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An Historical Phytogeography of the High Andean Flora*

Fitogeografía histórica de la Flora Altoandina

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ABSTRACT

Palynological and geological evidence have shown that the Andes were uplifted to their present elevations only within the last 5 million years. Consequently, the floras of all of the high Andean habitats (those above treeline) must be very young and have ultimately been derived from older, lower elevation habitats. However, some low elements which colonized high elevation habitats subsequently underwent authochthonous radiations giving rise to endemic groups. This study examines the relative contributions of the 1) initial source pool, 2) habitat severity, and 3) *in situ* speciation to modern levels of species diversity within the major phytogeographical regions of the high Andes (páramo, puna, austral alpine).

It is suggested that initial floristic differences along the Andes were due to receipt of propagules from dissimilar regions and differential survival of immigrants. The Northern Andes received a more diverse array of colonizing elements than any of the other high elevation regions and at the same time provided a habitat that was conducive to establishment and persistence. Consequently, during the period of their formation, the northern Andes became increasingly diverse compared to montane regions farther south. Superimposed on these Tertiary factors were the effects of the Pleistocene climatic events which were of major importance in determining the level of autochthonous speciation. A combination of Tertiary and Pleistocene, ecological and geological factors are thus needed to explain the modern patterns of diversity seen throughout the high Andean habitats. Various phytogeographical classifications proposed for the Andes are compared to floristic regions expected on the basis of ecological and historical events.

Key words: Biogeography, Evolution of Andean Flora, Paleoclimates.

RESUMEN

Las evidencias palinológicas y geológicas han mostrado que los Andes se levantaron hasta sus altitudes actuales solamente a partir de los últimos 5 millones de años. En consecuencia, la flora de todos los hábitats altoandinos (aquellos por encima del límite arbóreo) debe ser muy joven y en última instancia habría derivado de los hábitats de menor altura. Sin embargo, algunos de los elementos que colonizaron los hábitats altoandinos experimentaron radiación autóctona, originando grupos endémicos. En este trabajo se examinan: 1) la fuente inicial de la biota, 2) el rigor del hábitat, y 3) la especiación *in situ* hasta los niveles modernos de la diversidad de especies dentro de las principales regiones fitogeográficas de los altos Andes (páramo, puna, austral-alpina).

Se sugiere que las diferencias florísticas iniciales a lo largo de los Andes se deben a la recepción de propágulos desde regiones distintas y sobrevivencia diferencial de los inmigrantes. Los Andes septentrionales recibieron una gama más diversa de colonizadores que cualquiera de las otras regiones altas, y al mismo tiempo proporcionaron hábitats más adecuados para el establecimiento y sobrevivencia. Consecuentemente, durante el período de su formación llegaron a ser mucho más diversos en comparación a las regiones montañosas más meridionales. En forma adicional a los factores terciarios, los efectos de los eventos climáticos pleistocénicos fueron de gran importancia en la determinación de los niveles de especiación autóctona. Por lo tanto, se requiere una combinación de factores terciarios y pleistocénicos, geológicos y ecológicos para explicar los patrones modernos de diversidad existentes actualmente en los hábitats altoandinos. Se comparan varias clasificaciones fitogeográficas propuestas para los Andes con las regiones florísticas esperadas sobre la base de eventos geológicos y ecológicos.

Palabras claves: Biogeografía, Evolución Flora Andina, Paleoclimas.

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INTRODUCTION

Phytogeography, the study of the geographical distributions of plants, can consist of static descriptions of species that occur in particular areas, or it can include an analysis of the development of vegetative patterns. Most phytogeographers have an insatiable desire to explain the evolution of modern floras, and it is the historical aspects of plant geography that interest me most. Consequently when asked to present an overview of the phytogeography of the Andes, I decided to trace the evolution of the modern vegetation types of the high (supraforest) regions.

Many contemporary ecologists (following MacArthur and Wilson 1967) are prone to state that the number of species in an area is determined by: the time available for colonization, the size of the area to be colonized, the biotic interactions between species, the number of potential colonizers, and the distance over which colonizers must travel. These factors are indeed of major importance in explaining diversity within communities, but any model that relies on these criteria alone, assumes that the areas under consideration are all within the same climatic zone, have the same diversity of habitats per unit area, and can all draw from the same pool of colonizers. Attempts to explain the diversity of organisms within a community by only these factors also assumes that the areas under consideration have been stable (climatically and edaphically) over the time spans involved. For the most part, these are unrealistic assumptions. During the time over which the Andes were colonized, conditions within the high elevation habitats were continually changing and constantly altering the pools of "potential" colonizers.

What I would like to do here, therefore, is present a dynamic picture of the development of the modern floras of the high Andes and show how and why the supraforest habitats of the Andes differentiated into the main types of vegetation we now see. For these reconstructions, I examine not only the effects of area and absolute time of availability for colonization, but also the effects of changing climate. By tracing their histories, we can see why different areas of the high Andes would necessarily develop certain vegetative structures and from what extra-Andean regions they ultimately drew the majority of their floras. In a sense, therefore, this kind of analysis allows predictions to be made about types of vegetation in, and the floristic affinities of, various regions of the Andes.

In tracing the history of the high Andean vegetation, I first examine the effects of geological, and consequently climatic, changes on the original, low elevation communities present at the beginning of the Tertiary. I then discuss why, during the course of the Cenozoic, these climatic changes caused the percentages of the floras derived from various source areas to change in predictable ways along the cordillera. Finally, I examine the effects of the Pleistocene in shaping the modern high Andean floras. I then assess various phytogeographical classifications previously proposed for the high Andes in light of the historical development of the vegetation.

THE EFFECTS OF UPLIFT

The geological events that resulted in the raising of the Andes to their present elevations did not happen instantaneously (even in geological time). Supra-forest habitats were not suddenly created and ready for colonization, even though it is easy to speak of them as if they were (Simpson 1975). Moreover, the rise of the Cordillera over the 65 odd million years from the end of the Cretaceous to the end of the Pliocene was correlated with a progressive generation of climatic zonality from the equator to the poles and of the development of intracontinental patterns of aridity.

Consequently, as the Andes rose, the effects of altitude were confounded by factors that produced a disparity in climatic conditions from north to south along the Andes and from low to high elevations within particular latitudes (Figs. 1, 2). Figure 3 schematically indicates the relative elevations of the north, central, and southern parts of western South America during the middle Eocene, the middle Miocene, and at the end of the Pliocene, and suggests the kinds of vegetation that would have been present in these regions at these times. The elevations suggested for all of the periods except the end of the Pliocene are speculative, but are suggested by fossil evidence from Patagonia (Patterson & Pascual 1972), Bolivia (Ahlfeld & Branisa

