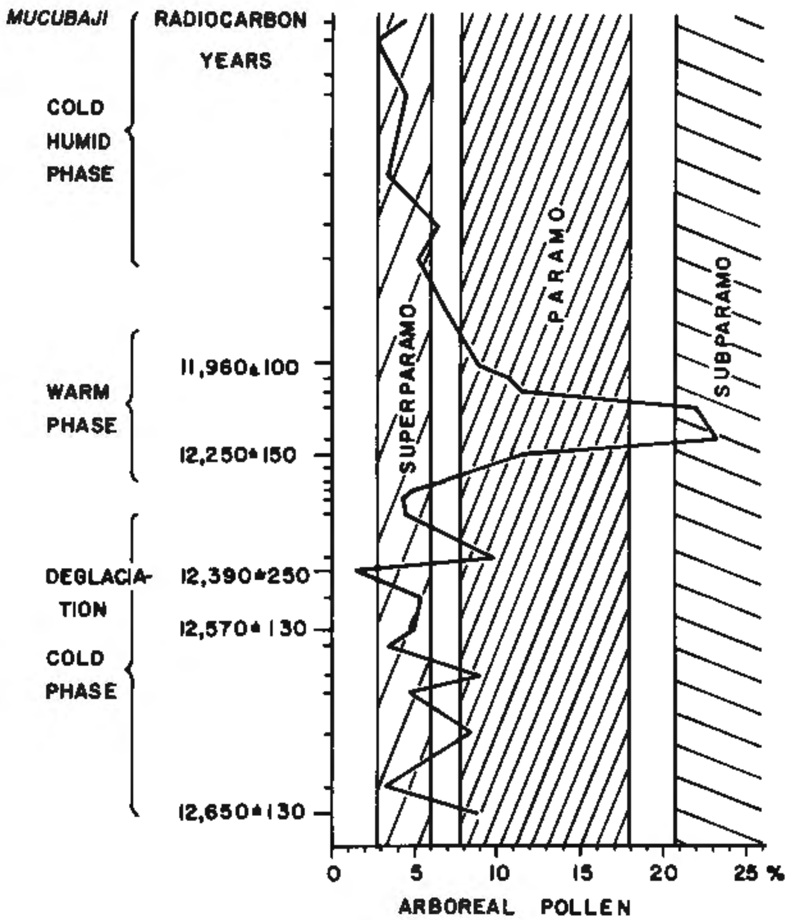

Fig. 8. Oscillation of the tree line at the end of the Pleistocene. The curve represents the total percentage of tree pollen per level in the Mucubaji terrace. It is plotted against the percentage of modern tree pollen that is being deposited in the páramos according to the altitude. Based on SALGADO-LABOURIAU, SCHUBERT and VALASTRO (1977) and SALGADO-LABOURIAU (1979).

Table 1. Late-Quaternary climatic oscillations in the Mérida andes.

Radiocarbon year before present (*interpolated dates)	Vegetation and climate at 3500 to 4000 m elevation
0 (present)	humid páramo. Humid and cold montane climate: average temperature 5.3 °C; absolute minimum −9 °C; absolute maximum + 22 °C, in 24 hours cycles; average precipitation 1084 mm per year
2520 to 5270	vegetation and climate similar to present
6150	scarce páramo vegetation; climate cooler and drier than present (La Culata dry phase)
6240 to 7530	vegetation and climate similar to present
ca. 11 000* to ca. 11 700*	humid superpáramo vegetation; climate cooler than present, average temperature probably 2–3 °C below present; humid (Mucubaji cold humid phase)
11 960 to 12 250	humid páramo vegetation; climate similar to present (Mucubaji warm phase)
ca. 12 280* to 12 650	superpáramo with scarce vegetation. Climate colder and drier than present, average temperature c. 2.9 °C deglaciation
Before 12 650	Mérida glaciation

Based on SALGADO-LABOURIAU and SCHUBERT (1976); SALGADO-LABOURIAU, SCHUBERT and VALASTRO (1977).

their maximum frequency to decrease again shortly after (11 960 B.P.) when a cold phase started. The same sequence of colonization of the newly deglaciated soil was found at another site, in the Páramo de Piedras Blancas at 4000 m elevation (RULL and SALGADO-LABOURIAU, unpublished data).

In the Sierra Nevada de Santa Marta (Colombia) the pollen analysis of a peat core in a glacial valley at 4760 m elevation shows a similar sequence. The glacier has a retreat at about 1700 A.D. when *Montia*, Cyperaceae and Compositae occupied the site. They were followed by *Plantago* and finally by *Lycopodium*, Caryophyllaceae, Cruciferae *(Draba)* and Scrophulariaceae (VAN DER HAMMEN, 1979).

The results from these three sites suggest that Fig. 6 represents general pattern of colonization in new deglaciated soils from the páramos: *Montia* and a few Compositae (together with Gramineae or Cyperaceae) are the first to establish, and they are followed later by *Lycopodium* and Caryophyllaceae with a few other elements that varies according to the mountain.

The pollen assemblages in Mucubaji from 12 650 to 12 280 B.P. are similar to those of modern superpáramo assemblages. Nevertheless, pollen frequency is lower in the old sediments indicating a scarce vegetation spread over almost bare soil. At 12 250 B.P. the pollen assemblage is abundant, and new elements have reached the valley (SALGADO-LABOURIAU, SCHUBERT and VALASTRO, 1977). Long-distance tree pollen which was scarce after deglaciation increases in this phase reaching values similar to those of modern páramo (Fig. 8). The abundance of páramo elements and the uplift of the forest indicate that a warm interval took place at that time. This phase is correlated with the Guantiva Interstadial of Colombia (GONZALEZ, VAN DER HAMMEN and FLINT, 1965). Shortly after the temperature must have decreased again because the forest has retreated to lower elevations (Fig. 8). The site gradually returned to superpáramo conditions, and a cold and humid interval began after 11 960 B.P.

Table 1 shows the climatic oscillations from the end of the Pleistocene to modern time at the Páramos of Mucubaji and La Culata based in the pollen analysis of sediments from fluvio-glacial terraces. Three cold phases with different degrees of humidity were detected: > 12 650–12 280 (relatively dry); 11 700–11 000 (humid); and 6150 B.P. (dry) (SALGADO-LABOURIAU, SCHUBERT and VALASTRO, 1977; SALGADO-LABOURIAU and SCHUBERT, 1976).

The main retreat of the last glaciation ice sheet at about 13 000 B.P. in the Venezuelan and Colombian Andes shows that the soils in the páramo belt are recent when compared with the montane forest belt. Below 3000 m elevation the soil has not been continuously destroyed by the readvances of the glaciers during the Pleistocene.

4. The Polylepis Forest

The small trees of *Polylepis sericea*, 4 to 6 m tall, grow above the montane forest in the Venezuelan Andes. They are found in the ecotone páramo-forest, between 2400 and 3000 m elevation, and along streams, in gallery forests that penetrate into the páramo. They also form small clusters of trees or woodlands enclaved in the páramos from 3200 a 4200 m elevation, usually in rocky slopes (Fig. 9) or along rivers. Sometimes they are the only trees; in other instances they are associated with small trees of the genus *Gynoxys* and with several types of shrubs (SALGADO-LABOURIAU, 1979, and literature within). The reduced size of these dwarf forests and their anomalous distribution is illustrated in Figs. 10 and 11.

Recently, the genus *Polylepis* was reviewed by B. B. SIMPSON (1979) and reduced to 15 species. As well as *P. sericea*, the other fourteen species have a similar distribution, and occur in the highest parts of the Andean mountains, from Northern Chile and Argentina to Colombia, with many species reaching 4000 to 5200 m elevation. According to the species, they are found in rocky slopes, valley bottoms or along rivers. Rare as an isolated tree, the *Polylepis* species form small woodlands surrounded by open plant

Fig. 9. Páramo landscape: La Aguada Station, Mérida, Venezuela, at 3400 m elevation. Arrow indicates a dwarf *Polylepis* forest at the background.

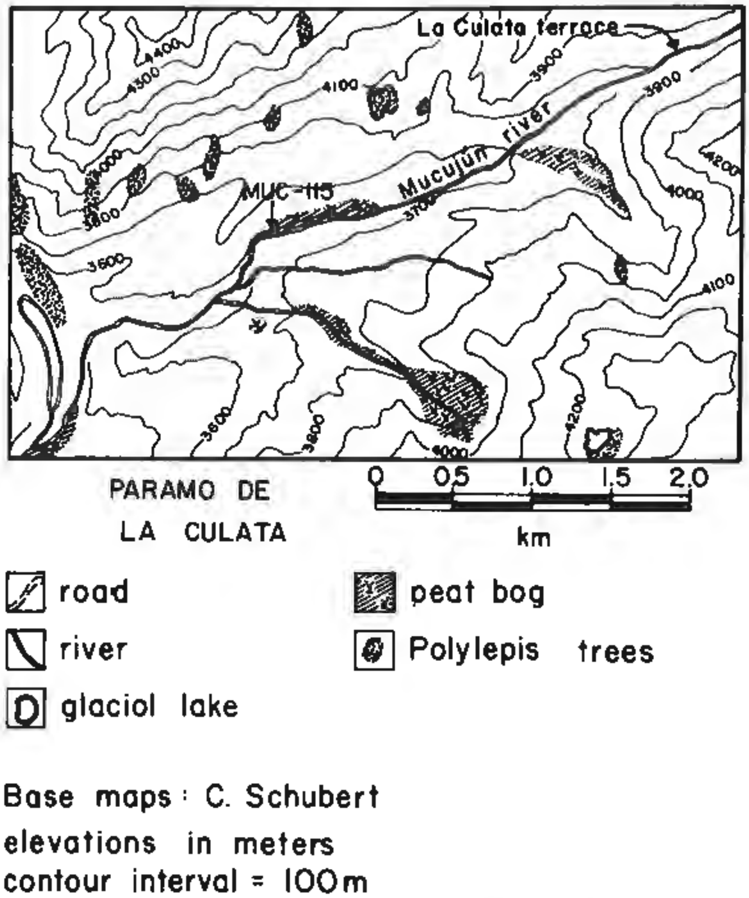

Fig. 10. Map of the Páramo of La Culata indicating the modern occurrence of the *Polylepis* dwarf forests.

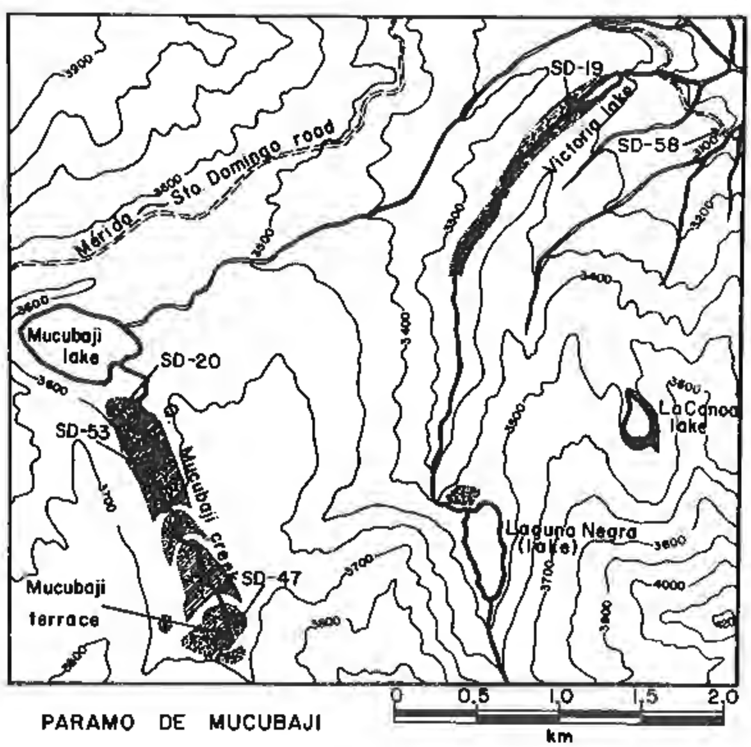

Fig. 11. Map of the Páramo of Mucubaji indicating the small areas occupied by *Polylepis* trees at present.

formations, as páramos and punas. These dwarf forests are specialized type of vegetation restricted to certain areas in the cold belt of the Andes.

The use of *Polylepis* as firewood and fence in these otherwise treeless regions, is drastically reducing its member (HUECK, 1972). The pollen analysis of a core in a bog close to the Laguna Victoria (3250 m elevation), in the Venezuelan Andes (SALGADO-LABOURIAU and SCHUBERT, 1977) has shown the existence of a *Polylepis* woodland around this small glacial lake in the last millenia, up to modern times. Nevertheless, at present the lake is surrounded by a recent plantation of exotic coniferous, and no *Polylepis* remains in the site.

The ability to grow above the montane forest in soils which freeze almost every night, and the distribution in dwarf woodlands is still a problem to ecologists and physiologists. WALTER and MEDINA (1969) suggested it is mainly due to favorable soil temperature. There is very little information about the development and microclimatic conditions for all the species of *Polylepis*, and the problem can only be solved by ecological and physiological investigation on this genus.

Recently, ELLENBERG (1979) reaffirmed his early theory that the *Polylepis* dwarf forests in the Altiplano of Peru and surrounding regions are remnants of a continuous evergreen woodland above the present montane forest. *Polylepis* is supposed to be one of the dominants in this woodland and would have declined by man interference clearing trees for pasture, timber and firewood, and also by domestic animals destroying the seedlings. Other authors (HUECK, 1972; SIMPSON, 1979; among others) oppose ELLENBERG's view, although recognizing that these small woodlands could have been larger than today.

In the last 30 years pollen analysis data have been accumulated for the Northern Andes in Colombia (VAN DER HAMMEN, 1974, 1979). They have shown that *Polylepis*-type of pollen started to be found in the Pliocene of the high plain of Bogotá and has been a constant element in the Quaternary high altitude

Fig. 12. Modern pollen grains:
F – *Polylepis incana* H. B. K., scanning electron microscopy photograph, x 700;
G – *Polylepis sericea* Wedd., light microscopy photograph, obj. x 40/1.0;
H – *Acaena cylindrostachya* R. & Pav., light microscopy photograph, objective x 40/1.0.

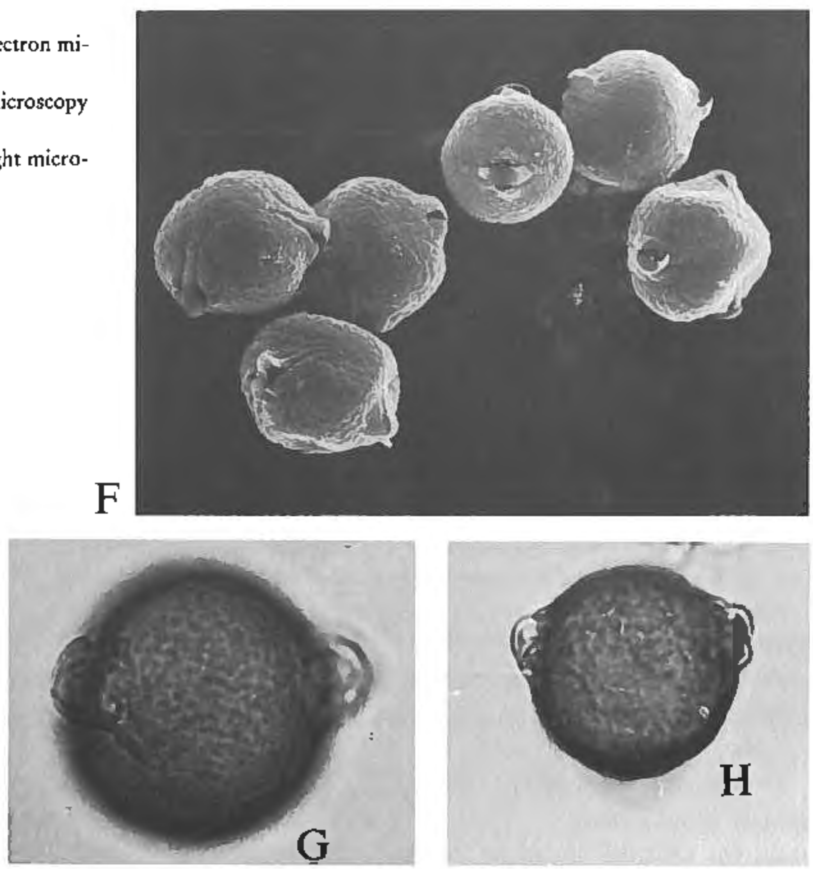

Table 2. Modern pollen grains of the genera *Acaena*, *Margyricarpus* and *Polylepis*. Measurements of the equatorial diameter in polar view.

	Collector	Average ($\bar{x}$)	95% Confidence Interval ($x \pm t \cdot s_{\bar{x}}$)
Margyricarpus pinnatus (Lam.) Ktze.	Asplund 6902	23.95	23.23–24.67
Acaena argentea R. & Pav.	Vareschi 5712	27.32	26.66–27.98
A. elongata L.	Badillo 913	28.40	27.37–29.43
A. cylindrostachya R. & Pav.	Baruch s/n	28.73	28.26–29.20
A. cylindrostachya R. & Pav.	Lasser & Adams 4489	28.92	28.28–29.56
Polylepis racemosa R. & Pav.	Hodge 6221	30.70	29.79–31.61
P. lanuginosa H. B. K. (*P. lehmanii* Hieron.)	M. Giler 2773	32.84	31.64–34.04
P. besseri Hieron.	B. Vuilleumier 468	33.32	32.54–34.10
P. australis Bitter	Schreiter 9814	33.52	32.82–34.22
P. incana H. B. K.	B. Simpson 8554 D	34.85	33.64–36.06
P. ciliata Maguire, Isotype	W. H. Camp E-2000	35.74	34.84–36.61
P. sericea Wedd.	Cuatrecasas 28145	36.21	34.89–37.53
P. sericea Wedd. (*P. quindiensis* (Cuatr.)	Cuatrecasas 23257	38.18	37.02–39.34
P. sericea Wedd.	Aristeguieta 7886	38.63	37.27–39.99
P. multijuga Pilg.	Hutchinson 6463	38.99	37.93–40.05
P. tomentella Wedd.	F. Schlegel 4815	39.28	37.58–40.98
P. quadrijuga Bitter (*P. boyacensis* Cuatr.)	Cuatrecasas 27834	41.22	40.16–42.28

sediments up to the Holocene. Toward the end of the Pleistocene it reached a marked maximum that is better observed in the sediments from Lake Fúquene (VAN GEEL and VAN DER HAMMEN, 1973). It declines at 20 600 radiocarbon years B.P. and disappears from the region after about 10 000 B.P. (VAN DER HAMMEN, 1974, Fig. 6). The pollen analysis of Quaternary sediments from several sites of the Colombian Andes (VAN DER HAMMEN, 1974, 1979, and literature therein) shows small maxima and minima of *Polylepis*-type probably indicating expansions and contractions of local *Polylepis* populations but, except for the Fúquene maximum, they do not indicate large forests because their percentage is always much smaller than the pollen sum.

It is difficult to distinguish between the pollen grains of *Polylepis* and those of the genus *Acaena*, which includes small shrubs and herbs of the páramo (VAN DER HAMMEN and GONZALEZ, 1960; HEUSSER, 1971; SALGADO-LABOURIAU, 1979; SIMPSON, 1979) (Fig. 12). Separation for several modern species was attempted using scanning electron microscopy (SMIT, 1978) and grain size (SALGADO-LABOURIAU, 1979). Table 2 presents pollen grain measurements of ten species of *Polylepis* compared with the andean species of *Margyricarpus* and *Acaena*. This table indicates that all the modern species of *Polylepis* studied have pollen grains significantly larger than those of the other two genera. Although both criteria of separation may be applied for recent sediments, they have to be used with care for old deposits. Nevertheless, if all the grains belonging to the Polylepis-type and found in Quaternary sediments are assigned to the genus *Polylepis*, they still do not reach the high frequency that allows the assumption of a continuous *Polylepis* belt above the cloud forest nor an evergreen woodland in which it was one of the dominants.

ELLENBERG's hypothesis that *Polylepis* "declined" in Perú by human interference cannot be applied to Venezuela. *Poylepis*-type of pollen is not abundant in post-glacial sediments from the Páramos of la Culata, Mucubaji, Laguna Victoria and Piedras Blancas (SALGADO-LABOURIAU and SCHUBERT, 1976, 1977; SALGADO-LABOURIAU, SCHUBERT and VALASTRO, 1977; RULL and SALGADO-LABOURIAU, unpublished).

Human settlements are unknown in the highest parts of the Venezuelan Andes prior to the arrival of the Spanish in XVI century. The region which is covered today by páramo vegetation was only used in short visits for religions purposes and probably as mountain paths to reach other low mountain regions

(WAGNER, 1967, 1979). Population was fairly large only after the Spanish invasion. Moreover, the pre-Colombian inhabitants of Venezuela had no herds of domestic animals, and European cattle was introduced in 1570 (WAGNER, 1967, 1979). Agriculture was practiced at elevations below 2000 m (ZUCCHI, 1973; WAGNER, 1973) which does not include the páramo region. Any change in the pollen assemblages from post-glacial páramo sediments prior to the last four hundred years are not caused by human interference. Any expansion or contraction of local *Polylepis* population or other montane vegetations would be climatically controlled, except for the possibility of pathogenic agents interfering in a specific plant, as suggested by M. B. DAVIS (1977).

Because of the absence or at least infrequent presence of man during post-glacial times, as well as the lack of domesticated animals during most of the Holocene, the Venezuelan páramos present a climatic model for the interpretation of other regions such as those of Perú and Equador where men and their large herds of camelidians (FLORES, 1979) had an important role for millenia in the modifications of plant communities.

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Summary

The results of the palynological studies of sediments from five different sites in the highest part of the Northern Andean mountains are discussed, and compared with modern assemblages.

The analysis from a fluvial terrace at 2490 m elevation shows that a humid gallery forest existed from 50640 to 33710 B.P. The pollen assemblages in all levels are dominated by *Alnus*, followed by *Podocarpus*, and spores of forest ferns; bamboo pollen is frequent in some levels. Glaciers have extended to 3000–3500 m elevation in the region. The Northern Andes was in a glacial period during the time, and the Tuñame gallery forest could have been a forest refuge area.

Information from 3500–4000 m elevation (in the páramo belt) shows that glaciers have retreated from Mucubaji valley at 12650 B.P., and páramo vegetation started to establish at the region. The first elements to reach the newly deglaciated valley were *Montia*, and a few Compositae and Gramineae. Shortly after they were followed by Caryophyllaceae and *Lycopodium*. The other paramo elements started after. The same sequence is found in post-glacial sediments from Piedras Blancas at 4000 m elevation and in a Holocenic glacier retreat at 4760 m, in Colombia. These results indicate that the Mucubaji sequence represents the general pattern of colonization of newly deglaciated soils in the Northern Andes.

At altitudes from 3500 to 4000 m three cold phases with different degrees of humidity were detected during post-glacial time:

1. > 12650–12280 B.P. (relatively dry);
2. 11700–11000 B.P. (humid);
3. 6150 B.P. (dry).

A warm phase occurred from 12250 to 11900 B.P.

The paleoecological data suggest that the *Polylepis* dwarf forest could have been somewhat larger in some phases during the Quaternary, but they do not support the hypothesis of a continuous evergreen woodland above the present montane forest. Expansions and contractions of the local *Polylepis* populatins are mainly climatic controlled.

References

ANDERSEN, S. T. (1978): Identification of wild grass and cereal pollen. Danmarks Geologiske Undersøgelse. Årbog, 69–92.

CALDERÓN, C. E. and T. R. SODERSTROM (1980): The genera of Bambusoideae (Poaceae) of the American Continent: key and comments. Smithsonian Contributions to Botany, 14.

CAMPOS, S. M. and M. L. SALGADO-LABOURIAU (1962): Pollen grains of plants of the "Cerrado" – III. Grasses. An. Acad. Brasil. Cienc., 34 (1), 101–110.

CUATRECASAS, J. (1957): A sketch of the vegetation of the Northern-Andean Province. Proceedings of the Eighth Pacific Science Congress, vol. IV, 167–173.

DAVIS, M. B. (1976–1977): Outbreaks of forest pathogens in Quaternary History. Proceedings of the IV International Conference on Palynology, Lucknow, India, vol. III, 216–227.

ELLENBERG, H. (1979): Man's influence on tropical mountain ecosystems in South America. Journ. Ecology, 67, 401–416.

FLORES OCHOA, J. A. (1979): Desarrollo de las culturas humanas en las altas montañas tropicales: Estrategias adaptativas. In: SALGADO-LABOURIAU, M. L. (Ed.): El Medio Ambiente Páramo. Ediciones Centro de Estudios Avanzados IVIC, Venezuela, 225–234.

GONZALEZ, E., T. T. VAN DER HAMMEN and R. F. FLINT (1965): Late Quaternary glacial and vegetational sequence in the Valle de Lagunillas,Sierra Nevada de Cucuy, Colombia. Leidse Geol. Meded., 32, 157–182.

GRABANDT, R. A. J. (1980): Pollen rain in relation to arboreal vegetation in the Colombian Cordillera Oriental. Rev. Palaeobot. Palyn., 29, 65–147.

HEUSSER, C. J. (1971): Pollen and Spores of Chile. Univ. Arizona Press, Tucson, U.S.A.

HUECK, K. (1972): As Forestas da America do Sul. Editora da Universidade de São Paulo, Brasil.

SALGADO-LABOURIAU, M. L. (1979): Modern pollen deposition in the Venezuelan Andes. Grana, 18, 53–68.

– (1982): Pollen morphology of the Compositae of the Northern Andes. Pollen et Spores, 24 (3–4), 397–452.

– and C. SCHUBERT (1976): Palynology of Holocene peat bogs from the Central Venezuelan Andes. Palaeogeogr., Palaeoclim., Palaeoecol., 19, 147–156.

– , – (1977): Pollen analysis of a peat bog from Laguna Victoria (Venezuelan Andes). Acta Cient. Venezolane, 28, 328–332.

– , – and S. VALASTRO Jr. (1977): Paleoecologic analysis of a Late-Quaternary terrace from Mucubaji, Venezuelan Andes. J. Biogeogr., 4, 313–325.

SCHUBERT, C. (1974): Late Pleistocene Mérida Glaciation, Venezuelan Andes. Boreas, 3, 147–152.

– (1984): The Pleistocene and Recent Extent of the Glaciers of the Sierra Nevada de Mérida, Venezuela. Erdwiss. Forschung, XVIII, 269–278.

– and S. VALASTRO Jr. (1980): Quaternary Esnujaque Formation, Venezuelan Andes: Preliminary alluvial Chronology in a tropical mointain range. Z. dt. geol. Ges., 131, 927–947.

SIMPSON, B. B. (1979): A revision of the genus *Polylepis* (Rosaceae: Sanguisorbae). Smithsonian Contributions to Botany, 43.

SMIT, A. (1978): Pollen morphology of *Polylepis boyacensis* Cuatrecases, *Acaena cylindristachya* Ruiz et Pavon and *Acaena elongata* L. (Rosaceae) and its application to fossil material. Rev. Palaeobot. Palynol., 25, 393–398.

VAN DER HAMMEN, T. (1974): The Pleistocene changes of vegetation and climate in tropical South America. J. Biogeogr., 1, 3–26.

– (1979): Historia y tolerancia de ecosistemas parameros. In: SALGADO-LABOURIAU, M. L. (Ed.): El Medio ambiente Páramo. Ediciones Centro de Estudios Avanzados, IVIC, Venezuela, 55–66.

– and E. GONZALEZ (1960): Upper Pleistocene and Holocene climate and vegetation of the "Sabana de Bogotá" (Colombia, South America). Leidse Geol. Meded., 25, 261–315.

VAN GEEL, B. and T. VAN DER HAMMEN (1973): Upper Quaternary vegetational and climatic sequence of the Fuquene area (Eastern Cordillera, Colombia). Palaeogeogr., Palaeoclim., Palaeoecol., 14, 9–92.

WAGNER, E. (1967): The Prehistory and Ethnohistory of the Carache Area in Western Venezuela. Yale University Publications in Anthropology, 71, New Haven, U.S.A.

– (1973): The Mucuchies Phase: an extension of the Andean cultural pattern into Western Venezuela. Am. Anthropol., 71, 195–213.

– (1979): Arqueología de los Andes Venezolanos; los páramos y la Tierra fría. In: SALGADO-LABOURIAU, M. L. (Ed.): El Medio Ambiente Páramo. Ediciones Centro de Estudios Avanzados, IVIC, Venezuela, 207–218.

WALTER, H. (1973): Vegetation of the Earth. Heidelberg, Science Library, vol. 15.

– and E. MEDINA (1969): La temperatura del suelo como factor determinante para la caracterización de los pisos subalpinos y alpinos de los Andes de Venezuela. Bol. Soc. Venez. Cienc. Nat., 115/116, 201–210.

ZUCCHI, A. (1973): Prehistoric human occupations of the Western Venezuelan Llanos. American Antiquity, 38 (2), 182–190.

Discussion to the Paper Salgado-Labouriau

Prof. Dr. W. Lauer:

Which interpretations of the *Polylepis*-problem result from your studies in Venezuela?

Dra. M. L. Salgado-Labouriau:

The results we have at present show that *Polylepsis* has not formed large extensions of forest at post-glacial times in Venezuela. *Polylepis* trees had probably grown as small woodlands isolated one from the other.

Prof. Dr. J. R. Flenley:

What was the change in temperature between the Mucubaji phase and the succeeding cold phase?

Dra. M. L. Salgado-Labouriau:

Mucubaji warm phase, characterized by a rapid upward displacement of the vegetational belt, possibly had an average annual temperature about the same as today (5.3 °C; average minimum of 1.9 °C; average maximum of 10.8 °C). The succeeding cold phase, with a retreat of the forest belt, perhaps was 2–3 °C below today average; but we need more sites to be sure.

Prof. Dr. B. Messerli:

The time of deglaciation was described with a radiocarbon data of about 12 500 B.P.
My questions are: When began the deglaciation, approximately, following your pollen diagrams?
Did the deglaciation begin at nearly the same time all over the Andes or were significant differences in time?

Dra. M. L. Salgado-Labouriau:

At 12 650 radiocarbon years B.P., the first pollen grains started to be deposited in peat sediments from Mucubaji. Before this date, only sand was found. Therefore, we believe deglaciation occurred shortly before 12 650 B.P., in this glacial valley. At present we have no other site analysed at this elevation (3650 m) to compare. Another site at higher elevation (4000 m) that is now beeing analysed shows a later date for the beginning of pollen deposition. The phases found in Mucubaji sediments are similar to those for the Columbian Andes (see VAN DER HAMMEN and collaborators); but there are not enough data for the Andes in general to answer the second question.

Miss J. M. Kenworthy, M. A.:

Can any participant in the discussion explain to me what is behind the assumption of a steeper lapse-rate in the past – throughout the equatorial zone, when the laws of physics and local topography must have at all times been relevant?

Dr. C. Schubert:

Concerning lapse-rates: lapse-rates may vary significantly from low elevations to higher elevations. So, it might be useful to subdivide lapse-rates into elevation segments.

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Ecological Diversity and Human Settlements in the Tropical Northern Andes

Los Pueblos del Sur: A Pilot Project of Integral Analysis in the Cordillera de Mérida

Maximina Monasterio and Guillermo Sarmiento

With 10 Figures

1. Ecological Diversity in the Venezuelan Andes

Starting at the Colombian border, the main Andean belt in Venezuela extends for 450 km to northwest direction (Fig. 1). All along its length the cordillera has an average width of nearly 100 km. This huge continuous massif appears deeply dissected by large structural valleys that give rise to systems of parallel chains. Most of the population is concentrated along these valleys, particularly in the middle and upper parts. Here, a rich and diversified agriculture occupies the terraces and alluvial fans. Thus along the Bocono, Motatan, Chama and Mocoties rivers, stand Bocono, Valera, Timotes, Mucuchies, Merida, Tovar, Bailadores and other minor urban centres. Beyond these main valleys, most slopes and secondary valleys remain sparsely populated.

In the central part of the Venezuelan Andes, in Merida, the Chama-Mocoties valleys separate the Cordillera de la Culata, to the north, from the Sierra Nevada de Merida to the south. Our study area, Los Pueblos del Sur, occupies both slopes of the Sierra Nevada (Figures 1 and 2) to the northwest, that drains into the Chama river towards the Lake of Maracaibo, and to the southeast that is draind by several rivers descending to the Llanos, which is then collected by the Apure, one of the major tributaries of the Orinoco.

