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THE PHYTOGEOGRAPHY AND ECOLOGY OF THE COASTAL ATACAMA AND PERUVIAN DESERTS[1]

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ABSTRACT

The Atacama and Peruvian Deserts form a continuous belt for more than 3500 km along the western escarpment of the Andes from northern Peru to northernmost Chile. These arid environments are due to a climatic regime dominated by the cool, north-flowing Humboldt (Peruvian) Current. Atmospheric conditions influenced by a stable, subtropical anticyclone result in a mild, uniform coastal climate nearly devoid of rain, but with the regular formation of thick stratus clouds below 1000 m during the winter months. Where coastal topography is low and flat, the clouds dissipate inward over broad areas with little biological impact. However, where isolated mountains or steep coastal slopes intercept the clouds, a fog-zone develops. This moisture allows the development of plant communities termed *lomas* formations. These floristic assemblages function as islands separated by hyperarid habitat devoid of plant life. Since growth is dependent upon available moisture, an understanding of climatic patterns is essential in efforts to interpret present-day plant distributions. Topography and substrate combine to influence patterns of moisture availability. The ecological requirements and tolerances of individual species ultimately determines community composition. Species endemism exceeds 40% and suggests that the lomas formations have evolved in isolation from their nearest geographic neighbors in the Andes. While the arid environment is continuous, there appears to be a significant barrier to dispersal between 18° and 22°S latitude in extreme northern Chile. Less than 7% of a total flora, estimated at nearly 1000 species, occur on both sides of this region. Viable hypotheses concerning the age and origins of these desert floras will require continued study of the ecology and biogeography of their component species.

INTRODUCTION

The Atacama and Peruvian Deserts form a continuous belt from La Serena (29°55′S) in north-central Chile northward for more than 3500 km to the Peru/Ecuador border (5°00′S) (Fig. 1). Modern scientific investigation of these areas began with the monumental floristic works of Philippi (1860) in Chile and Weberbauer (1911) in Peru, but our knowledge of the flora and geography of these remarkable coastal deserts has progressed slowly.

These deserts owe their severe aridity to a climatic regime dominated by a constant temperature inversion generated, in large part, by the cool, north-flowing Humboldt (Peruvian) Current. Also important is the influence of strong atmospheric subsidence associated with a positionally stable, subtropical anticyclone (Trewartha 1961). The result is a mild, uniform coastal climate with the regular formation of thick stratus cloud banks below 1000 m during the winter months. Where coastal topography is low and flat, this stratus layer dissipates inward over broad areas with little biological impact. However, where steep coastal slopes are present, this stratus layer forms a fog-zone concentrated against the hillsides (Fig. 2A, B). These fogs, termed the *camanchaca* in Chile and the *garúa* in Peru, are the key to the extent and diversity of vegetation in the Atacama and Peruvian Deserts. Their moisture allows the development of fog-zone plant communities termed *lomas* formations, which literally means small hills in Spanish. Other authors have referred to these communities as the “fertile belt” (Johnston 1929), “fog oases” (Ellenberg 1959) or “meadows on the desert” (Goodspeed 1961).

Since much of the available data on the climate, geography and vegetation structure of the coastal Atacama and Peruvian Deserts are highly scattered and uneven in coverage, there has long been a need to provide a modern synthesis for this region. Topics covered here include discussions of (1) the climate of the region and its influence upon the overall ecology, (2) the geomorphology and floristic community structure of each desert, and (3) speculation on the age and origins the modern-day flora.

COASTAL DESERT CLIMATE IN WESTERN SOUTH AMERICA

Three particularly notable climatic anomalies are present in the Atacama and Peruvian Deserts (Trewartha 1961). First, extremely arid conditions exist for an extended latitudinal distance (ca. 3500 km) with relatively abrupt climatic transitions both to the north and south. As a result, a steppe climate is poorly developed along these margins. Second, brief periods of heavy rainfall and relatively high temperatures occasionally affect the northern parts of the desert, bringing wet tropical conditions. These periods are associated with rare, but recurrent, El Niño events. Lastly, there is remarkable temperature homogeneity along the entire latitudinal extent of the deserts. This pattern of temperature stability results from the influence of cool, sea-surface temperatures associated with the south to north flow of the Humboldt (Peruvian) Current.

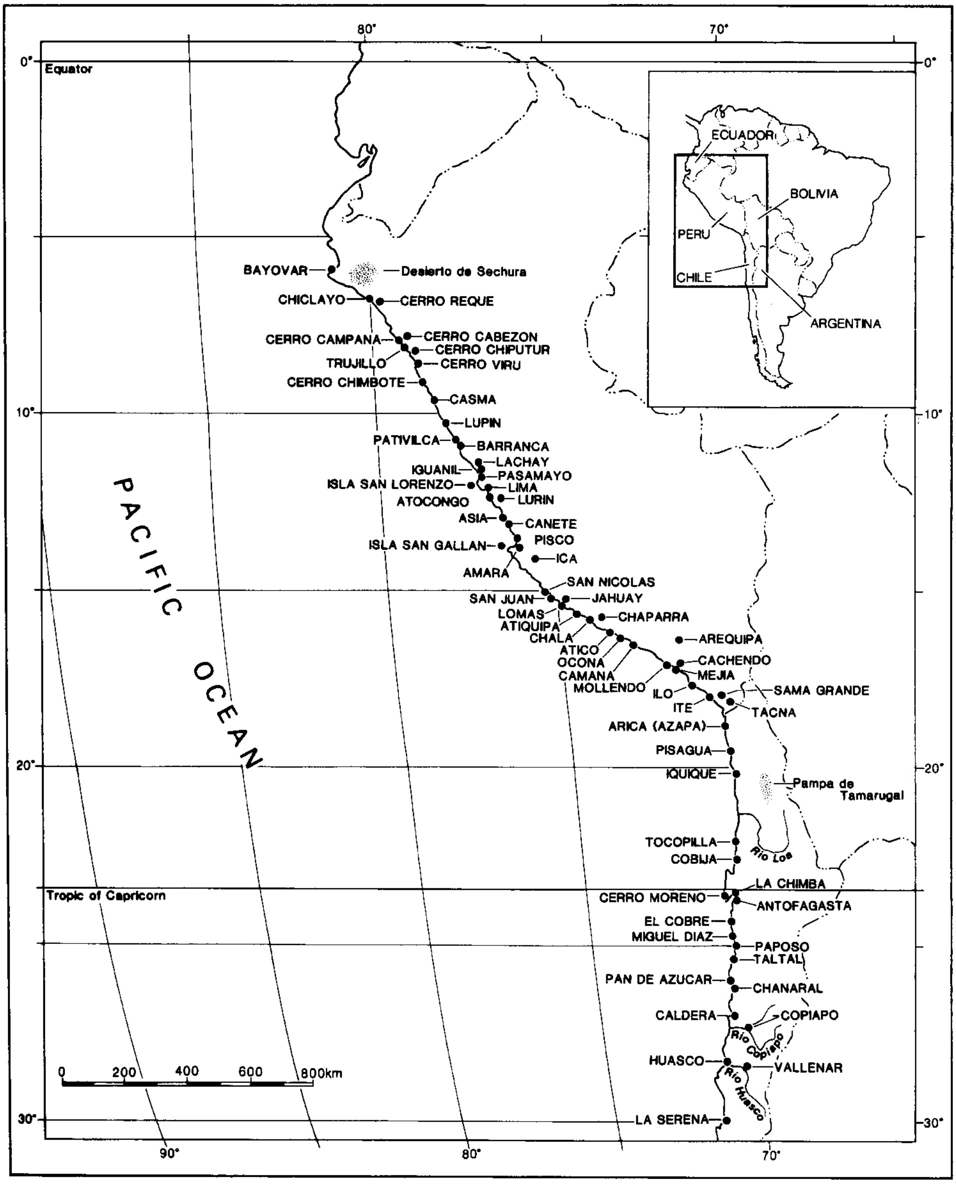


Fig. 1. Geographic features, including lomas localities referred to in text, within the Atacama and Peruvian Deserts.