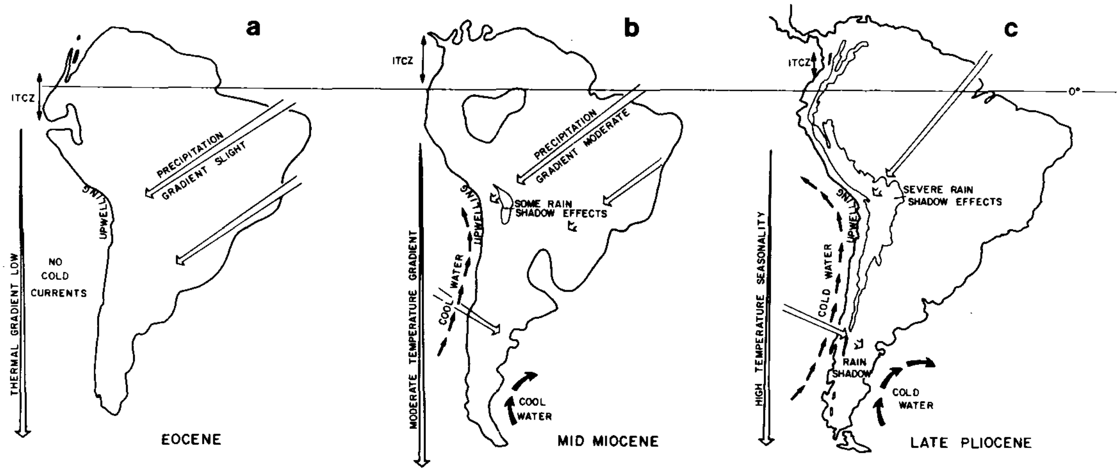

Fig. 1: Development of the latitudinal thermal gradient during the Tertiary. a) During the Eocene there was very little difference in temperatures between the equator and poles. The rotation of the earth did cause an upwelling on the western side of the continent that would have affected coastal regions. b) By mid-Miocene, there was ice in Antarctica and there was a definite equator to pole thermal gradient. The modern wind and current systems would have been more or less developed and the Andes were high enough to cause some rainshadow effects. c) By the end of the Pliocene, the modern climatic pattern of South America was established.

Desarrollo del gradiente latitudinal térmico durante el terciario. a) Durante el eoceno hubo una diferencia muy pequeña de temperaturas entre el ecuador y los polos. La rotación de la Tierra provocó corrientes ascendentes en el sector occidental del continente que habrían afectado las regiones litorales. b) En el mioceno medio, hubo hielo en la Antártica y un gradiente térmico definido desde el ecuador hacia los polos. Los sistemas de vientos y corrientes habrían estado más o menos desarrollados y los Andes alcanzaron una altitud suficiente como para condicionar algún efecto de "sombra de lluvias". c) Al término del plioceno se establecieron los patrones climáticos modernos de Sudamérica.

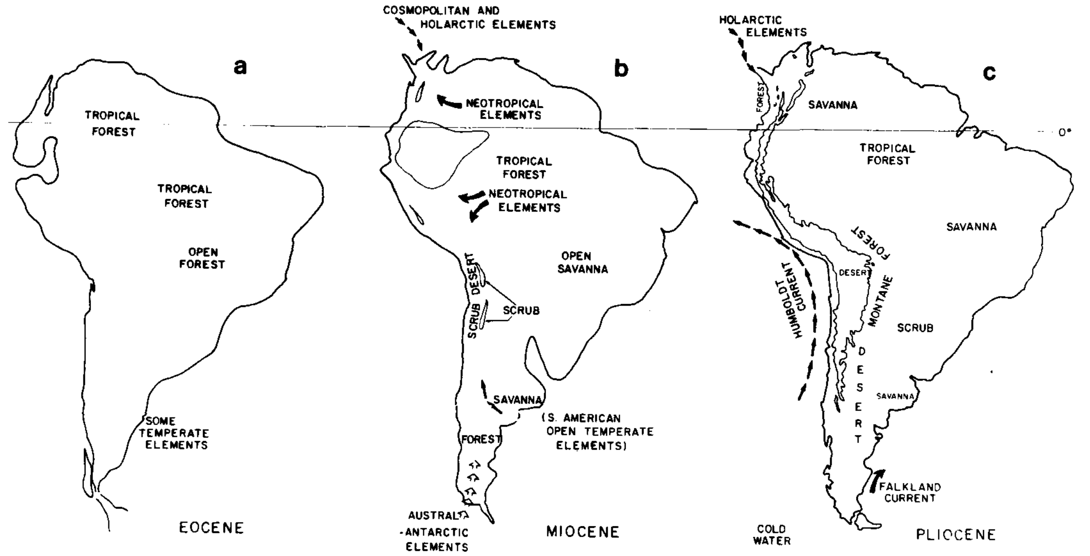

Fig. 2: Effects on the vegetation of the climatic developments of the Tertiary indicated in Fig. 1. a) Eocene. b) Mid-Miocene. c) End of the Pliocene. Also indicated are the various source areas of propagules that began to be important in the Miocene.

Efectos sobre la vegetación de los eventos climáticos del terciario señalados en la Fig. 1. a) Eoceno. b) Mioceno medio. c) Finales del plioceno. También se indican las diversas áreas de origen de propágulos que llegaron a ser importantes en el mioceno.

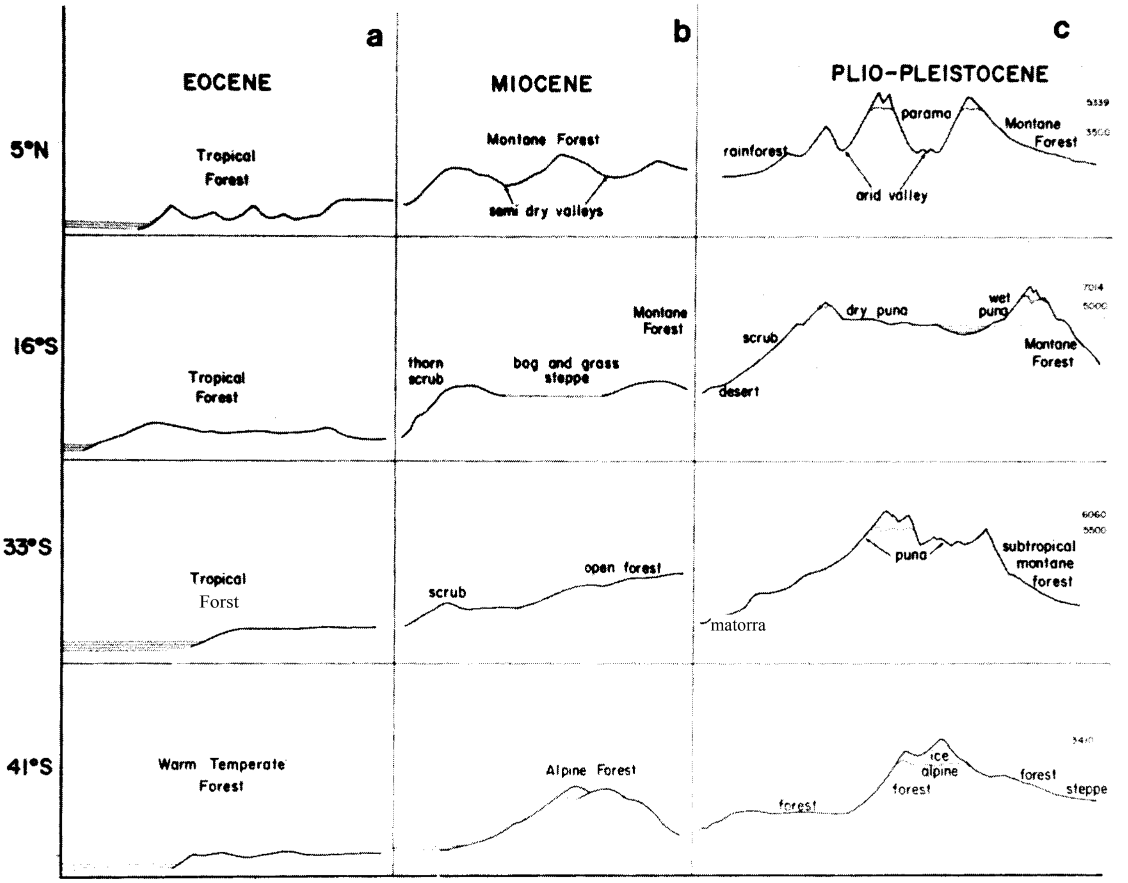

Fig. 3: Schematic cross-sections at various latitudes across the Andes showing possible elevations and vegetation types during the a) Eocene; b) mid-Miocene; c) end of the Pliocene.