Los Pueblos del Sur are thus bordered on the northwest by the Chama and Mocoties valleys; the highest peaks of the Sierra Nevada: Humbolt, Bonpland and Bolivar, reaching 5000 m, close the region to the north; while a large transversal range, el Batallon, acts as its natural southern frontier. Towards the llanos, the only natural limit that imposes itself is one of human occupation, since settlements are restricted to the slopes above 1000 m. The whole lower slopes remain almost completely unoccupied. The area thus defined has a total surface of about 300 000 ha (Fig. 2).

Due to the wide altitudinal range in this section of the Andes (500 to 5000 m), together with the diversity of rainfall regimes, almost every type of tropical mountain environment can be encountered (Fig. 3). Under each major climatic type a particular altitudinal zonation of vegetation and land-use belts may be found (SARMIENTO et al., 1971; MONASTERIO, 1980) (Figures 4 and 5). The constitutive elements of this zonation, as well as the precise altitudinal limits between them, vary in function of rainfall amount and its annual distribution. Thus, in the driest slopes facing the Chama valley, the vegetation sequence begins with a cactus shrub and ends with a dry type of paramo that already appears at 2500 m. In the moister areas of this same inner slope, most of the mountain side is covered by cloud forests (Fig. 6) that rise to 3300 or more meters, and that still remain mostly untouched because this area belong to the Sierra Nevada National Park. Above the cloud forest a wet type of paramo occurs, that is replaced higher on the slope by the Desert Paramo (Fig. 7), then by the periglacial desert and finally, above 4700 m, by the nival zone.

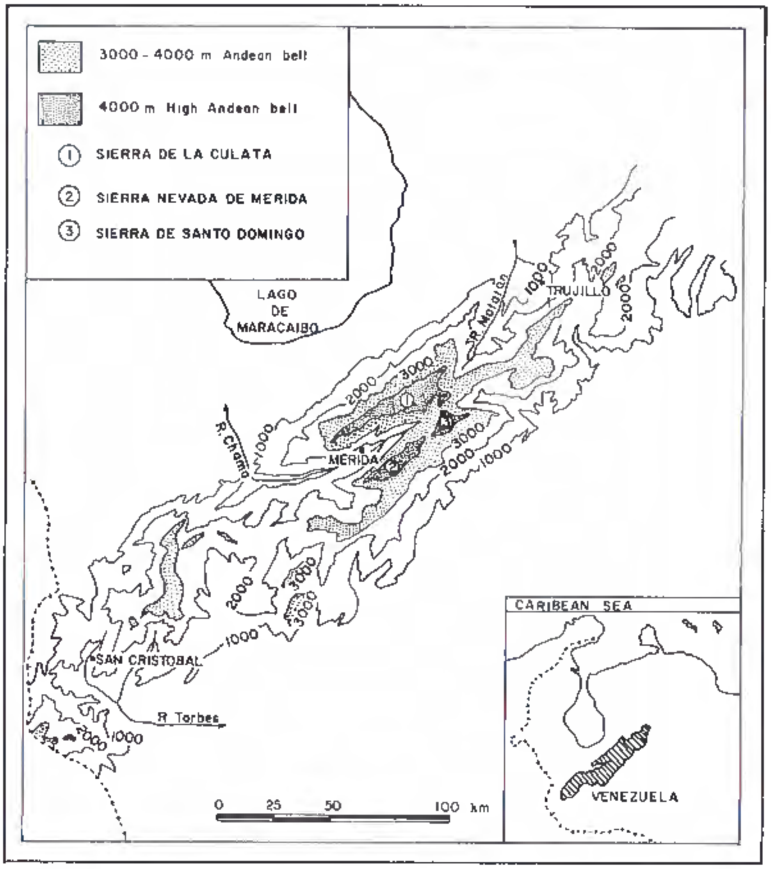

Fig. 1. Surface corresponding to different altitudinal levels in the Cordillera de Mérida, Venezuela.

Another sharp climatic contrast appears between the two slopes of this Andean chain (Fig. 8). The NW inner slope that drains into the Chama and Mocoties rivers, has a typical bimodal rainfall regime with two peaks of rainfall (April-May and September-October), while the SE outer slope, looking towards the llanos, shows an unimodal distribution, with a single annual peak in the midyear months and an accentuated drought from December to March (MONASTERIO and REYES, 1980).

Geology is another important factor which plays a major role in environmental diversity. Several geologic formations outcrop in this area, characterized as most mountain regions by a moving geological history (SCHUBERT, 1980). The main contrast in habitat condition for vegetation and cultures arise from

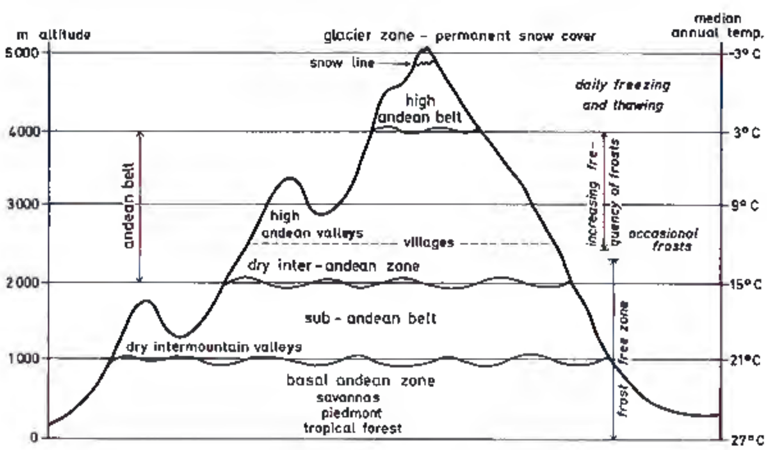

Fig. 3. Idealized profile of altitudinal zonation in the Cordillera de Mérida. The human population, distributed in "islands", is primarily in the two valley zones of Andean and sub-Andean belts (after MONASTERIO, 1980).

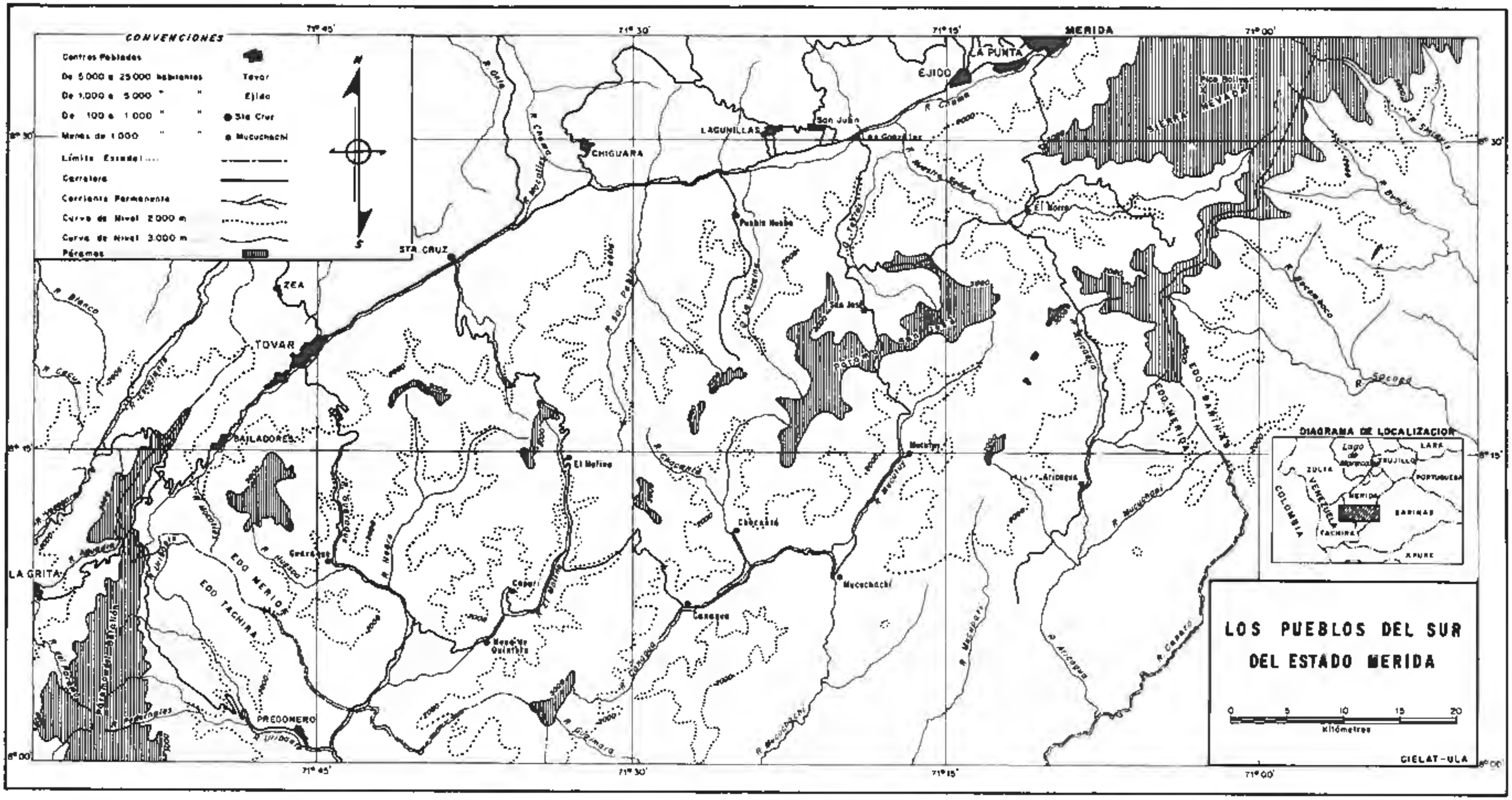

Fig. 2. Area of Los Pueblos des Sur de Mérida.

the occurence of three quite different rock types: metamorphic rocks, mostly gneisses and schists, giving rise to a massive relief; hard sedimentary rocks, like conglomerates and sandstones, that produce a contrasted faulted relief of crests and monoclines; while softer sedimentary rocks, such as shales and limestones, produce a gentler topography where deeper soils may develop. In this way, lithological influences through its effect on structure and differential erosion, the kind of surface modelling, the degree of soil development and hence the possibilities of land utilization (MESSER, MONASTERIO and SARMIENTO, 1982).

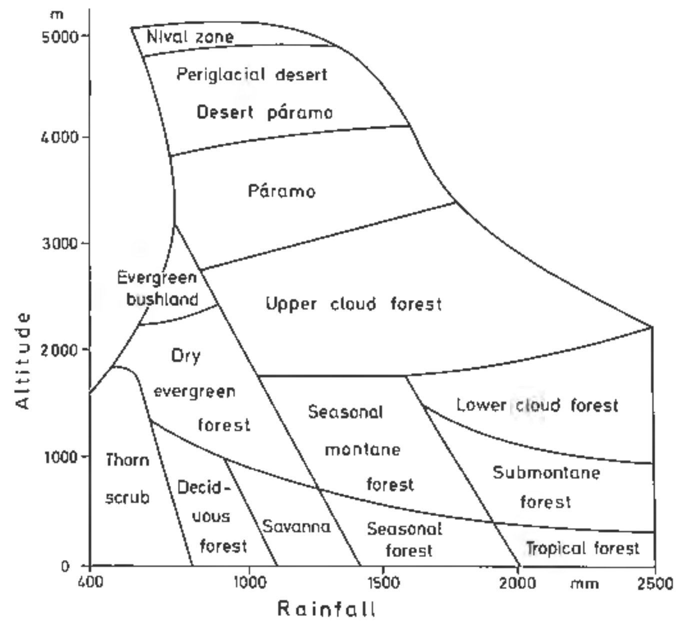

Fig. 4. Wide diversity of primary ecosystems existing in the northern tropical Andes (Cordillera de Mérida), according to altitudinal and rainfall gradients.

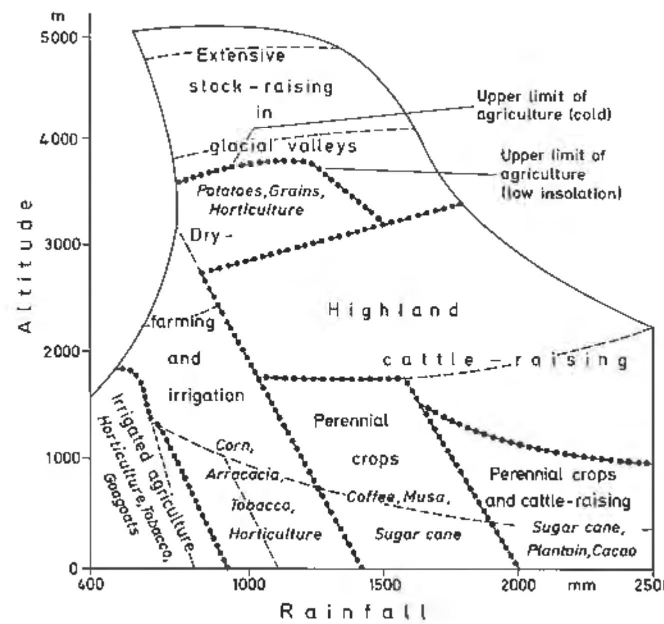

Fig. 5. Main land-use patterns in correlation with primary ecosystems existing in the Cordillera de Mérida (compared with Fig. 4). Thus, in the cloud-forest area, we have cattle raising for milk and meat production, the seasonal montane forest corresponds to perennial crops, mainly coffee, etc.

2. General Outlook and Some Key Methodological Premises

The primordial aim of this project, already in progress, is an ecological and socioeconomic study of the Pueblos del Sur in the Cordillera de Merida (see Fig. 2). This should provide a basic contribution to the establishment of developmental policies in harmony with the natural environment having their main focus on the stabilization of the local population and the improvement of their living conditions.

The Pueblos del Sur constitutes an area of striking regional individuality resulting from both ecogeographic factors and the historical development of its economy. Until very recently this area was relatively isolated from the macroregional context, even considering the isolation patterns characteristic of the high Andean valleys. Modernization is just beginning and most of the area remains as a marginal zone of traditional agriculture. However, public works are already in progress: roads, electricity, irrigation, etc. They will certainly lead to a dramatic change in all aspects of rural life. For this reason it becomes still more urgent to undertake an integral study that might lead to further knowledge of the overall regional picture of its agricultural systems, the local technologies and their ecological rationality. It is also important to study the possible alternatives created by better access to regional and national markets, the intensification of land use, and new pressures upon natural resources.

Furthermore, this region shows a diversity of temperature and other agroclimatic conditions given by the extension of its altitudinal belts. These range from the tropical lowlands in the Andean piedmont to the coldest paramos bordering the snowcovered peaks. The diversification of agroeconomic activities

Fig. 6. A view of the cloud-forest at 3000 m, in the Pueblos del Sur.

Fig. 7. A view of the Desert Páramo ecosystem with *Espeletia timotensis* at 4200 m in the Cordillera de Mérida. Snowfall is frequent at this altitude.

made possible by this rich variety of natural environments the relative persistance of production and conservation, and of local cultivars, render particularly interesting. It is especially important to analyze and characterize these systems or to define the conditions under replacement by socially more productive forms could be envisaged.

It is also worth emphasizing that, even if the traditional practices of management have allowed a relative equilibrium of the local environments and ecosystems, the strong slopes prevailing everywhere in this high mountain area, together with the climatic stresses to which it is normally subjected, determine the potential fragility of most natural and secondary ecosystems. Every technological innovation and infrastructural work has to be based on a thorough knowledge of the dynamics of the ecological units.

One of the most important elements considered in this project refers to the human resources of the region. Its peasants, heirs of aboriginal and hispanic traditions, remain warmly attached to the land. In spite of their isolation, they were open to trade both during the colonial and the republican periods. Any developmental programme must therefore take into account local traditions and feelings, avoiding the mechanical extrapolation of experiences and results coming from completely different socio-cultural backgrounds. High priority will be given to promote policies whose main objective is the well-being of the local peasantry and the maintenance of a long-term natural and social equilibrium.

To cope with the forementioned premises, it becomes absolutely necessary to implement methodologies ad hoc, adapted to the tropical mountains of Latin America. A multidisciplinary approach is essential, where the various personal and institutional participants can integrate their viewpoints and abilities in a process of mutual learning and gradual self-correction leading to the improvement of the whole team. Many methodologies are supposed to use an integral approach to regional problems as a basis for agricultural planning and rural development, but apparently none of them are entirely satisfactory nor have they resulted in direct application to all real situations. In our case, the existing agricultural systems, as well as the environmental conditions and the natural ecosystems, suggest the need for a global systemic approach rooted in a solid understanding of the physico-natural and socio-historical factors. From these factors may be derived the most rational alternatives to improve land-use and increase land and human productivity. We will try to set out, and to test in practice, certain methodological principles that could be applied by a small multidisciplinary and interinstitutional team. These principles could be adapted to the previous knowledge and to the working conditions of the tropical Andean environments. The two institutions already engaged in this project are the FONAIAP (National Organization for Agricultural Research), and the CIELAT (Center for Ecological Research of the Los Andes University).

One of the major interests of the project may lie in its possible value for future programmes of regional analysis on a large scale, by demonstrating an integrated approach, focused towards a clearly established practical goal. Quite often the programmes of rural development or regional planning, in Latin America and elsewhere, have neglected the ecological processes and constraints, either by lack of pertinent information or by straightness of vision, thus imposing a heavy handicap to the success of the project. On the other hand, regional analysis undertaken on sounder ecological basis have suffered from a distinctly academic bias. Scale problems are also evident, many studies are designed on such an excessively small scale that makes them useless for regional planning in mountain areas.

3. Patterns of Settlement and Land-Use

According to the figures of the last available National Census (1971) the total population of the Pueblos del Sur was approaching 40 000. In this essentially rural area, a dual pattern of human settlement appears: an archipelago of small villages together with a sparse population of isolated farms. There are about 30 villages, that in the humid areas always lie in valleys between 1200 and 1800 m. In the drier zone, where valley bottoms are excessively dry, most settlements stand on slopes between 1600 and 2800 m. In any case they range from small groups of a few houses to villages of a few hundred inhabitants.

Human occupation in the Pueblos del Sur follows divergent historical patterns according to agricultural possibilities given by the ecological conditions. On dry slopes, wheat (Fig. 9), seconded by other temperate-zone grains, constituted the major market crops. During most of the colonial period, and in spite of the non-existence of carriage roads, this area exported wheat not only to regional markets in the Andes

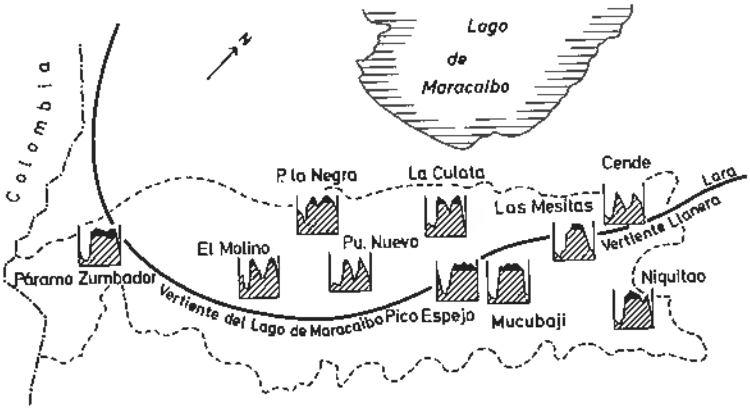

Fig. 8. Diversity of rainfall patterns in the Venezuelan Andes. Northwestern slopes show a bimodal rainfall distribution, while southeastern slopes show the typical unimodal tropical regime, with a dry season from January to March.

Fig. 9. Ancient wheat village at 2700 m in the Cordillera de Mérida. the wheat system is relictual and persists on dry slopes. There is a clear trend towards diversification and market crops beginning in alluvial fans.

Fig. 10. Threshing the wheat, traditionally a community activity. Cordillera de Mérida at 2700 m.

but even to Maracaibo and through this port to other regions. In the last decades of the nineteenth century, this wheat cycle was replaced by the coffee cycle. Coffee is cultivated in the Seasonal Montane Forest. Nowadays, wheat appears as a relictual crop directed mostly to self consumption (Fig. 10). During many periods, smallholders maintained a subsistence agriculture on these dry slopes, but recently modernization has progressed slowly through a diversified agriculture oriented to regional and local markets. Maize, blackbeans, arracacia, garlic, carrots, stand among the principal crops.

The southeastern slopes, as well as the moister inner slopes draining into the Mocoties, were colonized much later than the drier areas that already maintained aboriginal populations before the Spanish conquest. Until coffee cultivation and export came to play a significant role in the last decade of the century, most of these humid slopes remained sparsely populated. The coffee cycle persisted until the world crisis of 1930 that, together with the oil boom, induced dramatic changes in the whole Venezuelan society. Nowadays coffee production, complemented by subsistence crops, is regaining importance, but a new boom in horticulture results from ease of access to the national market and modernization. Most of the fertile alluvial soils are dedicated to a variety of crops like potatoes, onions, garlic, carrots, and many other vegetables, i.e. market gardening.

We have to recall here the fact that the Andes was not only but still remains, a major area of coffee production in Venezuela. However because of its unique agroecological conditions given by its mountain climates within a predominantly tropical warm country, the high andean valleys represent the sole area where many temperate crops become possible. In this way, this mountain areas, in spite of adverse slope conditions, become the necessary complement to the tropical agriculture of the warm lowlands.

Finally, a recent trend clearly apparent in the Pueblos del Sur, as in many other highlands in Venezuela, is the tremendous expansion of cattle raising on lands gained from the mountain forest. This upwards extension of rangelands not only changes the whole economic picture of the region, but also is subjecting the high ranges to new pressures of unpredictable consequences. Thus, the development of large hydroelectric projects points out the incompatibility between stockraising in the catchment areas and large dams and water reservoirs in the middle and low basins.

4. Some Objectives of this Research Project

a) Delimitation, characterization and mapping of the regional ecological units.
b) Identification and evaluation of the physical and biotic factors conditioning or limiting the use of natural resources in each ecological unit.
c) Inventory of the agricultural systems by ecological units.
d) Farm typology definition, characterization and analysis of agricultural systems.
e) Understanding of the regional agrarian systems on the basis of the existing agricultural systems and their interrelationships.
f) Analysis of the interrelationships between ecological factors, and agroeconomic structure and use of natural resources.
g) Identification of socioeconomic factors affecting or promoting the efficient utilization of natural resources in this region.
h) Analysis of the impact of past and present land-use practices on the stability of the ecosystems.
i) Consideration of the local technological traditions and their ecological and economic rationality.
j) Evaluation of possible impacts of new agronomic technologies on the agricultural systems, agroecosystems and natural ecosystems.
k) Analysis of the ecological, economic and social consequences of various infrastructural works undertaken in the last years: roads, irrigation systems, education and health-care centers, etc.
l) Discussion of methodological principles applicable to the agroecological zonification and agroeconomic analysis of tropical mountain regions.

5. Some Final Remarks on Methodology

During the last two or three decades, the problems posed by developmental urgencies in many regions, particularly in the underdeveloped countries, initiated the search for appropriate methodologies that could afford a rapid and efficient gathering of relevant information to sustain governmental or private actions. Though many useful tools were increasingly available, especially in the field of remote sensing, a lot of unsolved problems remained in this multidimensional research area.

The actual knowledge on climates, morphodynamics, soils, ecosystems and many human and social aspects, is so fragmentary that even guiding principles, not to speak of hard facts of scientific laws, are difficult to support or extrapolate. Obviously the underdevelopment also has a scientific dimension. This lack of hard facts and quantitative data is still more dramatic in tropical or in mountainous regions. Probably, the mountain regions of tropical countries accumulate the most handicaps.

It is our intention in this project to start with a quite restricted goal, taking into account the sea of ignorance around us. Our aim is to analyze a few aspects in a particularly restricted area that by its near location to our daily activities could be carried out by a small team having some previous experience both in the area and in the general ecological, agricultural and socioeconomic problems.

Two rather divergent types of approach have been followed in regional land and resources inventories. One is multi-sectorial approach, where specialists analyze each component of the natural and social environment. Once the sectorial aspects have been accomplished more or less independently, all this information is added in some way to produce an a posteriori synthesis. These seems to have been the methodological guiding principles in some ambitious and successful programmes carried on in various countries. Perhaps the best example might be the RADAM BRASIL program of inventory of natural resources in the huge Amazonian region of that country.

The second alternative is to start with a synthetic viewpoint, delimiting units resulting either from physico-natural conditions or from social pressures. That is, to have a first reading of the landscapes to be used later in the analysis and characterizatiou of factors and processes. The leading thread towards a synthesis has been land forms in the CSIRO methodology (CHRISTIAN and STEWART, 1963); natural vegetation in many European mappings; surface dynamics in the ecographic approach of Strasbourg (TRICART and KILIAN, 1979); or the global landscape as a product of environment and people in their actual and past actions in some geographic approaches (BERTRAND, 1970).

This approximation to integral regional analysis through an initial synthetic lecture of the landscape continued by a further analysis leading to a new synthesis, seems more adequate to small projects involving a reduced multidisciplinary team and limited resources. On the other hand, it may be argued that this synthetic approach would be more adequate than the multisectorial one, in mountain regions where all factors physical, biotical and social, are strongly linked with each other.

The system we propose to follow is one of successive approximations through interdisciplinary discussion of the conclusions obtained during each stage of the research work. It may be started with a preliminary delimitation of homogeneous landscape units through both interpretation of remote imagery and field work. Then each unit is sampled in its natural parameters and in its agroeconomic organization. The sampling may lead to some reinterpretation of units and may suggest the consideration of some previously neglected factors or processes. The zonification is thus improved and further data collection is suggested. Within this process, various kinds of information are pooled, from field data to imagery interpretation, from available statistics to questionnaires submitted to rural producers or other qualified informers, from various laboratory data to a collective discussion with landowners in their villages.

In this way, the art of regional ecological analysis, taking the word ecology in its wider and wiser sense, may be developed through a gradual process of learning and giving, what we hope would lead to a deeper understanding of this fascinating world of the Tropical Andes.

Acknowledgements

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References

BERTRAND, G. (1970): Ecologie de l'espace géographique. Recherches pour une science du paysage. Comtes rendus de la Societé de Biogeographie, 195–205.

CHRISTIAN, C. S. and G. A. STEWART (1963): Methodology of integrated surveys. In: Serial Surveys and Integrated Studies, UNESCO, Paris, 233–380.

MESSER,T., M. MONASTERIO and G. SARMIENTO (1982): Elementos para un análisis de la diversidad ambiental en los Pueblos del Sur (Estado Merida). Acta del VII. Congreso Venezolano de la Ciencia del Suelo. San Cristobal, 14 al 20 de Noviembre.

MONASTERIO, M. (1980): Poblamiento Humano y Uso de la Tierra en los Altos Andes de Venezuela. En: MONASTERIO, M. (Ed.): Estudios Ecologicos de los Paramos Andinos. Ediciones de la Universidad de los Andes, Merida. 170–198.

– and S. REYES (1980): Diversidad Ambiental y Variacion de la Vegetacion. En: MONASTERIO, M. (Ed.): Estudios Ecologicos en Los Paramos Andinos. Ediciones de la Universidad de los Andes, Merida. 47–91.

SARMIENTO, G., M. MONASTERIO, A. AZOCAR, E. CASTELLANO and J. SILVA (1971): Vegetación Natural. Estudio Integral de la Cuenca de los Rios Chama y Capazon. Sub-Proyecto N III. Facultad de Ciencias, Universidad de los Andes, Merida, Venezuela.

SCHUBERT, C. (1980): Aspectos Geológicos de los Andes Venezolanos: Historia, Breve Sintesis, El Cuaternario y Bibliografía. En: MONASTERIO, M. (Ed.): Estudios Ecológicos en los Paramos Andinos. Ediciones de la Universidad de los Andes, Merida, Venezuela. 29–46.

TRICART, J. and J. KILIAN (1979): L'Eco-Géographie et L'amenagement du Milieu Naturel. Paris.

Discussion to the Paper Monasterio

Dra. M. L. Salgado-Labouriau:

I find your project very interesting. I would like to ask if the rural settlements in the area have remained fairly stable or if they have expanded in the last 50 years.

Prof. Dra. M. Monasterio:

According to the various populations censuses (the last one in 1981), the total rural population in the Pueblos del Sur remained fairly stable during the last 50 years in spite of the large migration to other regions of the country. Various processes of internal displacement are also apparent, such as the seasonal or permanent migration from the relictual wheat system to the more dynamic coffee system or even to the expanding cattle raising areas in the Cloud Forest belt. These migratory currents were compensated by the high rates of population growth and the improved health conditions.

Prof. Dr. B. Ruthsatz:

Is there some knowledge about symbiosis between species of *Espeletia* and fungi, such as some type of mycorrhiza that could improve the uptake of mineral nutrients?

Prof. Dra. M. Monasterio:

Preliminary observations suggest the occurence of mycorrhiza in several species of *Espeletia.* This may obviously constitute a great selective advantage for species colonizing páramo environments where nutrient supply may be critical.
Specialists interested in a more systematic approach to this relevant problem are certainly needed.

Prof. Dr. W. Eriksen:

In what concerns your first map, why there are no páramos southward from Peru, at least on the eastern, more humid, Andean slopes?

Prof. Dr. M. Monasterio:

In our map (not published), we show the páramos extending from 11 °N, in the Sierra Nevada de Santa Marta (Colombia) to 8 °S in northern Peru. These limits frame the páramos in equatorial or mostly equatorial areas – where they occur as islands conforming a continental archipelago. Southwards from 8 °S, the high tropical moutain appears as a more continuous area, drier and less equatorial. Even if the eastern slopes are wetter, as in the case with the Peruvian Jalca zone, we prefer to relate these systems to the punas. Both types of formations: punas and páramos occur inside wide humidity gradients, therefore we do not emphasize this aspect as a basis for their ecological distribution. There are quite dry páramos, with 600 mm of rainfall, in the Cordillera de Mérida.

Then, to represent the continental extension of punas and páramos, we rely more on the particular features, structural and functional, of both types of ecosystems, as well as on the actual or potential land-use patterns.

Prof. Dr. F. Klötzli:

The parallelisms between Andean and East African Páramo vegetation are well known. But less thought has been given to special adaptations of typical Páramo organisms (e.g. *Espeletia*, *Senecio*, *Lobelia*). There must be a special reproduction or regeneration strategy, because in certain cases (as in Ethiopia with *Lobelia thynchopetralum*) such organisms are more or less growing solely under extreme solifluction conditions. Are details known from Venezuela concerning their regeneration?

Prof. Dra. M. Monasterio:

In the Cordillera de Mérida, all species of *Espeletia* growing in the Desert Páramo (that is above 4000 m), reproduce only sexually. We undertook a detailed analysis of their reproductive cycles and annual phenodynamics using permanent plots along a period of seven years (1976–1983). Some forms of vegetative regeneration by means of basal stems have been observed in species of *Espeletia* that occur at lower elevations (3000-3800 m).

Given that the solid surface maintains the most extreme habitat conditions in the Desert Páramo (daily frost cycles), with the related phenomena of solifluction and cryoreptation, it seems that all species of *Espeletia* have avoided a concentration of their biomass in the lowest, most unfavourable layers, exhibited by the contrary one upright life form and very sparce distribution pattern, in a similar way to that showed by the high-altitude Ethiopian Lobelias. Other characteristic features of the reproductive patterns of these species are presently under analysis and will be the subject of a coming publication.

Prof. Dr. W. Lauer:

Which climatic conditions characterize the individual páramo-types mentioned by you?

Prof. Dr. M. Monasterio:

In the Andes of Mérida it is possible to fix at about 4000 m the lower limit of undoubted periglacial features. This level marks the boundary between two clearcut ecological zones: the Andean belt, downwards, and the High Andean belt, towards the summits. The Desert Páramo corresponds with the periglacial belt of low latitude mountains where frost action and daily cycles of freeze-thaw promote specific geomorphogenetical processes and soil movements of deep ecological consequences. This climatic effects are reinforced by the open nature of the vegetation cover, giant rosettes of *Espeletia*, that leaves large areas of bare ground, favouring thus the rapid cooling and heating of the soil surface that lead to daily cycles of freeze and thaw along most of the years. Below 4000 m, the Desert Páramo is replaced by various páramo formations characterized by a continuous vegetation cover. Frosts in this belt are either mostly seasonal phenomena or they occur sporadically.

