COMPOSITAE VERSUS GRAMINEAE IN POLLEN ANALYSIS

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ABSTRACT

Three grass pollen minima are shown in the pollen analysis from a fluvio-glacial terrace. Geological and palynological data suggest that the first minimum (12,600 BP) was probably due to very cold climate following deglaciation of the region. The second minimum (12,250-11,900 BP), simultaneous with tree pollen maximum, was probably due to the scarcity of grasses in the adjacent region which was mostly occupied by forest. The third minimum, occurring at the same time as the great increase of Compositae pollen is found at the uppermost level, close to the soil surface, suggesting contamination from modern pollen.

Comparison between modern and old pollen assemblages has shown that the pollen now being deposited present higher Compositae and lower Gramineae pollen frequency than in the past. Geological, palynological and archaeological evidences suggest that this reversion in the pollen dominants was caused by the intense use of the land, specially by the introduction of cattle in the last 400 years. If overgrazing of the grassland can somehow increase the number of Compositae plants, a new method to detect the beginning of cattle raise may be developed.

INTRODUCTION

THE last twenty years have shown an increased interest in the study of the Quaternary in the tropics. The discovery of old moraines (Pl. 1, fig. 1) in the high tropical mountains of South America and Africa pointed towards the existence of glacial periods, and the last episode was correlated with the last glaciation of the Northern temperate zone (Wurm, Wiscosin). The idea of the " stability " of the tropical climate during the Pleistocene was shaken. Pollen analysis in these high mountains gave support to the glacial studies, and new evidence of glacial and interglacial episodes was found (Zinderen-Bakker & Coetzee, 1972; van der Hammen, 1974; Livingstone, 1975).

In the tropical high mountains the forest is replaced at higher elevations by an open plant formation, usually a low stratum of Gramineae with scattered shrubs and rosette mainly of Compositae (Pl. 1, fig. 1). These are the afro-alpine grassland, the páramos, the New Guinea mountain grassland, among others. The modern pollen deposition in these high sites reflects the vegetation, and the assemblages are dominated by pollen of Compositae and Gramineae.

The low tropical lands are covered by a mosaic of forest, savannas and semi-arid vegetation. No proof of climatic contrasting periods has been found so far for the low tropical areas, such as glacial and interglacial periods. Nevertheless, the succession of very cold and warm periods in the higher elevations must have been reflected somehow in at least the adjacent lowlands.

The palynological studies have just started in the lowlands (van der Hammen, 1974; Livingstone, 1975; Flenley, 1973) but only a few places have been analysed and no long core has yet been studied. Therefore information on the history of the lowland vegetation is scarce. Nevertheless, the study of speciation in birds (Haffer, 1969), in reptiles (Vanzolini & Williams, 1970), in plants (Prance, 1973) from South America, and others from Africa gave support to an hypothesis to explain the existence of different forms of animals and plants in places where there are no geographical or reproductive barriers. This hypothesis, first postulated by Moreau, proposes the existence of a succession of dry and wet periods. When climate was very dry, savanna and semi-arid vegetation would expand their territory, and forest would be restricted to small areas. Forest animals cornered into these refuge areas would migrate, differentiate or became extinct. The same would have happened to forest trees. More humid climate permitted the expansion and overlap of these refuge areas, and by then speciation probably had already occurred, and new forms had been created. Vice versa, the savanna and semi-arid vegetation would expand during the dry periods, and would contract into refuge areas during the wet periods. The choice of pollen analysis is only natural to verify this hypothesis, and it is easy to predict that it will give important data concerning it.

Another question can be answered by pollen analysis and it concerns the origin of the savannas and "cerrados". It is still frequently assumed that such types of vegetation are artificially created by man using axes and fire. For a person born in the tropics, who knows the big contrast between the dry and the rainy season, it is difficult to believe in this explanation. Contrasting seasons are releva t factors of macroclimate which cannot yet be changed by man, and human presence in South America is no older than ca. 20,000 years. During this time, husbandry only began during the last 400 years, and agriculture probably in the last 4,000 years. Also, it is difficult to think, for instance, that the 1,000 species of the Cerrados, all different from the ones of the neighbouring forests, could have speciated during such a short time. Furthermore, it has been pointed out by Labouriau (1966) that it is highly unlikely that 35 pairs of closely related species (one in the Cerrado, and one in the adjacent forest) of 16 different families could appear if such a contact were only recent. The South American savannas must be older than man in America.