Chilean Atacama

The position of the southern geographic limit of the Atacama Desert is subject to a variety of views, with most opinions favoring either La Serena (29°55′S) or the Río Copiapó (27°20′S), 280 km to the north. On a floristic basis, La Serena is clearly the most appropriate choice. North of the valley of the Río Elqui at La Serena, the semiarid coastal scrub vegetation is replaced by succulent desert communities with floristic affinities to desert regions to the north. Although La Serena

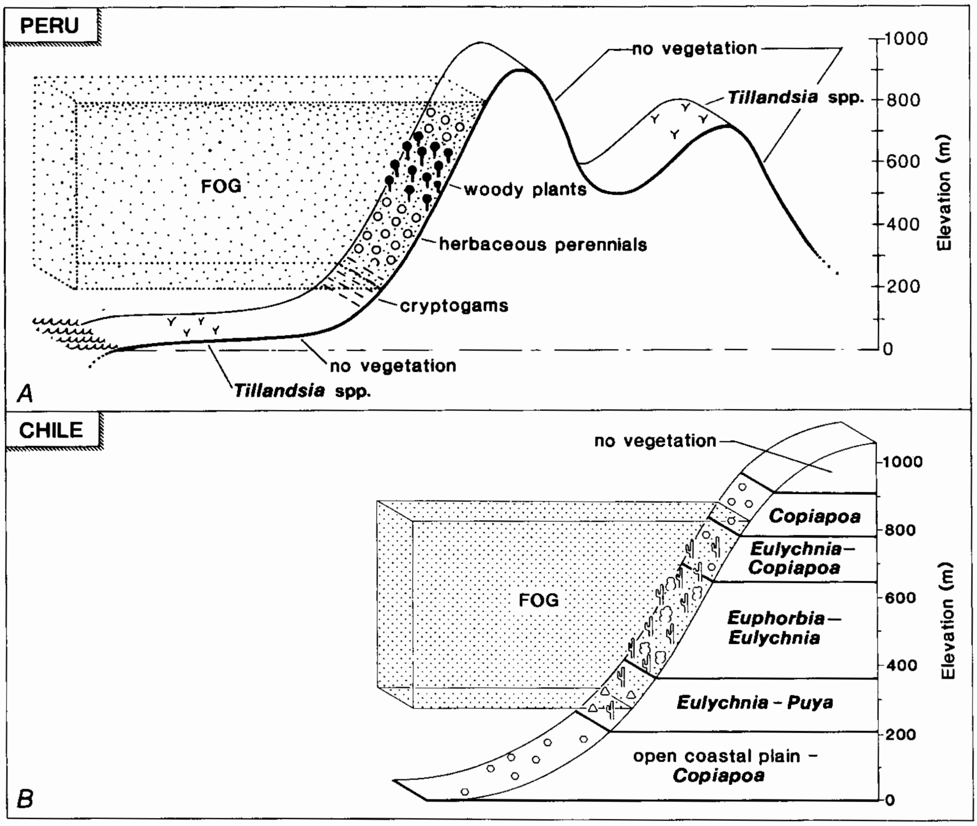


Fig. 2. Diagrammatic view of vegetation zonation in the coastal fog zone of (A) southern Peru (redrawn from Ellenberg 1959) and (B) northern Chile at Paposo (Rundel and Mahu 1976).

receives less than 130 mm of precipitation per year, a level far lower than the temperate margins of most desert regions, the city is nevertheless influenced by occasional incursions of polar air which provide the winter aspect of the Mediterranean climate of central Chile. The Río Copiapó, on the other hand, marks the southern limit of the extremely arid northern desert region where the influence of slowly moving air along the eastern margin of the Pacific anticyclone is a year-round phenomenon which deflects polar air masses. Westward movement of air masses across the continent from the Atlantic are effectively blocked by the high Andean Cordillera which has few passes less than 4000 m. As a result of these influences, the mean annual precipitation drops from only 29 mm at Copiapó to virtually zero through much of northern Chile (Fig. 3).

Values of mean annual precipitation reported for coastal cities of northern Chile are the lowest for many long-term records in the world. Iquique and Arica with nearly 50 years of precipitation records average 2.1 and 0.6 mm respectively. Even these low figures are misleading, however, because of the extreme rarity of days with precipitation. A single storm that dropped 10 mm of precipitation on Arica in January of 1918 accounted for nearly a third of all the precipitation received by the city over the past half century. In fact, Miller (1976) reported that there have been only about half a dozen days in the past 30 years when more

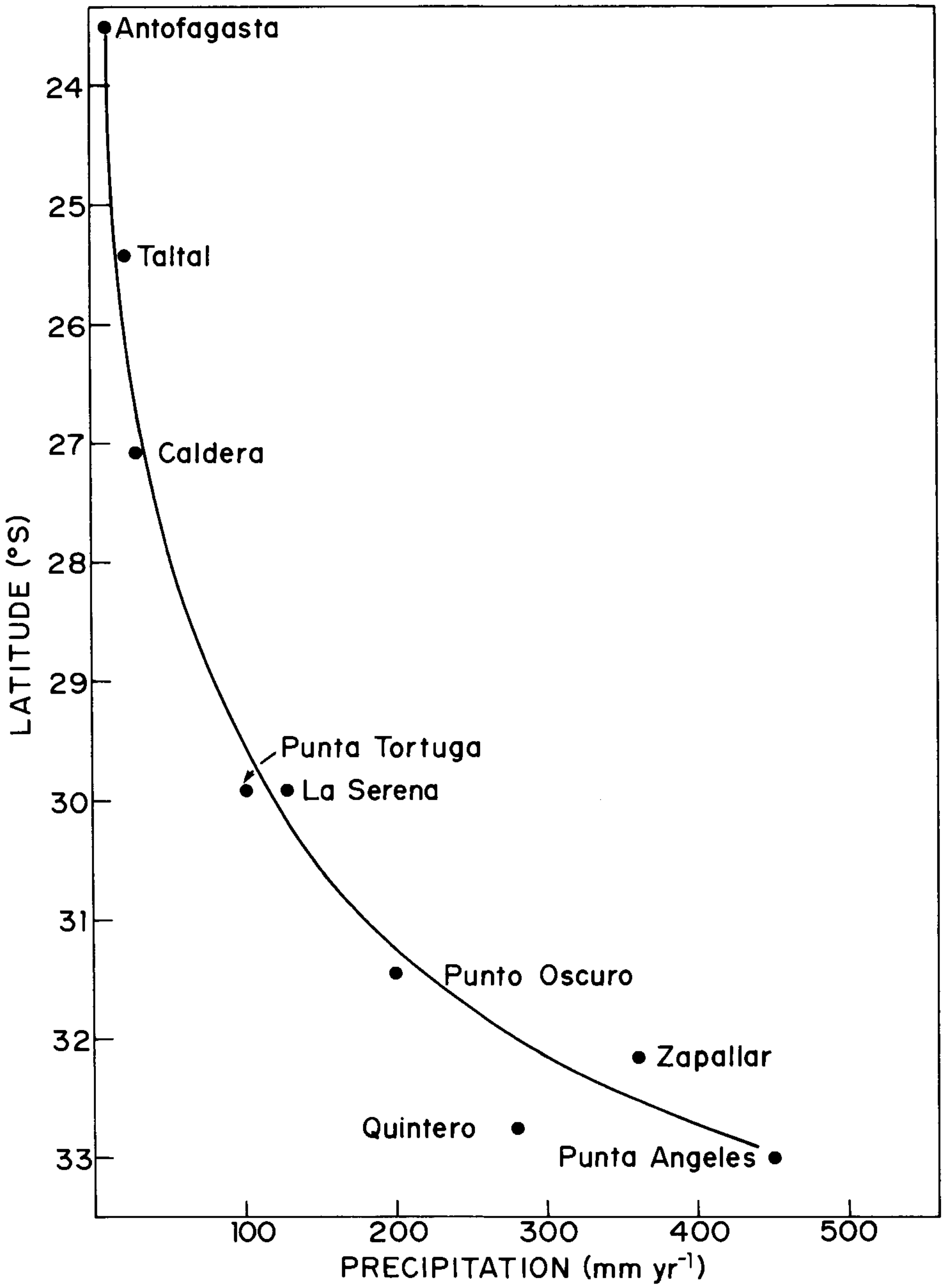


Fig. 3. Gradient of precipitation reduction with decreasing latitude in central and northern Chile.

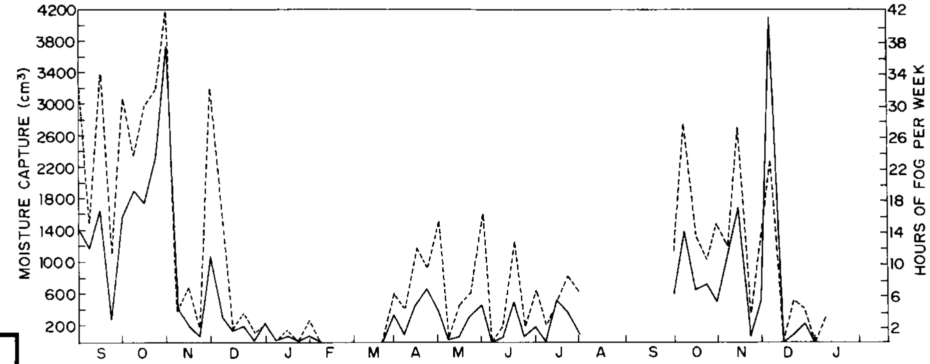
than 1 mm of precipitation fell at any of the coastal cities from Antofagasta north. Only about two out of five years on the average have any measurable precipitation, and drought periods of four to eight years are relatively common. Precipitation levels are higher as one moves southward in the Atacama. La Serena, at the southern margin of the desert, has a mean of 127 mm per year, but with high variability.

Although the northern Peruvian coastal cities occasionally receive torrential rains associated with El Niño conditions, heavy storms are virtually unknown along the north coast of Chile. The maximum recorded precipitations for a 24-hour period for Antofagasta, Iquique, and Arica are 28, 13, and 10 mm respectively (Miller 1976). There may be some connection between these storms and El Niño conditions, nevertheless, and the nature of the El Niño phenomenon is discussed in more detail below. Johnston (1929) reported 17 mm of precipitation falling in Antofagasta on a single day in 1925, a strong El Niño year. Other El Niño years, however, have failed to produce increased precipitation in northern Chile. The relatively strong El Niño of 1965 failed to increase precipitation levels in central Peru and areas to the south. In contrast, the El Niño event of 1983 produced conditions leading to heavy rains from northern to southern Peru, and a relatively high 7.3 mm of precipitation in Iquique, but no notable rains further south (Romero and Garrido 1985; Rutllant 1985). Nevertheless, the fogs appear to have been unusually dense that year, producing excellent flowering conditions in the coastal lomas formations (Prenafeta 1984).