Erdwissenschaftliche Forschung, Bd. XVIII, 307–320
Franz Steiner Verlag Wiesbaden GmbH · Stuttgart (1984)

Zur klimaökologischen Stellung der Gattung *Araucaria*

Winfried Golte

Mit 7 Abbildungen

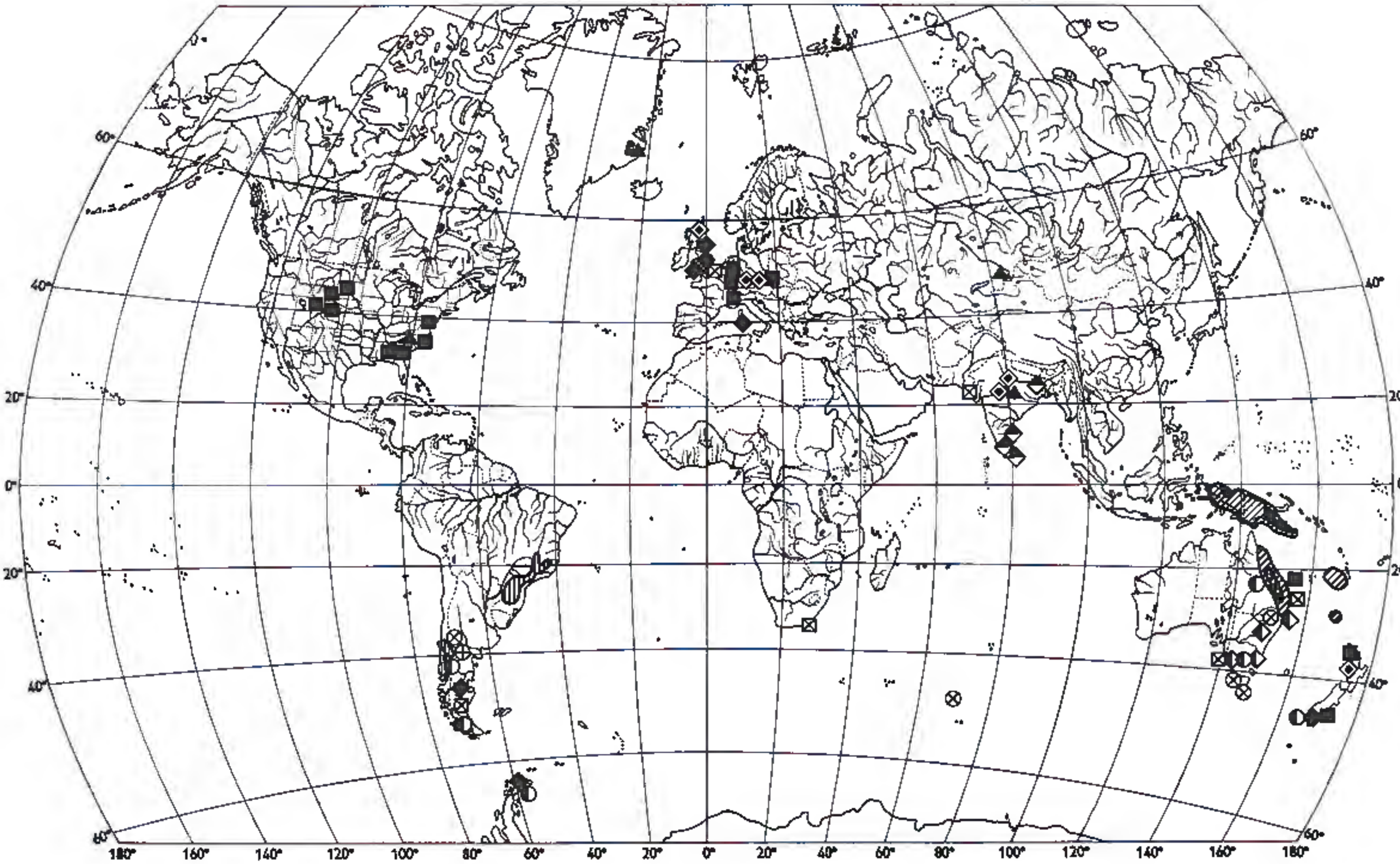
Unter den heute lebenden Coniferengattungen ist *Araucaria* eine der phylogenetisch ältesten, wenn nicht *die* älteste überhaupt (vgl. FLORIN, 1963). Früheste, noch spärliche Funde stammen aus der späten Trias, doch schon vom unteren Jura an ergeben die fossilen Nachweise ein zwar disjunktes, jedoch – über die langen Zeiträume hinweg – bis ins Tertiär hinein bemerkenswert konsistentes und stetiges Verbreitungsbild, dem sich auch die lebenden Vorkommen zwanglos anfügen (Abb. 1). Araukarien beherrschen – zusammen mit Podocarpaceen – vom Jura an die südhemisphärische Coniferenflora. Mit der Verbreitung ihrer gegenwärtig 19 Arten erscheint die Gattung als rein südhemisphärisch, sie war jedoch entweder selbst oder mit einem ihr sehr nahestehenden Genus im Mesozoikum auch auf der Nordhalbkugel verbreitet. Das hohe Alter der Gattung wird durch die Tatsache unterstrichen, daß sich noch deren lebende Vertreter in ihren vegetativen Organen durch eine Anhäufung primitiver Merkmale auszeichnen. Im Habitus zeigen Araukarien, namentlich *A. heterophylla* (= *excelsa*) von der Insel Norfolk auffallende Übereinstimmungen mit den sog. Urconiferen (Sammelgattung *Walchia*) des Jungpaläozoikums. Auch im Feinbau des Holzes (Xylotomie) vertreten die Araukarien (und die Schwestergattung *Agathis*) einen Urtypus, wie er in den Gymnospermenhölzern jener Zeit auftritt und bei keiner anderen lebenden Coniferenfamilie mehr erhalten ist (GREGUSS, 1955).

Angesichts dieser Befunde liegt es nahe, die heutige Verbreitung der Gattung *Araucaria* einmal im Hinblick auf die zugrundeliegenden Gesetzmäßigkeiten zu untersuchen und die Frage zu stellen, wieweit diese Ausdruck vorzeitlicher Verbreitungsverhältnisse sind. Damit sollen Gedanken weitergeführt werden, die ich in früheren Arbeiten zur Coniferenflora der Südhalbkugel (GOLTE, 1978 a) und in einem ökologischen Vergleich der beiden in Südamerika heimischen Araukarien (GOLTE, 1978 b) niedergelegt habe. Da die Ergebnisse der letztgenannten Arbeit in besonderer Weise Ausgangspunkt der nachfolgenden Betrachtungen sind, müssen sie hier zunächst kurz resümiert werden.

1. Ökologischer Vergleich von *Araucaria angustifolia* und *A. araucana* in Südamerika

A. angustifolia (Abb. 2) hat ein recht großes Verbreitungsgebiet im südlichen Brasilien und dem angrenzenden argentinischen Territorium Misiones. 2000 km davon entfernt, in den chilenisch-argentinischen Anden, befindet sich das viel kleinere Areal von *A. araucana*. Der ökologische Vergleich beider Arten drängt sich vor allem deshalb auf, weil sie in der Systematik einander sehr nahe stehen[1], die klimatischen Bedingungen in ihren Verbreitungsgebieten aber auf den ersten Blick gegensätzlich zu sein scheinen. *A. angustifolia* gedeiht am äquatorwärtigen Rand der Subtropen bei – jedenfalls im größten Teil des Areals – überwiegenden Sommerniederschlägen. Umgekehrt befindet sich das Areal von *A. araucana*

[1] Beide Arten bilden innerhalb der Gattung die Sektion *Colymbea*, die sich von den anderen Sektionen vor allem durch die relativ großen Nadelblätter und Zapfen (und Samen), sowie hypogäische Keimung unterscheidet.



Araucaria: **Present distribution: Sect.** ***Bunya*** **▤; Sect.** ***Columbea*** **▥; Sect.** ***Eutacta*** **▨ (incl. ▤ and ⬬); Sect.** ***Intermedia*** **⬬.**
Fossil Araucarians (excl. ***Agathis*****). Distribution: late Triassic ▲, early Jurassic ⬖, middle Jurassic ◆, late Jurassic ◈, Jurassic (indeterm.) ⬗,**
early Cretaceous ⊠, late Cretaceous ■, Eocene ⊕, Oligocene ◐, Tertiary (indeterm.) ⊗.

Abb. 1. Heutige und frühere Verbreitung der Gattung *Araucaria;* aus: FLORIN, 1963. (Present and past distribution of *Araucaria;* from: FLORIN, 1963).

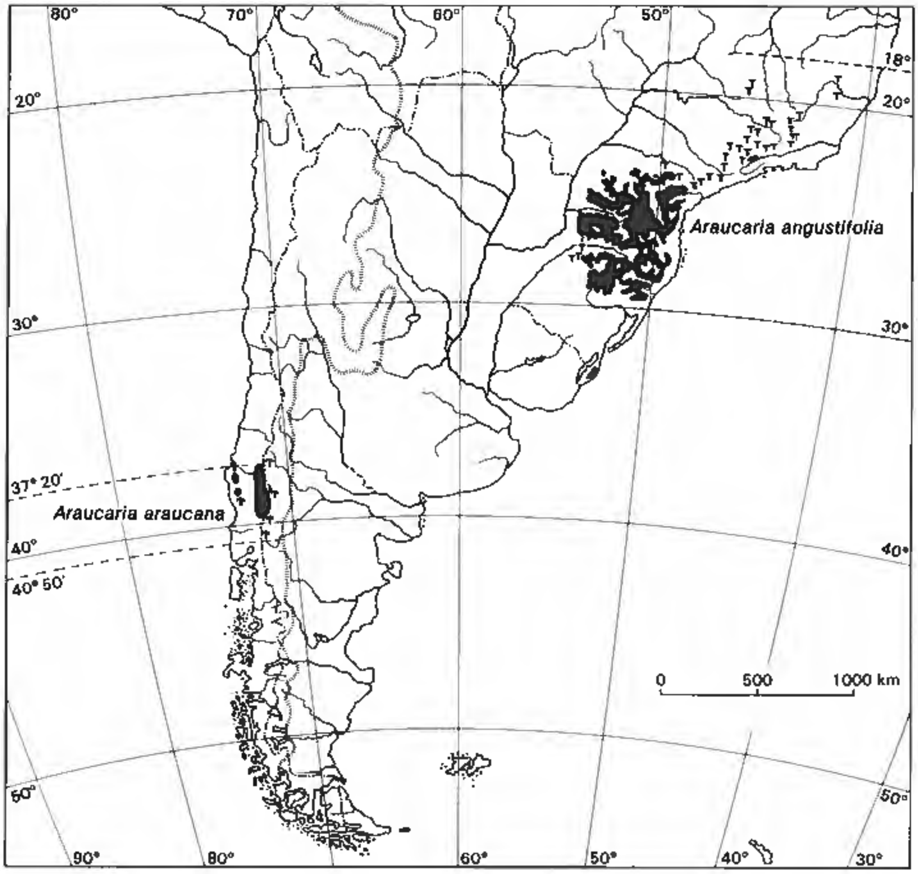


Abb. 2. Die Verbreitung von *Araucaria angustifolia* und *A. araucana* in Südamerika; aus: GOLTE, 1978 b. Kleinere Vorkommen sind durch Baumsymbole dargestellt.

(Distribution of *Araucaria angustifolia* and *A. araucana* in South America; from: GOLTE, 1978 b. Smaller occurences are represented by tree symbols).

am polwärtigen Rand der Subtropen im Übergangsbereich zur außertropischen Westwindzone, d. h. in einem Gebiet mit überwiegenden Winterniederschlägen.

Sehen wir uns zunächst die Verhältnisse bei *A. angustifolia* genauer an. Ihr Areal scheint die Grenze der Tropen (V. WISSMANN, 1948) geradezu zu „verhüllen", d. h. es liegt in einem Gebiet, das in sich tropische und außertropische Züge des Klimas vereinigt. Tropische und außertropische Zirkulation treten hier in Wechselwirkung.

Dies zeigt sich zunächst bei den Niederschlägen. Um deren jahreszeitlichen Gang zum Ausdruck zu bringen, habe ich in einem Meridionalschnitt längs durch das Areal den prozentualen Anteil der monatlichen Niederschläge an der jeweiligen Jahressumme dargestellt (Abb. 3). Wir sehen, daß sich innerhalb der Araukarienregion als Folge der Beteiligung von tropischer und außertropischer Zirkulation eine Umkehrung der jahreszeitlichen Niederschlagsverteilung vollzieht. Im Sommerhalbjahr kommt es, und zwar mit polwärts abnehmender Häufigkeit und Intensität, zu ergiebigen Niederschlägen vorwiegend konvektiven Typs, während im Winterhalbjahr, und zwar mit äquatorwärts abnehmender Häufigkeit und Intensität, außertropische Zyklonalniederschläge auftreten. Im Winter wird das vom atlantischen Subtropenhoch geprägte stabile Wetter immer wieder – etwa allwöchentlich – von instabilem Wetter mit Niederschlägen abgelöst, die den Durchzug einer Kaltfront begleiten. Diese Kaltfronten setzen auch bei den winterlichen

Temperaturen einen außertropischen Akzent (Abb. 4). Generell ist festzustellen, daß *A. angustifolia* nur dort vorkommt, wo die Mitteltemperatur mindestens eines Wintermonats 13 °C nicht übersteigt. Dazu kommt aber auch eine gewisse Häufigkeit von Frösten und sogar Schneefällen. Winterliche Niederschläge, Frost- und Schneefallhäufigkeit sind am größten im südlichen Teil der Araukarienregion. Und von diesen Bedingungen ist es nur noch ein Schritt zu den Verhältnissen, unter denen *A. araucana* in den Südanden gedeiht.

Das Diagramm der dort gelegenen Station Lonquimay (Abb. 5) zeigt ein ausgeprägtes Wintermaximum der Niederschläge, die in dem obersten Waldgürtel, in dem die Art auftritt, großenteils als Schnee fallen und zu einer mächtigen – bis über 2 m hohen – Schneedecke führen. Der Schnee hat nun verschiedene ökologische Konsequenzen. Erstens schützt er den Boden vor der Einwirkung der – gelegentlich sogar unter – 20 °C reichenden – tiefen Lufttemperaturen, so daß es zu keiner ausgeprägten Bodengefrornis, mithin auch zu keiner Sistierung der Assimilationstätigkeit kommen kann. Zweitens führt der Schnee zu einer Speicherung des Winterniederschlags und – da er erst im Frühsommer (Dezember/Januar) völlig abtaut – damit zu einer Annäherung des Optimums der Bodenfeuchte an das thermische Optimum.

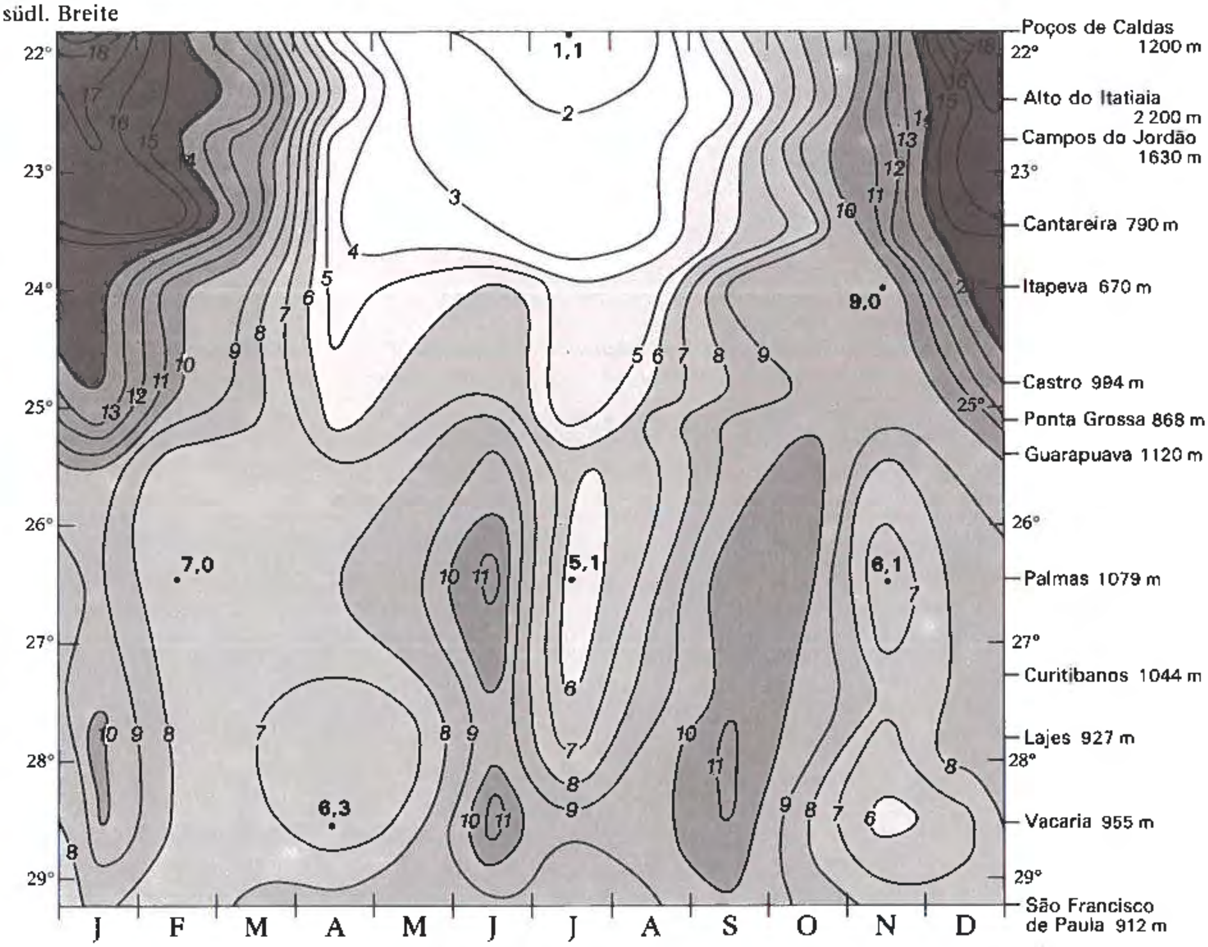


Abb. 3. Die jahreszeitliche Verteilung des Niederschlages in der Araukarienregion Südbrasiliens, dargestellt in Prozent der Jahressumme entlang eines Stationenschnittes zwischen 22° und 29° s. Br.; aus: GOLTE, 1978 b.

(The seasonal distribution of precipitation in the Araucaria region of Southern Brazil, presented as percentages of the annual total along a cross section of stations between 22° and 29° South; from: GOLTE, 1978 b).

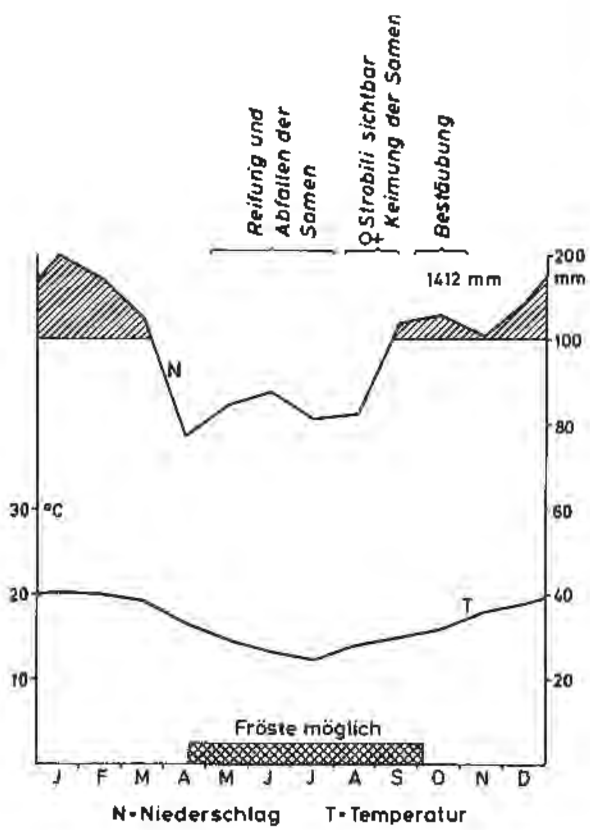


Abb. 4. Jahreszeitlicher Gang des Klimas (Station Curitiba, 25°26′ s. Br., 49°14′ w. L.; 959 m) und reproduktiver Zyklus bei *Araucaria angustifolia* (die angegebenen Zeiten gelten etwa für den mittleren Abschnitt des Verbreitungsgebietes); aus: GOLTE, 1978 b.

(Seasonal Course of the climate (station Curitiba, 25°26′ s, 49°14′ w; 949 m) and reproductive cycle of *Araucaria angustifolia* (the periods indicated apply approximately to the central section of the distribution area); from: GOLTE, 1978 b).

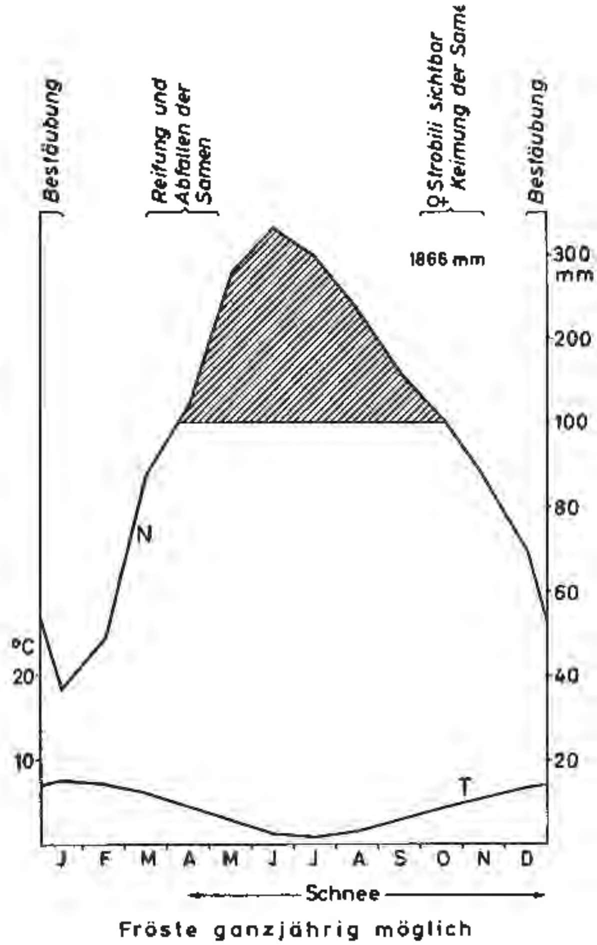


Abb. 5. Jahreszeitlicher Gang des Klimas (Station Lonquimay, 38°26′ s. Br., 71°15′ w. L.; 900 m) und reproduktiver Zyklus bei *Araucaria araucana;* aus GOLTE, 1978 b.

(Seasonal course of the climate (Station Lonquimay, 38°26′ s, 71°25′ w, 900 m) and reproductive cycle of *Araucaria araucana;* from: GOLTE, 1978 b).

Ähnlich wie das Areal von *A. angustifolia* in Südbrasilien die Tropengrenze gleichsam verhüllt, so verhüllt *A. araucana* mit ihrem Verbreitungsgebiet eine andere wichtige Klimagrenze, nämlich die zwischen der subtropischen Hochdruckzone und der außertropischen Westwindzone. Im Winterhalbjahr unterliegt die südandine Araukarie ganz dem zyklonalen Geschehen der Westwinddrift, während im Sommerhalbjahr zyklonale und antizyklonale Witterung einander abwechseln. Es fällt auf, daß der Niederschlagsgang (Wintermaximum) bei *A. araucana* die genaue Umkehrung dessen (Sommermaximum) darstellt, was wir im nördlichen Teil des Areals von *A. angustifolia* vorfinden. Wir haben aber gesehen, daß durch die Speicherung des Winterniederschlags in einer mächtigen Schneedecke bei *A. araucana* eine starke Annäherung an das Sommermaximum bei *A. angustifolia* zustandekommt. Daß die jahreszeitliche Umkehrung letztlich für die ganzjährig – wenn auch mit schwankender Intensität – wachsenden Araukarien von untergeordneter Bedeutung ist, können wir auch daraus schließen, daß sie sich bereits innerhalb des Verbreitungsgebietes von *A. angustifolia* abzeichnet, so daß im südlichsten Brasilien Verhältnisse herrschen, die denen bei *A. araucana* stark angenähert sind.

Der ökologische Vergleich der beiden südamerikanischen Arten zeigt also, daß die Araukarien einem ganz bestimmten jahreszeitlichen Niederschlagsgang angepaßt sind. Die Jahressummen der Niederschläge (1500–über 3000 mm) sind recht hoch, aber durchaus ungleichmäßig über das Jahr verteilt. Mehr oder weniger niederschlagsreiche Jahreszeiten wechseln mit solchen, die – ohne daß es dabei zu echter periodischer, d.h. regelmäßig einen Monat oder gar länger anhaltender Regenlosigkeit käme – eine Häufung trockener, von Strahlungswetter bestimmter Abschnitte aufweisen. Nur im Ausnahmefall einzelner Jahre – dies ist allerdings charakteristisch – kann dieses jahreszeitliche Nachlassen der Niederschläge das Ausmaß einer Dürre (drought) annehmen. Die Jahresschwankungen der Temperatur sind in den Verbreitungsgebieten beider Araukarien verhältnismäßig gering (6–8 °C), so daß von daher ein ganzjähriges Wachstum möglich ist. Andererseits sind diese wenn auch geringen jahreszeitlichen Schwankungen der Temperatur für die Araukarien offensichtlich von Bedeutung, wie übrigens klar auch aus der Verbreitung von *A. angustifolia* abzulesen ist (vgl. GOLTE, 1978b).

Die Frage ist nun, welche Anpassungen der Bäume sich hinter der Bindung an die skizzierten Klimaverhältnisse verbergen. Zunächst einmal sind die Araukarien vermöge ihrer ausgeprägten Hartlaubigkeit (Sclerophyllie) auf eine gewisse Verschlechterung der hygrischen Bedingungen, wie sie ja mit dem jahreszeitlich gehäuften Auftreten von Strahlungswitterung und der Verringerung der Niederschläge verbunden ist, eingestellt. Die Tatsache, daß sie mit ihren schirmförmigen Kronen im ausgewachsenen Zustand stets aus dem übrigen Kronendach herausragen und ihre assimilierenden Organe den möglichen hohen Sättigungsdefiziten geradezu exponieren, zeigt auch, daß sie die jahreszeitliche Trockenheit in gewissem Umfang brauchen. Es ist auch sehr auffällig, daß die Bäume nur dann Zapfen und Samen hervorbringen, wenn sie in dieser Weise der Sonne ausgesetzt sind. Und hier, in der Samenbildung, liegt nun, wie mir scheint, eine sehr bedeutsame Anpassung an eine jahreszeitliche Verschlechterung der hygrischen Bedingungen vor.

Diese Anpassung ist nur zu verstehen, wenn man bedenkt, daß die Gymnospermie, das Hervorbringen von (frei auf den Fruchtblättern liegenden) Samenanlagen, phylogenetisch eine Fortentwicklung des Generationswechsels der Pteridophyten darstellt. Bei den Farngewächsen durchläuft bekanntlich die Ontogenie noch zwei selbständige Generationen, eine geschlechtliche (Gametophyt) und eine ungeschlechtliche (Sporophyt). Das, was uns als Samenpflanze entgegentritt, ist der Sporophyt, der den einst selbständigen Gametophyten unter mehr oder weniger starker Reduktion gleichsam in seine Obhut genommen hat. Der für die Araukarien – und nicht nur für diese – entscheidende Umstand besteht demnach darin, daß die Megaspore im Megasporangium am Sporophyten verbleibt und sich hier die Entwicklung des Gametophyten von der Keimung bis hin zur Hervorbringung des Embryos, d.h. des neuen Sporophyten, vollzieht. Wenn auf diese Weise in der Samenbildung die geschlechtliche Generation gleichsam aufgehoben wird, dann deshalb, weil diese zu ihrer Entwicklung auf gleichmäßig hohe Feuchtigkeit und für die Verschmelzung der Gameten auf freies Wasser angewiesen ist. Der ökologische Sinn der Gymnospermie besteht also in der Überbrückung der für einen selbständigen Gametophyten zu ungünstigen oder zumindest risikoreichen trockenen Jahreszeit.

Diese ökologische Funktion der Samenbildung läßt sich deutlich an der Entwicklungsperiodizität der beiden Araukarien ablesen. Wir sehen bei *A. angustifolia* (Abb. 4), daß sich Reifung und Abfallen der Samen im Übergang zu der für das Wachstum ungünstigen, d.h. verhältnismäßig trockenen Jahreszeit, vollziehen. Etwa Mai bis Juli zerfallen die Zapfen. Die Samen keimen in der Regel schon 1–4 Monate später, und zwar in Zusammenhang mit dem Wiederansteigen der Niederschläge. Das Ruhestadium der Araukariensamen ist also relativ kurz und es läßt sich auch nicht lange ausdehnen, weil nämlich schon nach wenigen Monaten ein rascher Abfall der Keimfähigkeit eintritt. Dieser verhältnismäßig rasche Abfall der Keimkraft der Samen gilt nun für alle Araukarien (vgl. NTIMA, 1968), und er ist umso schneller, je höher die Temperaturen sind. Versuche von forstlicher Seite haben gezeigt, daß durch die Aufbewahrung der Samen im Kühlschrank dieser Abfall der Keimkraft merklich hinausgezögert werden kann. Daraus wird auch die Bedeutung der Tatsache verständlich, daß bei *A. angustifolia* die Samen zu einer Zeit fallen, in der zugleich die Temperaturen relativ niedrig sind und mit einer gewissen Häufigkeit Fröste auftreten.

Sehr aufschlußreich ist in dieser Hinsicht der Vergleich mit *A. araucana* (Fig. 5). Deren Samen reifen und zerfallen zwischen März und Ende Mai, d.h. gegen Ende der niederschlagsarmen Jahreszeit, und sie fallen – da Ende April/Anfang Mai die Schneefälle einsetzen – in eine Art natürlichen Kühlschrank, in dem sie ihre Keimfähigkeit regelmäßig über etwa ein halbes Jahr bis zum Beginn der Schneeschmelze und damit der Hauptwachstumszeit erhalten.

2. Die Araukarien Australasiens

Nur in Form eines kurzen Überblicks kann im folgenden gezeigt werden, daß die beim klimaökologischen Vergleich der beiden südamerikanischen Species erkannten Gesetzmäßigkeiten – mutatis mutandis – auch für die übrigen 17, in Australasien heimischen Araukarien (Fig. 1), gelten. Eine eingehende Darlegung und Begründung der diesbezüglichen Befunde mit Ausbreitung des umfangreichen in der botanischen, klimatologischen, geographischen, boden- und forstkundlichen Literatur verstreuten Belegmaterials wird an anderer Stelle vorgelegt werden. Insbesondere muß bei den folgenden Ausführungen auf eine nähere Interpretation der klimaökologischen Beziehungen und die – dabei unerläßliche – Einbeziehung der bodenkundlichen Gegebenheiten verzichtet werden. Die 17 weiteren *Araucaria*-Arten verteilen sich auf Ostaustralien und Neuguinea (zus. 3), die Norfolk-Insel (1) und Neu-Kaledonien (13). Sie werden drei weiteren Sektionen der Gattung zugeordnet[2].

2.1. *Ostaustralien*

Unter jenen 17 Arten ist es die ostaustralische *A. bidwillii*, die sowohl im Habitus, als auch ökologisch die größte Ähnlichkeit mit den beiden südamerikanischen Araukarien hat. Sie hat eine sehr begrenzte Verbreitung mit dem Schwerpunkt im gebirgigen südöstlichen Queensland (Hinterland von Brisbane, bei etwa 27° s. Br.), wo sie in Höhen zwischen 150 m und über 1000 m feuchte Talgründe (in tieferen Lagen) und Hänge (höhere Lagen) bevorzugt (vgl. MCARTHUR, 1949; NTIMA, 1968). Dazu gesellen sich zwei kleinere Reliktvorkommen weiter nördlich, über die bisher wenig bekannt ist.