In these savannas the Gramineae are the dominant plant type, followed by a large number of species of Leguminosae. The Compositae are also very abundant in species number in the Cerrado. The dominance of these families must be reflected in the pollen assemblages. Therefore, in order to verify changes in climate and succession of vegetation in the tropics, as well as to study the origin of the savannas, pollen analysis research has to be intensified. A better knowledge of these families as regards their pollen deposition, and the ratio between their pollen and the total pollen deposited, will help to answer these inquiries.

Grass pollen has been used in the interpretation of pollen diagrams by several authors. Among them Coetzee and Zinderen-Bakker interpreted the dominance of grass pollen in high mountains of Eastern Africa as an indicator of dry and very cold climate (Zinderen-Bakker, 1969). In the interpretation of pollen diagrams from Uganda, Hamilton (1972) suggests that abundance of grass pollen larger than 60 μ points towards disturbed conditions in the montane forest belt. Compositae versus Gramineae pollen was used to indicate climatic changes in Southern Africa (Zinderen-Bakker & Butzer, 1973). The information given by these two families are certainly important and they must lead to a good interpretation. But they cannot point towards the right conclusions if they are taken by themselves.

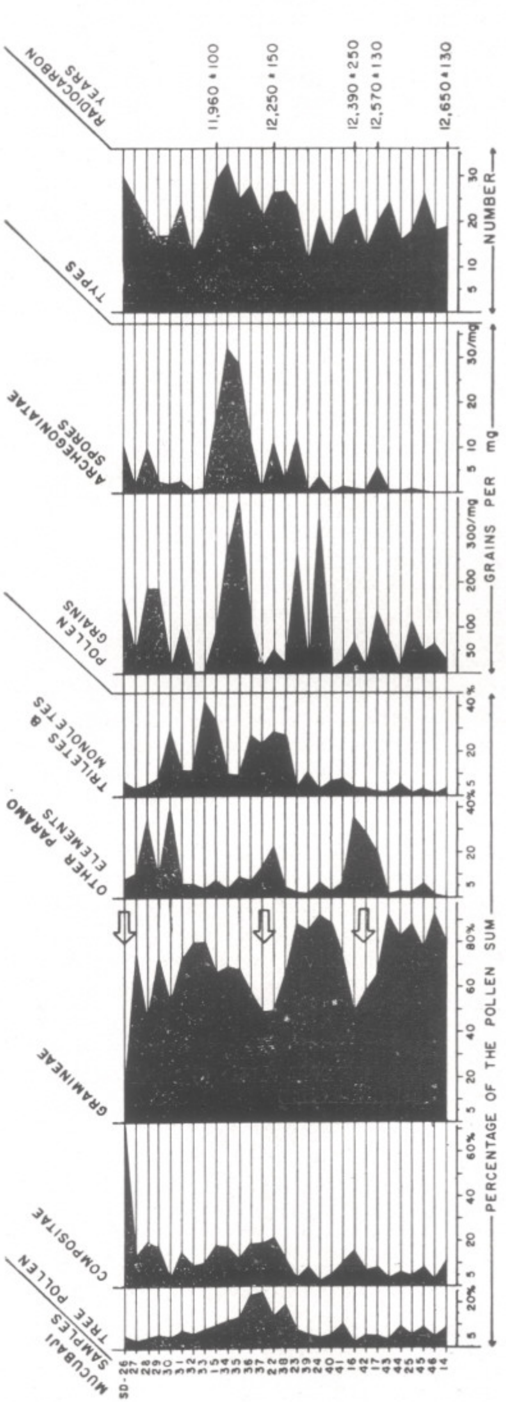
In this paper, two problems raised by Compositae and Gramineae pollen will be presented, and solutions will be proposed in order to exemplify the importance of the two families in the interpretation of the pollen diagrams from the tropics.

AN INTERPRETATION OF THREE GRASS POLLEN MINIMA

In the pollen analysis of a post-glacial terrace at Mucubaji (Venezuelan Andes) there were three clearly defined decreases of grass pollen (Salgado-Labouriau, Schubert & Valastro, in preparation; Salgado-Labouriau, 1977). In each of the three cases a different interpretation had to be adopted in order to fit the other pollen data, and knowledge from other research fields (Text-fig. 1).