Secciones transversales esquemáticas a varias latitudes a través de los Andes mostrando las posibles altitudes y tipos de vegetación durante el: a) eoceno; b) mioceno medio, y c) finales del plioceno.

1960) and Colombia (Van der Hammen 1974).

At the beginning of the Tertiary, fossil floras (Gerth 1941, Patterson and Pascual 1972, Archangelsky and Romero 1974, Báez and Gasparini 1979) indicate that there was some, but very little zonation across the latitudes spanned by South America even though the continent was in its present position. Most of the continent, at least most of the exposed western portions, appear to have been forested, with a slight gradation from tropical rainforest in equatorial latitudes to subtropical forest in the extreme south. In the Eocene, the first indications of temperate forest have been found (Archangelsky & Romero 1974). Oxygen isotope data from the Antarctic Ocean indicate cooling of the bottom water by mid-Eocene (Kennett 1977). This marine data correlates well with the Eocene appearance of *Nothofagus* in Patagonia (Archangelsky & Romero 1974) (Figs. 1-3). By the Oligocene, the surface waters of the Antarctic Ocean were cold and by the mid-Miocene, transient glaciations occurred on the Antarctic continent (Kennett 1977, Kerr 1982). Thus, by at least 14 million years ago, the modern thermal gradient between the equator and the poles was in place.

These changes would have had pronounced effects on the emerging Andes. Once the low to high latitude thermal gradient had been established, the modern system of heat balance (or a similar one) would have been created. The earth's pattern of heat balance, or latitudinal energy contrasts, combined with the rotation effects of the planet cause the modern wind and pressure systems. Consequently, the establishment of a thermal gradient not only dictated that the high latitudes would be colder than the low latitudes, but also that the high and low latitudes would be under different wind and pressure regimes. Most of the area of South America north of the Tropic of Capricorn came to lie within the influence of the trade winds and the area south of the Tropic within the westerly wind zone. Once this global circulation pattern developed, the Andes themselves began to play an increasingly important role in the climate of South America because the mountains created rainshadows to the lee side of the prevailing winds.

It is well known (Humboldt 1817, Troll 1959, Walter 1979) that mountains within a given biome have a sequence of altitudinal belts reflecting changes in vegetation. This change is caused, all other factors (e.g., total precipitation) being equal, by the decrease in temperature, increase in direct irradiation, and decrease in diffuse irradiation with elevation. The rate of temperature decrease with increasing elevation is called the lapse rate. The average lapse rate is considered to be about .65°C/100 m rise in elevation. However, in practice, the rate is often not linear and it can vary from place to place. For example, in the north central Andes of Peru and Ecuador, the lapse rate between sea level and 1000 m is about normal. From 1000 to 2500 m, the rate is only .32°C/100 m rise in elevation. Between 2500 and 4500 m elevation the decrease is relatively linear and approaches the average value of .65°C. Above this elevation, on clear nights, the rate can be as high as 1°C/100 m (Johnson 1976). Eventually an elevation is reached where the temperature decreases to 0°C. The actual altitude of this zero degree isotherm varies with latitude and with the season of the year. Likewise, there is an elevation above which temperatures never rise above 0°C. This constitutes permanent snow or frost line. Since the average annual temperature at the base of a mountain in high latitudes is much lower than that at the base of a tropical mountain, the elevations of the zero degree isotherms and permanent snowlines are much higher in the tropics than in high latitudes.

Reduction in plant growth expressed as reduction in productivity, has been shown to follow altitudinal decreases in temperature, although the decrease is not linear (Whittaker 1975, Whittaker and Marks 1975). The most conspicuous elevation at which productivity declines is treeline.

In temperate regions, treeline usually occurs at elevations at which the ground is permanently frozen below 20-30 cm because trees are not able to absorb enough moisture from the soil to sustain their large biomasses. When air temperatures reach 0°C, the xylem can be frozen with the result that water lost from exposed branches (or leaves) by inadvertent transpiration can not be replaced. If not reversed rapidly enough, death of the exposed plant parts occurs. The "hardening" of plants before the winter freezes in cold temperate regions serves to protect trees from this kind of damage, but at high enough elevations, conditions eventually become too severe even for hardened tissues to withstand the low temperatures if exposed. Plants that are low growing and protected under the snow cover avoid this sort of frost damage.

In high elevation tropical habitats, stress conditions leading to the reduction and finally elimination of plant growth are somewhat different. There is no temperature seasonality, but as elevations become higher and higher, there is a more and more pronounced diurnal fluctuation in temperatures (Hedberg 1964, Monasterio 1979) (Fig. 4). As elevations increase up to

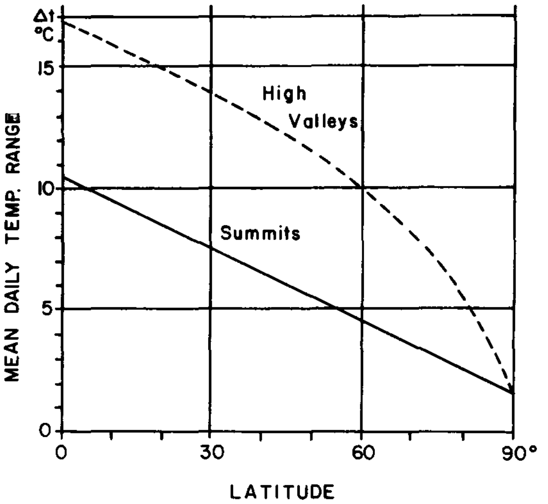

Fig. 4: The diurnal change in temperature plotted against latitude for several high elevation stations. (Redrawn from Barry 1979).

Cambios diurnos de las temperaturas graficadas en relación con la latitud para varias estaciones de alta-montaña. (Redibujadas de Barry 1979).