Ebenso wie das Areal von *A. angustifolia* ist auch dasjenige von *A. bidwillii* schwerpunktmäßig in ausgesprochen subtropischer Position unmittelbar an der Tropengrenze (vgl. v. WISSMANN, 1948) angesiedelt. Entsprechend greifen auch hier tropische und außertropische Zirkulation ineinander. Die reichlichsten und zuverlässigsten Niederschläge fallen zur Zeit des weitesten südlichen Ausgreifens der ITC in den Sommermonaten (Januar–März), während im übrigen Teil des Jahres häufiger trockene Phasen eingeschaltet sind, die aber nur ausnahmsweise die Form einer Dürre annehmen. Ähnlich wie in Südbrasilien setzen winterliche Kaltlufteinbrüche in SE-Queensland einen außertropischen Akzent. Von Neusüdwales her reicht ein „Kältestreifen" mit wirksamen Frösten und (seltenen) Schneefällen gerade noch in das Verbreitungsgebiet von *A. bidwillii* hinein (vgl. GENTILLI, 1955). An ihren tiefstgelegenen Standorten sind Fröste noch relativ selten, doch treten in den höher gelegenen Vorkommen bis zu etwa 30 Frostwechsel-

[2] Zur Einteilung der Gattung in Sektionen vgl. NTIMA (1968), der freilich die ostaustralische *A. bidwillii* entgegen der von WILDE & EAMES (1952) vorgeschlagenen Revision noch gemeinsam mit den südamerikanischen Arten in die Sekt. *Colymbea* stellt. Sie wird seither in der monotypischen Sektion *Bunya* geführt. Alle weiteren Arten – ausgenommen *A. hunsteinii* von Neuguinea – sind in der Sekt. *Eutacta* zusammengefaßt, die sich durch relativ kleine Blätter (pfriemenförmig u. gebogen, Folgeform z.T. schuppenartig) und Zapfen, sowie epigäische Keimung von den Sekt. *Colymbea* und *Bunya* unterscheidet. Eine Mittelstellung nimmt die in eine eigene Sekt. *Intermedia* gestellte *A. hunsteinii (= klinkii)* ein.

tage im Jahr auf (NTIMA, 1968). Tatsächlich besitzt die Art eine ausgeprägte Frostresistenz. Erst bei unter – 6 °C können Schädigungen auftreten.

Es ist gewiß kein Zufall, daß auch das viel größere Areal von *A. cunninghamii* im subtropischen SE-Queensland und dem angrenzenden Neusüdwales einen ausgesprochenen Schwerpunkt hat, von wo es über die „Passatküste" des nördlichen Queensland (GENTILLI, 1955) bis in das westliche Neuguinea sich fortsetzt. Allein in Ostaustralien erstreckt sich das Vorkommen dieser Art über etwa 20 Breitengrade (31°–12° s. Br.; vgl. WEBB & TRACEY, 1967). Zusammen mit dem Verbreitungsgebiet in Neuguinea, das nahe an den Äquator heranreicht, ergibt sich eine Erstreckung des Areals über mehr als 30 Breitengrade. Es liegt nahe, hinter dieser erstaunlichen meridionalen Verbreitung eine besonders breite physiologische Valenz der Art zu vermuten, doch deutet alles darauf hin, daß hier im Zusammenspiel von Klima und Relief innerhalb des Areals tatsächlich so einheitliche Wachstumsbedingungen zustandekommen, daß von „relativer Standortkonstanz" (im Sinne von H. & E. WALTER) gesprochen werden kann. Infolge seiner Lage auf dem südlichen Ast des südostasiatisch-australischen Monsungebietes weist der gesamte Raum ein Sommermaximum (Dezember–März) der Niederschläge auf, dessen Ausprägung im Mittelabschnitt des Areals, der Passatküste zwischen Bundaberg (25° s. Br.) und Cooktown (15° 28′ s. Br.), am stärksten ist und sich sowohl gegen den polwärtigen Rand (außertropische Westwindzone), als auch gegen den äquatorwärtigen Rand (äquatoriale Westwindzone) zugunsten gleichmäßiger verteilter Niederschlagsregime abschwächt. Im Winterhalbjahr herrscht Hochdruckeinfluß vor. Das Niederschlagsminimum fällt in Queensland in die Monate August (Südabschnitt) bzw. September (Nordabschnitt). Es kommt aber auch hier nicht zu länger anhaltender periodischer Regenlosigkeit. Vielmehr treten mit einer gewissen Regelmäßigkeit Niederschläge auf, die teils orographisch bedingt sind (in Queensland polwärts abnehmend), teils von den zwischen den wandernden Antizyklonen durch die gegenläufigen Winde unter Einbeziehung außertropischer Luftmassen entstehenden Kaltfronten herrühren. Nur unperiodisch, d. h. in extremen Jahren treten im küstennahen östlichen Queensland während der Wintermonate (April–November) ausgesprochene Dürren auf.

2.2. *Neuguinea*

Das Vorkommen von Araukarien im Zentralgebirge von Neuguinea muß in engem Zusammenhang mit demjenigen in Queensland gesehen werden. Bis zum Beginn des Pliozäns und – durch Trockenfallen der nur etwa 50 m tiefen Torresstraße – noch während der Kaltzeiten des Pleistozäns war eine Landverbindung gegeben. Auch klimatisch stehen, wie im vorigen Abschnitt für *A. cunninghamii* bereits herausgestellt wurde, beide Gebiete in engem Zusammenhang (vgl. FITZPATRICK et al., 1966). Neben der letztgenannten Art, die nicht nur im östlichen Teil der Insel (Papua New Guinea), sondern auch bis in den äußersten Westen des indonesischen Teils (Irian Jaya) vorkommt, gedeiht dort noch – allerdings beschränkt auf Papua New Guinea – *A. hunsteinii*. Die Vorkommen beider Arten in Papua New Guinea hat GRAY (1973) kartographisch zusammengestellt. Dabei zeigt sich, daß die beiden Arten, mögen sie auch großräumig gesehen den gleichen Einflüssen unterliegen, standörtlich deutlich divergieren. *A. cunninghamii* wächst zwischen 600 m und 2800 m (zumeist 900–2200 m) vornehmlich auf steilen Hängen und Rücken, während *A. hunsteinii* in durchschnittlich etwas tieferen Lagen, zwischen 550 m und 2100 m (zumeist 750–1500 m), vorzugsweise in Tälern verbreitet ist. Trotz dieser Unterschiede, die hier nicht näher erörtert werden können, ist offensichtlich, daß beide Arten mit ihren Vorkommen die Stufe des Übergangs vom Tieflandsregenwald in den Bergwald besiedeln (vgl. GRAY, 1975). Entsprechend treten in den Araukarienbeständen als Begleiter Elemente aus beiden Höhenstufen auf. Es liegt demnach hier in der Vertikalen ein ähnliches „Verhüllen" der Warmtropengrenze vor, wie wir es im Falle der südbrasilianischen *A. angustifolia* und auch bei *A. bidwillii* bereits in der Horizontalen konstatiert haben. Daß es sich tatsächlich um ein analoges Verhalten handelt, ist schon daraus zu schließen, daß *A. cunninghamii* als einzelne Art innerhalb ihres von der warmgemäßigten Zone bis in die inneren Tropen reichenden Areals

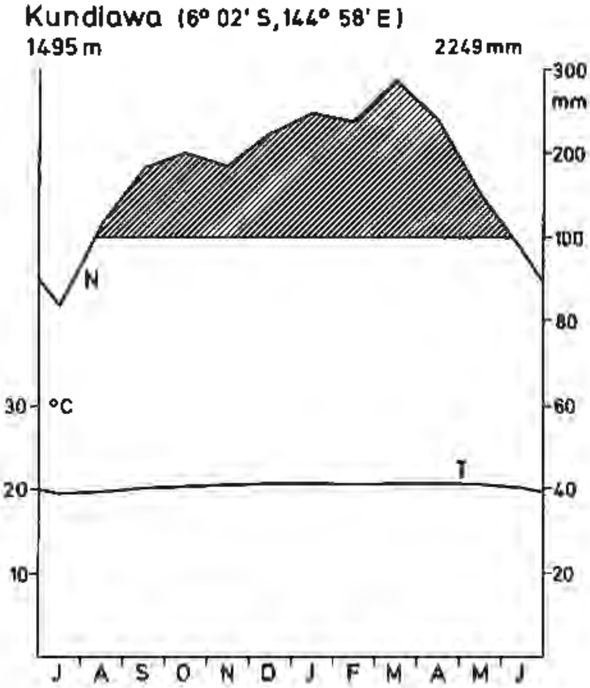


Abb. 6. Klimadiagramm von Kundiawa (Verbreitungsgebiet von *Araucaria cunninghamii*), Neuguinea.

(Course of the climate of Kundiawa (distribution area of *Araucaria cunninghamii*), New Guinea).

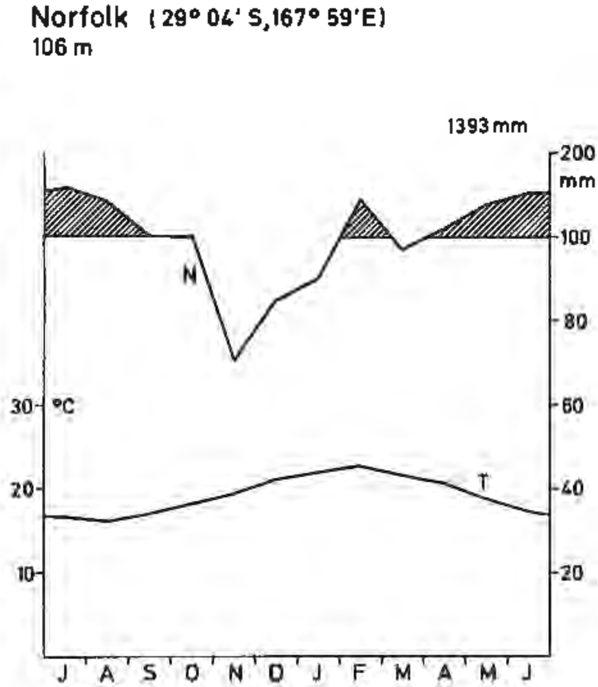


Abb. 7. Klimadiagramm von Norfolk Island (Verbreitungsgebiet von *Araucaria heterophylla (= excelsa)*).

(Course of the climate of Norfolk Island, distribution areas of *Araucaria heterophylla (= excelsa)*).

beide Verbreitungstendenzen erkennen läßt. Die Bestände von *A. cunninghamii* und *A. hunsteinii* reichen gerade in die Höhenstufe hinein, in der Frostwechsel auftreten. Bodenfröste setzen – abhängig von der Topographie – bei etwa 1500 m ein, und ab 2000 m sind leichte Fröste eine regelmäßige Erscheinung (BROWN & POWELL, 1974). Dabei ist hinsichtlich der im Vergleich etwas tiefer liegenden Vorkommen von *A. hunsteinii* zu berücksichtigen, daß diese gerade die für Ansammlung von Kaltluft besonders empfänglichen Tal- und Beckenlagen besiedelt.

Die Bedeutung einer akzentuierten nächtlichen Abkühlung für die Araukarien muß auch hier in einem Zusammenhang mit dem gesamten jahreszeitlichen Witterungsablauf gesehen werden (Abb. 6). Die Frostwechsel treten in mittleren Höhen nur während der Saison des SE-Passats (Mai–Oktober) auf, die in großen Teilen des Zentralgebirges – bei scharf ausgeprägten orographischen Effekten – eine „Trockenzeit" ist. Freilich ist diese auch hier nur als eine Zeit verminderter Häufigkeit und Intensität der Regenfälle zu verstehen. Die Hauptniederschläge fallen in der Zeit des indonesisch-australischen NW-Monsuns (Dezember–März). In dieser Zeit starker konvektiver Aktivität wird die Niederschlagsverteilung nur schwach von der Orographie beeinflußt. In Zeiten stabiler SE-Strömung jedoch besteht in weiten Teilen des Hochlandes eine Tendenz zu Wolkenarmut und Strahlungswetter, wodurch bei Tage die potentielle Evapotranspiration kräftig ansteigen und bei Nacht die Temperatur unter den Gefrierpunkt absinken kann. Bezeichnenderweise – unter dem Gesichtspunkt des Vergleichs mit anderen Araukariengebieten – können diese Phänomene in einzelnen Jahren extreme Ausmaße annehmen, so beispielsweise 1940 oder 1941 und 1972, als im Hochland Neuguineas über Wochen und Monate Dürre und scharfe Fröste bis in Höhen unter 2000 m verzeichnet wurden (vgl. BROWN & POWELL, 1974).

Wenn die Araukarien im Zentralgebirge Neuguineas – trotz der etwa bei den südamerikanischen Arten noch wesentlich stärker ausgeprägten Frostverträglichkeit – nicht in noch höhere Lagen aufsteigen, so dürfte das vor allem damit zusammenhängen, daß sie andererseits auf strahlungsreiche, trocken-warme Witterungsabschnitte angewiesen sind, Luftfeuchtigkeit und Bewölkungsgrad aber gerade mit Annäherung an das Kondensationsniveau aufwärts sprunghaft zunehmen.

2.3. Norfolk Island

Die 34 km^2 große, bei 29° s. Br. und 168° ö. L. vor der Ostküste Australiens gelegene Insel (höchster Punkt 330 m) war zum Zeitpunkt der Entdeckung durch James Cook (1774) noch vollständig von einem immergrünen Regenwald bedeckt, in den *A. heterophylla (= excelsa)* – die bei uns bekannte „Zimmertanne" – als beherrschendes Element in mehr oder weniger dichten Beständen eingestreut war. Norfolk liegt nach den Kriterien H. v. WISSMANNS (1948) noch im Randbereich der Tropen, doch zeigen schon die Mittelwerte des wärmsten und des kältesten Monats (Fig. 7: Februar 22,8 °C, August 16,1 °C) und erst recht die absoluten Extrema (31,7 °C bzw. 7,8 °C) der Temperatur – gemessen in 17 m Seehöhe –, daß das Klima subtropisch genannt werden muß. Dies kommt auch im jahreszeitlichen Gang der Niederschläge zum Ausdruck, der sich dadurch auszeichnet, daß die Winterregen hier reichlicher und zuverlässiger sind als die Sommerregen (vgl. SCHOTT, 1938). Die Sommerregen entsprechen dem tropischen Regime des SW-Pazifiks, während die Winterregen im Gefolge außertropischer Wanderdepressionen niedergehen.

2.4. Neu-Kaledonien

Nirgendwo auf der Erde findet sich auf engstem Raum eine solche Ansammlung archaischer Gewächse wie auf Neu-Kaledonien. Dazu gehören auch die nicht weniger als 13 Vertreter der Gattung *Araucaria*, die in der Gymnospermenflora der Insel von D. J. DE LAUBENFELS (1972) beschrieben werden. Dieser Reichtum an altertümlichen endemischen Pflanzen hat – abgesehen von der Inselnatur als solcher und ihrem Gebirgscharakter (größte Höhe 1634 m) – vor allem klimatische und geologisch-pedologische Ursachen. Die letzteren beziehen sich auf die Serpentinmassive, die weite Teile, besonders im südlichen Drittel der Insel (in dem auch die Araukarien ihre Hauptverbreitung haben) einnehmen. Mit ihrer extremen Kieselsäure- und Basenarmut (völliges Fehlen von Quarz, Feldspäten und Feldspatvertretern) bilden diese hier wie auch anderswo auf der Erde günstige Substrate für Coniferen (vgl. GOLTE, 1978 a). Tatsächlich sind alle neu-kaledonischen *Araucaria*-Arten – mit einer Ausnahme – auf Serpentingebiete beschränkt. Auf die verschiedenen Arten kann hier nicht näher eingegangen werden (vgl. u. a. VIROT, 1956; DE LAUBENFELS, 1972). Die meisten von ihnen sind Bestandteile der Berg- und Nebelwälder (oberhalb von etwa 300 m) auf den Serpentinmassiven. Besonders bemerkenswert – und mit den extremen Eigenschaften des ultrabasischen Gesteins zu erklären – ist allerdings, daß einzelne Arten (*A. muelleri, A. biramulata, A. rulei*) hier am Tropenrand auch noch im Tiefland heimisch sind.

Ein Baum des Tieflandes schließlich ist auch die eigenartige *A. columnaris (= cookii*; „pin colonnaire"), die einzige nicht auf Serpentin gedeihende Araukarie Neu-Kaledoniens. Sie steht *A. heterophylla* von der Norfolk-Insel nahe und wächst – bei etwa 2000–3000 mm Jahresniederschlag – auf Korallenkalken im Küstenbereich des südlichen Neu-Kaledonien sowie der nahegelegenen Loyalty-Inseln und der Ile des Pins.

Entsprechend seiner Lage nahe dem Wendekreis lassen sich in Neu-Kaledonien bereits deutlich eine wärmere (Mitte Oktober–Mitte April) und eine kühlere Jahreszeit (Mitte April–Mitte Oktober) unterscheiden (die Jahresschwankung beträgt etwa 6 °C). Während des ganzen Jahres, verstärkt aber im Südwinter, unterliegt die Insel dem Einfluß des SE-Passats. Die Hauptniederschläge fallen, verbunden mit veränderlichen, teilweise stürmischen Winden, im Sommer und entsprechen dem von der Südwärtswanderung der ITC bestimmten tropischen Regime (vgl. FAIVRE et al., 1955). Sie sind im Norden der Insel reichlicher als im Süden. Tropische Zyklonen können gelegentlich schwere Regenfälle bringen. Ab April/

Mai gerät Neu-Kaledonien mit dem Rückzug der ITC zunehmend unter antizyklonalen Einfluß. Die winterliche Situation (Juni–August) ist durch wandernde Hochdruckzellen gekennzeichnet, zwischen denen wärmere Luftmassen aus NE und Polarluft aus S bis W gegeneinander geführt werden. Der Durchzug dieser Kaltfronten ist mit mäßigen Niederschlägen verbunden, die den Süden der Insel stärker befeuchten als den Norden.

SARLIN (1954) hat am Beispiel von Nouméa gezeigt, daß sich die Niederschläge in Neu-Kaledonien durch beträchtliche Variabilität auszeichnen. Grundsätzlich ist in allen Monaten des Jahres Trockenheit möglich. Allerdings waren von 564 Beobachtungsmonaten (= 47 Jahren) nur 8 absolut regenlos, wovon wiederum nur die Monate September bis Dezember betroffen waren, die auch mit relativ größter Häufigkeit „trocken" sein können. Insgesamt zeigen der jahreszeitliche Witterungsablauf und die räumliche Niederschlagsverteilung deutlich, daß Neu-Kaledonien im Übergangsbereich der tropischen und der außertropischen Zirkulation liegt, deren Wechselwirkung offenbar das ganze Jahr über Häufigkeit und Menge der Niederschläge beeinflußt, dabei aber eine hohe Niederschlagsvariabilität zur Folge hat.

3. Schlußfolgerungen

Die knappe Übersicht der Araukarienvorkommen Australasiens zeigt in Übereinstimmung mit den beim Vergleich der südamerikanischen Arten gewonnenen Erkenntnissen, daß die Gattung ungeachtet der bei ihren 19 Arten zum Ausdruck kommenden Spielbreite an ganz bestimmte Klimaverhältnisse gebunden ist, die sich aus einer synoptischen und jahreszeitlichen Wechselwirkung der tropisch-subtropischen Zirkulation (ITC und Passat) einerseits und der außertropischen Zirkulation (Westwinddrift) andererseits ergeben. Der verbreitungsmäßige Schwerpunkt liegt eindeutig in den Subtropen, und zwar in den Sattelgebieten zwischen den subtropischen Hochdruckzellen als den Bereichen intensivster Wechselwirkung der tropischen und der außertropischen Zirkulation. In diesen Gebieten ist der subtropische Hochdruckgürtel quasi-permanent durchbrochen, so daß ganzjährige, wenn auch deutlich schwankende Niederschläge möglich sind. Dynamisch-klimatologisch entsprechen diese Feuchtebrücken im Trockengürtel den quasistationären Höhentrögen, in denen die ektropische Westwinddrift weit gegen den Äquator vorstößt bzw. ihn sogar überschreitet (vgl. FLOHN, 1971). Auf diese nicht nur für die Araukarien, sondern auch für die Verbreitung zahlreicher anderer Reliktconiferen entscheidenden Zusammenhänge habe ich bereits in der erwähnten früheren Arbeit (GOLTE, 1978 a) hingewiesen. Am Beispiel der beiden südamerikanischen *Araucaria*-Arten konnte gezeigt werden, in welcher Weise die Bäume mit dem xeromorphen Bau ihrer assimilierenden Organe (Sclerophyllie) und der Art ihrer Reproduktion (Gymnospermie) auf den jahreszeitlichen Gang der Wachstumsbedingungen eingestellt sind.

Wie nun sind Verbreitung und standörtliches Verhalten der Araukarien über die bloße Feststellung der Zusammenhänge hinaus zu erklären? Wie wenig zweckmäßig es wäre, die Verbreitungsverhältnisse und ökologischen Beziehungen lediglich aus dem gegenwärtigen Verhalten zu beurteilen, zeigt eine einfache Rechnung. Das gesamte Quartär, wenn man es einmal grob auf 2 Millionen Jahre veranschlagt, macht gerade 1% der mehr oder weniger überschaubaren Verbreitungsgeschichte der Gattung *Araucaria* aus. Alles spricht dafür, daß die noch heute erkennbare verbreitungsmäßige und ökologische Spielbreite, die sich deutlich an bestimmten dynamischen Klimagrenzen orientiert, Ausdruck eines weit in die Vergangenheit zurückreichenden, genetisch festgelegten Potentials ist. Die ohne Zweifel noch lückenhafte und teilweise schwer deutbare Verbreitungsgeschichte der Gattung (vgl. Abb. 1; u. FLORIN, 1963) läßt gleichwohl bestimmte Tendenzen erkennen, die dann zu erklären sind, wenn man von einer weitgehenden Konstanz dieser Spielbreite ausgeht.

Betrachten wir einmal nur das südhemisphärische Vorkommen beiderseits des Pazifiks! Legen wir die gegenwärtige Position der Kontinente zugrunde, dann finden wir die jurassischen Vorkommen zwischen etwa 30° (Ostaustralien) und 63° s. Br. (Westantarktis). Im Falle Australiens ist aber wegen der Kontinentalverschiebung in Wirklichkeit eine polnähere Lage anzunehmen. In der Kreidezeit fand offenbar eine geringfügige äquatorwärtige Verschiebung des Verbreitungsgebietes statt. Im frühen Tertiär scheint zunächst ein ebenso geringfügiger polwärtiger Rückzug erfolgt zu sein, bevor im Jungtertiär und Quartär das Areal sich auf seine heutige Position in Richtung auf den Äquator verschob.

Wir finden also die Gattung *Araucaria* im Mesozoikum und Alttertiär eindeutig in mittleren Breiten (vermutlich bis in die Nähe des Polarkreises), während die niederen Breiten in auffälliger Weise gemieden wurden. Diese (wohl kaum durch Lücken im Fossilbestand bloß vorgetäuschte) Tatsache deutet darauf hin, daß das Klima niederer Breiten in jener Zeit anders ausgesehen haben muß als heute. Auch andere Indizien machen es unwahrscheinlich, daß ein äquatorialer Regengürtel in einer der heutigen ähnlichen Form existierte. Entsprechend dürften auch transäquatoriale Feuchtebrücken – die etwa für *Araucaria* oder ihre Stammformen „gangbar" gewesen sein könnten – nur zeitlich und räumlich sehr begrenzt bestanden haben – ein Umstand, der das von FLORIN (1963) als nicht gesichert betrachtete bihemisphärische Vorkommen der Gattung zu einem interessanten, aber schwer lösbaren Problem der Florengeschichte macht. Aufschlußreich ist in dieser Hinsicht das Beispiel Vorderindiens, das im älteren Mesozoikum zum Verband der Südkontinente (zwischen Antarktis und SE-Afrika) gehörte. Hier befand sich von der späten Trias bis wahrscheinlich in die frühe Kreidezeit eines der alten Verbreitungsgebiete von *Araucaria*. Dann driftete – wie ein Floß – Indien im Laufe der Kreide in die Nähe seiner heutigen Position. Dabei mußte es den Äquatorialbereich queren – mit der Folge, daß die Gattung hier ausstarb.

Das Klima der Mittelbreiten, in denen die Araukarien, hauptsächlich in Faltengebirgszonen entlang den Kontinentalrändern, gediehen, muß in der Zeit des eisfreien (akryogenen) Zustandes der Erde recht warm gewesen sein, aber eben nicht tropisch, wie so oft behauptet wird. Es war – nach dem heutigen Verhalten dieser Gattung zu urteilen – ein Mischtyp, der tropische und außertropische Merkmale in sich vereinigte, nicht nur im Sinne eines jahreszeitlichen Alternierens, sondern auch im synoptischen Sinne.

Literatur

BROWN, M. and J. M. POWELL (1974): Frost and Drought in the Highlands of Papua New Guinea. Journ. of Trop. Geogr., vol. 38, 1–6.

FAIVRE, J.-P., J. PORTIER et P. ROUTHIER (1955): Géographie de la Nouvelle Calédonie. Paris.

FITZPATRICK, E. A., D. HART and H. C. BROOKFIELD (1966): Rainfall Seasonality in the Tropical Southwest Pacific. Erdkunde, Bd. 20, 181–194.

FLOHN, H. (1971): Tropical Circulation Pattern. Bonner Met. Abh., H. 15, Bonn.

FLORIN, R. (1963): The Distribution of Conifer and Taxad Genera in Time and Space. Acta Horti Bergiani, Bd. 20, Uppsala, 121–312 and 319–326.

GENTILLI, J. (1955): Die Klimate Australiens. Die Erde, 206–238.

GOLTE, W. (1978 a): Die südhemisphärischen Coniferen und die Ursachen ihrer Verbreitung außerhalb und innerhalb der Tropen. In: TROLL, C. und W. LAUER (Hrsg.): Geoökologische Beziehungen zwischen der temperierten Zone der Südhalbkugel und den Tropengebirgen. Erdwiss. Forsch., Bd. 11, Wiesbaden, 93–123.

– (1978 b): Die südandine und die südbrasilianische Araukarie. Ein ökologischer Vergleich. Erdkunde, Bd. 32, 279–296.

GRAY, B. (1973): Distribution of Araucaria in Papua New Guinea. Res. Bull., No. 1, Port Moresby.

– (1975): Size-Composition and Regeneration of Araucaria Stands in New Guinea. J. Ecol., 63, 273–289.

GREGUSS, P. (1955): Xylotomische Bestimmung der heute lebenden Gymnospermen. Akademia Kiadó, Budapest.

HAVEL, J. J. (1971): The Araucaria forests of New Guinea and their regenerative capacity. Journ. of Ecol., vol. 59, 203–214.

DE LAUBENFELS, D. J. (1972): Flore de la Nouvelle-Calédonie et Dépendances. No. 4: Gymnospermes. Paris.

MCARTHUR, W. M. (1949): The Genus Araucaria in its Geographical Aspects. Res. Rep., Nr. 5, Geogr. Lab., Nedlands.

NTIMA, O. O. (1968): The Araucarias. Fast Growing Timber Trees of the Lowland Tropics, No. 3, Commonw. For. Inst., Univ. of Oxford.

SARLIN, P. (1954): Bois et Forêts de la Nouvelle-Calédonie. Centre Techn. For. Trop., Nogent-sur-Marne.

SCHOTT, G. (1938): Klimakunde der Südsee-Inseln. In: Handbuch der Klimatologie, hrsg. v. W. KÖPPEN und R. GEIGER, Berlin.

VIROT, R. (1956): La Végétation Canaque. Mém. Mus. Nat. d'Hist. Nat., N. Sér. B, T. 7, Paris.

WEBB, L. J. and J. G. TRACEY (1967): An Ecological Guide to New Planting Areas and Site Potential for Hoop Pine. Austral. Forestry, vol. 31 (3), 224–230.

WILDE, M. H. and A. J. EAMES (1952): The ovule and "seed" of Araucaria Bidwillii with discussion of the taxonomy of the genus. II. Ann. Bot., N. Ser., 16, 27–47.

VON WISSMANN, H. (1948): Pflanzenklimatische Grenzen der warmen Tropen. Erdkunde, Bd. 2, 81–92.

Diskussion zum Beitrag Golte

Dra. M. L. Salgado-Labouriau:

The map of distribution of *Araucaria* (present and fossil) do not indicate the presence of this genus in Africa in the Cenozoic and Mesozoic (Exept for one occurence in South Africa Tertiary). How do you explain it?

Dr. W. Golte:

Das weitgehende – wohl kaum durch lückenhaften Fundbestand bloß vorgetäuschte – Fehlen von *Araucaria* in Afrika dürfte m. E. u. a. damit zusammenhängen, daß dieses im ehemaligen Zusammenhang der Südkontinente (Gondwana) stets eine relativ äquatornahe (Binnen-)Lage einnahm und daher (s. meine obigen Ausführungen) verhältnismäßig trockene Klimabedingungen aufwies.

Priv.-Doz. Dr. P. Frankenberg:

Sie haben sehr deutlich aufgezeigt, daß sich die *Araucaria* in ihrem Verbreitungsgebiet an den Übergangsbereich Tropen/Außertropen orientiert. Dieser hat sich ja in den letzten Jahrtausenden seit dem Kältemaximum verschoben. Hat sich damit auch das Gattungsareal von *Araucaria* verlagert?

Dr. W. Golte:

Von großräumigen Verschiebungen der Araukarienareale während des Holozäns ist mir aus der Literatur nichts bekannt. Vielleicht sind die von HUECK in Südbrasilien festgestellten Verschiebungstendenzen im Mosaik Subtropischer Feuchtwald – Araukarienwald – Campograsland als Ergebnis von Klimaänderungen zu deuten.

Prof. Dr. W. Haffner:

Araucarien sind in fast allen frostfreien oder doch sehr wintermilden Gebieten der Erde als Zierbäume verbreitet. Wie steht es mit der Samenreife außerhalb des natürlichen Verbreitungsgebietes? Sollten Araucarien nur im heutigen Verbreitungsgebiet Samen bilden, wäre dies ein eindeutiger Beleg für die von Ihnen herausgestellten besonderen Klimaansprüche.

Dr. W. Golte:

Ich habe vielerorts außerhalb der natürlichen Vorkommen angepflanzte Araukarien beobachtet, die z. T. auch Samen hervorbrachten. Stets jedoch fiel auf, daß keinerlei natürliche Verjüngung stattfindet – ein Phänomen, das ja auch für den größten Teil unserer Nadelholzforsten gilt, in denen die „Konkurrenz" künstlich ausgeschaltet ist.

Prof. Dr. B. Ruthsatz:

Ich möchte zu bedenken geben, daß man das aktuelle Verbreitungsgebiet der *Araucaria*-Arten nicht als ihr potentiell mögliches ansehen darf, weil dabei sicher die Konkurrenz von Laubbäumen eine große Rolle spielt. Viele unserer Nadelbäume sind sehr konkurrenzschwache Arten, die auf Extremstandorte abgedrängt werden von den Konkurrenten.

Prof. Dr. F. Klötzli:

Wenn wir das von Frau RUTHSATZ angefangene Strategie- und Konkurrenzdenken noch etwas ausweiten, so sehen wir, daß sich im *Araucaria*-Areal ganz ähnliche Beziehungen ergeben, wie z. B. zwischen Fagaceen und Pinaceen auf der nördlichen Halbkugel. Auch auf der südlichen Halbkugel erscheint z. B. *Araucaria araucana* auf speziellen edaphisch geprägten Standorten, wo *Nothofagus* deutlich an Vitalität verliert, im Bereich des Lago Conguillo z. B. auf grusigen jungen Lavaböden. Ich frage mich nun, wie die Beziehungen im *A. angustifolia*-Areal beschaffen sind. Konzentrieren sich die Araucarien auch dort auf Spezial-Standorte? Haben Sie entsprechende Bodenanalysen?

Prof. Dr. W. Weischet:

Als Information zu den Diskussionsbemerkungen von Frau RUTHSATZ und Herrn KLÖTZLI scheint es mir bemerkenswert, daß die singuläre Verbreitung der Araucarien tatsächlich mit singulären dynamisch-klimatologischen Bedingungen zusammenfällt. Ähnliche klimatologische Situationen gibt es m. E. sonstwo in der allgemeinen Zirkulation nicht.