Along the coast of northern Chile, cool moisture-laden marine air is confined below a temperature inversion, with a layer of warm dry air above. The mean height of the inversion at Antofagasta is about 900 m, while at Quintero in central Chile it is only 500 m (Miller 1976). As a result, persistent fog-zones of stratus clouds form below the inversion and frequently extend hundreds of kilometers westward out over the Pacific. These cloud banks are readily apparent in satellite photographs of the coastal area. Usually, the cloud bank is less than 250 m thick, forming somewhere between 400 and 800 m in elevation. This pattern is quite different from that seen along most of the Peruvian coast and central Chile where the lower margin of cloud bank is often 200 m or less.

Because the lower margin of the cloud bank (or fog-zone) is relatively stable, as well as its upper margin beneath the temperature inversion, the lowest few hundred meters of elevation along the coast north of Chañaral have surprisingly low relative humidities and only rarely experience ground-level fog. Antofagasta has a mean annual fog frequency of less than two days per year, while Iquique and Arica average 0.1 and 0.4 days respectively. By comparison La Serena at the southern margin of the desert averages 26 days of fog per year and Valparaíso in central Chile has 54 days per year (Miller 1976). Coastal fogs also occur along the central Peruvian coast.

Few data are available on the seasonal frequency and moisture contents of the stratus layer in northern Chile. Muñoz (unpubl.) reported volume of moisture captured in a mechanical fog collector and the hours of fog per week over a 16-month period in the fog-zone north of Antofagasta at about 800 m elevation (Fig. 4). His data indicate that fogs are important from late March to December, peaking in late spring, while the summer months of January through mid-March had little or no fog. Earlier work by Espinosa (1961) at a nearby site found that fog condensed on collectors on nearly two-thirds of the days over a 16-month study period and no more than 10 consecutive days occurred without precipitation. These patterns roughly parallel seasonal values of mean cloudiness reported for Antofagasta, Iquique, and Arica. Semiquantitative data on fog frequency and moisture content have also been collected at Fray Jorge in the semiarid coastal ranges south of La Serena (Kummerow 1966).



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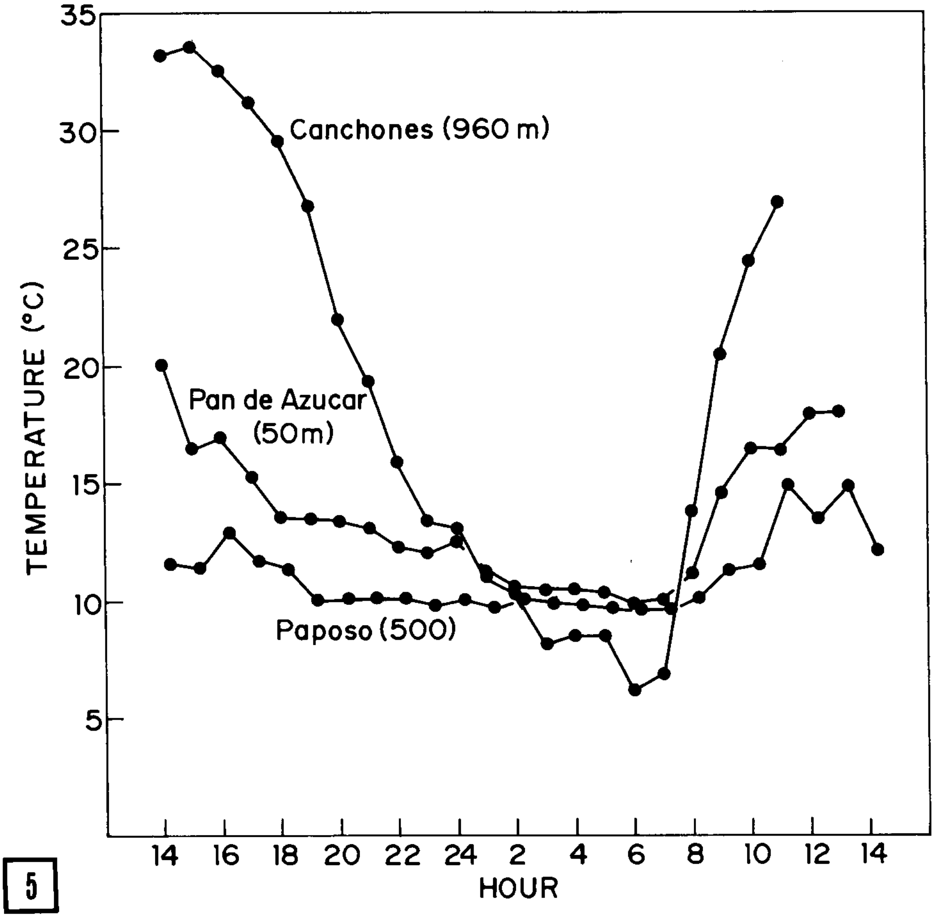

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Fig. 4. Seasonal occurrence of *camanchaca* conditions at 800 m elevation north of Antofagasta during 1963–64. Data are shown for relative moisture capture by screens (solid line) and hours of fog per week (dashed line). Adapted from Espinosa (1961).

Fig. 5. Diurnal cycle of air temperature at coastal (Pan de Azúcar), fog belt (Paposo) and inland valley (Canchones) stations in northern Chile during spring 1978.

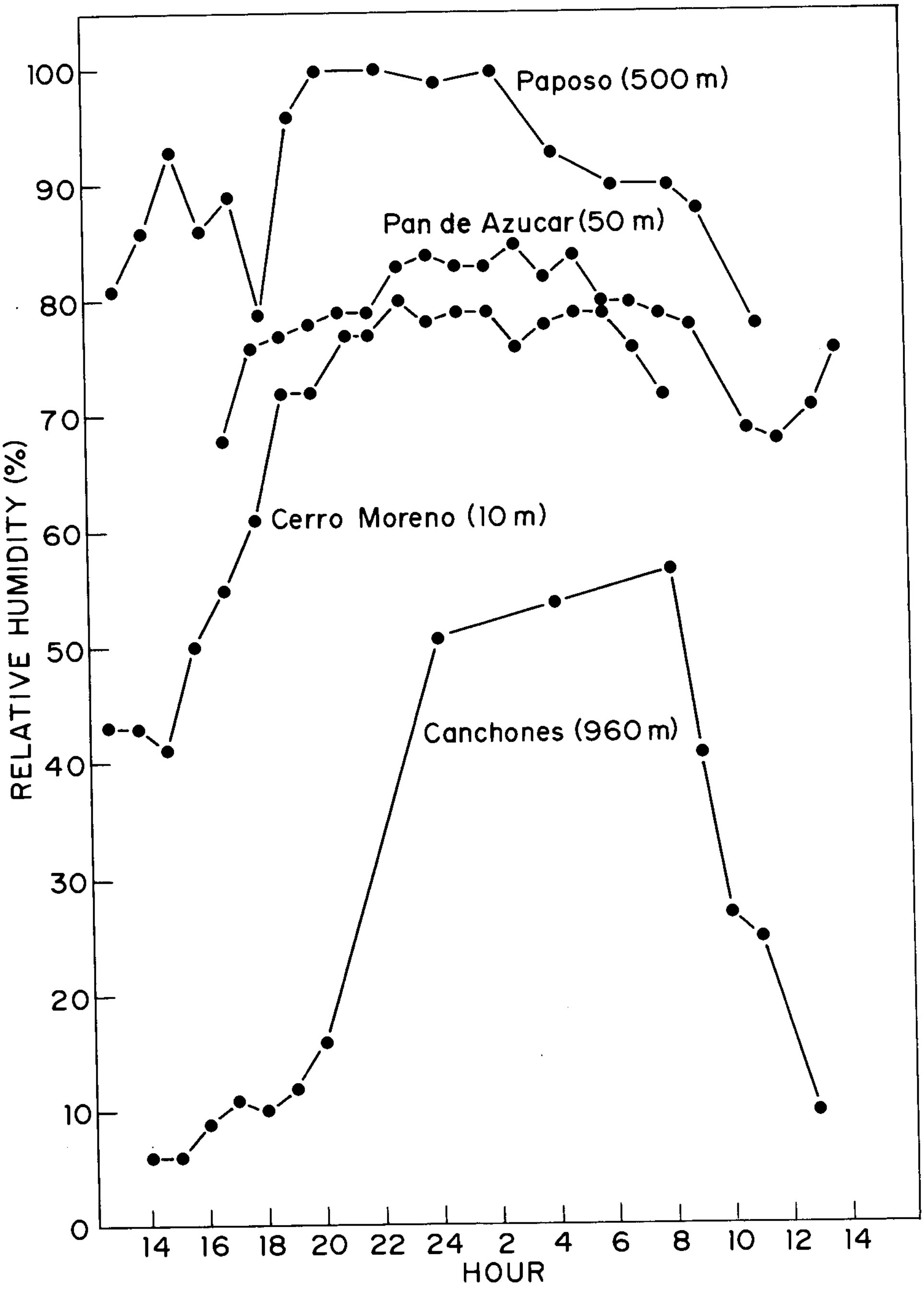

Fig. 6. Diurnal cycle of relative humidity at coastal (Pan de Azúcar and Cerro Moreno), fog belt (Paposo) and inland valley (Canchones) stations in northern Chile during spring 1978.