5200 m and above, the number of hours of freezing per day increases to the point at which the ground becomes permanently frozen and growth for rooted plants becomes impossible. Below this zone, there is often freezing at the soil surface, reducing the amount of water that can be absorbed. Mean night minima are normally about -10°C on the altiplano (Johnson 1976). Temperatures of 1 to 4°C are supposed to be lethal for tropical forest plants (Bielb 1965). In addition, above 2500-3000 m in tropical regions, rainfall decreases relative to lower elevations. It is not clear whether the limit of tree growth in high tropical regions is determined by aridity, the large number of hours during which freezing can occur, or both, but the fact that treeline in the tropics is higher in valleys than on ridges suggests that drought is the dominant factor. Although trees can not grow under such conditions, shrubs, grasses, and perennial herbs can grow well. Obviously, plants can not become dormant each day, but must still deal with the problem of nightly freezes. The most general solution to avoid the effects of short bouts of freezing temperatures is to insulate the living tissues (Hedberg 1964). If properly insulated against damage that could be caused during the few hours of freezing each night, and if sufficient soil moisture is present, "caulescent" herbs can grow in these habitats. Such plants constitute a vegetation stratum that is lacking in high elevation arid regions and alpine meadows and, as such, add to the diversity of tropical humid versus tropical dry or temperate high elevation habitats.

It has been shown that, across biomes, diversity varies predictably in the same way as productivity. Diversity decreases from the tropics to the poles and from the bases to the summits of mountains (cf., MacArthur 1972). The reasons for these patterns have been debated for years (Pianka 1966), but one argument (MacArthur 1969, Connell and Orias 1964) relates differences in diversity directly to differences in primary productivity. As conditions become so severe so as to permit the growth of fewer and fewer individuals, the maintenance of populations of sufficient size for reproduction becomes a problem. The species that dominate at environmental extremes are those that are able successfully to maintain effective breeding populations.

As the equator-pole gradient increased during the Tertiary and the Andes progressively rose, we would therefore expect that there was a gradual development of a gradient in productivity from low to high latitudes and from low to high elevations. Correlated with these trends in productivity, we would expect a progressive decrease in numbers of species in high latitudes and high elevations from that present in the same terrestrial localities in the Eocene. In effect, the development of global thermal zonality and increased elevations both had the same effect, the reduction in primary productivity and the elimination of species (reduction in diversity). Where these effects are strongest, as in the high vegetation zones of the southern Andes, reductions would have been most severe. By the time the latitudinal thermal gradient became a strong force in the mid-Miocene, the southern Andes would have been raised to elevations of at least 1500 m, sufficiently high for the development of an alpine type of vegetation (Fig. 3). The northern Andes would have also been raised to similar elevations, but the temperatures at low elevations would have been much higher than those at the southern end of the Andes. Following the lapse rate up the tropical Andes shows that elevations of 1500 m are too low for temperatures to decrease to the point at which trees can no longer grow. Evidence for the lack of supra-forest habitats before the end of the Pliocene (3-5 million years ago) in Colombia has been presented by Van der Hammen (summarized in Van der Hammen 1974). Van der Hammen's data suggest that the Eastern Cordillera of Colombia did not rise above 2000 m before the end of the Pliocene and, until that time, was covered with montane forest. Open habitats at elevations above 3500 m, became available and were colonized in Colombia only within the last 5 million years. In terms of time, therefore, the oldest kind of supra-forest habitat in the Andes is the austral-alpine. However, any advantage of being available for colonization at an earlier time than other Andean regions would have been negated by the extreme selection exerted by the combination of temperateness and high elevation.

The development of a tropics to pole thermal gradient was not the only climatic change that occurred during the Tertiary. For certain regions of the Andes, concomitant changes in precipitation were as important as increases in elevation for the historical development of the vegetation. Unlike temperature, the rainfall patterns developed were not correlated in a straightforward manner with latitude. Changes occurred not only in the total amount of precipitation that was received, but also in the dispersion of the precipitation over the year. The rainfall pattern developed by the end of the Tertiary showed a decrease in total precipitation from the northern Andes to the southern end of the altiplano and then a gradual increase in total annual precipitation toward southern Chile. In addition, a seasonality of rainfall developed from Colombia south to the same region. Within the Central Andes a gradient of precipitation from semi-arid to extremely arid developed from east to west across the altiplano (Figs. 1-3). The development of these patterns of rainfall was gradual over the first half of the Tertiary as latitudinal thermal gradient set into motion the major wind patterns we now see. The extremes of aridity that resulted in the western part of the central Andes was, however, a consequence of the final uplift of the Eastern Cordillera and probably did not exist in its present form until very late in the Pliocene. The aridity in this region is now so severe that it produces one of the driest deserts in the world.

As in the case of increased temperateness and the attainment of very high elevations, the formation of desertic conditions had the effects of reducing total productivity (Murphy 1975) and of reducing diversity by eliminating more and more of the species that had grown in the Andean regions when they were low, warm, and humid. Within the tropics there is a progression of vegetation types across aridity gradients. Forest gives way to grassland, grassland to scrub, and scrub to barren soil with no perennial biomass. In the high Andes, the first, forest, stage is not present, but the remainder of the sequence is followed with one notable difference in the last stages. Annuals never become as important in the extremely dry regions of high elevations as they are in low, equally dry, elevation deserts. Solifluction (freezing and thawing of the surface layers of the soil) strongly inhibits seedling establishment and makes the annual habit a precarious one.

While the central Andes probably did not become extremely dry until very late in the Tertiary, pockets of arid habitats developed relatively early in interandean valleys. These valleys formed a scattered network from the northernmost regions of Colombia to central Chile and Argentina. It is difficult to assign an absolute age to any of the interandean valleys, but some of them must have existed since Miocene times when the first major upthrusts of the most of the Andean units occurred. These valleys were undoubtedly of importance in providing migration routes for some of the taxa preadapted to arid conditions that eventually colonized the dry regions of the altiplano.

POTENTIAL COLONIZERS

We mentioned above that the number of species in an area (and, of course, the kinds of species) are dependent in part on the number of potential colonizers. Usually, all individuals of neighboring "source areas" are considered potential colonizers. The source areas of colonists for all of the high montane regions would originally have been the tropical and subtropical forests that covered them and which now abut most of the high tropical Andes. In a sense, these taxa would never have been colonists and any modern elements derived from them are actually natives rather than immigrants. As so often happens, however, in the onslaught of changing conditions, most of the original inhabitants were replaced by successful alien colonists. The most successful of these immigrants came from areas ecologically similar to the new kinds of habitats being created.

Some Neotropical elements did respond to the selection pressures exerted by altitude and/or aridity and became incorporated into the high elevation floras, but although selection over time can modify the tolerance limits of many species, whether or not such changes occur depends on the original amount of variation present in a species, the severity of the selection, the time span over which selection has to act, and competition from other taxa. In the case of the central, and to some extent the southern, high Andes, selection was strong, time was short, and the demands made of species adapted to life in the lowland humid tropics were beyond the limits of variation present in most of them. As conditions became more and more disparate from lowland tropical conditions, fewer and fewer species of the original lowland vegetation survived. The highest number survived in those high elevation habitats most similar to their lowland counterparts and fewest survived in the vastly different high elevation arid and temperate habitats. Consequently, we expect the fewest Neotropical elements in the high arid habitats and the supra forest habitats of the austral regions, and the most in the high elevation humid tropical habitats.

As the mountains rose and conditions changed, other sources of colonists besides the lowland or montane forests became increasingly important (Fig. 2). Among these were open habitats in various parts of the Neotropics and the interandean dry regions, both of which provided taxa pre-adapted to arid or semi-arid conditions. While the Patagonian flora is often considered to be a "source" area for Andean elements, it is equally probable that Patagonia was colonized by taxa that had become adapted to open, cold environments in the Andes. North America likewise provided a source of taxa pre-adapted to cool conditions because of its well developed non-forest temperate biota.