Dr. W. Golte:

Das Argument der „Konkurrenzschwäche" wird immer wieder zur Erklärung von Coniferenstandorten angeführt. Ich habe mich aber in meinem Beitrag zu zeigen bemüht, daß die Areale der Araukarien mit ganz bestimmten klimatischen Bedingungen und deren räumlicher Ausdehnung in Zusammenhang stehen. Insofern freue ich mich über die Bestätigung durch Herrn WEISCHET, daß es sich tatsächlich um singuläre dynamisch-klimatische Verhältnisse handelt. Im übrigen bin ich der Auffassung, daß die Araukarien (und andere Nadelhölzer) auch heute noch im Pflanzenkleid der Erde genau jenen Platz besetzt halten, der ihnen nach ihrer Stellung in der Phylogenie und der Entwicklung in der anorganischen Welt zukommt. Der Begriff „Extremstandorte", der in diesem Zusammenhang von Frau RUTHSATZ verwendet wird, ist m. E. Ausdruck eines „angiospermozentrischen" pflanzengeographischen Weltbildes. Auf Standorten mit derartigen physikalisch-chemischen Eigenschaften sind offensichtlich seit ihrer Entstehung (Oberkarbon) die Coniferen zu Hause. Wie sollte man sich etwa das über mehr als 30 Breitengrade reichende Areal von *Araucaria cunninghamii* als das einer „konkurrenzschwachen" Conifere noch gut 100 Millionen Jahre seit der explosionsartigen Ausbreitung und Differenzierung der Angiospermen erklären? Gerade für Ostaustralien und Neuguinea konnte durch verschiedene Arbeiten (WEBB & TRACEY, 1967; HAVEL, 1971) festgestellt werden, daß die dortigen Araukarien unter bestimmten ökologischen Bedingungen „normale" Komponenten des voll entwickelten Regenwaldes sind und sich entsprechend regenerieren. Gleiches gilt nach eigenen Erfahrungen für die südamerikanischen Araukarienwälder. Dort habe ich zwar Bodenanalysen gemacht (wiedergegeben in: GOLTE, 1978 b), jedoch nicht speziell unter dem Gesichtspunkt des Vergleichs mit Nachbarstandorten. Eine überragende Rolle spielt der Wasserhaushalt der Böden, hinsichtlich *A. angustifolia* ist durch die Arbeiten von K. HUECK bekannt, daß innerhalb des Areals gewisse standörtliche Verschiebungen stattfinden, im Zuge derer der subtropische Feuchtwald in tieferen Lagen den Araukarienwald „unterwandert", während dieser seinerseits sich auf Kosten der Höhengrasländer (Campos) ausdehnt. Diese Verschiebungen tragen aber höchstwahrscheinlich klimatischen Veränderungen Rechnung.

Prof. Dr. U. Schweinfurth:

Zur Verbreitung von *Araucaria hunsteinii:* Sie kommt auch im früheren Kaiser-Wilhelm-Land (= ‚New Guinea') vor, nicht nur in ‚Papua'. Die Station Kundiawa wäre zu ersetzen vielleicht durch Station Bulolo-Wau, wo *A. hunsteinii* verbreitet vorkommt.

Dr. W. Golte:

Hinsichtlich Punkt 1 (*A. hunsteinii* im früheren Kaiser-Wilhelm-Land) muß ich natürlich zustimmen. Zu Punkt 2: Die Station Kundiawa habe ich gewählt, weil sie von GRAY (1973) unter denjenigen genannt wird, die sich in enger Nachbarschaft zu Araukarienbeständen (innerhalb von höchstens 2 km Entfernung), in diesem Falle *A. cunninghamii*, befinden.

Prof. Dr. W. Lauer:

Inwieweit haben ausgebildete, wenn auch kürzere Trockenzeiten generell eine Bedeutung für den Samenabfall der Araukarien-Früchte? Nach den von Ihnen für Neuguinea gezeigten Diagrammen scheint hier die kurze Trockenzeit von großer Bedeutung zu sein für den Lebensrhythmus der Araukarien.

Dr. W. Golte:

Xerochastische Bewegungen (Trockenspalten) spielen bei Coniferen generell für die Freisetzung der Samen eine große Rolle. Sie sind uns von *Pinus*-Zapfen in besonderer Weise vertraut. Bei *Araucaria*, deren Samen durch die Verwachsung von Deck- und Samenschuppe vollständig mit einer festen Schale umhüllt sind, erfolgt diese Freisetzung durch Zerblättern des Zapfens, d. h. durch Abfallen der Schuppenkomplexe von dessen spindelförmiger Achse. Nach eigenen Erfahrungen genügt bei vorzeitig gepflückten Zapfen schon die geringste nachfolgende Austrocknung, um diese zum Zerfallen zu bringen. Auch etwa in Neuguinea findet die Freisetzung der Samen (in der Regel September bis November, standörtlich variierend) in Zusammenhang mit der Jahreszeit statt, in der gehäuft trockene Phasen auftreten. Darin kommt sicher die Synchronisierung des physiologischen Geschehens mit dem hygrischen Jahresgang zum Ausdruck; allerdings ist zu berücksichtigen, daß es sich zugleich um endogen gesteuerte Vorgänge handelt.

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Vertical Distribution of Palaearctic and Oriental Faunal Components in the Nepal Himalayas[1]

Jochen Martens

With 14 Figures

From the viewpoint of biology, the geographical position of the Himalayas is significant in several respects:

1. The Himalayas separate the uplands of Central Asia from the Indian Subcontinent, thereby forming an effective barrier between two large areas of Asia, which are quite different climatically: cold High Asia and tropical South and South-east Asia.
2. The Himalayas themselves enforce the contrast. Exchange of air between the two regions is difficult and the Himalayas create their own climate, when during the South-west monsoon orographic precipitation occurs on the southern flanks, though it is greatly reduced on the northern slopes. This striking function as a climatic barrier holds true only for the central parts of the mountains, that is approximately the areas of Kumaon, Nepal, Sikkim and Bhutan. In the western Himalayas, the aridity of Central Asia extends across to the southern slopes, while in the eastern parts rainstorms, though declining in amount and frequency, reach as far as South-east Tibet (SCHWEINFURTH, 1957; TROLL, 1967).

This sharp climatic separation by the Central Himalayas is of great importance biologically and in many respects influences the distribution of plants and animals of the mountain chain. The Himalayas are regarded as a region of contact between the two great biogeographic realms which meet and intermesh in various ways. The criteria for classification differ somewhat for phytogeography and zoogeography, but both show that the Himalayas are a meeting place for florae and faunae of different origins and ecological requirements. All areas north of the Central Himalayas belong to the Palaearctic realm as do the highest parts of the southern flanks occupied by animals. The lower and lowest altitudes of the southern flanks are associated with the Oriental realm. The border between the two regions is, however, not striking and abrupt, but forms over vast distances a transition area, which comprises varying combinations of representatives of each of the areas in question. This holds especially true for the eastern Himalayas. In the Central parts, it is easier to delimit the boundaries due to the sharp contrast in climate and vegetation between northern and southern slopes.

Within the general terms Palaearctic and Oriental, however, we find a great variety of plant and animal groups according to their differing geographical origin. We must take into account that the Himalayan fauna is predominantly one which invaded the Himalayas at the time of or after the uplift of the mountain chain during the Tertiary and that the Himalayan fauna has only partially undergone an evolution of its own. As we might expect, recent distributions reflect the route by which individual species or species groups migrated into the Himalayas and can be deduced from the habitat or forest community to which each species is adapted.

[1] Results of the Himalaya Expeditions of J. MARTENS since 1969. Senckenbergiana biol., 65 (1/2), 1984. – J. M. sponsored by Deutscher Akademischer Austauschdienst and Deutsche Forschungsgemeinschaft.

As the Himalayas are predominantly forest covered, at least on the southern slopes and in many areas of the Inner Valleys, it is analysis of the forest vegetation that will provide the first indications of the origin and vertical distribution of the exceedingly rich fauna. For Himalayan faunae, we can distinguish three main areas of origin, as far as the Palaearctic is concerned. In each different climatic conditions prevail and the flora and fauna have undergone different development during the Pleistocene.

1. **Species of the High Steppe and of the Mountains above Timberline.**
   Predominantly these are adapted to cold temperate climates at high altitudes and are always found in open habitats: in the rock and rubble zone with sparse vegetation, on the high mountain steppes and naturally above the timberline, not usually below 4000 m, but upwards to the limits of animal life near to 6000 m and locally even higher (SWAN, 1961). In Nepal, the species in question have reached the Himalayas from Tibet and most do not extend southwards further than the northern slopes. Only a few reach the uppermost parts of the southern flanks (Central Asian species).
2. **Species of the Xerophilic Forests, which penetrate into the Central Himalayas from the West.**
   These species belong to the West Asian fauna and correspond largely to the Mediterranean subregion of the Palaearctic. They are adapted to relatively dry forest habitats, much less exposed to the monsoon. The forest habitats in question reach into the Central Himalayas as a narrow belt, mainly to North-west Dhaulagiri and also, though with fewer typical species, as far as North Annapurna and North Manaslu (West Asian Himalayan species).
3. **Species of the Moist Forests of the Subalpine Belt.**
   These have reached Nepal mainly from the east from various areas of western China. They are distributed mainly in a narrow belt extending westward along the southern slopes of the Himalayas. The species concerned are not well adapted to high precipitation rates typical of the Eastern and Central Himalayas, but they tolerate them, and so we find them in both the eastern and wetter and in the western and drier forest types. Vertically, they are found from the temperate *Rhododendron*-Coniferous zone to the timberline, that is from about 2800 to 4200 m. The zoogeographic relationships of this species group are clearly indicated by the fact that closely related species are found in northern parts of the Palaearctic, while areas in which Himalayan species are found point far into northern regions (West Chinese Himalayan species).

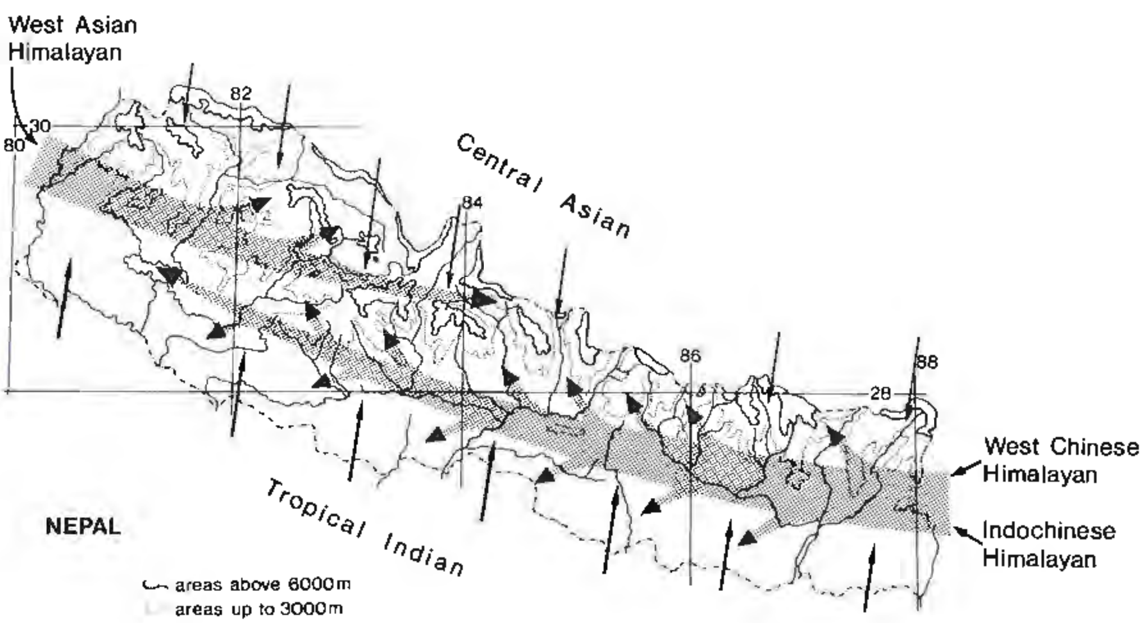

Fig. 1. Map of Nepal indicating main immigration routes of faunal components into the Central Himalayas.

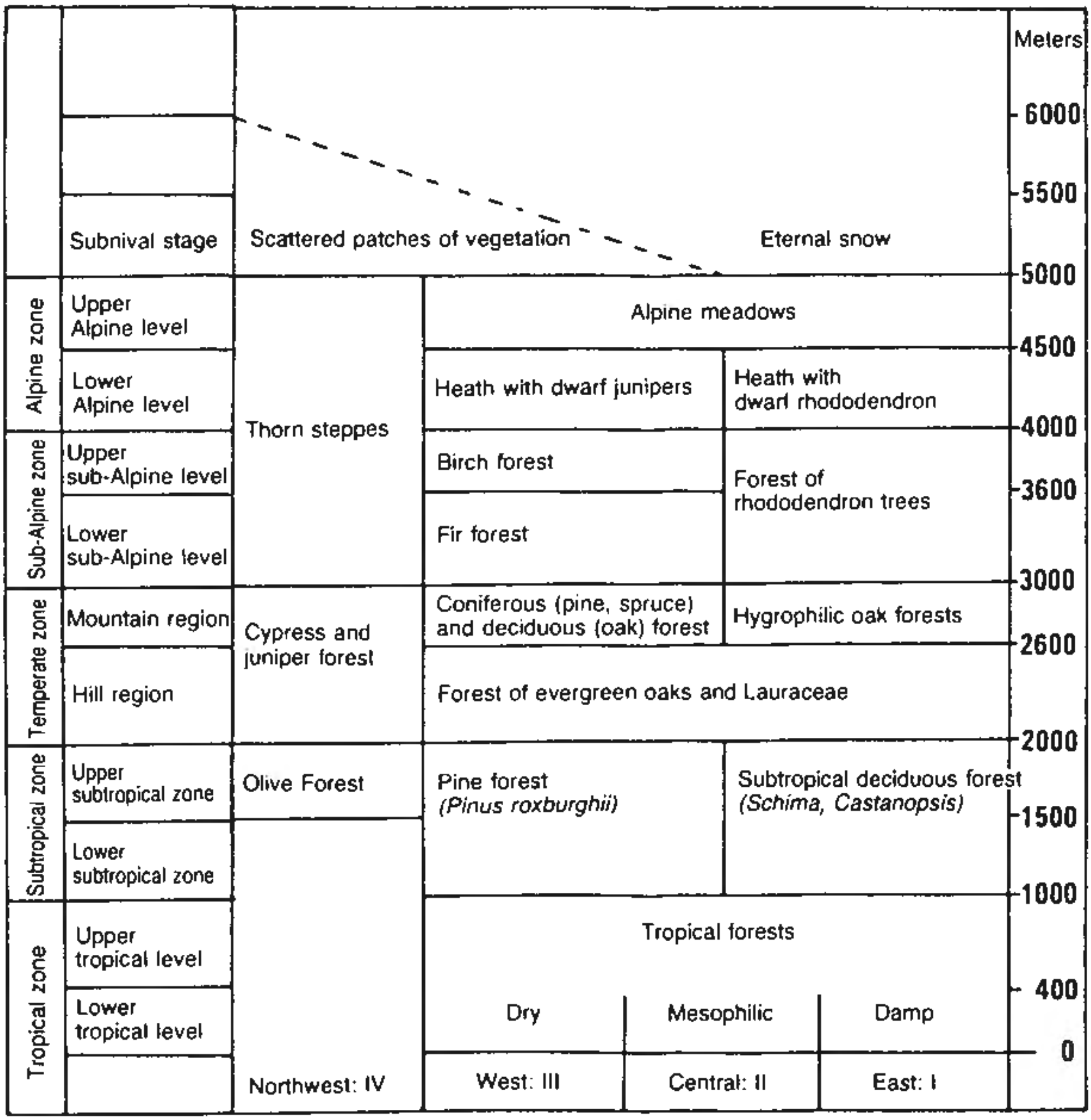

Fig. 2. The vegetation belts with the most important plant communities in Nepal. The Roman numerals at the bottom of the Table indicate the floral regions of Nepal (after: DOBREMEZ, 1972).

The Oriental faunal elements belong to two major groups:

4. Tropical/Subtropical Oriental Species of Southeastern Origin from the Indochinese Subregion, mainly Burma and Indochina.

Those species migrated in high numbers westward along the southern slopes of the Himalayas. Their diversity is greatly reduced from east to west in response to the diminishing monsoon rainfall. Within the zone of *Castanopsis-Quercus*-laurel forest and partly within the tree *Rhododendron* belt (2000–3500 m), they are distributed in a great variety of genera and families, and, only in the subalpine coniferous forest, are they greatly reduced in numbers (Indochinese Himalayan species).

5. Tropical Oriental Species, broadly distributed in the Indian Peninsula.
These reach the southern Himalayan mountains from the south and along deeply cut river valleys, may penetrate right into the main mountain chain. Their vertical distribution rarely exceeds 2000 m, and is in many cases much less (Tropical Indian species or Peninsular Indianspecies).

Thus, the Himalayan faunal elements, though emphasized by various authors, are not an independent group confined to the Himalayas, but are a mixture of species groups which invaded the Himalayas from various directions. Himalayan palaeo-endemics, with no closely related species outside the Himalayas, are rare but neo-endemics, especially among arthropods, currently occur (MARTENS, 1979 and 1981 b).

To be able to assess individual components in the fauna, we have to know first their environmental limits, then their region of origin, their recent distributional extent and the history of their establishment in the Himalayas. The ecological limits of the animal groups – in so far as the forest fauna is concerned – are, on the other, dependent on the vertical zonation of the vegetation and very often follow the climatic gradient. Frequently, there are far-reaching correspondences between the zonal gradation of the vegetation and its faunal communities.

First let us glance at a classification of the vegetation belts, as proposed by DOBREMEZ (1972) in a simplified diagram for Nepal (Fig. 2). From a mainly zoological point of view, it provides sufficient information and from it we can see that on the southern slopes tropical forests prevail to an altitude of

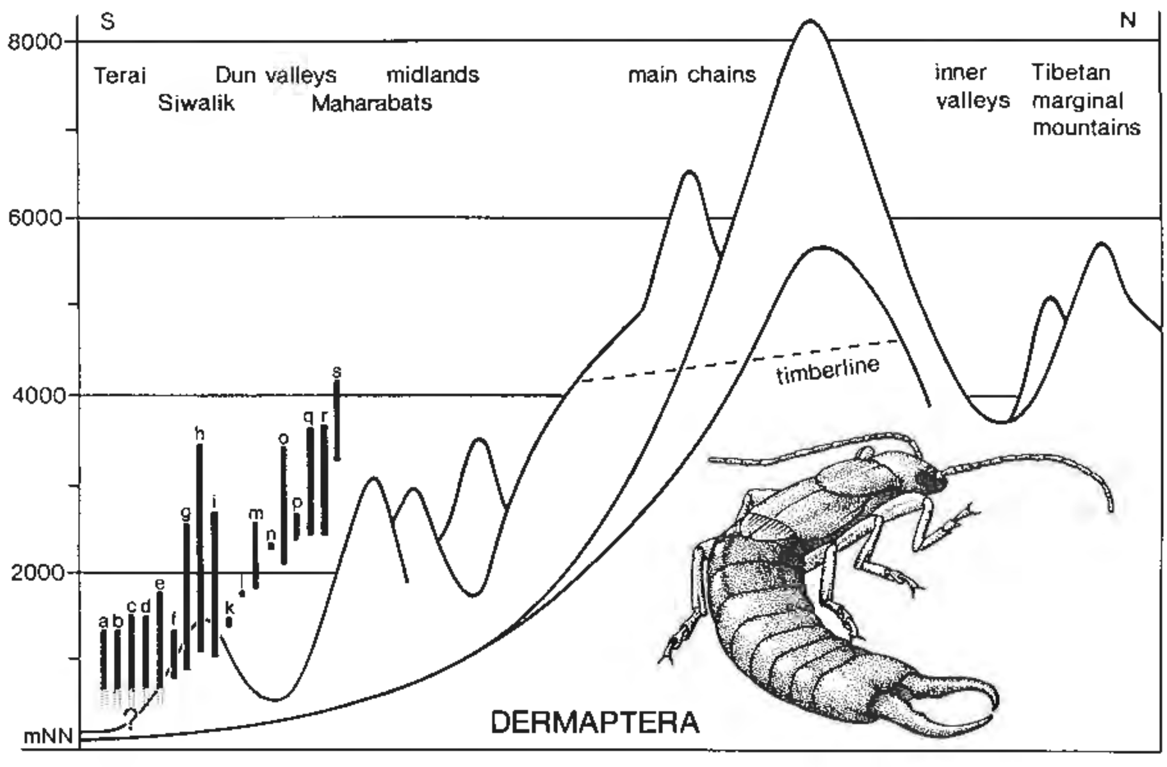

Fig. 3. Vertical distribution of 18 earwig species (after the collections of J. MARTENS; combined after: BRINDLE, 1974 and 1983). Stippled parts of the columns: distribution in the lower parts unknown. – a) *Labidura riparia* (600–1350 m), b) *Nala lividipes* (600–1350 m), c) *Forcipula trispinosa* (600–1500 m), d) *Diplatys transversalis* (600–1500 m), e) *Eudohrnia metallica* (600–1770 m), f) *Forcipula borellii* (700–1300 m), g) *Forcipula decolyi* (800–2250 m), h) *Forficula beelzebub* (1100–3450 m), i) *Aborolabis nepalensis* (1000–2700 m), k) *Diplatys rileyi* (1350–1450 m), l) *Nala nepalensis* (1750–1800 m), m) *Eparchus oberthuri* (1800–2600 m), n) *Diplatys rufescens* (2250–2300 m), o) *Allodahlia martensi* (2100–3400 m), p) *Allodahlia macropyga* (2350–2700 m), q) *Forficula schlagintweiti* (2400–3650 m), r) *Anechura stoliczkae* (2400–3700 m), s) *Forficula beebei* (3250–4200 m).

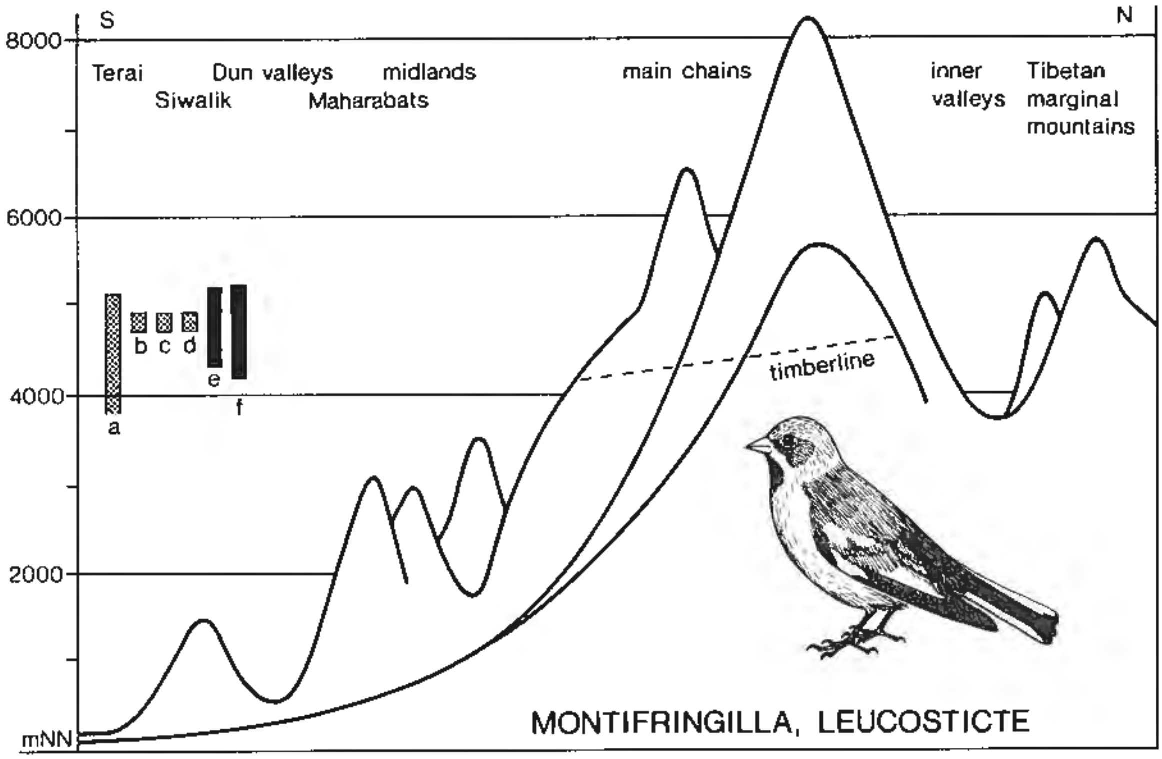

Fig. 4. Vertical distribution of snowfinches (after: DIESSELHORST, 1968; FLEMING et al., 1980; pers. obs.). Stippled columns: species restricted to dry Tibetan mountain steppe habitats. – a) *Montifringilla adamsi* (3900–5200 m), b) *M. taczanowskii* (4750–4900 m), c) *M. ruficollis* (4750–4900 m), d) *M. blanfordi* (4750–4900 m), e) *Leucosticte nemoricola* (4300–5190 m), f) *L. brandti* (4200–5200 m).

1000 m, which receive reduced rainfall from east to west. Transition areas with strongly changing vegetation between eastern and western parts of the Central Himalayas are the Arun valley in East Nepal and the Dhaulagiri area in West-central Nepal. This belt is almost exclusively inhabited by Oriental Indian species. Above it, we find subtropical montane forest, where – mainly in the western parts – *Pinus roxburghii* prevails, a species adapted to soils which dry quickly after rainfall. At altitudes up to 2000 m, the tropical influence is steadily reduced and between 1000 and 2000 m are found the greatest number of Indochinese species.

Of particular significance is the vegetation between 2000 and 3000 m and locally even higher. This belt receives more convective-type precipitation and the high altitude causes a cooler climate. Plant species and genera occur which belong to the temperate zone and which are known for example from the European flora, like *Quercus*. With regard to the fauna and flora, we call this belt the Himalayan West Chinese. The arthropod fauna especially contains many neo-endemic species.

In the belt between approximately 3000 and 4000 m are found the *Rhododendron*-Coniferous forests, in the drier western parts mainly fir and birch forest. The timberline is near to 4000 m, locally higher, meeting the scrub formation subject to Central Asian influence. Strikingly divergent is a region, north of Dhaulagiri, Annapurna and other West Nepal parts of the main mountain chains, which is forestless except for a few lower parts. The high altitude and dryness bring about strong similarities with Tibetan plateau conditions and it is actually from Tibet that the region has been colonized by plants and animals.

This rough floristic differentiation can provide the zoologist with but a guideline, since individual animal species are only broadly associated with plant communities typical of their geographical origin. On the contrary, in the Himalayas, many separate evolutionary trends have succeeded. We can identify

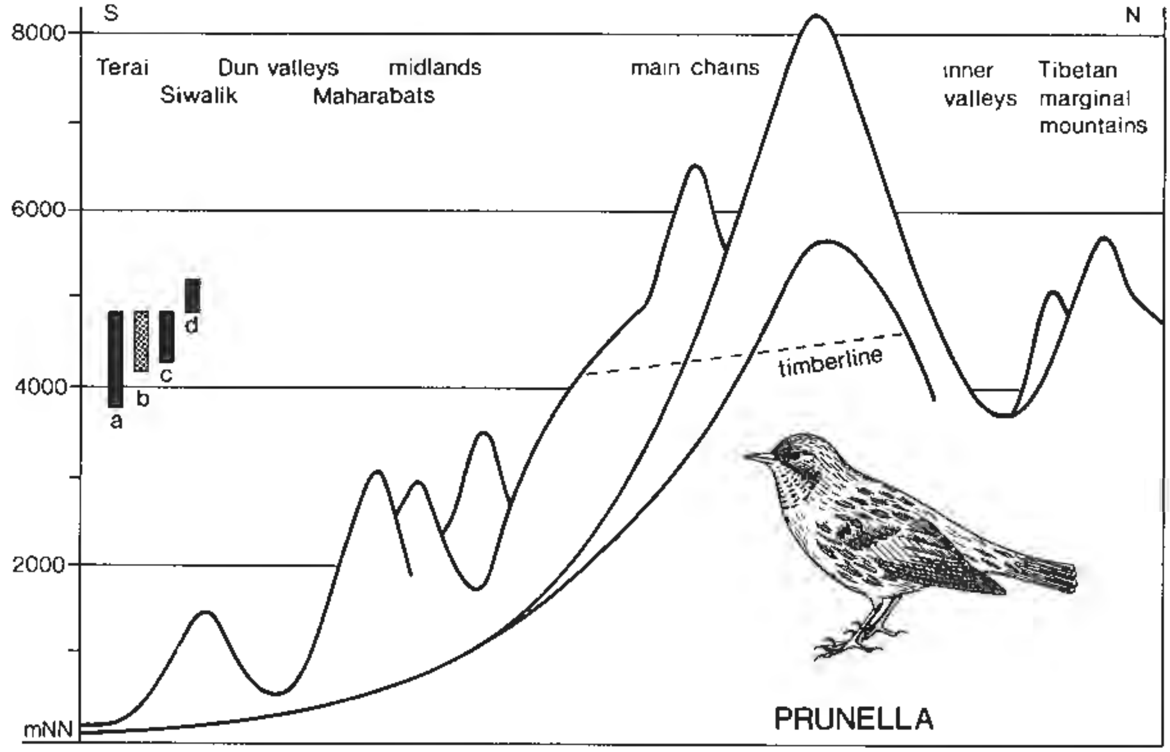

Fig. 5. Vertical distribution of hedgesparrows (after: DIESSELHORST, 1968; FLEMING et al., 1980; pers. obs.). Stippled column: species confined to dry Tibetan mountain steppe habitats. – a) *Prunella strophiata* (3800–4800 m), b) *P. fulvescens* (4200–4800 m), c) *P. rubicilloides* (4300–4800 m), d) *P. collaris* (4800–5200 m).

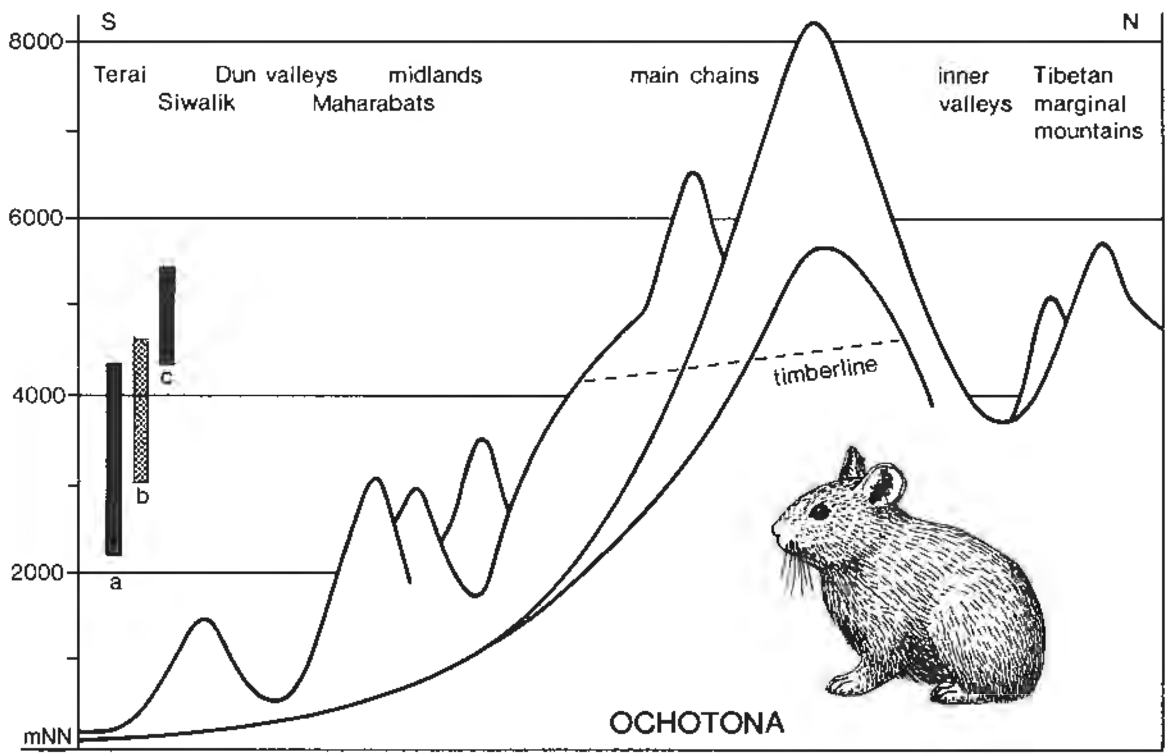

Fig. 6. Vertical distribution of pikas (after: ABE, 1971; KAWAMICHI, 1971; MITCHELL and PUNZO, 1975; pers. obs.). Stippled column: species restricted to dry Tibetan mountain steppe habitats. – a) *Ochotona roylei* (2200–4300 m), b) *O. thibetana* (3050–4600 m), c) *O. macrotis* (4300–5400 m).