The relative stability of the stratus cloud layer from Chañaral to Antofagasta produces distinctive elevational zones along the coast. Microclimate data from four sites demonstrated this gradient during the spring growing season in September and October 1978. Pan de Azúcar (50 m elevation) and Cerro Moreno (10 m elevation) are coastal sites situated below the fog-zone. The Paposo site is a classic area of well-developed lomas formation in the central fog-zone, and Canchones (20°27'S, 69°37'W, 960 m elevation), to the north within the Pampa del Tamarugal, is above the fog-zone east of the coastal hills. Typical diurnal patterns of temperature and relative humidity are shown for these sites in Figures 5 and 6. Paposo had an extremely stable pattern of temperature, with a diurnal amplitude of temperature change of only 5 C. Maximum temperatures reached were only 15 C. Pan de Azúcar along the coast had a greater but still moderate temperature amplitude. Temperatures ranged from a low of 10 C to a high of 20 C. The temperature amplitude at Canchones was very high. Afternoon temperatures rose above 33 C and then dropped to only 6 C at night.

Diurnal patterns of relative humidity change are also very distinctive in the three elevational zones. At Canchones relative humidity was only 6% at midday and rose above 55% just before dawn. Despite the lack of the characteristic heavy fogs at the Paposo site on this date, relative humidities still remained above 80% almost continuously. Values were at or very near saturation for much of the evening. Diurnal patterns of relative humidity at the two coastal sites were intermediate. It is interesting to note that relative humidities stayed at a maximum near 80%, despite the close proximity of the ocean. Farther north along the central Peruvian coast and southward in central Chile relative humidity frequently reaches the saturation point at night or in the early morning.

Differences in microclimate exist between these elevational gradients from the coastal plain up the slopes of the coast range and into the interior valleys (Rundel and Mahu 1976). This pattern is best developed in the coastal zone between Chañaral and Antofagasta where precipitation is very low but sufficient to allow vegetation development.

Peruvian Desert

The most prominent feature of the coastal climate of Peru, much as in Chile, is its extraordinary stability. Dense stratocumulus clouds form along the coast almost continuously from May to October, particularly in central and southern Peru. Prohaska (1973) described the winter of 1967 in Lima, in which 90% of all days were overcast and continuous periods of cloud cover remained as long as 44 days. Clear skies occurred only 1.6% of the time over this period. Such conditions can be considered typical. The summer months, in contrast, are characterized by clear and sunny weather, although occasional clouds do form.

Despite stable winter cloudiness in central Peru, with ceilings often between 150 and 300 m, fog is infrequent below 100 m (Johnson 1976). Mean humidities along the coast, however, are considerably higher than those of the northern Chilean coast (Fig. 7). The presence of coastal fog near Lima has been associated with calm periods of air movement, since the height of the stratus layer is inversely related to wind speed (Graves in Prohaska 1973).

The fog forms in the same manner as that described for Chile, as long-wave radiation loss to the atmosphere cools the upper surface of the stratus bank. Fog is a steady winter feature of virtually the entire coastal region of Peru from Chiclayo south. Below 100 m, fog is primarily a phenomenon of the night and early morning hours but it may be continuous in the lomas formations from 100 to 800 m. Studies by Prohaska (1973) at Jorge Chávez International Airport, on the coast near Lima, found that drizzle occurred 27% of the time through the winter. Despite nearly 900 hours of fog precipitation, only 6.1 mm of moisture collected in rain gauges. Although little moisture collects in this manner in rain gauges, the lomas vegetation and rock outcrops in the upland fog-zone intercept moving fog droplets and act to condense considerable quantities of water. It is fog drip, both from plant structures and outcrops, that allows the existence of plant growth. An artificial moisture capture system, a pyramid four meters in height and 25 m^2 at its base, has been reported to trap as much as 100 liters of fog moisture per day at the Lomas de Lachay (Oka 1986).

Precipitation levels are extremely low all along the coast of Peru, but the extreme variability of annual levels gives little significance to mean values. There is no clear latitudinal pattern of change along the coast. Many cities in southern and central Peru have drought periods similar to those already discussed for northern Chile. Pisco (13°42′S, 10 m elevation), for example, sits below the fog-zone and averages only 2 mm yearly precipitation. Tacna in southern Peru sits inland within the fog-zone at 558 m elevation and receives 44 mm yearly, much of this fog drizzle in August and September (Johnson 1976). The major problem in interpreting climatic records for most other Peruvian coastal cities, however, is the rare episodes of heavy rain which may obscure the long-term pattern of virtually zero precipitation. Some inland cities receive occasional showers spilling over from stratus in the Andes but these are less a heavy problem than those of the El Niño years.

Temperature gradients along the coast of Peru are strongly moderated by the cooling effects of the Humboldt Current. Overall the Peruvian coast shows a pattern of gradually increasing mean July minimum temperatures and mean January maximum temperatures moving from south to north (Fig. 7). The temperatures are remarkably cool for these latitudes. In Lima, for example, winter temperatures are 9 C below characteristic coastal temperatures at the same latitudes on the eastern side of the continent (Prohaska 1973). The dense cloud cover of the winter season effectively restricts input of solar radiation and thus keeps air temperatures strongly dependent on water temperatures. As a result the winter diurnal temperature extremes along the Peruvian coast are rarely over 6 C (Johnson 1976). Clearer weather conditions in summer produce higher temperatures.

El Niño Phenomenon

The El Niño phenomenon describes infrequent, but recurrent, perturbations of normal marine and meteorological currents of the Tropical Pacific Basin (Wyrtki 1975; Graham and White 1988; Glynn 1989). During these conditions, the coastal waters along northern and/or central Peru warm considerably in the winter months, thereby breaking down the inversion and allowing the intrusion of moist Pacific air masses. This complex phenomenon has been described in detail (Schweigger 1959; Schütte 1968; Doberitz 1968; Prohaska 1973; Caviedes 1975; Johnson 1976; Graham and White 1988). It was formerly thought that the Humboldt (Peruvian) Current was physically displaced by warm south-flowing currents from equatorial waters, but the data to support this idea are not clear.

The impact of the phenomenon on precipitation in western South America is well illustrated by data from 1925, when strong El Niño conditions were present. Chicama (7°51′S) with a mean annual precipitation of 4 mm per year and Lima,

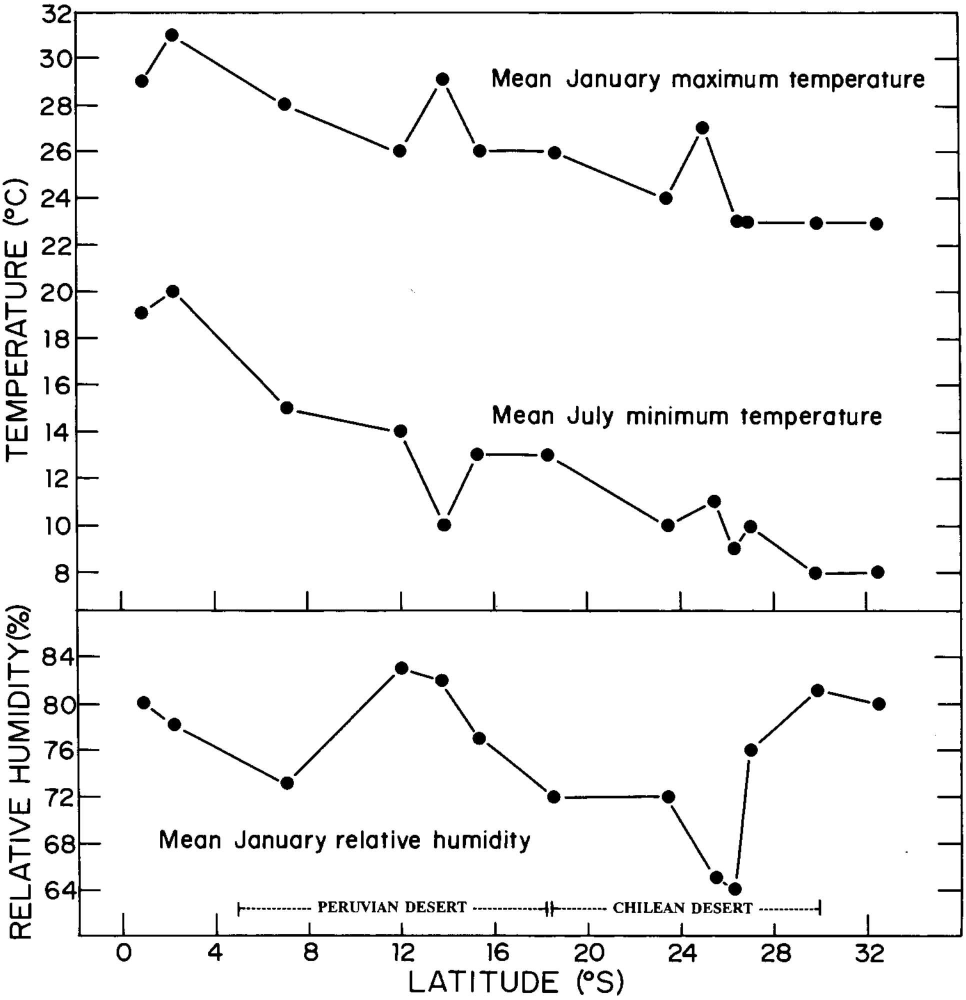

Fig. 7. Latitudinal gradients of mean January maximum temperature, mean July minimum temperature and mean January relative humidity through the Atacama and Peruvian Deserts.

with 46 mm yearly, were deluged by 394 mm and 1524 mm of rain respectively in that year (Goudie and Wilkinson 1977). Trujillo recorded 395 mm of precipitation in March 1925 alone, despite a mean annual level of 35 mm for the preceding seven years (Knoch 1930). Similar strong El Niño conditions occurred in 1891, 1953, 1965, and 1972, with weaker effects felt commonly but not invariably at about seven year frequencies (Johnson 1976; Moseley, Feldman, and Ortloff 1981; Quinn, Neal, and Antunez de Mayolo 1987).