Colonization by Nearctic species probably occurred gradually from the mid Miocene onward. The final closing of the Panama gap per se about 3.5 million years ago would actually have had little effect on the colonization rate of the supraforest habitats of the Andes since the uplift of the lowland connection between Colombia and Panama would not have changed the distance between montane peaks. The fact that most of the colonization of the high Andes occurred after the middle of the Pliocene is due to the final raising of these habitats at that time, not the production of a continuous lowland connection between Panama and Colombia. Relative to North America or Eurasia, South America did not develop a sizable non-forest temperate flora because the continent lacks a large temperate land mass. There were, of course, some native austral herbaceous elements and many of these would have served as the original colonizers of the southern Andes when they rose to heights above which trees could survive. Nevertheless, it is likely that many of the propagules that successfully colonized the southern open, high elevation habitats would have arrived via long distance dispersal and would have belonged to groups that ultimately became cosmopolitan because of their colonization abilities.

Since, in general, we expect the number of propagules received to be inversely related to distance, it seems clear that the northern Andes would have received more propagules from North America than any other Andean region. Yet, if we could make predictions as to the relative contributions of the various sources of species that populated in the high elevation habitats by the end of the Tertiary, we might predict that the northern high Andes would have the largest absolute number of taxa derived from North American stocks, but it terms of percentages of the floras of various regions, Holarctic taxa might constitute higher percentages of the central and southern Andean floras than of the northern regions. Likewise, weedy cosmopolitan elements would probably constitute greater percentages of the floras of the Central Andes than of the northern Andes. In the southermost Andes, we also expect a high percentage of cosmopolitan elements, austral elements and, although distances from North America are great, a significant proportion of widespread temperate elements that colonized via North America.

EFFECTS OF THE PLEISTOCENE

By the end of the Pliocene, we would expect that the northern Andes would have had the richest floras of any of the high elevation habitats and would have contained a high percentage of Neotropical elements. During the Pleistocene, the differences between the floras of the northern, central, and southern Andes were magnified. This intensification of patterns already laid down by the end of the Tertiary was caused by the promotion of speciation within the high elevation zones of the northern Andes and the further reduction of species diversity in the extreme south. In the central Andes, the Pleistocene was a time of differentiation of some taxa, but the effects were not as pronounced as in the north.

In the Colombian Andes, Van der Hammen (1974 and references therein) has shown that by the beginning of the Pleistocene, a flora similar to the modern high elevation flora existed. During the Pleistocene his studies have documented the occurrence of several glacial advances that lowered snow and vegetation lines about 2000 m. Overlapping with these periods of cold were periods alternately more, then less, humid than modern times. The combined effects of the various climatic oscillations would have been expansions of ranges of almost all of the kinds of plants present in the high northern Andes. Van der Hammen's pollen profiles (Van der Hammen 1974) clearly show that at some times, *Polylepis* greatly expanded its range and at other times the areas dominated by grasses increased in size. This multiple and varied set of opportunities for expansion followed inevitably by restrictions would have provided perfect conditions for speciation. Some groups such as *Espeletia, Diplostephium,* and *Loricaria* emerged from the Pleistocene as speciose groups with almost all of their species endemic to the high elevations of the northern Andes. This same pattern, but to a lesser extent, would have affected the mountain tops of the Ecuadorian and northern Peruvian Andes.

The Central Andes would have been affected somewhat differently. First, the altiplano is a large expanse of high elevation habitat. There are not a series of isolated "islands" of habitat in this region. Consequently, species distributions are usually determined by climatic, rather than geographical factors. During the Pleistocene, ranges across the altiplano were undoubtedly also modified (Simpson 1975, 1979) and some elements that now have restricted ranges would have experienced times of conditions favorable for range expansion. On the other hand, even at times when conditions were most different from now, when lakes dissected the altiplano, and glaciers wiped out populations and severed connections between populations to the north and south of Lake Titicaca, there would never have been the kind of isolation that now exists (and existed during previous interglacials) in the northern Andes. Consequently, differentiation was not as common, nor in most cases, as complete as, that in the northern Andes. Some authochtonous speciation would have occurred, but not on the scale of that to the north.

In the southernmost Andes, supraforest habitats are distributed along the edges of the large glaciers in the extreme south and atop peaks to the north of the ice fields. Consequently, these habitats are distributed in part in an island-like fashion similar to the northern high elevation habitats (Fig. 5). As in the northern Andes,

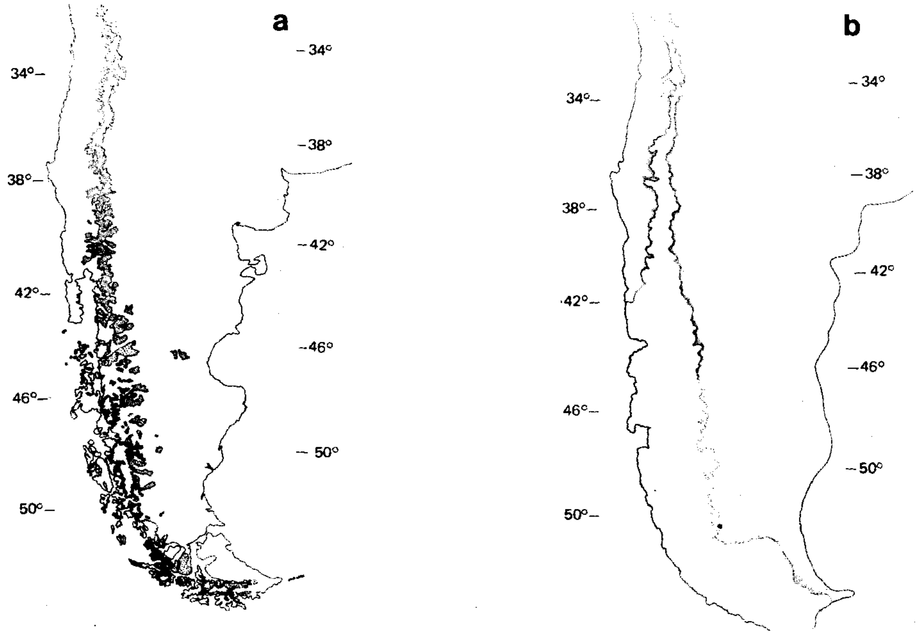

Fig. 5: The distribution of Austral-alpine (stippled) habitats at the present time (a) and during the maximum glaciation (b) in southern South America.

Distribución de los hábitats austral-alpinos (punteados) en la actualidad (a) y durante la máxima glaciación (b) en el sur de Sudamérica.

Pleistocene glacial events lowered snow and vegetation zones and hence expansion latitudinal, and longitudinally of high elevation zones. The extent to which this occurred, however, differed greatly from that in the northern Andes. In southernmost South America, glaciations effectively wiped out all of the alpine habitats south of 44°S. Alpine elements could have existed north of Chiloe Island, along the base of the Andes in Argentina and at lowered elevations between the latitudes of 32° and 42° in south-central Chile (Fig. 5). While there is some evidence that suggests vegetation zones moved north in Chile, the movement was not great and when climatic conditions changed, islands of alpine habitat were not left behind. The effect of the habitat changes would have been extinction and the promotion of some differentiation, but not an extreme proliferation of species.