First Grass Pollen Minimum — It occurred at the same time as the tree pollen minimum, and a maximum of Compositae pollen. Radiocarbon date is 12,600 BP for that level.

Geological evidence pointed out that during the glaciation the site was covered by glaciers (presence of well-preserved lateral and end moraines), and that the glaciation period was coeval to the last glaciation of Europe and North America (Schubert, 1970). Deglaciation probably started at about 13,000 BP as it occurred in the nearby Eastern Cordillera of Colombia (van der Hammen, 1974). Ecological studies of the Venezuelan páramos (Sarmiento *et al.*, 1971; Vareschi, 1956) show that the highest part of the páramo now belongs to a type of high altitude desert (*páramo*



TEXT-FIG. 1 — Pollen diagram from the Mucubaji terrace, simplified after Salgado-Labouriau, Schubert & Valastro (1977).

desértico) in which grasses are almost absent, and tall rosettes of *Espeletia* (Compositae) are scattered over the bare rocky soil (Pl. 2, figs. 3, 4). The present site is ca. 500 m below the beginning of the desertic páramo, and has a grassland type of páramo.

The minimum of grass pollen at 12,600 radiocarbon years could be due to the absence of grasses in the region because of very cold climate. In fact, the pollen assemblage is very similar to the modern ones from the desertic páramos. Therefore, the first grass pollen minimum was probably due to very cold climate.

Second Grass Pollen Minimum — It occurred at the same time as the tree pollen maximum, and a raise in Compositae pollen, during an interval dated at 12,250 to 11,900 radiocarbon years. During this interval there was an increase in absolute number and in types of pollen grains and spores of Archegoniatae. All of this indicates a rise of the montane forest, which probably occupied the region just below the site, suggesting an increase in the average temperature, and that grass pollen could only come from the site and from higher elevations. The second grass pollen minimum was probably due to an increase in temperature. Other data from this pollen analysis show that humidity increased at this interval.

Third Grass Pollen Minimum — It occurred at the uppermost level, a few centimetres from the soil surface. At this level Compositae pollen reaches its largest maximum throughout the terrace (69·6% of the total pollen deposited, whereas the next higher percentage is 20·7%). One may infer that a new factor came into play. The comparison with modern pollen deposition (see below) shows that Gramineae and Compositae reach their modern values at this level. But it cannot represent modern time because radiocarbon dating of peat layers in the lower part of the section reaches only 11,900 BP, and soil and pollen assemblages of the upper part seem to be continuous, and are consistent with the lower level (Text-fig. 1). Therefore, the third grass pollen minimum occurring together with the great increase of Compositae pollen is most probably caused by contamination by modern pollen, due to the proximity to the surface.

REVERSION OF THE RATIO GRAMINEAE-COMPOSITAE IN MODERN TIMES

All the old sediments from the Venezuelan páramos so far analysed present a lower frequency of Compositae pollen than the modern pollen assemblages. On the other hand, the frequency of grass pollen was always higher than today. Table 1 shows the data obtained up to the present and it shows that a reversion took place during modern times in which Compositae pollen dominates over Gramineae pollen. This must have occurred after 2,500 BP because at that time, in La Culata, grass pollen was still higher than Compositae pollen. The reversion of dominants can be seen in the Laguna Victoria core which represents a continuous section of 2·50 m reaching modern time.

At the bottom of this section, conditions are similar to the other old sediments analysed. Nevertheless, Compositae pollen increases steadily towards the top (although with oscillations) whereas grass pollen decreases (Text-fig. 2). What could be the cause of this reversion?

Geological studies do not indicate drastic changes during the last 2,500 years, such as glaciation and vulcanism. The climate seemed to be relatively warm, compared with conditions during the Mérida Glaciation, which ended about 13,000 years ago. Humidity is not low today even in the dryer parts of the mountains, and the Laguna Victoria section indicates that the lake was larger in the recent past. The answer must lie in other causes besides climate.