What is being estimated as the most severe El Niño perturbation of the century began in June 1982. By early 1983, rains had moved down the length of coastal Ecuador and Peru, and showers continued through June 1983. The climatic effects upon Ecuador were devastating and have been summarized by Naranjo (1985). The amount of rain falling in northern and central Peru was remarkable as well, with torrential rains and associated catastrophic floods destroying homes, roads, and agricultural irrigation systems (Feldman 1983; Dillon 1985). Piura, with a mean annual precipitation of 50 mm, received more than 1200 mm between December 1982 and April 1983 and over 2000 mm for all of 1983 (Mujica 1984; Hansen 1990). Likewise, Tumbes with 1537 mm, Chiclayo with 211 mm, Trujillo with 8.8 mm, and Chimbote with 32.4 mm, all received levels of precipitation several times greater between December 1982 and April 1983 than 20–30-year averages. To the south, actual recorded rainfall did not reflect the increased duration and density of the fog. These conditions led to increases in plant diversity and extensive development of herbaceous vegetation throughout the Peruvian Desert (Dillon and Rundel 1990).

GEOMORPHOLOGY AND VEGETATION OF THE CHILEAN ATACAMA

In the region north of La Serena, the geomorphology of the coastal margin is dominated by the Cordillera de la Costa, a line of faulted cliffs which rise abruptly from a narrow coastal plain seldom exceeding a few kilometers in width. The principal port cities of northern Chile are all built on this narrow plain—Antofagasta, Tocopilla, Iquique, and Arica. Sandy beaches are rare along much of the coast and steep rocky escarpments are common. Fault movements are still active as indicated by the frequency of earthquakes. Raised beach terraces are present along the narrow coastal plain, most notably between Taltal and Paposo, and south of Tocopilla. These terraces, which indicate a pattern of recent uplift (Paskoff 1967, 1970), attain elevations up to 400 m, and even include occasional former rocky islands capped with preserved guano (Harrington 1961). South of Antofagasta the coastal ranges rise to an average elevation of 1300 m, but in the area around Paposo the Sierra Vicuña Mackenna reaches 3000 m. The Cordillera de Domeyko of the Andean Cordillera begins its rise some 100–175 km to the east and reaches heights of well over 4000 m. The presence of the steep coastal escarpment within 15–20 km of the ocean is largely responsible for the development of a rich lomas formation around Paposo (Rundel and Mahu 1976). North of Antofagasta the coastal ranges are commonly to 700 m but may reach 1000–1500 m; however, this general pattern is broken by Cerro Moreno, a prominent headland northwest of Antofagasta that will be discussed in more detail below.

A major change in topography occurs just south of Arica at the northern tip of Chile where the escarpment of the coastal range gives way to broad and gently rising coastal terraces which are characteristic of the coastal zone of southern Peru. This topographic change also correlates with an abrupt change in floristic relationships (see FLORISTIC PATTERNS AND COMMUNITY STRUCTURE).

Several broad floristic descriptions, which include the coastal Chilean Atacama, have been published since the pioneering work of R. A. Philippi (1860). Reiche (1907, 1911, 1934–37) contributed a series of papers containing descriptions and notes on the flora of northern Chile. Johnston (1929) and Werdermann (1931) both described the flora of the northern area from field studies in 1925, a strong El Niño year. Muñoz-Schick (1985) compiled a photographically illustrated flora for a portion of the southern Atacama known as the "El Norte Chico" (north of La Ligua-Petorca to south of Chañaral). Schmithüsen (1956), Rauh (1985), and Walter and Breckle (1986) provided broad overviews of the vegetation. Marticorena and Quezada (1985) and Gajardo (1987) have recently compiled catalogs of the vascular flora of Chile. A floristic inventory of the coastal Atacama and

Fig. 8. Coastal vegetation north of La Serena, Chile, dominated by *Trichocereus coquimbanus* and *Oxalis gigantea.*

Peruvian Deserts (Dillon, unpubl. data), including field collections and herbarium material, was utilized in the preparation of the following discussion.

La Serena to the Río Copiapó

Along the coast north of La Serena (Fig. 8), precipitation is sufficient to support relatively high vegetation coverage in a community with representatives from the coastal matorral of central Chile (Rundel 1981). Frequently encountered species include: *Trichocereus coquimbanus* (Mol.) Br. & R., *Oxalis gigantea* Barn., *Lobelia polyphylla* Hook. & Arn., *Myrcianthes coquimbensis* (Barn.) Landrum & Grifo, *Puya chilensis* Mol., *Lithraea caustica* (Mol.) Hook. & Arn., *Heliotropium stenophyllum* Hook. & Arn., *Nolana coelestis* (Lindl.) Johnst., *N. crassulifolia* Poepp., and *N. sedifolia* Poepp. Coastal dunes are dominated by *Nolana divaricata* (Lindl.) Johnst. and *Tetragonia maritima* Barn. (Kohler 1970), and associated species include, *Nolana* (*Alona*) *carnosa* Lindl., *Ephedra breana* Phil., and *Skytanthus acutus* Meyen. Numerous ephemeral geophytes, including *Alstroemeria* spp., *Tecophilaea* spp., *Leucocoryne* spp., *Rhodophiala* spp., and *Leontochir ovallei* Phil., are present when rare rains fall in this area (Muñoz-Schick 1985).

Desert vegetation of interior valleys between La Serena and Copiapó is much more sparse but regularly present compared to the more arid regions to the north. North of the Cuesta Buenos Aires where the Pan American Highway leaves the coast, the rugged topography supports only sparse vegetation. Beginning about 40 km south of Vallenar, however, the vegetation coverage increases markedly, and continues to north of the city. Succulent communities with mound-forming species of *Eulychnia* and *Tephrocactus* are dominant and the shrubby *Heliotropium steno-*

phyllum, Balsamocarpon brevifolium Clos, and *Bulnesia chilensis* Gay are common. Shrubs, such as *Cordia decandra* Hook. & Arn., *Adesmia argentea* Meyen, *A. microphylla* Hook. & Arn. and *Ephedra,* are important in wash habitats.

Between Vallenar and Copiapó, vegetation is virtually or totally absent over extensive areas. Both the climate and the effects of man's activities have been important in producing this arid landscape. Thin veneers of sand cover gentle rocky slopes over much of this region. Perennials, such as, *Argylia radiata* (L.) D. Don, *Bulnesia chilensis, Encelia canescens* Lam., *Frankenia chilensis* Roem. & Schult., *Caesalpinia angulata* (Hook. & Arn.) Baillon, *Polyachyrus fuscus* (Meyen) Walpers, *P. poeppigii* (Less.) Less., *Nolana rostrata* (Lindl.) Miers, and *N. pterocarpa* Phil., are the only significant species along many kilometers of the Pan American Highway. Although occasionally fog does penetrate these inland valleys, it has no apparent effect on the vegetation. Lichens are virtually absent. The valley of the Río Copiapó, however, does allow sufficient intrusion of moist maritime air masses to support scattered populations of coastal lichen species on the rocky hills around the city nearly 50 km inland.

North of La Serena, agricultural activities are restricted to limited areas in the river valleys of the Río Huasco around Vallenar and the Río Copiapó around Copiapó. Expanded agricultural activities upstream from Vallenar in recent years have completely eliminated surface flow in the Río Huasco except in years of extremely high runoff from the Andes (Lloyd 1976). The water table remains shallow, however. Downstream from Vallenar, natural summer evaporation has resulted in rapid increase in ground water salinity to over 3450 mg/g, restricting its use by natural vegetation and agriculture (Lloyd 1976). Dune formations near Huasco support a well-developed cover of halophytic species, most notably *Sarcocornia fruticosa* (L.) A. J. Scott., *Carpobrotus chilensis* (Mol.) N.E. Br., *Distichlis spicata* (L.) Greene (Kohler 1970). Some smaller transverse valleys arising in the foothills of the Andes east of Vallenar have impounded ground water supplies as a result of faulting along their lower margins. These valleys provide limited water resources for such cities as Domeyko and Castilla. Tritium evidence has indicated that these are fossil water supplies, and human usage has dramatically lowered water tables in the past 40 years (Lloyd 1976).

The narrow valley of the Río Copiapó is heavily used for agricultural production from 40 km east of Copiapó to the river's mouth. Salinity problems are present, however, and stands of large native *Atriplex* become increasingly frequent moving westward. Increased use of water in recent years for both agricultural and mining purposes have lowered the water table somewhat (Lloyd 1976). Minor transverse valleys in the Río Copiapó drainage, which once had stands of native vegetation and supported limited agriculture, are now largely barren, apparently due to exhaustion of fossil ground water supplies.

Historical records indicate that the valleys of both the Ríos Huasco and Copiapó once supported dense stands of phreatophytic trees. Vallenar, founded in 1789, was originally constructed entirely of local wood occurring in the valley west of the city. Flooding of the Río Huasco in 1887 uncovered a large quantity of willow trunks near the mouth of the river (Klohn 1972). Copiapó, founded in 1714, was once known as San Francisco de la Selva because of the extensive and dense stands of trees which covered the valley (Klohn 1972).