PHYTOGEOGRAPHICAL CLASSIFICATIONS OF THE HIGH ANDES

The previous analysis would lead us to believe that different types of vegetation developed in the northern, central, and southern Andes. That this did, in fact, happen is reflected in the common recognition of three major high Andean phytogeographical units, the Páramo, Puna, and Austral-alpine. Still, various authors have classified the vegetation in different ways.

Perhaps the most generalized phytogeographical scheme proposed for the high Andean flora is that of Cabrera and Willink (1973) (Fig. 6). These authors have placed the high Andean vegetation within a larger unit they call the Andean-Patagonian Dominion which includes all the high elevation vegetation types from Venezue-

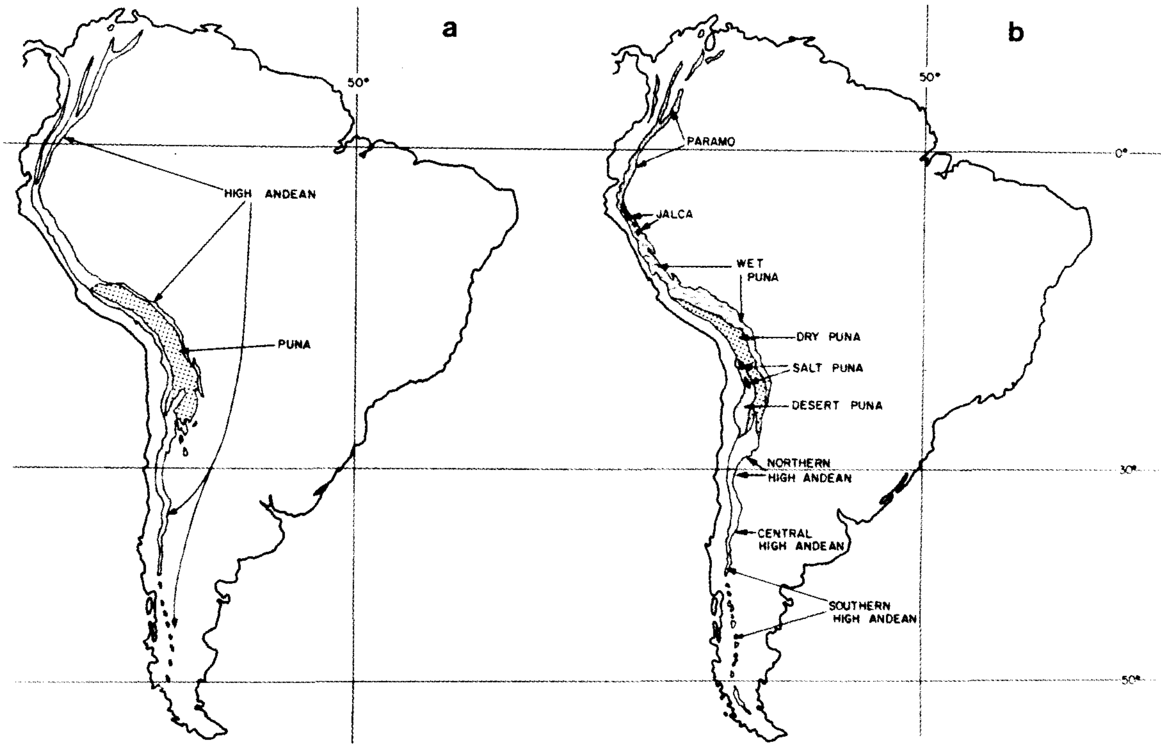

Fig. 6: Phytogeographical schemes proposed for the high Andean vegetation. a) The most generalized scheme proposed by Cabrera and Willink (1973). b) A composite scheme combining studies of Weberbauer (1945), Cabrera (1951, 1968), Troll (1959), Van der Hammen (1974), Simpson (1975).

Esquemas fitogeográficos propuestos para la vegetación altoandina. a) El esquema más usual propuesto por Cabrera y Willink (1973). b) Un esquema compuesto combinando estudios de Weberbauer (1945), Cabrera (1951, 1968), Troll (1959), Van der Hammen (1974), Simpson (1975).

la to Tierra del Fuego, the coastal deserts of Perú and Chile, and the Patagonian steppes of Neuquén, western Rio Negro, Chubut, and Santa Cruz in Argentina. Within this dominion, they circumscribed a High Andean Province extending across all the high elevations of Venezuela, Colombia, and Ecuador, the eastern and western edges of the altiplano and all of the supra-forest habitats south of the altiplano to the tip of the continent. They also delineated a second province, the Puna Province which included the central portions of the altiplano. Physiognomically this scheme has some merit because it lumps all of the grass-perennial forb associations and separates out the arid shrub-dominated types of vegetation. Yet, Sarmiento (1975) has shown that parts of the Puna (the "high Andean desert" of Sarmiento) has a higher floristic similarity with Patagonia than with the Puna proper. Likewise, Cleef (1979) has shown that almost half of the Páramo flora is derived from local tropical taxa and that almost half of these are monotypic genera. Floristically, therefore, the Puna of Cabrera and Willink (1974) seems to be composed of more than one natural vegetation type and the Páramos appear distinct from the other grass-dominated high Andean vegetation types.

Hueck and Siebert (1972) divided the high altitude vegetation of the Andes into Páramo, Puna, Salar vegetation, and "High-Andean Vegetation without Major Classification". They used the term Páramo to refer to areas in which *Espeletia* grows. The "unsubdivided" high elevation vegetation included everything else from Venezuela to Tierra del Fuego that was not Puna (altiplano scrub) or Salar vegetation. While this scheme does recognize the Páramo vegetation as distinct, it is hard to understand the existence of a high-Andean non-Páramo type of vegetation in Colombia and Venezuela. Species that Hueck and Siebert (1972) listed as characteristic of this kind of vegetation are all either widespread taxa or groups restricted to the central Andes.

Many other authors (cf. Walter 1971) have followed Troll (1959) and divided the tropical Andes into Paramo and Puna, but subdivided the Puna into Wet Puna, Dry or Thorn Puna and Salt Puna. The Wet Puna included all of the grass and forb dominated parts of the high central Andes and the Thorn or Dry Puna the high elevation vegetation types dominated by shrubs. Troll (1959) based his divisions on climate and the structure of the vegetation. He differentiated Páramo from Puna on the basis of the presence of a pronounced dry season in the latter with the transition occurring in northern Peru. Across the Puna from northeast to southwest there is an increase in the length of the dry season. Although the reduction in precipitation and increase in seasonality is gradual across this expanse, there are areas where the structure of the vegetation and the floristic composition undergoes a noticeable change. The break between a predominantly grass steppe to an open shrubland constitutes the boundary between Troll's Wet and Dry Puna. Cabrera later (1968) further divided the Dry Puna of Troll into Wet Puna, Dry Puna, and Desert Puna (Fig. 6). Vegetation that falls under Troll's classification of Salt Puna is scattered about the western altiplano in saline areas. Salt Puna is therefore an edaphically, and not a climatically, determined vegetation type.

It is unfortunate that Troll did not travel in the southern Andes because the high elevation flora there has been little studied as a unit compared to the Páramo or Puna. Most workers are content simply to call everything south of the Puna, "high Andean vegetation". The few attempts to subdivide the vegetation phytogeographically have been done on a limited scale.