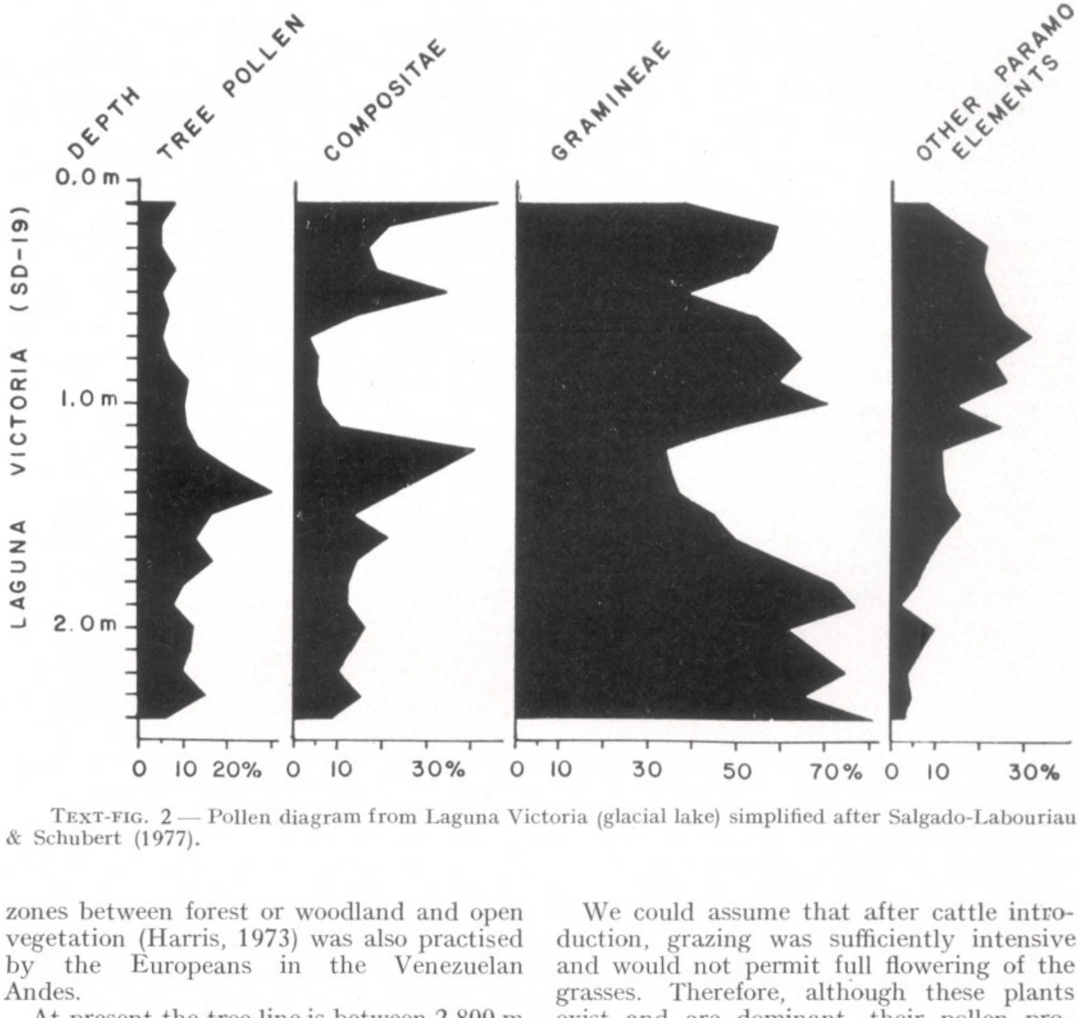
Although grass pollen has declined in modern times, Gramineae are today the dominant low stratum (Sarmiento *et al.*, 1971; Vareschi, 1970), covering most of the ground up to about 4,000 m elevation, where the desertic páramo starts. Therefore the plants are present in abundance although its representation in the pollen assemblages has declined.