Río Copiapó to Chañaral

The inland region north of Río Copiapó to Chañaral marks the northernmost portion of the "El Norte Chico" (Muñoz-Schick 1985). The region has open communities of scattered low shrubs of *Skytanthus acutus* Meyen, *Encelia canescens* Lam., *Frankenia chilensis,* and *Nolana* (*Alona*) *rostrata.* Annuals and short-lived perennials in favorable habitats include, *Perityle emoryi* Torr., *Oenothera coquimbensis* Gay, *Adesmia latistipula* Phil., *Astragalus coquimbensis* (Hook. & Arn.) Reiche, *Cruckshanksia verticillata* Phil., *Fagonia chilensis* Hook. & Arn., and *Tetragonia angustifolia* Barn. Numerous geophytes are also present in this area when sufficient moisture is available.

The coastal strand and dune formations of the littoral belt from the Río Copiapó to Chañaral possess many of the same species found in the interior with additional characteristic species, such as *Nolana divaricata, Heliotropium stenophyllum* Hook. & Arn., *H. linearifolium* Phil., *H. pycnophyllum* Phil., *Oxalis gigantea, Ophryosporus triangularis* Meyen, *Ephedra andina* C. A. Mey., *Euphorbia lactiflua* Phil., *Bahia ambrosioides* Lag., *Senna cumingii* (Hook. & Arn.) Irwin & Barneby var. *coquimbensis* (Vogel) Irwin & Barneby, *Tetragonia maritima, Trichocereus coquimbanus,* and *Eulychnia acida* Phil. (Kohler 1970; Reiche 1911; Opazo and Reiche 1909). Immediately to the south of Chañaral, several species find their southernmost distribution, including *Gypothamnium pinifolium* Phil., *Dinemandra ericoides* Adr. Juss., *Nolana aplocaryoides* (Gaud.) Johnst., and *Tiquilia litoralis* (Phil.) A. Richardson.

A variety of species of low globular cacti are also present, most notable *Neochilenia* and *Copiapoa.* Several species of *Copiapoa* form broad, multiheaded mounds. *Eulychnia iquiquensis* (Schum.) Br. & R., an arborescent cactus reaching 2–3 mm in height is present as scattered individuals. Total vegetation cover averages 15–20% over much of the area. Coastal fogs descend to low elevations along this portion of the coast, supporting a considerable diversity of saxicolous and corticolous lichens.

Ground water resources near Chañaral are highly restricted. The lack of surface flow in the Río Salado is largely due to limited catchment area in the Andes. Areas which were once the upper elevation catchment of this river have been tilted to the northeast to form the Salar de Pedernales with internal drainage. Runoff from the Andes flows onto the salar and some of this overspills as ground water flow into the upper Río Salado where the river is perennial for several kilometers before it infiltrates into alluvial deposits. The high salinity of this water makes it of little value for plant growth. Dissolved salts in springs at El Salado east of Chañaral are over 73,000 mg/g (Lloyd 1976). Trace element contamination is also a problem with 1–3 mg/g of arsenic and 15–20 mg/g of boron in the water (Klohn 1972). Potable water supplies for Chañaral are piped from the Copiapó Valley.

Chañaral to Antofagasta

The coastal region between Chañaral and Antofagasta is the center of pronounced endemism with a large number of species restricted to the area or with distributions ranging only slightly to the north or south. The flora of this region was the focus of R. A. Philippi's first collecting efforts in Chile (1853–54), culminating in the *Florula Atacamensis* (1860). This is, therefore, the type locality for nearly 200 of Philippi's species described from this region. During the last century, a few other notable collectors visited the area, including F. San Roman (1883–84), A. Larrañang (1888), A. Borchers (1887–89), and L. Darapsky (1889). In 1925, I. M. Johnston intensively collected from Barquito (just south of Chañaral) to near Miguel Diaz (Fig. 1). Werdermann also collected in northern Chile during 1925 (Werdermann 1931).

The vegetation in this area is largely restricted to the coastal escarpment and the initial portions of numerous quebradas that traverse it. These quebradas are essentially dry river valleys formed during past pluvial periods. The greatest diversity and density of plant cover exists within the quebradas, from their mouths near the coast to distances of 5–20 km inland. As the quebradas increase in elevation, plants do not extend above the upper level of the fog at 900–1000 m. Many of the shrubs, which were only occasional elements further to the south, are numerous in this region. In fact, with exceptions, nearly all the species encountered in the area north of Copiapó can be found in this area as well. Important shrubby species primarily confined to this region include: *Anisomeria littoralis* (Poepp. & Endl.) Moq., *Atriplex taltalensis* Johnst., *Berberis litoralis* Phil., *Adesmia viscidissima* Johnst., *Croton chilensis* Müll. Arg., *Haplopappus deserticola* Phil., *Stevia hyssopifolia* Phil., *Gutierrezia taltalensis* Phil., *Senecio almeidae* Phil., *Monttea chilensis* Gay, *Nicotiana solanifolia* Walp., *Teucrium nudicaule* Hook. and *Balbisia peduncularis* (Lindl.) D. Don. This region is a center of diversity for family Nolanaceae (Fig. 9), with several species typically occuring sympatrically. Frequently encountered species include, *Nolana mollis* (Phil.) Johnst., *N. salsoloides* (Lindl.) Johnst., *N. sedifolia, N. peruviana* (Gaud.) Johnst., *N. leptophylla* (Miers) Johnst., *N. villosa* (Phil.) Johnst., and *N. aplocaryoides.*

At numerous locations within the region, but typically within the lower reaches of quebradas, underground aquifers make their way to the surface. Where the water is trapped, due to catchment topography, small pools of highly saline water, termed *aguadas,* support vegetation. Nearly 100 such aguadas occur within this sector. Communities are mixtures of more mesic halophytes and typically arid species. Mesic communities existing in or near water sources include, *Cressa truxillensis* H.B.K., *Cyperus laevigatus* L., *Cotula coronopifolia* L., *Baccharis juncea* (Lehm.) Desf., *Scirpus cernuus* Vahl, *Limonium plumosum* (Phil.) Kuntze, *Juncus acutus* L., *Sarcocornia fruticosa, Distichlis spicata,* and *Zannichellia palustris* L. Arid species also typically inhabit these sites and can reach exceptional dimensions when sufficient water is available.

Several species are notable accumulators of salts (Rundel, Ehleringer, Gulmon, and Mooney 1980), and slopes near the coast typically are marked with white halos of salts marking sites where shrubs once grew (Fig. 10). The foliar content of mineral ash in these shrubs is a remarkable 20–40% (Rundel et al. 1980), producing a highly stable 'shadow" in this dry climate. The most common species producing these white circular spots is *Nolana mollis,* a long-lived perennial shrub common in quebradas. The leaves of this species are covered with salt glands and water has been shown to condense on its leaves in unsaturated atmospheres (Mooney, Gulmon, Ehleringer, and Rundel 1980*a*). Other salt accumulators in-

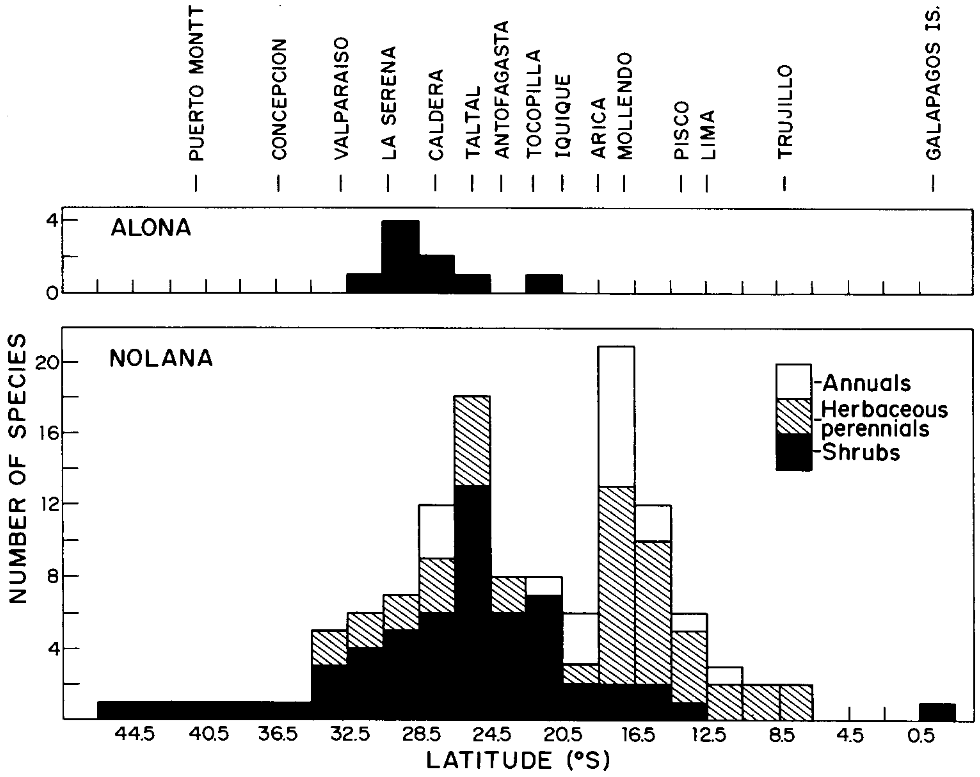

Fig. 9. Diversity of species of *Nolana* (sections *Alona* and *Nolana*) along a latitudinal gradient in relation to species life-form. Data from Johnson (1936) and Ferreyra (1961*b*).