There are numerous other phytogeographical schemes portions of the high Andean vegetation but these finer subdivisions have usually been made by workers within particular countries or for a region of a country with little attempt to relate their schemes to those proposed for the same kind of vegetation in a contiguous country. In the Páramos, for example, Cuatrecasas early (1958) subdivided the Colombian vegetation above treeline into altitudinal zones which he designated SubPáramo, Páramo proper, and SuperPáramo. These distinctions have been followed by recent workers in Colombia (cf. Van der Hammen 1974, Cleef 1978). In Venezuela a different set of vertical belts was worked out by Vareschi (1970) and still a third by Monasterio (1980).

In Ecuador, perhaps because of the lack of in depth studies, there has been little controversy about the name for the vegetation of the high elevations and few attempts have been made to subdivide it. The term Páramo is applied without problems by botanists and local inhabitants alike to all of the vegetation above treeline with the exception of isolated "bosques de quinoales" *(Polylepis)* that appear in scattered localities. In Peru, Weberbauer (1945) used the term Jalca for the southern extension of the Páramo, but he clearly indicated that he considered it Páramo and stated that it differed from the Puna to the south because it received a larger amount of precipitation and a greater proportion of the precipitation in the form of sleet than the Puna. The southern limit of the Páramo he indicated was at 8° 30' S latitude in the region west of the Marañon Valley.

South of 8-9° S in Peru, the Puna begins. Weberbauer did not subdivide the Peruvian Puna into smaller vegetation units either altitudinally or latitudinally and he thus did not distinguish between the kind of vegetation south of the Jalca but north of 13°S and the vegetation of the Peruvian altiplano. He considered that the floristic relationships of the Puna vegetation were with the western slopes of the Andes and the interandean valleys. *Pernettya* (Ericaceae) is one of the few dominant Puna elements that is clearly derived from the eastern side of the Andes. In Bolivia and northern Argentina, the area covered by Puna vegetation is greatly expanded longitudinally and is thus affected by the precipitation gradients that lead to the physiognomic and floristic associations recognized by Troll (1959). Floristically as one goes west across the altiplano, the Neotropical-derived taxa drop out and the floras correspondingly have a greater and greater portion of their species belonging to widespread temperate or cosmopolitan groups.

South of the Puna, the high elevation vegetation has been divided differently by botanists depending upon whether they were working on the Chilean or the Argentina side of the Andes. Schmithüsen (1956) delineated a Northern Andean Formation that extended from the northern limit of Chile to 39° S and, south of this, a Southern High Andean Region. The northern part was characterized by having only three "favorable" months for plant growth. In the southern area, there were nine "favorable" months. Cabrera (1951) placed the Argentine high Andean flora, other than the Puna, into the Altoandean vegetation province, but he subdivided this into a northern, central and southern component. The northern extended from Jujuy to La Rioja (22-29° S), the central from the southern part of San Juan across Mendoza to the northern part of Neuquén (30° to about 38° S), and the southern from southern Neuquén across the western part of Rio Negro, Chubut, Santa Cruz and Tierra del Fuego. It appears to me that the flora of the Andes south of the altiplano consists of a gradual transition from dry Puna vegetation to austral alpine vegetation in much the same way as the high mountains of southern Ecuador and northern Peru form a bridge between the Páramo and the Puna.

CONCLUSIONS

How one determines phytogeographic regions is a matter, to some degree, of personal preference. Some authors rely exclusively on physiognomy as the basis for their division. Others use floristic analyses to ascertain relatively coherent groups of species but the Andes as a whole are not well enough known floristically to permit rigorous phytosociological analyses although such techniques have been used by several workers in restricted regions (Oberdorfer 1960, Monasterio 1980, Villagrán 1980). In general the phytogeographical divisions of the Andes have therefore been primarily based on the presence or absence of certain "key" taxa such as *Espeletia.* An examination of the climates of the mountainous regions of western South America shows that these physiographic units are correlated with the major climatic provinces. An understanding of the historical development of these climatic provinces allows us to understand why and when the major types of Andean vegetation developed and to predict what future studies will show about the floristic affinities of different parts of the high Andes.

It is impossible to test these tentative predictions with any rigor, but a few suggestive studies have been made. The first of these by Cleef (1979) is the only in depth study. Cleef systematically collected over a large number of the colombian Páramos and examined the taxa in the light of their ancestral derivations. Even though he sampled only a portion of the total area covered by Páramo vegetation, he collected 259 genera, indicating a very high diversity. His studies of these genera indicated that almost half (41%) of the genera were derived from tropical elements growing in adjacent regions. Another 10.4% are related to groups distributed widely throughout the tropics. Eleven percent of the genera apparently colonized from North America (the Holarctic element), 19.6% belonged to widespread temperate groups, and 7.7% are cosmopolitan. Most of these probably also arrived from North America. A small, but significant, proportion (9.2%) of the flora is apparently of austral origin.

There are really no other data sets comparable to that of Cleef. Weberbauer (1945) lists plants "characteristic of the Puna", or "plants with their greatest development in the Puna", but it is impossible to ascertain the completeness of the lists. Herzog (1923) enumerates plants of microhabitats at several localities in northern Bolivia, but the brevity of the lists suggests that they contain only the most common species. Two other studies farther south in the Andes contain plants lists that provide a suggestion of what more extensive work in the future might show.

The first, a study of the vegetation of thé cordillera of La Rioja, Argentina, by Hunziker (1952) contains an extensive list of the plants collected over a wide area of the mountains of La Rioja. Hunziker also indicated which species grew at high elevations (Dry Puna). While this study is much less extensive than that of Cleef, the presence of only 38 genera in Hunziker‘s collections from the southern Dry Puna habitats suggests a much lower diversity than in the north. An analysis of these genera shows that 47% are South American and without exception restricted to the Andes or south temperate regions. The tropical elements so prominent in the north are completely lacking. Twenty-two percent of the genera in the high habitats sampled by Hunziker are cosmopolitan and 31% of widespread distribution in temperate regions. There are no genera of definite austral origin.

The second study by Thomasson (1959) is a survey of the high alpine vegetation near Lago Nahuel Huapi in Neuquén, Argentina. Thomasson's lists appear to include most of the species in the area and indicate that about 49 genera are the normal number for a island of Austral-alpine habitat. The diversity is again much lower than in the north, although in this case, only one of the many areas of such vegetation was sampled. In terms of the relationships of these genera, 27% are of South American origin (over one-third are "Andean"), 22% belong to cosmopolitan groups, 27% belong to widespread, primarily temperate groups, and 24% are of austral origin. This flora thus appears to be more similar in the origin of its flora to the Páramos than to the geographically closer Puna. Undoubtedly, this similarity is due to the comparable effective precipitations in the two regions.

It is thus clear that the floras of the various regions of the high Andes have been drawn from different source areas and that the relative importance of these source areas depends on the distance from the source to some extent, but primarily to the degree of ecological similarity of the source area and the area under consideration.

LITERATURE CITED

AHLFELD F & L BRANISA (1960) Geología de Bolivia. Instituto Boliviano del Petróleo. La Paz.

ARCHANGELSKY S & E ROMERO (1974) Los registros más antiguos del polen de *Nothofagus* (Fagaceae) de Patagonia (Argentina y Chile). Boletín de la Sociedad Botánica de México 33: 13-30.