It is known from archaeological data that the inhabitants of the Venezuelan Andes had no permanent settlements in the páramos before the arrival of the Europeans. They lived below the páramos, and visited the high lands occasionally for short periods of time. They had no type of livestock, but agriculture was present up to 3,000 m elevation, and specially between 2,000 and 800 m (Warner, in press). They probably never had a dense population in the A des. Shortly after the Spanish arrival, in 1570 A.D., European cattle was introduced in the Andes (Wagner, 1967), and it was maintained up to 4,000 m elevation. Intense agriculture began at this time resulting in the almost total destruction of the lower montane forest (which limits with the savannas of the Llanos), as well as the use of the flat lands at higher elevations. During the last four hundred years, coffee has been cultivated on the lower slopes, and potato and wheat in the transition zone between páramo and montane forest (Pl. 1, fig. 2). Cultivation of the transition

TABLE 1 — RANGE OF RELATIVE FREQUENCY OF COMPOSITAE AND GRAMINEAE POLLEN IN MODERN AND OLD ASSEMBLAGES

(in stratigraphic order, oldest at bottom)

Samples		Gramineae		Compositae	
		% of the Pollen Sum	% of the Total pollen	% of the Pollen Sum	% of the Total pollen
Modern pollen deposition		7·7-51·4	7·4-40·4	30·3-80·4	21·2-78·1
Victoria Laguna	5 uppermost levels	37·8-58·9	30·2-49·8	16·5-46·1	12·6-27·6
	5 lowest levels	61·2-81·7	49·6-75·5	8·7-15·8	8·1-13·2
La Culata terrace		41·0-64·0	24·0-43·3	4·5-37·0	2·2-30·2
Mucubaji terrace		43·1-92·4	41·7-91·0	2·3-22·0	2·1-20·7



TEXT-FIG. 2 — Pollen diagram from Laguna Victoria (glacial lake) simplified after Salgado-Labouriau & Schubert (1977).

zones between forest or woodland and open vegetation (Harris, 1973) was also practised by the Europeans in the Venezuelan Andes.

At present the tree line is between 2,800 m and 3,300 m, and is at its highest on steep slopes or in protected areas such as National Parks, where access is difficult. The recent introduction of several species of exotic *Pinus* and *Eucalyptus* trees above the forest belt in the Sierra Santo Domingo shows that the region is potentially able to support trees up to 3,400 m. Therefore, human occupation of the land has resulted in the lowering of the tree line, and the widening of the transition zone between páramo and forest.

Since decline in Gramineae pollen and increase in Compositae pollen were found only in the top layers of the páramo soil, it is possible that land use resulted in a change of the ecological equilibrium of the páramo vegetation.

We could assume that after cattle introduction, grazing was sufficiently intensive and would not permit full flowering of the grasses. Therefore, although these plants exist and are dominant, their pollen production is low. This would account for the grass pollen decline, and would be limited to the last 400 years.

Today Compositae are abundant up to the highest elevation (snow line, approx. 4,700 m). This shows that the high frequency of its pollen is due to the presence of a large number of individual plants. The low frequency in the past must be a reflection of plant scarcity at that time. At present I am studying the pollen morphology of the different genera in order to identify them in the sediments, and to determine which ones have increased lately. Nevertheless, the increase of Compositae plants at present must be correlated with land use, but the role of man is not clear. Have man and cattle somehow increased the seed dispersal? Could seedlings develop better into adult plants provided grasses are kept low to the ground by continuous browsing?

In the Venezuelan Andes the reversion of the pollen frequencies of Compositae and Gramineae was probably due to the introduction of cattle, and it seems that this also caused the present-day dominance of Compositae. The grass pollen decline in this case has no climatic meaning.

This reversion of dominant pollen types may indicate the presence of cattle disturbing the environment in the past in other regions. Unfortunately, it is difficult to verify in other author's diagrams whether such a reversion occurs because each author has his own ways of selecting the elements of the Pollen Sum. It is common that Compositae and/or Gramineae are excluded from it. We believe this hypothesis can be better tested in the Old World where cattle raising has existed for thousands of years. In Britain, it was shown that overgrazing of the grassland causes an increase of clover (Leguminosae, in Spedding, 1971). It is possible that in the tropics the equilibrium shifts towards the Compositae. If this proves to be correct, a method to detect the beginning of cattle raising can be developed.

Mankind is continually altering his environment, and we can never be entirely sure of the disturbances introduced in the past. With time and pollen we can learn how to detect them.

ACKNOWLEDGEMENT

I am grateful to C. Schubert, E. Warner, E. Medina and L. G. Labouriau for useful discussions and for critical reading of the manuscript.

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EXPLANATION OF PLATES

PLATE 1

1. Páramo de Mucubaji, Venezuelan Andes (ca. 3600 m elevation . Two terminal moraines can be seen in the valley; in the foreground, a lateral moraine covered by grasses and by *Espeletia* in flower.