clude *Gypothamnium pinifolium, Heliotropium pycnophyllum, Tetragonia maritima* Barn., *Eremocharis fruticosa* Phil., and *Frankenia chilensis.*

In the area around Pan de Azúcar, the coastal communities below the fog-zone have been described in some detail (Rundel et al. 1980). Two types of communities are present, one composed of low succulents with virtually monospecific stands of *Copiapoa cinerea* Br. & R. var. *columna-alba* (Ritter) Backeb. or *C. haseltoniana* Backeb. (Mooney, Weisser, and Gulmon 1977; Gulmon, Rundel, Ehleringer, and Mooney 1979; Ehleringer, Mooney, Gulmon, and Rundel 1980). Small subterranean cacti, such as *Neochilenia malleolata* (Ritter) Backeb., are also present (Weisser 1967*a, b*). Open stands of less succulent shrubs on bajadas and in washes form a second community type (Rundel et al. 1980). The dominant shrub species are *Nolana mollis, Heliotropium linearifolium, Gypothamnium pinifolium, Oxyphyllum ulicinium* Phil., *Euphorbia lactiflua, Tetragonia maritima,* and *Eremocharis fruticosa.* Even the densest stands of these shrubs do not exceed 1–2% cover, and the great majority of the landscape lacks vegetation of any kind. Annual plants are rare in most years, but were abundant in 1987. Large areas of coastal terraces from Pan de Azúcar to north of Paposo were covered by annuals, most predominantly *Nolana aplocaryoides,* at that time. The moderately low relative humidity within this area restricts lichen growth to a few xerophytic crustose species (Rundel 1978).

Fig. 10. *Nolana villosa* with halo of salt from decomposing leaves at Paposo, Chile.

The slopes above the small mining village of Paposo (Fig. 11), 50 km north of Taltal, support the richest development of fog-zone vegetation in northern Chile with no fewer than 120 species of flowering plants and ferns (Dillon, unpubl. data). This development of vegetation results directly from the special topographic conditions at Paposo where steep coastal hills, rising over 1500 m, form a barrier against the movement of marine air into the interior valleys (Fig. 2b). As a result, the stratus cloud layer below the inversion forms fog between 300 m and 800 m, which allows a considerable condensation of moisture and protects the slopes from the extreme desiccation of the sun.

The central fog-zone at Paposo is dominated by *Euphorbia lactiflua,* reaching heights of 2 m or more (Fig. 12), and *Eulychnia iquiquensis* that reach over 3 m (Rundel and Mahu 1976). Vegetation in this central zone occurs from about 370 m to 640 m and commonly covers 50% or more of the ground surface (Fig. 13), compared to less than 5% total plant cover on the coastal plain below. Other important shrubby species are *Tricochereus coquimbanus, Oxalis gigantea, Lycium stenophyllum* Remy, *Proustia cuneifolia* D. Don, *Croton chilensis* and *Balbisia peduncularis.* Annual species include *Viola litoralis* Phil., *V. polypoda* Turcz., *Cruckshanksia pumila* Clos, *Alstroemeria graminea* Phil., *Malesherbia humilis*

11

12

Fig. 11. *Euphorbia lactiflua* at the lower margin of the fog zone vegetation (ca. 150 m) at Paposo, Chile.

Fig. 12. Central fog-zone vegetation at Paposo, Chile (ca. 440 m), dominated by *Euphorbia lactiflua* and *Eulychnia iquiquensis*.

Poepp. and *Chaetanthera glabrata* (DC.) Meigen. Relative humidity in this zone seldom falls below 80%, at least during the spring and winter seasons, and remains at 100% for long periods of time when the stratus layer is well formed. The humidity is normally high enough to support a lush growth of lichens and condensation is sufficient to allow the epiphytic growth of *Tillandsia geissei* Phil. In

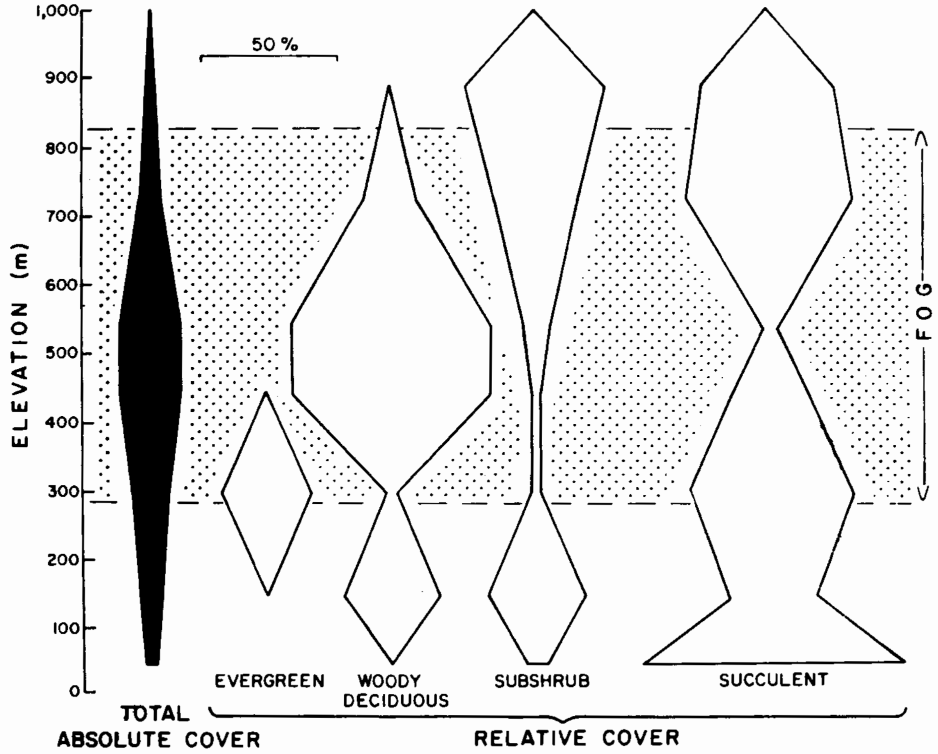

Fig. 13. Absolute and relative coverage of nonherbaceous perennial plants along the elevational gradient at Paposo, Chile. From Rundel and Mahu (1976).

1987, however, after an apparent period of prolonged drought, epiphytic lichens and *T. geissei* were largely absent from the Paposo fog-zone.

Above and below this central fog-zone the coverage of species drops sharply and the growth-forms of the dominates change (Fig. 13). While *Euphorbia lactiflua* and other tall drought-deciduous shrubs dominate this zone the importance of succulent cacti and low semiwoody subshrubs increases away from this center. Dense mounds of *Deuterocohnia chrysantha* (Phil.) Mez and *Puya boliviensis* Baker are locally common along the coastal flats and mark the lower margin of fog occurrence at about 300 m. Unlike the terrestrial *Tillandsia* species common to the Peruvian Desert, these are rooted species. The coastal plain below the fog-zone supports broad stands of *Copiapoa haseltoniana* and scattered shrubs, in communities similar to those at Pan de Azúcar to the south. Above the uppermost limits of regular fog occurrence at about 800 m, *Copiapoa* stands again become dominant along with *Polyachyrus cinereus* Ricardi & Weldt, *Oxalis caesia* Phil., *Nolana stenophylla* Johnst., *N. villosa, N. sedifolia,* and *N. peruviana.* Some shrub species such as *Gypothamnium pinifolium* and *Chuquiraga ulicina* (Hook. & Arn.) Hook. & Arn. occur both below and above the fog-zone (Rundel and Mahu 1976; Johnston 1929). The highest extreme of plant life along the gradient is reached by the shrubby *Loasa fruticosa* (Phil.) Urban & Gilg at 1060 m. Above this point, marking the extreme limit of fog influence, plant life is absent (Fig. 14).

North of the well-developed fog-zone of the Paposo region, vegetation on the

14

15

Fig. 14. Barren hills immediately above the fog zone at Paposo, Chile (ca. 900 m).

Fig. 15. *Copiapoa cinerea* var. *columna-alba* at Pan de Azúcar, Chile. Note the characteristic stem orientation facing towards the north.

coastal slopes along the Pacific Ocean becomes increasingly sparse. The slopes and coastal plain around Antofagasata are virtually free of any vegetation except scattered individuals of *Eulychnia iquiquiensis* and various *Copiapoa* species. Within Quebrada La Chimba, northeast of the city, vegetation tends to occur along the margins of dry river canyon where runoff concentrates. Johnston (1929) collected around the city in the spring following heavy rains in 1925 and obtained 34 species; however, recent collecting and herbarium records indicate that the number present is nearly 60 species (Dillon, unpubl. data).