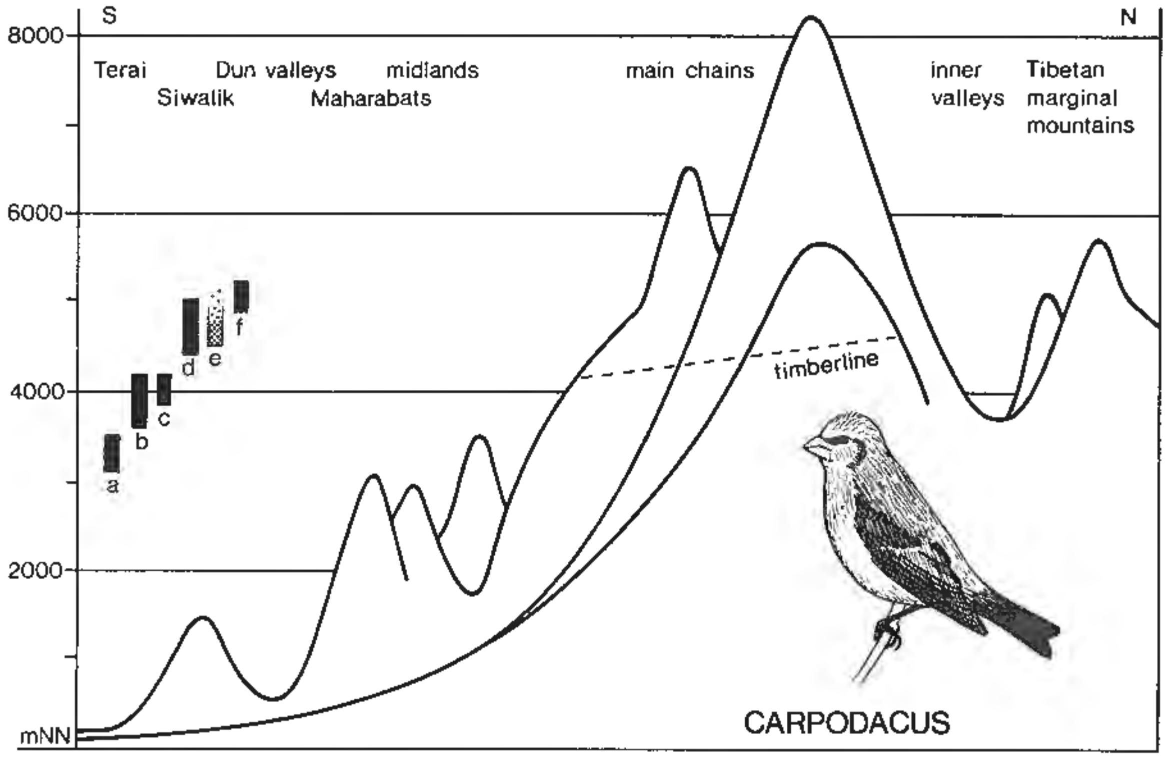

Fig. 7. Vertical distribution of rosefinches (after: DIESSELHORST, 1968; FLEMING et al., 1980; pers. obs.). Stippled column: species restricted to dry Tibetan mountain steppe habitats, upper limit unknown. – a) *Carpodacus erythrinus* (3100–3700 m), b) *C. pulcherrimus* (3600–4200 m), c) *C. thura* (3800–4200 m), d) *C. rubicilla* (4350–5000 m), e) *C. rubicilloides* (4450 to about 5000 m), f) *C. puniceus* (4800–5200 m).

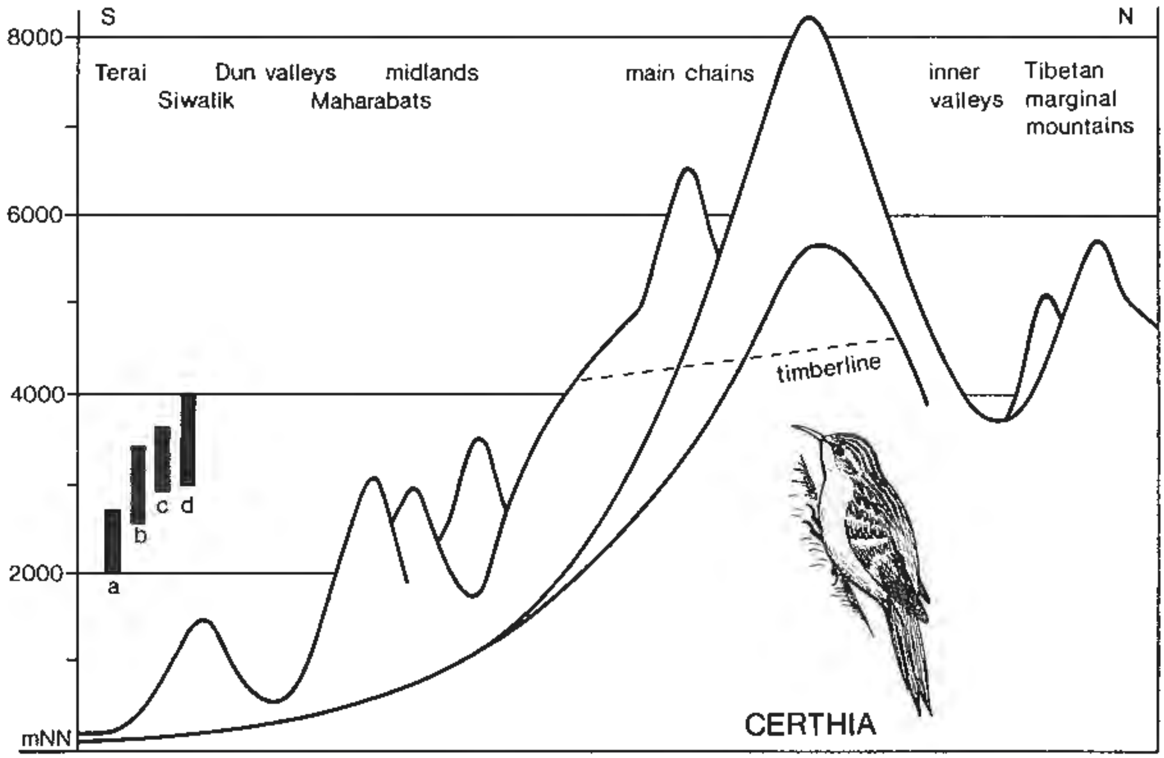

Fig. 8. Vertical distribution of treecreepers (after: DIESSELHORST, 1968; FLEMING et al., 1980; MARTENS, 1981 a). – a) *Certhia discolor* (2000–2700 m), b) *C. nipalensis* (2550–3400 m), c) *C. himalayana* (2900–3650 m), d) *C. familiaris* (3000–4000 m).

secondary adaptations to tropical, subtropical and cold-temperate altitudinal belts, which hardly conform to the area of origin of the species, genus or even family in question. This holds especially true for those animal groups, which after colonization of the Himalayas underwent heavy fragmentation of their populations and finally speciation into many neo-endemics now inhabiting small areas only. Such circumstances prevail for the small arthropods of the forest soils and litter. The vertical distribution of these closely related species is clearly graduated, covering altogether a wide range of altitude and climatic conditions (cf. Fig. 12).

Looking at a few examples, we shall try to identify the different types of vertical distribution in the Nepal Himalayas and to emphasize special developments.

Earwigs (Insecta: Dermaptera; Fig. 3): The only group of insects the vertical distribution of which is relatively well known. As many as 36 species have so far been listed. The vertical distribution of 18 of these is given in the figure. Species of Oriental origin and Indian affinities ascend up to about 1500 m, those of Palaearctic origin are found from 2000 to 4200 m and nearly all belong to the family Forficulidae (Forficulinae), "and the five species which occur at the highest altitudes all belong to the genera *Anechura*, *Allodahlia*, and *Forficula*" (BRINDLE, 1983). In the Central Himalayas all species but one – regardless of their zoogeographic affinities – are confined to the monsoon-influenced southern slopes. An exception is *Forficula beelzebub*, penetrating to the dry areas north of the main chain. Normally, the vertical belts are less than 2000 m broad, and *F. beelzebub*, covering 2500 m, is the only euryoecean species occupying a large variety of habitats. About half of the Nepal species, often endemics with small areas, are known in a few localities only. In such cases, their vertical distribution seems to be very limited, but detailed information is still lacking.

A more detailed classification of the patterns of vertical distribution starts with the Central Asian Palaearctic elements. They penetrate with few species only to the southern slopes.

Snowfinches (Aves: Ploceidae; Fig. 4): The genera *Montifringilla* and *Leucosticte* are mainly Palaearctic, *Leucosticte* extending to North America. Tibet is believed to be the centre of development of *Montifringilla*. Four species reach the northern flanks in Nepal in Tibetan mountain steppe habitats. Both the *Leucosticte* species are found also on the highest parts of the southern slopes (e.g. in Khumbu) and one of them, *nemoricola*, is a common winter visitor locally down to 2100 m (pers. obs.).

Hedgesparrows (Aves: Prunellidae; Fig. 5): Three of the four *Prunella* species of Nepal also breed on the northern slopes (one breeding only there), concentrated vertically between 4000 and 5000 m. None of the species penetrates from its lower limits into the forest belt, *strophiata* however inhabits tall willow bushes (down to 3800 m). *Rubeculoides* and *fulvescens* may occur side by side.

Pikas (Mammalia: Lagomorpha: Ochotonidae; Fig. 6): The species of the genus *Ochotona* are found only in the Northern Hemisphere, in the Southeast Palaearctic mainly at high altitudes and nearly exclusively outside forests and above the timberline. One species, however, *roylei*, has succeeded in adapting itself to the monsoon-influenced southern flanks, down to 2300 m in the subtropical zone. *Thibetana* inhabits dry northern areas. Beside *Alticola* voles, pikas are the only mammals settling permanently altitudes up to nearly 6000 m in the Himalayas.

Rosefinches (Aves: Fringillidae; Fig. 7): *Carpodacus* is a genus rich in species mainly in the Palaearctic realm of the Old World with the most important concentration of species in South-west China, in the Himalayas and in areas adjoining them to the north. Eleven species breed in Nepal. The distribution of several species is similar to that of *Ochotona*: they penetrate from Central Asia to Nepal (Fig. 7b, d, e, f) and are confined to high altitudes but not only on the northern slopes. Others are Himalayan West Chinese (7c) or are largely distributed in North Asia (7a). Only two of the species presented here (*erythrinus*, 7a; *thura*, 7c) are confined to the forest belt and only *thura* inhabits the dense forests proper. None of the Nepal species has breeding colonies below 3000 m.

Treecreepers (Aves: Certhiidae; Fig. 8): In Asia, all the species of the genus *Certhia*, except one, inhabit the Palaearctic realm and thus occupy only the upper forest belt. The four species in question

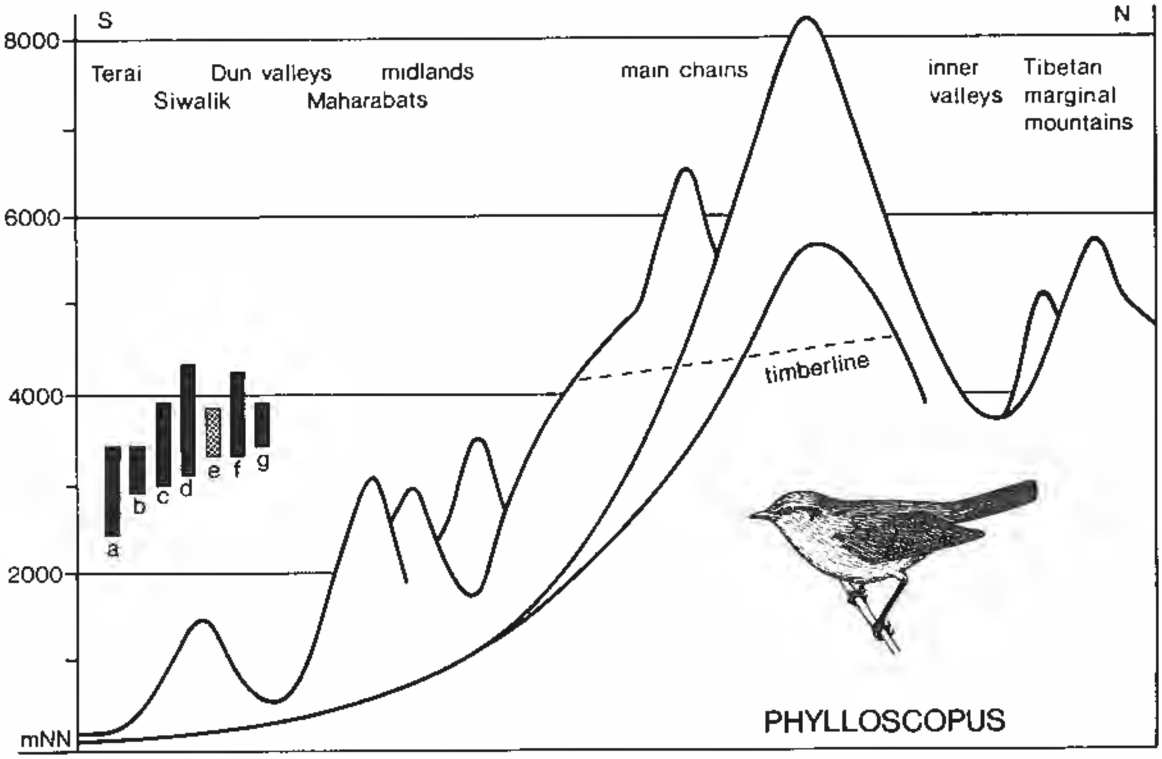

Fig. 9. Vertical distribution of leafwarblers (after: DIESSELHORST, 1968; FLEMING et al., 1980; MARTENS, 1980). Stippled column: species largely restricted to dry West Himalayan forests north of the main chain. – a) *Phylloscopus reguloides* (2400–3400 m), b) *P. maculipennis* (2900–3400 m), c) *P. proregulus* (3000–3900 m), d) *P. affinis* (3150–4300 m), e) *P. inornatus* (3300–3800 m), f) *P. trochiloides* (3300–4200 m), g) *P. pulcher* (3400–3900 m).

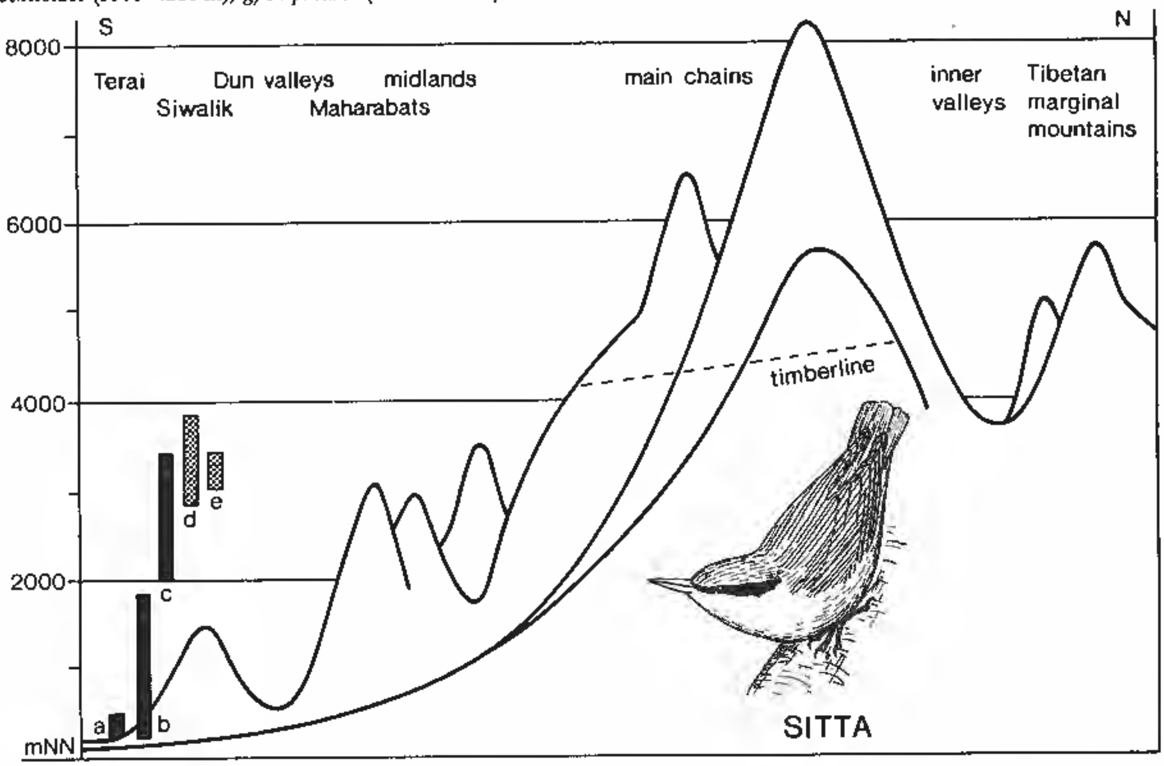

Fig. 10. Vertical distribution of nuthatches (after: DIESSELHORST, 1968; FLEMING et al., 1980; pers. obs.). Stippled columns: species restricted to dry West Himalayan forests north of the main chain. – a) *Sitta frontalis* (150–400 m), b) *S. castanea* (150–1800 m), c) *S. himalayensis* (2000–3400 m), d) *S. leucopsis* (2800–3800 m), e) *S. cashmirensis* (3050–3500 m).

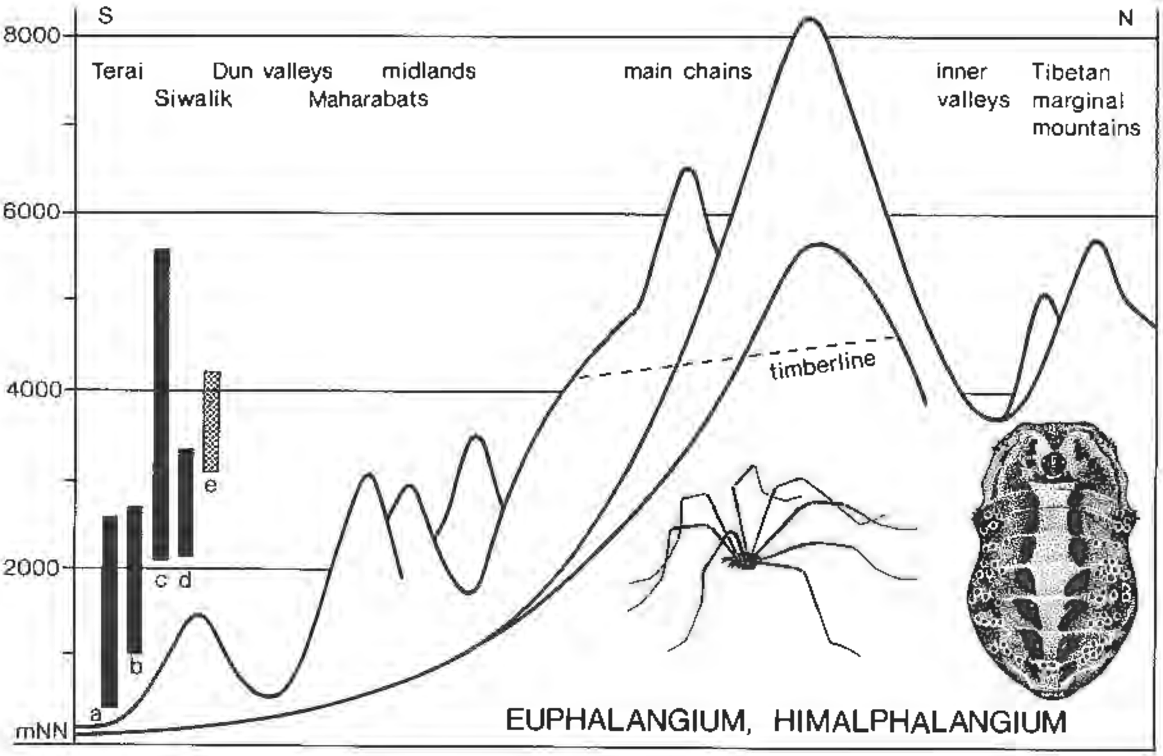

Fig. 11. Vertical distribution of harvestspiders (Phalangiinae) (after: MARTENS, 1973). Stippled column: species largely restricted to dry areas: forests and mountain steppe north of the main chain. – a) *Euphalangium nepalicum* (300–2600 m), b) *Himalphalangium nepalense* (1000–2700 m), c) *H. palpale* (2100–5550 m), d) *H. suzukii* (2150–3350 m), e) *H. dolpoense* (3100–4200 m).

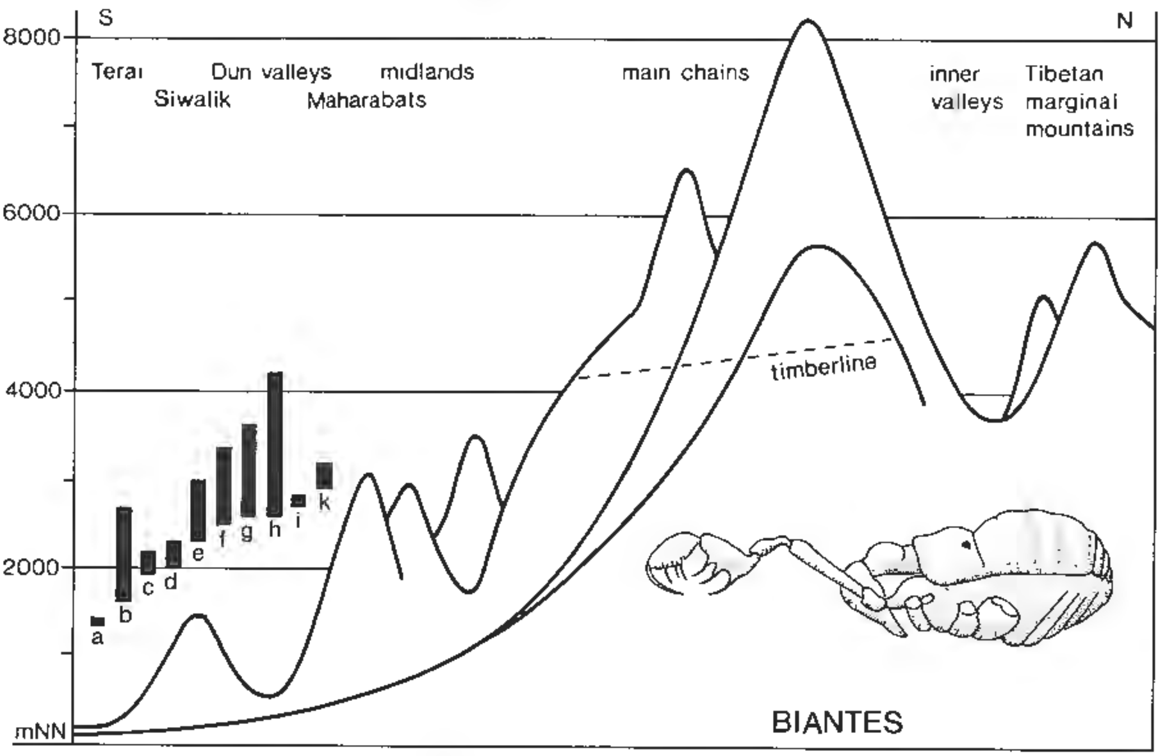

Fig. 12. Vertical distribution of harvestspiders (Biantidae) (after: MARTENS, 1978). – a) *Biantes brevis* (1300–1400 m), b) *B. newar* (1600–2700 m), c) *B. gandaki* (1900–2200 m), d) *B. gandakoides* (2000–2300 m), e) *B. thamang* (2300–3000 m), f) *B. dilatatus* (2500–3350 m), g) *B. thakkhali* (2600–3640 m), h) *B. pernepalicus* (2600–4250 m), i) *B. annapurnae* (2600–2850 m), k) *B. sherpa* (2900–3200 m).

reached the Himalayas of Nepal from different areas: from west (*himalayana*, 8 c), the east (*discolor*, 8 a) or, apparently, from east and west (*familiaris*, 8 d). *Nipalensis* is endemic to the Himalayas. Only *discolor* is confined to subtropical (i.e. to temperate) forest types, and occurs also in the Indochinese subregion, thus avoiding the tropical forest belt of the Himalayas. Each species inhabits a different altitudinal belt and forest formations, but vertical distributions overlap broadly. Two, or exceptionally three species may occur sympatrically. In the lower forest zone up to 2000 m, the ecological niche maintained by the treecreepers remains unoccupied (MARTENS, 1981 a).

Leafwarblers (Aves: Sylviidae; Fig. 9): The genus *Phylloscopus*, comprising about thirty species, is largely distributed in the Palaearctic and almost confined to this region. The heaviest concentration of species is in the Himalayas, and only few survive in the Indochinese subregion. In Nepal, only one species (*reguloides*, 9 a) descends to subtropical forest types, but it originated in West China and thus has adapted to a temperate climate. One species (*inornatus*, 9 e) reaches Nepal from the west inhabiting only dry forest types of western origin, the limit to its eastern distribution being in South Dolpo (North-west Dhaulagiri), perhaps further east in Thakkhola (Kali Gandaki Valley between Dhaulagiri and Annapurna).

Examples of genera of Palaearctic origin, penetrating into the Oriental Realm within the Himalayas with species restricted to low altitudes.

Nuthatches (Aves: Sittidae; Fig. 10): Nearly the whole forest belt is inhabited by *Sitta* species, but two are found only in the North-west in the dry forests of West Himalayan character as far east as North-west Dhaulagiri (*leucopsis*, 10 d; *cashmirensis*, 10 e). Two are restricted to the foothills (*frontalis*, 10 a; *castanea*, 10 b). Curiously enough, large areas, densely forested especially in the Inner Valleys (f.e. Thakkhola, Manang), are void of nuthatches; *himalayensis* avoids habitats not influenced by the monsoon; *leucopsis* and *cashmirensis* – though conditions are favourable for them – have not discovered the "hidden" Inner Valleys, separated by vast inhospitable areas from their easternmost breeding areas: These are the regions above the timberline to the north and wet areas to the south.

Harvestspiders (Arachnida: Opiliones: Phalangiidae; Fig. 11): The genera *Himalphalangium* and *Euphalangium*, both Phalangiinae, originate from the Palaearctic. *Himalphalangium* radiated in the Central Himalayas, now inhabiting the area and South Tibet with endemic species. One species lives mainly in the dry areas on the northern flanks (*dolpoense*, 11 e), others have adapted to a different extent to the forests of the lower subtropical zones and do not avoid the monsoon influence. Their adaptation consists of the biological peculiarity that embryonic and postembryonic development of the low altitude species takes place during the coldest part of the year, that is during the winter and pre-monsoon seasons.

Himalayan fauna of Oriental origin. These are throughout species relating to genera from India and Indochina, which entered the Himalayas mainly from the south, south-east and east.

Harvestspiders (Arachnida: Opiliones: Biantidae; Fig. 12): The family Biantidae is distributed in both Indias, though known only locally until recently, and also in Africa south of the Sahara. The genus *Biantes* consists of numerous species in the Himalayas, and, from Nepal only, as many as 18 species are described. We can be sure that the individual species developed within or at least near to their present distribution areas. Most surprisingly, a relatively large number of species have adapted to a temperate climate in the upper forest zone and one species (*pernepalicus*, 12 h) is even found above the (artificial) timberline. This case can be quoted as an illustration of how an originally tropical genus may reach – including the phenomena of speciation – up to altitudes forming part of the Palaearctic realm.

Sunbirds (Aves: Nectariniidae; Fig. 13): The genus *Aethopyga* is mainly Indochinese in distribution and of tropical origin. As for the Biantidae, purely tropical species exist beside others adapted to temperate montane forests (*nipalensis*, 13 c), and one is exclusively restricted to the Palaearctic *Rhododendron*-Conifer forest zone up to the timberline and is, in addition, endemic to the Himalayas (*ignicauda*, 13 d).

Shrews (Mammalia: Soricidae; Fig. 14): The genus *Suncus* is largely distributed in the Oriental realm, and the two Himalayan species (*etruscus*, *murinus*) invaded the area from the south. The musk shrew

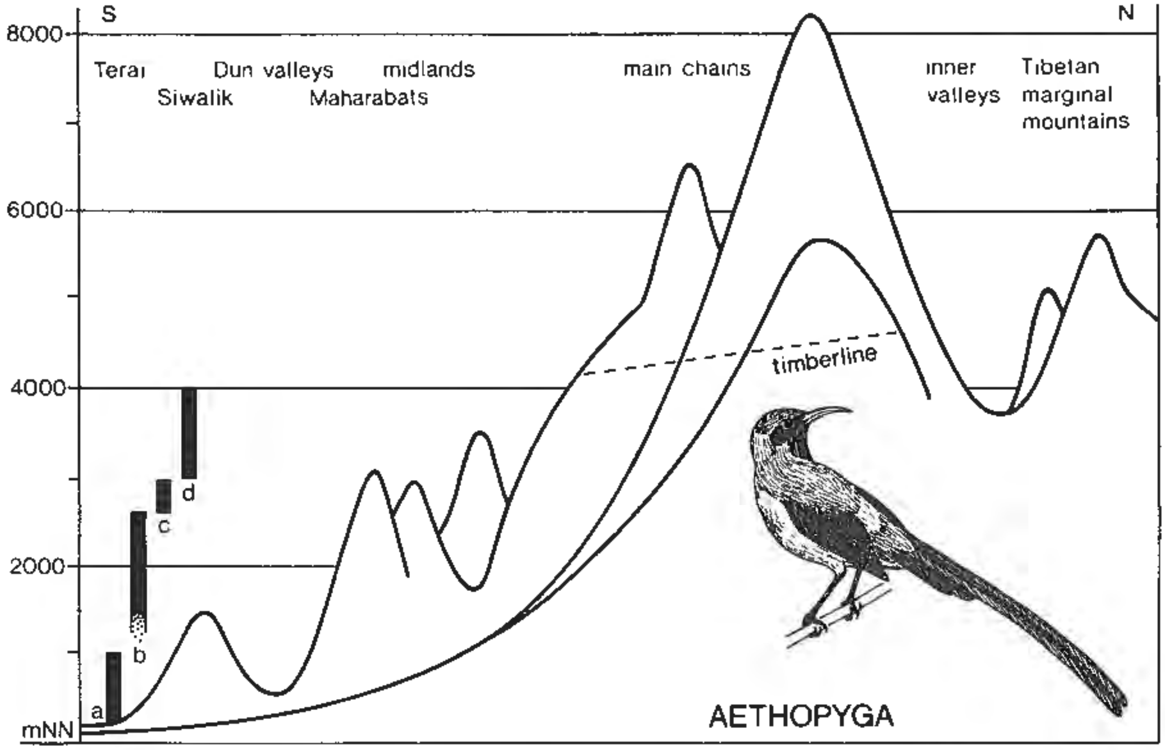

Fig. 13. Vertical distribution of sunbirds (after: DIESSELHORST, 1968; ALI and RIPLEY, 1972; FLEMING et al., 1980; pers. obs.). – a) *Aethopyga siparaja* (250–1000 m), b) *Ae. saturata* (1500–2600 m), c) *Ae. nipalensis* (2600–3000 m), d) *Ae. ignicauda* (3000–4000 m).