2. Cultivated fields at ca. 3000 m elevation. In the foreground a walled area to husk the wheat.

PLATE 2

3. Tall rosettes of *Espeletia* on rocky bare soil of the desertic páramo (4300 m elevation).

4. Páramo de Piedras Blancas, Venezuelan Andes (4300 m elevation). Note the absence of grasses.

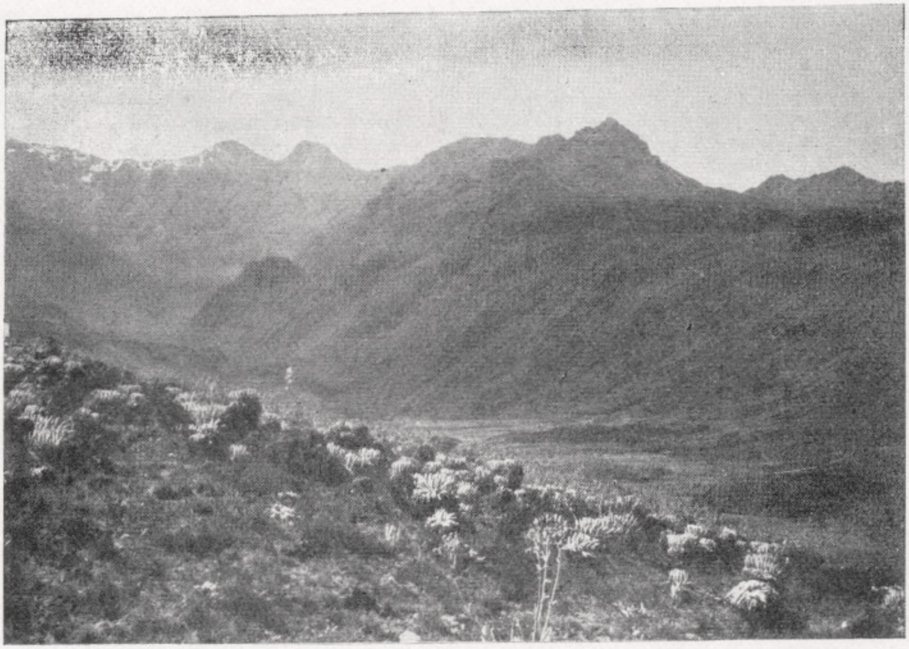

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PLATE 1

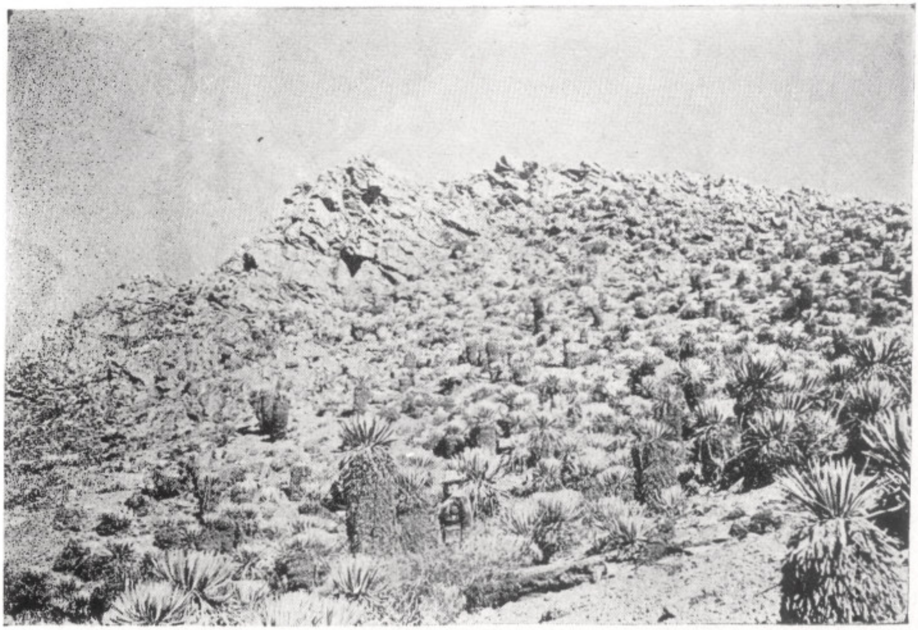

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PLATE 2