BAEZ AM & ZB DE GASPARINI (1979) The South American herpetofauna: An evaluation of the fossil record. In: Duellman WE (ed) The South American Herpetofauna: Its Origin, Evolution and Dispersal. Museum of Natural History, University of Kansas, Lawrence, Kansas: 29-54.

BARRY RG (1969) High altitude climates. In: PJ Webber (ed) High Altitude Geoecology. Westview Press. Boulder: 55-74.

BLIEB R 1965. Temperaturresistenz tropischer Pflanzen auf Puerto Rico. Protoplasma 59: 133-156.

CABRERA AL (1951) Territorios fitogeográficos de la República Argentina. Boletín de la Sociedad Argentina de Botánica 4: 21-65.

CABRERA AL (1968) Ecología vegetal de la Puna. In: C. Troll (ed) Geo-ecology of the Mountainous Regions of the Tropical Americas. Colloquium Geographicum. Geographisches Institut der Universität Bonn 9: 91-116.

CABRERA AL & A WILLINK (1973) Biogeografía de América Latina O.E.A. Washington, D.C.

CLEEF AM (1978) Characteristics of Neotropical Páramo vegetation and its subantarctic relations. In: Troll C & W Lauer (eds) Geological Relations Between the Southern Temperate Zone and the Tropical Mountains. Erdwissenschaftliche Forschung 11: 365-390.

CLEEF AM (1979) The phytogeographical position of the Neotropical vascular Páramo flora with special reference to the Colombian Cordillera Oriental. In: Larsen K and LB Holm-Nielsen (eds) Tropical Botany. Academic Press. New York: 175-184.

CONNELL JH & E ORIAS (1964) The ecological regulation of species diversity. American Naturalist 28: 399-414.

CUATRECASAS J (1958) Aspectos de la vegetación natural de Colombia. Revista de la Academia Colombiana de Ciencias Exactas, Físico-Químicas y Naturales 10: 221-268.

GERTH H (1941) Die Tertiarfloren des südlichen Südamerika und die angebliche Verlagerung des Südpols während dieser Periode. Geologische Rundschau 32: 321-336.

HAMMEN T VAN DER (1974) The Pleistocene changes of vegetation and climate in tropical South America. Journal of Biogeography 1: 3-26.

HEDBERG O (1964) Features of Afroalpine plant ecology. Acta Phytogeographica Suecia 49: 1-144.

HERZOG T (1923) Die Pflanzenwelt der bolivianischen Anden und ihres östlichen Vorlandes. Engelmann. Leipzig.

HUECK K & P SEIBERT (1972) Vegetationskarte von Südamerika. Fischer. Stuttgart.

HUMBOLDT A VON (1817) De Distributione Geographica Plantarum secundun colli temperiem et altitudiem montium. Prolegomena. Paris. (fide Troll 1959).

HUNZIKER JH (1952). Las comunidades de la cordillera de La Rioja. Revista de Investigaciones Agrícolas 6: 167-196.

JOHNSON AM 1976. The climate of Perú, Bolivia and Ecuador. In: Schwerdtfeger W (ed) Climates of Central and South America. Elsevier. New York: 147-218.

KENNETT JP (1977) Cenozoic evolution of Antarctic glaciation, the circum-Antarctic Ocean, and their impact on global paleoceanography. Journal of Geophysical Research 82: 3843–3860.

KERR RA (1982) New evidence fuels Antarctic ice debate. Science 216: 973-974.

LIETH H (1975) Some prospects beyond production management. In: Lieth H and RH Whitakker (eds) Primary Productivity of the Biosphere. Springer. New York: 285-304.

MACARTHUR RH (1969) Patterns of communities in the tropics. Biological Journal of the Linnaean Society (Lond.) 1: 19-30.

MACARTHUR RH (1972) Geographical Ecology. Patterns in the Distribution of Species. Harper and Row. New York.

MAC ARTHUR RH & EO WILSON 1967 The Theory of Island Biogeography. Princeton University Press. Princeton.

MONASTERIO M (1979) El Páramo desértico en el Altiandino de Venezuela. In: Salgado-Labouriau M (ed) El Medio Ambiente Páramo. Mérida: 117-146.

MONASTERIO M (1980) Las formaciones vegetales de los Páramos de Venezuela. In: Monasterio M (ed) Estudios Ecológicos en los Páramos Andinos. Universidad de los Andes. Merida: 93-158.

MURPHY PG 1975 Net primary productivity in tropical terrestrial ecosystems. In: Lieth H and RH Whittaker (eds) Primary Productivity of the Biosphere. Springer. New York: 217-231.

OBERDORFER E (1960) Pflanzensoziologische Studien in Chile. Weinheim.

PATTERSON B & R PASCUAL (1972) The fossil mammal fauna of South America. In: Keast A, FC Erk & B Glass (eds) Evolution, Mammals, and Southern Continents. State University of New York, Albany: 247-309.

PIANKA ER (1966) Latitudinal gradients in species diversity: a review of concepts. American Naturalist 100: 33-46.

SARMIENTO G (1975) The dry plant formations of South America and their floristic connections. Journal of Biogeography 2: 233-251.

SCHMITHÜSEN J (1956) Die räumliche Ordnung der chilenischen Vegetation. Bonner Geographische Abhandlungen 17: 1-86.

SIMPSON BB (1975) Pleistocene changes in the flora of the high tropical Andes. Paleobiology 1: 273-294.

SIMPSON BB (1979) Quaternary biogeography of the high montane regions of South America. In: Duellman WE (ed) The South American Herpetofauna: Its Origin, Evolution, and Dispersal. Museum of Natural History. University of Kansas. Lawrence, Kansas: 157-188.

SMITH JMB (1982) On the origins of the tropicalpine flora. In: Gressitt JL (ed) Biogeography and Ecology of New Guinea. Junk. Boston: 287-308.

THOMASSON K (1959) Nahuel Huapi. Plankton of some lakes in an Argentine National Park with notes on terrestrial vegetation. Acta phytogeographica suecia 42: 1-83.

TROLL C (1959) Die tropische Gebirge. Bonner Geographische Abhandlungen 25: 1-93.

VARESCHI V (1970) Flora de los Páramos de Venezuela. Universidad de Los Andes. Mérida.

VILLAGRAN C (1980) Vegetationsgeschichtliche und pflanzensoziologische Untersuchungen im Vicente Pérez Rosales National Park (Chile). Dissertationes Botanicae 54. Cramer.

WALTER H (1971) Ecology of Tropical and Subtropical Vegetation (trans. by D. Mueller-Dombois) Van Nostrand Reinhold. New York.

WALTER H (1979) Vegetation of the Earth and Ecological Systems of the Geo-biosphere. (ed. 2) Springer-Verlag. New York.

WEBERBAUER A (1945) El Mundo Vegetal de Los Andes Peruanos. Ministerio de Agricultura. Lima.

WHITTAKER RH (1975) Communities and Ecosystems (ed. 2) MacMillan. New York.

WHITTAKER RH & PL MARKS (1975) Methods of assessing terrestrial productivity. In: Leith H & RH Whittaker (eds) Primary Productivity of the Biosphere. Springer. New York: 55-118.