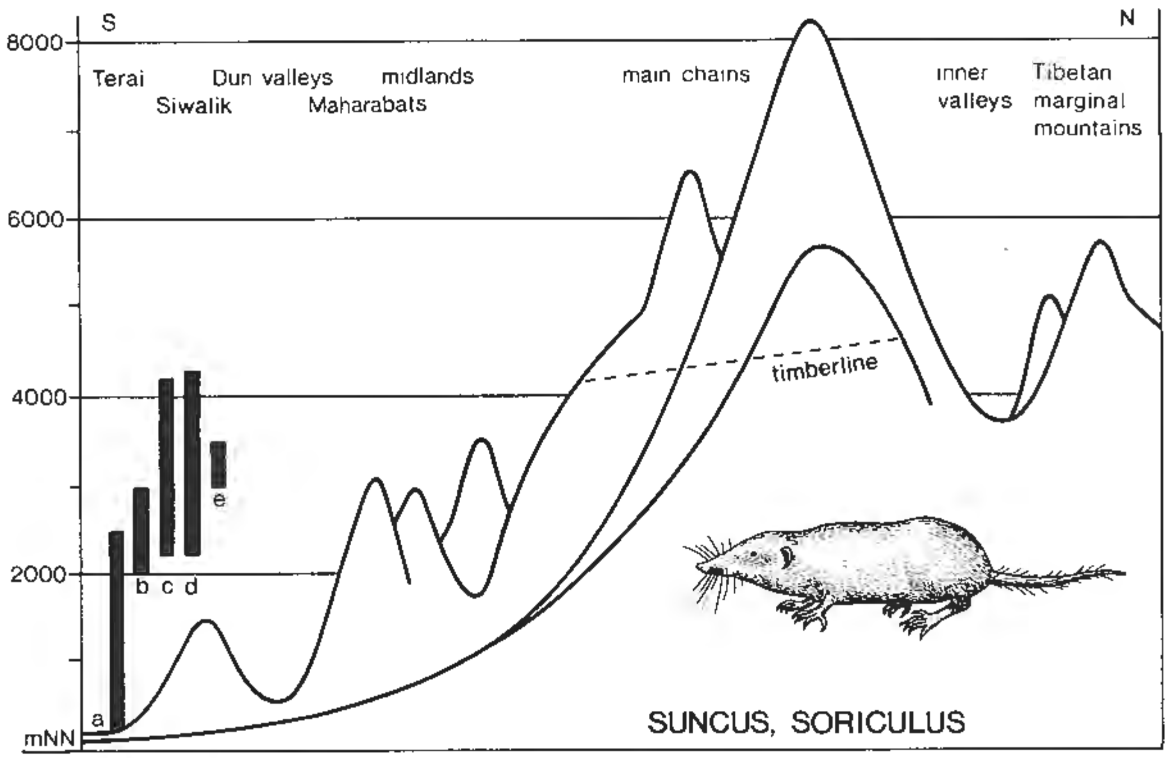

Fig. 14. Vertical distribution of shrews (after: ABE, 1971; GRUBER, 1969; MITCHELL, 1977; pers. obs.). – a) *Suncus murinus* (150–2750 m), b) *Soriculus leucopsis* (2000–3000 m), c) *S. nigrescens* (2200–4200 m), d) *S. caudatus* (2200–4300 m), e) *S. baileyi* (3000–3400 m).

(*Suncus murinus*, 14 a), though living frequently with human settlements, normally occurs upwards to 2000 m, rarely higher (recorded in Nepal to 2750 m), and it is evidently confined to the tropical/subtropical belt. *Soriculus* has mainly Indochinese and west Chinese affinities and, in consequence, inhabits the temperate forest zone with a tendency to reach altitudes even above the timberline (*nigrescens*, 14 c; *caudatus*, 14 d).

Discussion

The vertical distribution of no group of the Himalayan fauna is as yet satisfactorily known – not to mention the local variations reflecting exposure and vegetational differences within small distance. Comparatively sound is the information on birds, small mammals (excepting bats), a few soil dwelling arthropods (Carabidae: *Carabus;* Dermaptera; Opiliones), and butterflies (Lepidoptera: Rhopalocera). Moreover, as the diversity of the fauna is enormous, cataloguing will take many more years. Thus the examples given rely on the taxa mentioned elsewhere and which I have observed myself during Himalayan expeditions (six since 1969).

The examples show that vertical distributions are well defined and that they depend on the climatic conditions in the areas from where immigration into the Himalayas has taken place. The present vertical distribution is in agreement with the ecological adaptations acquired by the species/genera in their areas of origin. In the secondary Himalayan areas, however, adaptations to warmer or colder altitudinal belts have occurred quite frequently.

In comparison with the large vertical span of 6000 m inhabited by living beings, the vertical belts for individual species must be considered narrow. Often they cover hardly more than 1000 m and seem to be even smaller for endemics with limited areas. According to recent findings, this holds especially true for small arthropods of the forest litter and soil. Marked vertical gradation of closely related species is the rule and the species swarm covers a great variety of altitudes and climatic conditions – regardless of their faunal origin. Only a few species, not to mention ubiquitous ones with very large area spans, occupy belts of 2000 m or more. In several cases, we can recognize the reasons for such extensive belts:

a) The habitat may change little in essential detail at the different altitudes. This holds true for running water, which offers apparently similar conditions at different altitudes at least for several birds: Brown Dipper *(Cinclus pallasii)* and White-capped Redstart *(Chaimarornis leucocephala)*, each confined to the borders of mountain streams and occupying a very large extent of at least 4000 m (DIESSELHORST, 1968; pers. obs.).
b) The vertical zone may be colonized by two subspecies, which replace one another altitudinally. This holds true for the Jungle Crow *Corvus macrorhynchus)*, comprising in Nepal the subspecies *C. m. culminatus* up to about 2000 m, and *C. m. intermedius* up to timberline.
In the case of the Stonechat *(Saxicola torquata)*, the subspecies *S. t. indica* penetrates into the lower Himalayas from North India up to 2500 m. The Tibetan subspecies *S. t. przewalskii* descends from the Tibetan plateau to the Inner Valleys to the northern rim of the Main Chain, down to 3800 m. However, they do not meet and there is a belt of about 1500 m void of Stonechats (ALI and RIPLEY, 1973; MARTENS, 1972).
c) Habiats may be extended vertically by human activity. Frogs of still waters in the lowlands penetrate to the artificial rice terraces of the foothills and higher (DUBOIS, 1980).
d) Species associated directly with human settlements may reach even to the inhospitable northern slopes of the sparsely settled Main Chain – which could be impossible to sustain without human support. Good examples are the Tree Sparrow *(Passer montanus)* and the Cinnamon Tree Sparrow *(P. rutilans)*, which colonize even the highest villages in Dolpo, up to 4300 m.
Also the human flea *(Pulex irritans)* extends its area to the highest villages – a species living not permanent on men but during the adult stage (SMIT, 1974).

The data presented here can provide only a rough idea of the multitude of phenomena relating to vertical distribution in the vast Himalayan mountain chain. At present, we are occupied in collecting data in the field. Until now, we have understood only a few main factors acting on and limiting vertical distributions. But we are quite ignorant of how to explain which ecological factors and environmental peculiarities act on the fine structure of the vertical distributions.

Summary

a) The Himalayan fauna is to be understood as adapted to different climatic belts and vegetation zones.
b) Both climatic belts and vegetation zones are largely in accordance with the areas of origin outside the Himalayas of the various faunal elements.
c) The Himalayan fauna is mainly an immigration fauna. We distinguish five main centers of origin and thus five categories of Himalayan fauna, three of which fall into the Palaearctic (Central Asian, Himalayan West Asian, Himalayan West Chinese) and two in the Oriental realm (Himalayan Indochinese, Peninsular Indian).
d) Though the Palaearctic elements are more differentiated than the Oriental ones, they are represented by a greater number of species.
e) Vegetation belts and climatic zones provide only guidelines to our understanding of the faunal distribution. After immigration a large variety of special adaptations have occurred, mainly the colonization of vertical belts not matching areas of origin (tropical, subtropical, temperate). Speciation has played a major role in such special ecological adaptations.

Acknowledgment

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References

ABE, H. (1971): Small mammals of Central Nepal. J. Fac. Agr. Hokkaido Univ., 56 (4), 367–423.

ALI, S. and S. D. RIPLEY (1973): Handbook of the birds of India and Pakistan, 9, 25–30.

BRINDLE, A. (1974): The Dermaptera of Nepal. Senckenbergiana biol., 55 (1/3), 141–164.

– (1983): Dermaptera from Nepal (Insecta). Senckenbergiana biol., 63 (1/2), 91–104.

DIESSELHORST, G. (1968): Beiträge zur Ökologie der Vögel Zentral- und Ost-Nepals. Khumbu Himal, 2, 1–417.

DOBREMEZ, J.-F. (1972): Les grandes divisions phytogéographiques du Népal et de l'Himalaya. Bull. Soc. Bot. France, 119 (1/2), 111–120.

DUBOIS, A. (1980): L'influence de l'homme sur la répartition des Amphibiens dans l'Himalaya central et occidental. C.R. Soc. Biogéogr., 485, 155–178.

FLEMING, R. L. Sr., R. L. FLEMING Jr. and L. S. BANGDEL (1980): Birds of Nepal with Reference to Kashmir and Sikkim. Kathmandu.

GRUBER, J. (1969): Tiergeographische, ökologische und bionomische Untersuchungen an kleinen Säugetieren in Ost-Nepal. Khumbu Himal, 3 (2), 197–312.

KAWAMICHI, T. (1971): Daily activities and social pattern of two Himalayan pikas, *Ochotona macrotis* and *O. roylei*, observed at Mt. Everest. J. Fac. Sc. Hokkaido Univ., (6, Zool.), 17 (4), 587–609.

MARTENS, J. (1972): Brutverbreitung paläarktischer Vögel im Nepal-Himalaya. Bonn. Zool. Beitr., 23 (2), 95–121.

– (1973): Opiliones aus dem Nepal-Himalaya. II. Phalangiidae und Sclerosomatidae (Arachnida). Senckenbergiana biol., 54 (1/3), 181–217.

– (1978): Opiliones aus dem Nepal-Himalaya. IV. Biantidae. Senckenbergiana biol., 58 (5/6), 347–414.

– (1979): Die Fauna des Nepal-Himalaya – Entstehung und Erforschung. Natur u. Museum, 109 (7), 221–243.

– (1980): Lautäußerungen, verwandtschaftliche Beziehungen und Verbreitungsgeschichte asiatischer Laubsänger (Phylloscopus). Fortschr. Verhaltensforsch., 22, 1–71.

– (1981 a): Lautäußerungen der Baumläufer des Himalaya und zur akustischen Evolution in der Gattung *Certhia*. Behaviour, 77 (4), 287–318.

– (1981 b): Ornithogeography of the Himalayas. Coll. "Ecologie et Biogéographie de l'Himalaya" du CNRS, Toulouse 1979, 75–84.

MITCHELL, R. M. (1977): Accounts of Nepalese mammals and analysis of the host-ectoparasite data by computer techniques. Thesis, Iowa State University.

– and F. PUNZO (1975): *Ochotona lama* sp.n. (Lagomorpha: Ochotonidae): a new pika from the Tibetan highlands of Nepal. Mammalia, 39 (3), 419–422.

PAULUS, H. F. (1983): Paralasa nepalica n.sp. aus den Trockengebieten NW-Nepals (Insecta: Lepidoptera: Satyridae: Erebiinae). Senckenbergiana biol., 63 (5/6), 337–346.

SCHWEINFURTH, U. (1957): Die horizontale und vertikale Verbreitung der Vegetation im Himalaya. Bonn. Geogr. Abh., H. 20.

SMIT, F. G. A. M. (1974): Siphonaptera collected by Dr. J. Martens in Nepal. Senckenbergiana biol., 55 (4–6), 357–398.

SWAN, L. W. (1961): The ecology of the High Himalayas. Scient. Amer., 205 (4), 69–78.

TROLL, C. (1967): Die klimatische und vegetationsgeographische Gliederung des Himalaya-Systems. Khumbu Himal, 1 (5), 353–388.

Discussion to the Paper Martens

Priv.-Doz. Dr. P. Frankenberg:

Are any faunistic elements of the cold tropics to be found in the Himalaya?

Prof. Dr. J. Martens:

Yes, in the sense that groups of tropical, in our case of oriental origin, have adapted themselves to altitudes, which belong to the cold-temperate, palaearctic area of influence. Numbering among these groups are for example daddy-long-legs (harvestmen, Opiliones) of the families Biantidae and Assamiidae, which are to be found in few species even above 4000 m, that is to say clearly above the forest-line. Close relatives are living in lower altitude in (sub)tropical areas. The same is true for the Laughingthrushes (Timaliidae).

Priv.-Doz. Dr. P. Frankenberg:

Do breeding areas coincide with feeding areas in the bird's territories?

Prof. Dr. J. Martens:

This is quite variable. Many small birds defend territories, in which their nests are located and where at the same time food is searched. Other species, e.g. vultures in the high mountains, show very low (breeding-)settlement densities. They remove far from the breeding-place and may meet at the food-source, e.g. at a carcass, with others of their kind. Between these two extremes are many transitions, additionally modified by the extreme conditions in high mountains. Heavy snows during the monsoon may force non-breeding partners down into lower belts, e.g. *Grandala coelicolor*, a mountain thrush adapted to high altitude.

Prof. Dr. W. Haffner:

Can you quote examples of faunistic elements which are typical not only for the humid, cloudy *Rhododendron*-fir forest but also for the dry zones?

Prof. Dr. J. Martens:

Among the titmice (Paridae) *Parus rubidiventris* and *P. ater* settle in both biotopes, though more densely in areas where conifers dominate. Within the dry areas, both species live in the deep-cut valleys (Thakkhola), as well as on the northern flanks as far as they are covered with woodland (southern Dolpo, Manang). Among the small mammals the fieldmouse *Apodemus gurkha* and the shrew *Soriculus nigrescens* are spread respectively, as well as the daddy-long-legs of the Phalangiidae family. Generally, this type of distribution doesn't occur frequently; it demands high ecologic plasticism.

Prof. Dr. W. Haffner:

In Nepal there are also plant species with broad altitudinal belts, e.g. *Rhododendron arboreum*, a species which is to be found between 1200 m and 3500 m. Numbering among these, above all, are many species whose distribution was favoured by man.

Prof. Dr. J. Martens:

Culture plants are certainly favoured by man in the whole vertical zone, depending on climatic tolerance. Indirect supports of distribution, if new ecologic niches are created, do certainly occur. They may be less important, however, since it can be expected that climatic factors exercise an influence on vertical limitation. Certain species of some families are selectively favoured by pasturing, since they are shunned by the animals, e.g. *Primula* (Primulaceae) and *Arisaema* (Araceae). Particular, very adaptable adventive-plants spread along road borders, e.g. *Eupatorium* (Compositae).

Prof. Dr. B. Ruthsatz:

Are the examples of distribution which you demonstrated tied to the original plant societies in their areas? In how far do they tolerate a disturbance of biotopes by man, or can they even survive in anthropogenic substitutional societies?

Prof. Dr. J. Martens:

The dependence on primary vegetation is always especially high, if the species in question – independent of the altitudinal belt – settle on wood biotops. Slight interferences, e.g. moderate clearing without complete deforestation, are mostly tolerated. It is always fatal, if shading of the forest ground is strongly reduced and insolation increases. Soil-dwelling forms with high demands on constant air humidity and balanced temperature ranges do mostly not succeed in compensating the accompanying stress. Substitutional societies are only suitable to a limited number of species, mainly those, which are able to settle a larger spectrum of biotopes, anyway.

Dr. W. Golte:

In how far do the differences in exposition exercise an influence on the large vertical distribution of some species?

Prof. Dr. J. Martens:

The most marked differences are to be found on the southern resp. northern side of the main mountain chain in dependance on monsoon rains. The local variances of precipitation have their effect on the distribution of species. However, the influence of locally restricted differences in exposition haven't so far been judged; the data needed are still too sparse.

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The Position of Fagaceae and Myrtaceae on the Pacific Mountains

Frank Klötzli*

With 15 Figures and 2 Tables

1. Introduction

In almost all areas of the southern hemisphere, subtropical and tropical zones, Myrtaceae may take the role as dominant tree species, especially in middle and higher altitudes and even from the timberline. And also in the northern hemisphere, certain genera may dominate (e.g. *Syzygium*, *Eugenia*, *Tristania* etc. in evergreen broadleafed ["laurel"] forests.). But with preference on mountains in the specific area Myrtaceae may furnish the leading tree species, thereby often competing with Fagaceae of the genera *Quercus*, *Lithocarpus*, *Castanopsis* and *Nothofagus* (or then also with Pinaceae/Podocarpaceae, e.g. *Dacrydium*, *Phyllocladus*, *Papuacedrus*, etc.).

Leading Myrtaceae species are often recruited from the genera *Eucalyptus* (Australia, from northern Queensland to southern Tasmania, New Guinea, etc.) or *Metrosideros* (e.g. New Zealand, Tahiti, Hawaii, etc.), and on special sites (bog, subalpine belt) also *Leptospermum*.

On the other hand, Fagaceae play a decisive role in the more temperate areas, but also in montane and subalpine forests (compare the conditions in Indonesia, SE-Australia, incl. Tasmania, New Guinea, New Caledonia, New Zealand, but also between the Himalayas and Japan under subtropical conditions).

Between these two areas, dominating Myrtaceae under more tropical conditions, Fagaceae under more subtropical and temperate conditions, there is a large transition zone, where Fagaceae and Myrtaceae may be under heavy competition, thereby also meeting representatives of other dominating families, e.g. Podocarpaceae (incl. *Dacrydium*) on indomalaysian mountains (e.g. Kinabalu), Mimosaceae (*Acacia*, e.g. Tasmanian coastal heath) in eastern Australia.

On the northern boundaries of such areas, there are many relictic[1] sites of Fagaceae, a topic to be treated in this paper.

* Work of this type can only be achieved with the help of numerous colleagues. Therefore, I owe special thanks to the following "antipodial" botanists and ecologists, going from Australia to South America: Dr. R. K. Crowden, Hobart, Tasmania; Dr. J. M. Veillon, ORSTOM, Nouméa, Nouvelle Calédonie; Mr. St. Chambers, Waitakaruru, New Zealand (N), Dr. P. Wardle and Mr. R. Allen, Christchurch, New Zealand (S), Monsieur D. Drakni, Directeur ORSTOM, Papeete, Tahiti; Prof. Dr. C. Ramirez, Valdivia, Chile; Prof. Dr. R. J. C. León, Buenos Aires, Argentina. I am also very grateful for their hospitality and their conscientious preparation of all excursions and many fruitful discussions, in Europe especially also to my friend and teacher Prof. Dr. H. Ellenberg.
To finance this trip I got a grant from the Swiss Federal Institute of Technology. My coworker and friend Mrs. Anna Holström has done a good deal of all the evaluations. And the graphs have been drawn by Mrs. Erika Wohlmann. To all these institutions, persons and many other colleagues in the more subtropical and tropical parts of the area of *Nothofagus* I owe my heartfelt thanks, last, but not least also to my family that had to bear the consequences of such trips around the world.

[1] Not all of them, however, are true relictic stands, i.e. remnants of a former large area of distribution (compare Fig. 1, e.g. *Nothofagus moorei*, *Nf. cunninghamii*). Some stands would have to be called more correctly "special sites" or are part of an extrazonal pattern.
Similar relictic site conditions for nemoral broadleafed forests are also detectable in the southern Taiga (e.g. Scandinavia; KLÖTZLI, 1975).

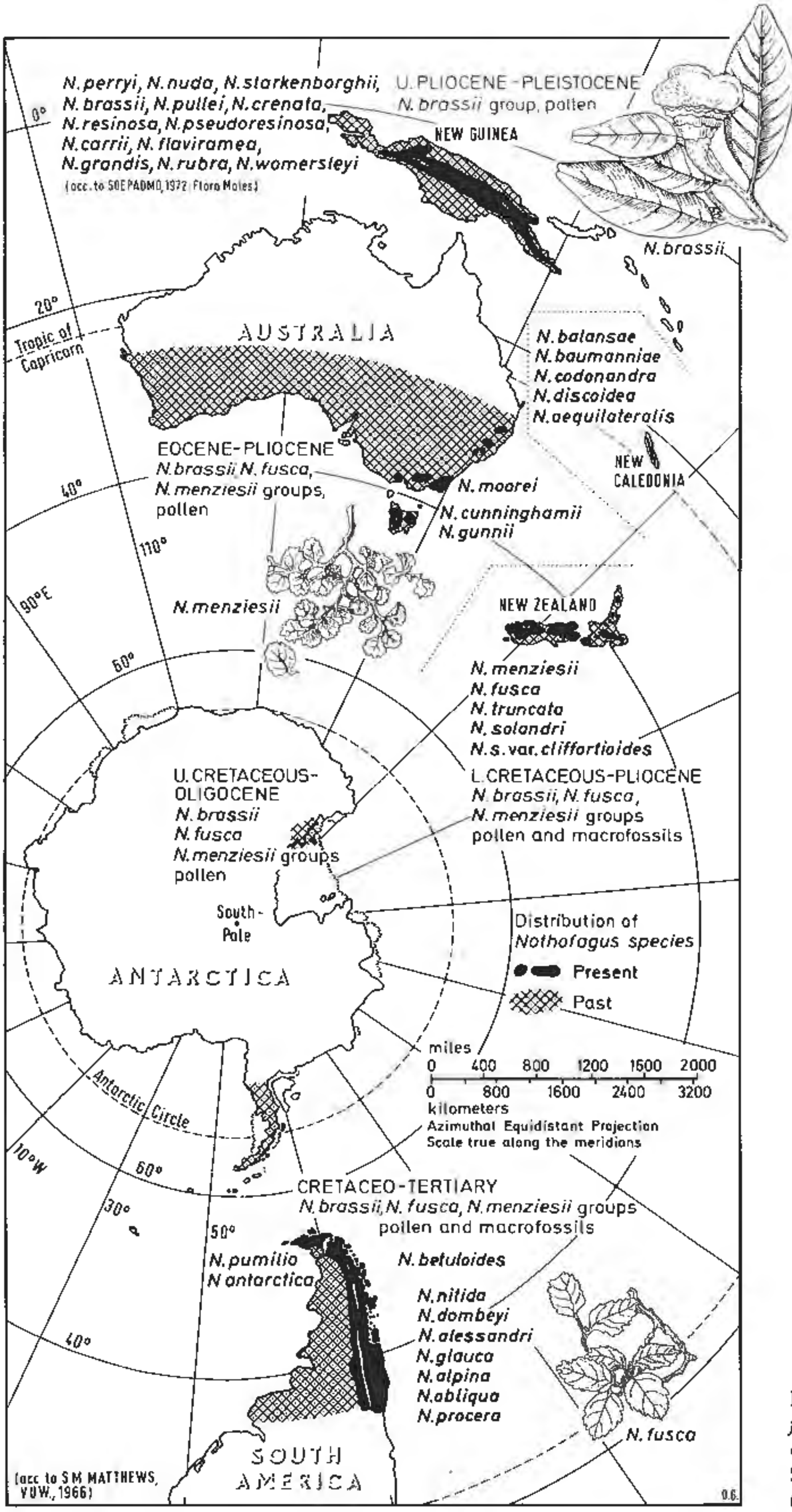

Fig. 1. Distribution of *Nothofagus* (s.l.) in the reach of former eastern Gondwana, compiled by S. M. MATTHEWS, N.Z., 1966 (part of display).

In these latitudes only *Nothofagus* s.l. (incl. *Trisyngyne*) is a representative of this family, but with many species having only very restrictive areas (compare e.g. Chapter 2.1.1., *Nothofagus moorei*; for New Guinea endemites see: ASH, 1982, *Nothofagus nuda, Nothofagus womersleyi*). Often they occupy very distinct patches in a multigenera forest, be it in Australia, the pacific area or in South America, thereby showing every aspect of relict species, sometimes due to difficulties of migration or because of dieback of unknown cause (see CARTLEDGE et al., 1975, in ASH, 1982).

2. Relictic Situations of Fagaceae in the Area of the Myrtaceae

In this transition zone, two distinct groups of relictic sites may be differentiated, namely those with and those without fire protection; i.e. in one case relictic sites are surrounded by vegetation which is regularly influenced by fire, and for the other group of sites this is not the case, vegetation all around being of a non-fire influenced type. In all regions, *Nothofagus* is highly fire-sensitive, therefore endemites may be endangered in fire-exposed areas because of insufficient regeneration (compare also: ASH, 1982).

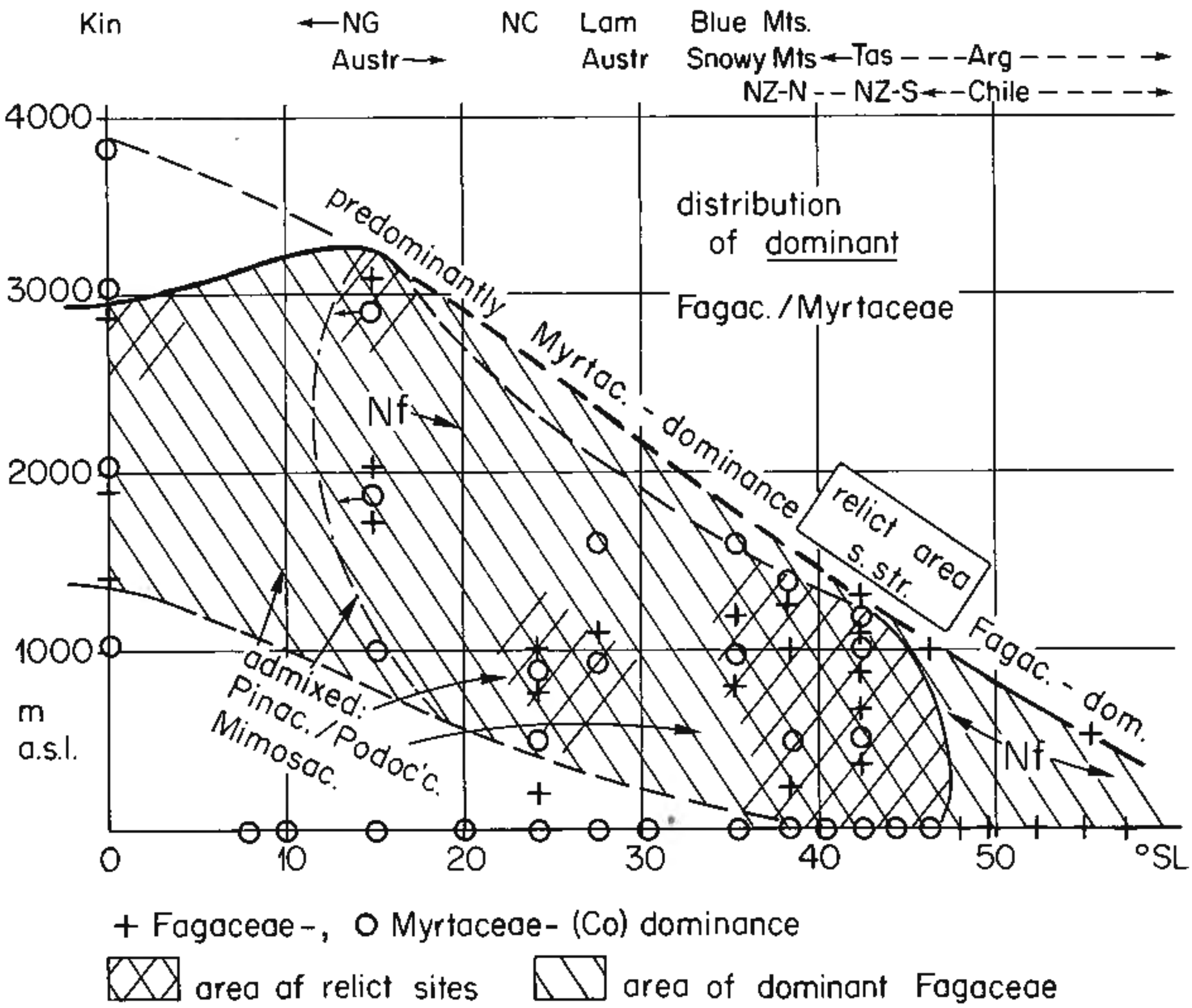

Fig. 2. Area of Myrtaceae and Fagaceae (only where dominant or codominant) in the southern hemisphere, showing zone of intense competition where boundaries overlap in their southern parts, i.e. area of so-called "relictic stands".

2.1. Relictic Sites without Fire Protection

In this group of sites, an eventual fire would not be prevented from spreading. According to ASH (1982) there is "no simple explanation for their topographic distribution". But most cases may be attributed to one of the six following types.

A good deal of topo- and orographic positions are possible, e.g. hill tops, ravine slopes, basin sites, but also flat sites.

2.1.1. Hill Tops

The summits (about 1000–1200 m a.s.l.) of round hills in the area of the Lamington National Park, south of Brisbane, Queensland, Australia, are often colonised by fragments of *Nothofagus moorei* forests. They are covering just the tops ($\Delta h \approx 10$ m!) and mostly monospecific in their tree layer, but also their shrub and herb layer is rather poor in species (dominant species are *Tasmannia* and *Doryphora* as a shrub and *Blechnum wattsii* and other ferns, some monocots e.g. *Dianella*, and also Hydrocotyle species, and occasionally *Dawsonia* moss).

Adjacent to these relicts of a former continuous carpet of *Nothofagus* rain forests, are as a rule different types of subtropical montane rain forest with dominating *Ficus wattsoniana, Agryrodendron trifoliolosum, Geissois benthamii, Pseudoweinmannia lasiocarpa* and admixed *Araucaria cunninghamii* and *Cryptocarya* species, carrying some climbers *(Calamus, Derris involuta)* and epiphytes *(Platycerium, Adiantum,* Orchids). The lower strata are governed by tree ferns (*Cyathea,* sometimes penetrating *Nothofagus* stands) and palms or ferns, Commelinaceae, Iridaceae, Cyperaceae and Poaceae, respectively (compare also WEBB, 1968, "Notophyll evergreen vineforest" and "Microphyll fern forest").

For similar conditions in lower altitudes in New Guinea, where *Nothofagus* escapes competition on hill tops, see ASH (1982; there also: DAWSON, 1966, for New Caledonia).

2.1.2. Ravine Slopes

On Mt. Do (about 1000 m a.s.l.) but also on other mountains of eastern New Caledonia, e.g. near Rivière Bleue, at about 200–300 m a.s.l.; there are many relict(-like) woodlands and forests with dominant endemic *Nothofagus* species which are on rather steep slopes of ravines (*Nothofagus aequilateralis, Nf. balansae* etc.; details on distribution see BAUMANN-BODENHEIM, 1983). They may be mono- to polyspecific, carrying a wealth of endemic species in all strata. Besides Fagaceae, also *Alphitonia novaecaledoniae, Myodocarpus fraxinifolius, Agathis ovalis* and many other broadleafed species (Table 1) may be prevalent. Some climbers, e.g. *Freycinetia, Smilax,* may be conspicuous, and quite a number of typical species of a true understorey, Cordyline, *Cyathea vieillardi,* palms *(Actinoquintia, Basolinia, Clinosperma),* but mostly young trees are dominating. An occasional herb layer is governed by ferns (e.g. *Blechnum, Schizaea, Sphaenomeros, Trichomanes, Elaphoglossis,* etc.) and tussocks of *Schoenus tendo.*

There is no chance for these Nothofagus species to grow on the adjacent plateaux (heavy metal soils, serpentine and peridotite), because dense heath (Table 2) or low bush with occasional stands of *Araucaria balansa* prevents any regeneration of more demanding species. Also, Myrtaceae are confined to the richer sites of the valleys and foothills *(Melaleuca leucadendron)* or occasionally admixed in the ravines (*Syzygium, Eugenia,* etc.).

In northern New Zealand, the situation is less evident, as the less steep slopes are cultivated. But also in this case, *Nothofagus truncata* is dominant with some *Phyllocladus trichomanoides, Agathis australis, Beilschmiedia tawa, Knightia excelsa,* overgrown with *Metrosideros* climbers and fern epiphytes, and a

Table 1. Tropical montane rainforest on Mt. Do/New Caledonia. List of genera in the tree layer (partly regeneration). (species names in brackets where verifiable)

Nothofagus (codonandra^{x})	(± dom.)	*Hibbertia*	[Dilleniac.]
Araucaria (bernieri and *muelleri)*	[Araucariac.]	*Ixora*	[Rubiac.]
Austrobuxus	[Buxac.]	*Myodocarpus (fraxinifolius^{+})*	[Araliac.]
Baloghia	[Euphorbiac.]	*Podocarpus (silvestris^{+})*	[Podoc'c.]
Baccariella	[Sapotac.]	*Pittosporum*	[Pittosporac.]
Balanops$^{\circ}$	[Balanopsidac.]	*Psychotria*	[Rubiac.]
Cupaniopsis	[Sapindac.]	*Rapanea*	[Myrsinac.]
Caryophyllus	[Myrtac.]	*Rauwolfia*	[Apocynac.]
Casearia	[Flacourtiac.]	*Scaevola*	[Goodeniac.]
Dysoxylon	[Meliac.]	*Salacia*	[Hippocrateac.]
Dutaillyea	[Rutac.]	*Styphelia*	[Epacridac.]
Guettarda	[Rubiac.]		
Gastrolepis	[Icacinac.]		
in lower altitudes also:			
Nothofagus (aequilateralis^{+})	(± dom.)	*Guioa (glauca)*	[Sapindac.]
Alphitonia (novae-caledonica)	(co-dom.) [Rhamnac.]	*Geissois*	[Cunoiac.]
Agathis (moorei$^{\circ}$)	[Araucariac.]	*Garcinia*	[Guttiferae]
Albizia (granularis)	[Mimosac.]	*Hugonia (penicillanterus)*	[Linac.]
Bocquillonia	[Euphorbiac.]	*Ochrothallus*	[Sapotac.]
Citronella (sarmentosa)	[Icacinac.]	*Schefflera*	[Araliac.]
Elaeocarpus	[Elaeocarpac.]	*Stenocarpus (tenellus)*	[Proteac.]
Euroschinus	[Anacardiac.]	*Syzygium (austrocaledonicum)*	[Myrtac.]
Eugenia	[Myrtac.]	*Tristaniopsis*	[Myrtac.]
Gardenia	[Rubiac.]		

^{x} upper, $^{\circ}$ middle, $^{+}$ lower } montane belt

Table 2. Tropical montane heath on Mt. Do/New Caledonia. List of genera in the shrub layer (S.) and field layer (F.), the only tree being *Araucaria balansa* [Araucariac.] at 1000 m a.s.l. (species names in brackets where verifiable).

S. *Dracophyllum*	[Epacridac.]	F. *Costularia (arundinacea)*	[Cyperac.]
Polyscias	[Araliac.]	*Caladenia*	[Orchidac.]
Rapanea	[Myrsinac.]	*Eriaxis (rigida)*	[Orchidac.]
Scaevola (beckii)	[Goodeniac.]	*Baeckia (ericoides)*	[Myrtac.]
Symplocos	[Symplocac.]	*Fistula*	[Caesalpiniac.]
Wickstroemia	[Thymelaeac.]	*Gleichenia*	[Gleicheniac.]
Epiphytes		*Lycopodium*	[Lycopodiac.]
Nepenthes (vieillardii)	[Nepenthac.]	*Schizaea*	[Schizaeac.]
Dendrobium (oppositifolium)	[Orchidac.]	*Thelymitra*	[Orchidac.]
		and carpets of *Cladonia* lichens	

(in lower altitudes [300 m] serpentine scrub with less ericoids and more sclerophyllous species and conifers as e.g. *Dacrydium araucarioides* [Podocarpac.] and *Agathis ovata* [Araucariac.])

According to the plantgeographical (chlorological) analysis of BAUMANN-BODENHEIM (1956) both stands of Table 1 and 2 may be interpreted as typically montane, with a tendency to middle-montane. The same time a considerable amount of possible distribution types of (sub-)tropical plant species are present, including extreme new-caledonian endemics in both cases, forest and heath.

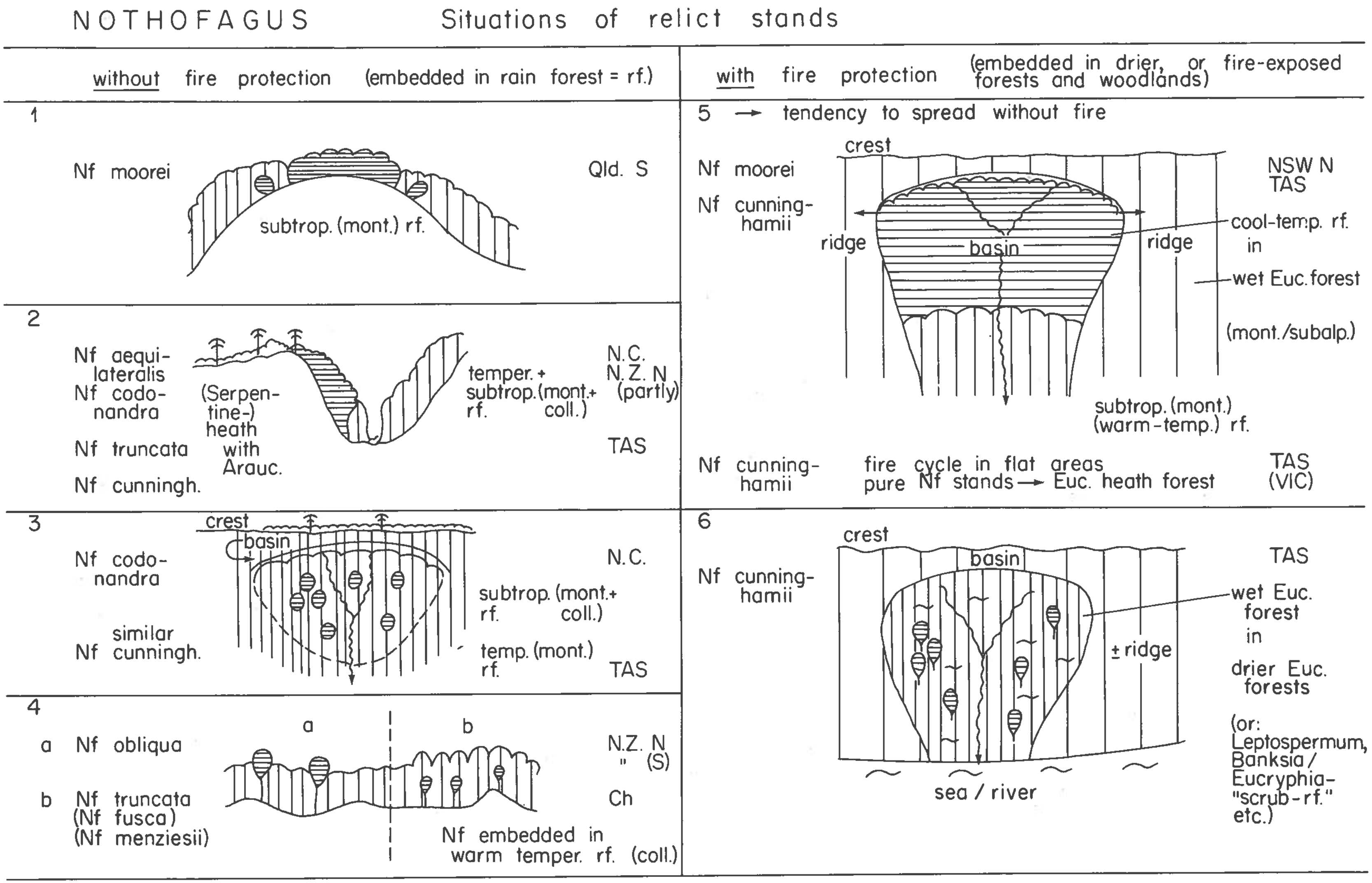

Fig. 3. Situation of "relictic stands" in the widest sense ("special sites") (compare also views in: KLÖTZLI, 1975).

dense undergrowth of some *Cyathea medullata,* some bushes *(Cyathodes, Olearia, Myrsine)* and *Pteridium* herds.

Under less steep conditions, the Fagaceae have apparently no advantage any more with their stabilising root system and capacity of sprouting from fallen trunks, and they are overgrown by Podocarpaceae (*Podocarpus, Dacrydocarpus* etc.) and/or Myrtaceae *(Metrosideros),* at the utmost forming subdominant understorey groups. In many areas, this type of forest is indicated by the hedge row species or some trees left in the pastures. Sometimes, also *Agathis australis* may prevail under these conditions admixed with the same species as above, especially *Beilschmiedia, Dysoxylon, Pseudowintera, Weinmannia racemosa* and *Podocarpus* species and a great number of shrubs (e.g. Coromandel Peninsula 400 m; compare e.g.: WARDLE, 1970; KUSCHEL, 1975).

2.1.3. Basin Sites with Isle-like Domes

Also Mt. Do and some other mountains in New Caledonia (Dividing range) have relict(-like) forests in moist basins (≈ 900 m, 30–40%/W) on steeper slopes with dome- or crest-like convex parts in the same basins. Under these conditions, *Nothofagus codonandra* is mostly codominant or just present with single stems surrounded by montane rain forest species (*Actinoquintia* as high palm, *Cyathea* as tree fern, *Pandanus* and many tree species as e.g. *Meryta coriacea, Beauprea, Elaeocarpus, Tapaeinosperma, Falcatifolius, Myodocarpus, Phellina, Guettarda,* etc., in the moister parts especially *Planchonella, Podocarpus silvestris, Austrocedrus, Oxera* etc.) (for further details see also: DAWSON, 1966, in ASH, 1982).

Nothofagus is probably prevented from colonising the more concave parts of these basins because of difficulties in seed-installation (fungus attack, see also GADEKAR, 1975, for similar conditions with *Fagus silvatica* in C-Europe). Also from New Guinea ERIKSON (pers. comm.) reports to have seen a similar pattern.

2.1.4. Climax Woodland on Flat Sites

In middle Chile, *Nothofagus obliqua,* sometimes *Nothofagus dombeyi,* may be found as protruding stems in climax forests with a great number of laurophyll ("Notophyll") trees and *Podocarpus (Pc.),* e.g. *Aextoxicum punctatum, Laurelia philippiana, L. sempervirens,* many climbers, fern epiphytes, often hard-leafed ("microphyll") shrubs, *Chusquea* bamboo and mesic herbs (e.g. near Lake Puyehue, 40–50 m a.s.l.) or then with *Pc. andinus, Austrocedrus chilensis, Lomatia hirsuta, Drimys winteri, Maytenus boaria* and many shrubs (e.g. near Cunco at 350–450 m a.s.l.). Near the coast similar forests occur in the montane belt with a physiognomy quite near to the *Podocarpus*-forests of New Zealand, often with *Weinmannia trichosperma, Laurelia philippina, Podocarpus nubigenus, Dasyphyllum, Saxegothea conspicua* and *Nothofagus obliqua* as dominants, normally with many climbers, fern-epiphytes, Bamboo, shrubs and mesic herbs (e.g. Cord. Pelada, 650 m; compare e.g.: OBERDORFER, 1960; HUECK, 1966; KLÖTZLI, 1983).

Regeneration is rather scarce, showing that *Nothofagus* is more or less on an outpost and not a fully emancipated species like dominant "colleagues" of them in the montane and subalpine temperate rainforests with dominant *Nothofagus dombeyi, Nothofagus betuloides* or *Nothofagus nitida* (compare lit. cit.) or in transitions from colline to montane temperate deciduous forests (with *Nothofagus procera* or *Nothofagus pumilio*), or then to colline, cool-temperate broadleafed ("laurel") forests with *Nothofagus obliqua, Persea, Laurelia,* etc. (e.g. to the north of Puerto Montt).

These forests are hard to ignite, therefore, do not need any fire protection to guarantee their existence (human influence excluded!) and the codominance of Fagaceae.

Fig. 4. Australia E, Queensland S, Lamington National Park: View on complex of wet *Eucalyptus*-forests, subtropical montane rain forest, and, background, on small hills with *Nothofagus moorei* (up to 1100 m).

Fig. 5. id.: *Nothofagus moorei* stand on Mt. Hobwee, 1100 m.

Especially in northern, but also on the westcoast of southern New Zealand, Fagaceae (*Nothofagus fusca, Nothofagus solandri, Nothofagus menziesii,* sometimes *Nothofagus truncata*) are never amongst the single highstemmed trees as the *Podocarpus.* They form, as a rule, an understorey, often dense, and are dominated or overgrown by *Podocarpus (Podocarpus ferrugineus, Pc. dacrydioides, Pc. spicata, Pc. totara, Pc. hallii, Dacrydocarpus cupressinus)* and sometimes *Metrosideros.* The understory is quite rich in ericoid and small leafed shrubs, in luxuriously growing herbs and ferns, but regeneration of *Nothofagus* may be quite satisfactory (for further details see e.g.: WARDLE, 1970; KUSCHEL, 1975; KLÖTZLI, 1983).

Withouth *Podocarpus* and *Nothofagus,* but with similar physiognomy, and dominating *Metrosideros, Weinmannia* and tree ferns, *Freycinetia,* ericoid shrubs, *Blechnum* and other ferns, such forests are in all warm-temperate and tropical montane areas of the Pacific (N.Z., Tahiti, Hawaii, and other pacific isles; see e.g.: KUSCHEL, 1975; PAPY, 1948 and 1954/55; MUELLER-DOMBOIS, 1983).

2.2. Relictic Sites with Fire Protection

Under this heading, little fire-endangered sites are collected or then – mostly – sites englobed by fire-influenced forests.

Fire protection in these relict stands is given by edaphic support, i.e. by moister soil, generally in basins or also flat sites. There is no chance of regeneration of the leading species outside of these fire-protected areas, because any young plant would be destroyed by the annual fire, which, on the other hand, does not prevent Myrtaceae from growing in dense fire adapted stands (details e.g. in: GILL et al., 1981; for Australia see also: KEAST, 1981).

2.2.1. Basin Sites

Especially in Tasmania (JACKSON, in SPECHT et al., 1974; JACKSON, 1981; WILLIAMS, 1974) but also along the eastern Australian Great Dividing range, *Nothofagus* relict stands are surrounded by often mono-specific *Eucalyptus* stands, where *Nothofagus* is only a "guest" tree in the understorey, if presence is possible.

In Tasmania, such stands occur on the south eastern coast (e.g. Signal Hill) where *Eucalyptus* (e.g. *E. obliqua, E. delegatensis*) are dominant with an often dense layer of ericoid and small-leafed shrubs – sclerophyll and "laurophyll" – and also tree ferns, *Nothofagus cunninghamii,* up to 15 m tall only, and *Atherospermum moschatum,* up to 25 tall, both being confined to rather moist seepage basins, and regenerating freely in a fern-rich herb layer with *Blechnum wattsii, Polystichum proliferum* and some monocots, e.g. *Dianella.*

But similar stands with similar shrubs and dominating ferns may also occur at higher altitudes, including the mainland, where also *Eucalyptus* is absolutely dominating the bordering areas, the transition zone being barely around 50 m wide, with e.g.:

1. *Euc. subcrenulata, E. delegatensis, E. coccifera, E. urnigera* in Tasmania on Mt. Field (at 600 m up to 1100 m), with *Nothofagus cunninghamii* and shrubs of the neighbouring forests, with Epacridaceae, Proteaceae and Asteraceae, all mostly needle-leafed or sclerophyll; also *Phyllocladus aspleniifolius* and *Anodopetalum biglandulosum* being mostly present.
2. *Euc. viminalis,* partly surrounded by *E. fastigiata, E. obliqua, E. pauciflora,* depending on altitudes, aspect and moisture (see also: WEBB, 1968; TURNER, 1976), in New South Wales on Barrington tops (at about 1000 m a.s.l.) with *Nothofagus moorei* and sclero- to laurophyll species as e.g. *Doryphora* and *Trochocarpus,* and predominance of ferns *(Blechnum, Polystichum).*

Other similar sites are treated in chapters 2.2.2. and 2.2.3. Furthermore, also *Eucalyptus oreades,* fire-sensitive, may survive under similar conditions.

Fig. 6. Nouvelle Calédonie, Mt. Do., ca. 1000 m: *Araucaria* in heath, to the right touching edge of slope carrying stands of *Nothofagus aequilateralis*.

Fig. 7. New Zealand N, Waitakaruru, ca. 60 km E of Auckland, ca. 150 m: Stand of *Nothofagus truncata* on slope leading to rivulet.

Fig. 8. Nouvelle Calédonie, Mt. Do., ca. 900 m, S-slope: Moist basin with (sub-)tropical montane rain forest, containing small stands of *Nothofagus codonandra* on small crests.

Fig. 9. New Zealand S, N-part of west coast: Temperate rain forest (climax) with *Dacrydocarpus cupressoides* and some *Nothofagus cliffortoides* in the lower tree layer. – In the Valdivian rain forest similarly *Nothofagus obliqua* may be conspicuous in the upper tree layer.

Fig. 10. Australia E, New South Wales N, Barrington Tops, ca. 1000 m: *Nothofagus moorei* stand in moist basin, surrounded by montane moist *Eucalyptus*-forests.

In these areas, *Nothofagus* may penetrate into surrounding natural, nutrient-poor heath sites, where even *Eucalyptus* and *Phyllocladus* show reduced vitality and grow there as small park-like trees under very light conditions, together with typical heath endemites (e.g. *Richea pandanifolia*, many ericoid Epacridaceae and sclerophyll Proteaceae, dominating, *Gahnia*, *Sphagnum*, *Hepaticae* and lichens), and menaced by occasional fires (for causes leading or characterising heath, see also: TRACEY and WEBB, 1969).

From New Guinea similar conditions are announced by ASH (1982), for *Nf. starkenborghii*, on peat for *Nf. rubra* (compare also other chapters in: GRESSITT, 1982).

2.2.2. Very Moist Basins

In very moist basins, *Nothofagus* species grow on rather crest-like domes, often on boulders (compare 2.1.3.), which are as a rule situated near the area, or near rivulets or streams. Again, these sites are surrounded by non-Fagaceae woodlands and drier forests (e.g. *Euc. pulchella*, *E. amygdalina* on triassic sandstone), on the Tasmanian southeastern coast by *E. delegatensis*/*E. obliqua* (often on jurassic dolerite), in the southwestern moist wilderness area, on soils of very low fertility, at about 300–400 m a.s.l., by "Scrub Rainforest" with *Eucryphia lucida* stands including *Anopterus glandulosus*, *Anodopetalum*, an

Fig. 11. Australia, Tasmania, Mt. Field, ca. 600 m: Heath woodland adjacent to basin with *Nothofagus cunninghamii*, surrounded by moist montane *Eucalyptus*-forests, still carrying some stems of *Nothofagus cunninghamii*, *Phyllocladus* and *Eucalyptus*.

Acacia, many ericoids and a variety of ferns forming a dense scrub of a "Krummholz-like" type, or then even by heath thickets with *Banksia* and *Lepidospermum*. Under such conditions, fire-sensitive *Nothofagus* avoids the drier ridges, and for *Eucalyptus* there is often too little light (JACKSON, 1981).

2.2.3. Moister Flat Sites

As in boreal coniferous forests, showing at fire-induced (birch-)pine-spruce cycle, also in Tasmania, the composition of forests on moister flat sites is ruled by frequence and intensity of fires, but also by nutrient regime (compare e.g.: JACKSON et al., 1981; "ecological drift": WALTER, 1968, pp. 267 ff.).

Therefore, pure or mixed *Eucalyptus-Nothofagus cunninghamii*-forest (with e.g. *Eucalyptus regnans*, up to 100 m tall, Ø 3–5 m(!), *E. obliqua* etc., on precambrian metamorphes) with tree ferns *(Dicksonia antarctica)* and a laurophyllous understorey *(Zieria arborea, Monotoca glauca, M. elliptica, Atherospermum moschatum, Anopteris glandulosa)* with many ferns (*Blechnum*, *Polystichum*, compare 2.2.1.) occur on moist flats around Mt. Field (e.g. near and on the Styx River) or then similarly in Victoria (SE-slopes), moist enough to secure the existence of *Nothofagus cunninghamii* – dominated stands in regions with annual fires (compare also: WEBB, 1968, "nanophyll mossy forest"; HOWARD, 1973; HOWARD and ASHTON, 1973).

Fig. 12. Australia, Tasmania, on Styx River, ca. 150 m: Moist flats with *Eucalyptus regnans* (up to nearly 100 m tall, here not visible) and tall *Nothofagus cunninghamii;* luxuriant tree ferns *(Dicksonia antarctica)* in foreground.

Fig. 13. Australia, Tasmania, nr. Gordon Dam, ca. 350 m (up to 800 m): Upper steeper slopes with scrub rain forest, on moist boulder basins partly with *Nothofagus cunninghamii/Eucryphia lucida*, on lower slopes with *Eucalytpus, Acacia mucronata* and different *Leptospermum* species.

Fig. 14. Australia, Tasmania, nr. Gordon Dam, ca. 350 m: Scrub rain forest with *Phebalium squamosum* [Rutaceae], *Acacia mucronata, Leptospermum* and *Epacris* (different species), and also *Anodopetalum biglandulosum*.

3. Considerations on the General Strategy of Fagaceae and Myrtaceae

Considering the above-mentioned site conditions, and now tracing the situation from "the other side", dominance of Myrtaceae has to be expected under the following conditions:

1. Less temperate but favourably at least subtropical to tropical climates at lower altitudes, also from the colline to the subalpine belts (E-Australia, Indonesia etc.).
2. In drier climates under the influence of regular fires (drier sites in the whole area).
3. At a given suitable temperature, or then even below optimum temperature, under more stress-rich conditions, as e.g.:
   - more pronounced mechanical factors (river, unstable slopes, browsing)
   - high water table
   - drought-exposed sites
   - nutrient-deficient (heath) sites inducing more open and consequently mostly more fire incidents and less shade to the detriment of shade-tolerant Fagaceae. An advantage is certainly given by an internal ability to spourt from roots (suckers), the base of stems, and by the fact that seed and seedling are fire-adapted.

Fig. 15. Australia, Tasmania, nr. Gordon Dam, ca. 350 m: Interior of scrub rain forest, on rather steep slopes, with dom. *Anodopetalum* (Photo: Australian Botanical Congress, slide series, 1981).

Under human influence, Myrtaceae, therefore, tend to increase their special area by taking over sites of less adapted families (on the other hand: for die-back compare: MUELLER-DOMBOIS, 1983; CARTLEDGE et al., 1975).

Fagaceae on the other hand, especially *Nothofagus*, are much less fire-adapted, and in the area of the Myrtaceae confined to less temperate (colder), moister and richer sites, or then, under conditions where neighbouring species tend to have more difficulties to establish as young trees or hold themselves on exposed sites due to mechanical factors. As a rule, they are very shade-tolerant under their parent trees or in canopy gaps of mixed forests (see: ASH, 1982; SCHULZE, 1982, p. 658). But under the extremely shady conditions of closed rain-forests, they are inclined to colonise more open areas, where seeds of often very low viability may also be deposited more readily. On the other hand, out of the area of the Myrtaceae, Fagaceae are capable to colonise all sites, from dry to moist, rich to poor, the colline to the subalpine belt (compare also: ASH, 1982).

Comparing both families, they both show maximum adaptation to the prevailing conditions under subtropical and temperate climates, respectively, and give way to other families, when regeneration is difficult under very shady conditions and/or production too slow under more tropical conditions.

Summary

1. On many mountains in the whole Pacific area Fagaceae (F.) and Myrtaceae (M.) play an essential role as dominant arborescent organisms (compare e.g. Kinabalu/Sabah, Malaysia, volcanic mountains in Tahiti, eastern Australia, New Guinea, New Caledonia, southern Andes etc.).
2. As a rule, M. reach the timberline and other higher altitudes in the tropical zone (incl. Podocarpaceae); in the more marginal areas towards the southern temperate zone rather F. are dominating (compare F. in SE-Australia, New Zealand, southern South America etc.).

3. In the transitional zone towards the temperate zones, these F. appear in ± relictic situations:

a) without fire protection

   1. hill tops in the subtrop.-montane rain forest (e.g. S-Queensland);
   2. ravine slopes in (sub-)tropical montane rain forest, surrounded by heath woodland (containing *Araucaria*, New Caledonia; New Zealand);
   3. basin sites with isle-like domes in subtropical rainforest (New Caledonia);
   4. flat sites protected by climax woodlands with leading dominants (middle Chile) or in the auxiliary stand (N- and partly S-New Zealand), within the area of colline to submontane warm-temperate rain forests or then transition to temperate deciduous forests or laurophyllous forests.

b) with fire protection (little fire endangered stands in fire influenced forests)

   1. basin sites with montane to subalpine warm to cool-temperate *Eucalyptus-Nothofagus*-rain forest surrounded by wet *Eucalyptus*-forests of high diversity (Tasmania, SE-Australia);
   2. very moist basins but on small isle-like crests in the vicinity of rivers or the sea, in colline to montane wet *Eucalyptus*-forests, surrounded by dry *Eucalyptus*-forests, *Eucryphia*-stands or then *Banksia/Leptospermum*-thickets (Tasmania);
   3. moister, flat sites as final stages of the *Eucalyptus/Nothofagus*-fire cycle, surrounded by wet *Eucalyptus*- or heather forests (Tasmania, SE-Australia (Victoria)), mostly in the montane belts.

4. The general strategy of both families is accentuated by the fact, that M. are starting to dominate where they are sponsored by higher temperatures, especially in their production, or then when M. as frequent pyrophytes have certain advantages (coppicing, viability of seed etc.), or are submitted to higher mechanical stress. Under humau influence the area of the M. is mostly widened to the detriment of the F.

References

ASH, J. (1982): The *Nothofagus* BLUME (Fagaceae) of New Guinea. In: GRESSIT, J. L. (Ed.): Biogeography and Ecology of New Guinea. Monograph. Biology 42, 355–380.

BAUMANN-BODENHEIM, M. G. (1956): Über die Beziehungen der neucaledonischen Flora zu den tropischen und den südhemisphärisch-subtropischen bis -extratropischen Floren und die gürtelmäßige Gliederung der Vegetation von Neu-Caledonien. Ber. Geobot. Forsch. Inst. Rübel, 1955, Zürich, 64–74.

– (1983): Morphologie und Klassifikation neu-caledonischer Arten der Fagaceen-Gattung *Trisyngyne*. Bot. Helv. 93, 281–321.

CARTLEDGE, E. G., D. E. SHAW and D. J. STAMPS (1975): Studies in relation to dead patches of *Nothofagus* in Papua New Guinea. Papua New Guinea Dept. Agr., Stock and Fish, Res. Bull. 13. (Cited in ASH, 1982.)

DAWSON, J. W. (1966): Observations on *Nothofagus* in New Caledonia. Tuatara 14, 1–7.

GADEKAR, H. (1975): Ecological conditions limiting the distribution of *Fagus silvatica* L. and *Abies alba* Mill. near Schwarzenberg (Lucerne), Switzerland. Veröff. Geobot. Inst. ETH, Stiftung Rübel, 54.

GILL, A. M., R. H. GROVES and I. R. NOBLE (Eds., 1981): Fire and the Australian Flora. Austr. Acad. Sci., Canberra.

GRESSITT, J. L. (Ed., 1982): Biogeography and ecology of New Guinea. I. & II. Monogr. Biol. 42. The Hague, Boston, London.

HOWARD, T. M. (1973): Studies in the ecology of *Nothofagus cunninghamii* OERST. 1–3. Austr. J. Bot. 21, 67–102.

– and D. H. ASHTON (1973): The distribution of *Nothofagus cunninghamii* rainforest. Roy. Soc. Vict. Proc. 86, 47–75.

HUECK, K. (1966): Die Wälder Südamerikas. Ökologie, Zusammensetzung und wirtschaftliche Bedeutung. In: WALTER, H. (Ed.): Vegetationsmonographien der einzelnen Großräume 2., Jena.

JACKSON, W. D. (Ed., 1981): The vegetation of Tasmania. XIII Intern. Bot. Congr., Field Trip 28 (Guide), Univ. of Tasmania.

KEAST, A. (1981): Ecological Biogeography of Australia. Vol. 1. Monogr. Biol. 41, The Hague, Boston, London.

KLÖTZLI, F. (1975): Edellaubwälder im Bereich der südlichen Nadelwälder Schwedens. Ber. Geobot. Inst. ETH, Stiftung Rübel, 43, 23–53.

– (1983): Standörtliche Grenzen von Fagaceen – ein Vergleich in beiden Hemisphären. Tuexenia (N.S.) 3, 47–65.

KUSCHEL, G. (Ed., 1975): Biogeography and ecology in New Zealand. In: Monogr. Biol. 27, Den Haag.

MÜLLER-DOMBOIS, D. (1983): Population death in Hawaiian plant communities: a causal theory and its successional significance. Tuexenia (N.S.) 3, 117–130.

OBERDORFER, E. (1960): Pflanzensoziologische Studien in Chile. Ein Vergleich mit Europa. In: TÜXEN, R. (Ed.): Flora et vegetatio mundi 2. Weinheim.

PAPY, H. R. (1948): Aperçu sommaire des étages de végétation à Tahiti. Bull. Soc. Hist. Nat. Toulouse 83.

– (1954/55): Tahiti et les îles voisins. Trav. Lab. for. Toulouse 5 (Vol. I, Sect. 2), 1–130, 163–386.

SCHULZE, E. D. (1982): Plant-life forms and their carbon-, water- and nutrient relations. In: LANGE, O. L., P. S. NOBEL, C. B. OSMONDY and H. ZIEGLER (Eds.): Physiological Plant Ecology II. (Encycl. Pl. Physiol., N.S. 12 B.) Berlin, Heidelberg, New York, 615–676.

SPECHT, R. L., E. M. ROE and V. H. BOUGHTON (1974): Conservation of major plant communities in Australia and Papua New Guinea. Austr. J. Bot., suppl. ser. 7.

TRACEY, J. G. and L. J. WEBB (1969): Edaphic differentiation of some forest types in eastern Australia. I. Soil physical factors. II. Soil chemical factors. J. Ecol. 57, 805–816, 817–830.

TURNER, J. C. (1976): An altitudinal transect in rainforest in the Barrington Tops area. Austr. J. Ecol. 1, 155–174.

WALTER, H. (1968): Vegetation der Erde in öko-physiologischer Betrachtung. 2. Die gemäßigten und arktischen Zonen. Stuttgart.

WARDLE, J. A. (1970): Ecology of *Nothofagus solandri*. For. Res. Inst., N.Z. For. Serv., Techn. Pap. 58 (also: N.Z.J. Bot. 8, 494–646).

WEBB, L. J. (1968): Environmental relationships of the structural types of Australian rainforest vegetation. Ecol. 49, 296–311.

WILLIAMS, W. D. (Ed., 1974): Biogeography and ecology in Tasmania. Monogr. Biol. 25, Den Haag.

Discussion to the Paper Klötzli

Dr. W. Golte:

1. How is the ecological relation of the deciduous *Nothofagus gunnii* to the *Eucalytpus* species (e.g. *E. coccifera*) in Tasmania?
2. How do you interprete the paleoclimatic and paleoecological development of Australia considering the fact that *Nothofagus* has played – mainly in the South – a dominant role dnring most of the Tertiary there?

Prof. Dr. F. Klötzli:

1. As far as I have experienced *Nothofagus gunnii*,it is usually forming a shrub layer under e.g. *Eucalyptus coccifera* at an altitude of about 900–1100 m a.s.l. (e.g. Mt. Field), sometimes up to the timberline, but always protected from fire.
2. Being not a paleobotanist I can only state that *Nothofagus* had a far greater area in the tertiary age dne to less warm-temperate to tropical conditions. Later the old Gondwane area was split up into more relict-like isles and the conterminous areas in New Zealand and southern South America, the Myrtaceae taking over the old, now warmer Fagaceae areas.

Prof. Dr. E. Löffler:

Your observations concerning the preferred supine position of *Nothofagus* correlate very well with my interpretations of aerial studies on New Guinea. My question refers to a phenomenon which I observed in extended *Nothofagus*-forests. Within the forest there appear roundish gaps which indicate a dying out of the forest. Do you have an explanation for this phenomenon?

Prof. Dr. F. Klötzli:

Possible explanations are: mechanical damages (wind, biting by herbivors) or/and locally superannuated groups of trees.

Prof. Dr. W. Eriksen:

Do you observe a comparable extension of Myrtaceaes in *Nothofagus*-areas in South America, e.g. after burnings?

Prof. Dr. F. Klötzli:

After burnings only Myrtaceae bushes which need much light (e.g. *Myrceugenia, Myrceugenella*) can extend more.

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