Cerro Moreno, a prominent rocky headland north of the city of Antofagasta, has a fog vegetation on its southwestern slope at a relatively high elevation (Follmann 1967). In contrast to the diverse community structure at Paposo, to the south, the Cerro Moreno fog-zone is poorly developed. The number of vascular plant species is less than half that of La Chimba with only 28 species recorded. Vegetation along the coast below the fog-zone is virtually absent, with only a few scattered individuals of *Nolana peruviana.* Several *Nolana* species and *Tetragonia angustifolia* increase in importance with increasing elevation on the southwest face of Cerro Moreno, but coverage is still very low and almost entirely restricted to washes. The lower margin of the fog-zone on Cerro Moreno is near 600 m and is marked by scattered populations of *Copiapoa.* The maximum development of the fog-zone occurs from 800 to 1000 m. The shrub strata is most notably absent, with only a few species present, such as, *Heliotropium pycnophyllum, Ephedra breana* Phil., and *Lycium deserti* Phil. Annual and perennial herbs include, *Cynanchum viride* (Phil.) Reiche, *Viola polypoda, Argythamnia canescens* (Phil.) F. Phil. *Eulychnia iquiquiensis* is dominant, as at Paposo, but the vigor of this species is poor. Two essentially nondesert species disjunct from central Chile, *Acaena trifida* Ruiz & Pavón and *Colliguaja odorifera* Mol., have small populations persisting at the site. Perhaps the most notable aspect of the flora is the lush cover of lichens on *Eulychnia* and *Copiapoa,* and on soil and rocks (Follmann 1967). These latter terricolous and saxicolous species are rare or absent at Paposo. The green alga *Trentepohlia* is so ubiquitous at Cerro Moreno that it colors many of the *Eulychnia* brick red. It is interesting to note in comparing Cerro Moreno and Paposo that atmospheric conditions enabling the development of unusually luxuriant lichen growth at the former site are not sufficient to affect vascular plant growth comparably.

Succulent species of the Cactaceae utilizing Crassulacean acid metabolism (CAM) form a very characteristic aspect of coastal areas in this part of the Atacama Desert. In general, the water relations of cacti are poorly studied, but studies of the genus *Copiapoa* have provided insight into how these species are adapted to the severe drought conditions of their habitat. *Copiapoa cinerea* var. *columna-alba* at Pan de Azúcar has been investigated in the most detail (Fig. 15). Despite a relatively high plant density of nearly two plants per square meter present in pure stands of this *Copiapoa,* there is no indication that competition is affecting stand density (Gulmon et al. 1979). While the ratio of horizontal root area to ground surface area exceeds 1.0, the mats of fibrous roots are neither uniformly distributed nor densely branched. Mean annual precipitation at Pan de Azúcar is less than 25 mm yr^{-1}, but this input exceeds the maximum potential water use for any of the stands. A precipitation level of 25 mm yr^{-1} equals 25 liter m^{-2} yr^{-1}. Assuming a minimum surface resistance to water transport of 5 s cm^{-1} and a boundary layer resistance of 1.5 g cm^{-1} (Kluge and Ting 1978) and using measured spring environmental values of 15 C night temperature, relative humidity ranging from 50 to 80%, and 10 hours of nightly transpiration through CAM, maximum annual water use in stands of *Copiapoa* at Pan de Azúcar would be only 2.4 to 6.0 liter m^{-2} yr^{-1} (Gulmon et al. 1979).

Since drought periods without measurable precipitation may extend as long as 6 years or more in northern Chile, water supply for *Copiapoa* growth is contingent on the storage capacity of the cactus stem. The total stem volume of *Copiapoa* at Pan de Azúcar is only about 1 liter m^{-2}, an amount much too low to store more than a fraction of the water supplied by precipitation (Gulmon et al. 1979). A mature *Copiapoa* 22 cm tall could be expected to maintain active transpiration for 143 days using its stored water, while a young plant 2 cm tall could only maintain 48 days. From these calculations it appears reasonable to suggest first that individuals of *Copiapoa* must maintain very high stomatal resistances for long periods of time during extended drought episodes to prevent water loss, and secondly that young plants would have much greater problems than large plants in maintaining positive carbon balance during these droughts. Difficulty of establishment under conditions of very irregular and infrequent rainfall, therefore, rather than competition for water is the primary limiting factor of population density in *Copiapoa.*

Efficient utilization of water is of very great importance to the survival of *Copiapoa* and it would not be surprising to find characteristics of growth form, morphology, and physiology that enhance the ability of these species to survive long periods of drought. Indeed, such adaptations are present. The most significant of these adaptations in *Copiapoa* is the characteristic orientation of stems in a northerly direction (Mooney et al. 1977). By angling north, *Copiapoa* gains one significant benefit by reducing the heat load on the sides of the cactus (Ehleringer et al. 1980). This positioning is particularly significant during late summer and fall when the sides of *Copiapoa* species may be absorbing only 70–80% of the energy taken up by randomly oriented cacti. This effect is accentuated by the presence of a reflective wax layer on the upper sides and top edges of the cactus stem. Reducing the quantum absorption of its sides is a clear advantage in maintaining water balance over long drought periods. Studies with other groups of cacti have shown that daily carbon gain is directly proportional to daily quantum absorption (Nobel 1977), and inversely proportional to level of water stress (Szarek, Johnson, and Ting 1973; Nobel 1977). Ehleringer et al. (1980) have therefore suggested that *Copiapoa* species in the arid Atacama should require relatively few quanta to reduce CO_2 captured during the previous night.

A second adaptation of northerly orientation in *Copiapoa,* not directly related to water relations, is the maximization of heat interception in the meristematic and reproductive regions on the top of the cactus stem. Since ambient air temperatures are relatively cool during the spring along the coast of northern Chile (15–20 C), increased temperatures (30–40 C) in the meristematic and reproductive areas on the top of the cactus stem enable more rapid growth. The angle of the cactus stem, as well as its orientation, is important in this effect since the angle strongly influences the absorbed quantum flux. Simulations by Ehleringer et al. (1980) suggest that the angle for maximum absorption in early spring (the time when flowering is initiated in *Copiapoa*) would be 50° in northern Chile with quantum absorption declining rapidly below 40° and above 60°. The mean measured cactus body angle of *Copiapoa cinerea* var. *columna-alba* is 52°. The increased heating of meristematic and reproductive regions of *Copiapoa* may be indirectly significant for water relations since this condition hypothetically reduces the necessary length of reproductive growth and thereby would allow maintenance of higher stem resistances for longer periods of time than would be otherwise possible. It is interesting to note that a southern (equatorial) orientation is present in several species of *Ferocactus* in the Sonoran Desert of North America (Humphrey 1936).

Antofagasta to Arica

The coastal zone, extending from just north of Antofagasta to Arica, has extremely low species diversity and density. Along the escarpment above 500 m, scattered individuals of *Eulychnia iquiquiensis* and *Copiapoa* species are present. The sparse vegetation developed is a subset of the species distributed south of Antofagasta. The communities near Cobija, with 15 species recorded, and Tocopilla, with 60 species recorded (Jaffuel 1936), have only a few endemic species. These include the rare *Malesherbia tocopillana* Ricardi (a close relative of *M. ardens* Macbr. of southern Peru), *Mathewsia collina* Johnst., and *Nolana tocopillensis* Johnst. Northward from here, the small fertile areas become smaller and increasingly scattered. Near Iquique, Johnston (1929) reported only weak development of vegetation in 1925 and Werdermann collected only about 12 species in Quebrada Huantajaya east of Iquique also in that year. An exception is the large community of terrestrial *Tillandsia landbeckii* Phil. growing on pure sand 10 km east of Iquique at 990–1100 m. Beyond this point, the coast is essentially barren to Arica.

Floristically, the formations from Antofagasta to Arica have little affinity to the Peruvian lomas formations to the immediate north. Of the 117 species of vascular plants recorded from this area by Johnston (1929), only five (4%) were Peruvian species reaching their southern limit. By comparison 89 species (76%) represented northern extensions of the richer flora found south of Antofagasta. The remaining 23 species (20%) were endemics to this zone, most notably, species of *Nolana* (Johnston 1936).

Inland Valleys of Northern Chile

Inland from the coastal zone of northern Chile, the slopes of the Cordillera de la Costa descend gently to extremely arid interior basins at about 1000 m elevation which are outside the direct influence of fog. These basins form relatively narrow north-south valleys broken up by low ranges south of Antofagasta, but to the north the broad Pampa del Tamarugal extends east to the slopes of the Andes. This basin is a structural continuation of the Valle Central from central Chile, with undulating terrain descending gradually from Arica to Taltal, nearly 1000 km to the south. Because the deposition of alluvium in this basin has resulted largely from runoff from the Andes to the east, the lowest points of the basins occur in the western margin of the pampa where the basin and coastal ranges meet. Dry *salares* at these low points of the basin from Antofagasta north to Iquique, as well as adjacent slopes, were the source of the past nitrate wealth of Chile.

With the single exception of the Río Loa north of Tocopilla, surface rivers are absent from the Pampa del Tamarugal and adjacent coastal regions. Relatively shallow ground water is present in aquifers originating in the Andes, however. Small settlements in the Pampa which date back to colonial or pre-Columbian times invariably mark the sites of artesian springs. Potable water supplies for the principal port cities of northern Chile at these latitudes must be piped in hundreds of kilometers from the high Andes. Water supplies in the Río Loa are unusually high in lithium, boron, and arsenic, with the former two elements in very high concentration in plant tissues (Rundel and Palma, unpubl. data). The high concentrations of arsenic, while not accumulated in plants, have produced significant human health problems (Klohn 1972). Characteristic plants along the Río Loa and other areas of the central valley where artesian springs are present include *Pluchea absinthioides* (Hook. & Arn.) H. Rob. & Cuatr., *Distichlis spicata, Atriplex atacamensis* Phil. and *Acantholippia trifida* (Gay) Mold.

Widespread fluvial deposits and dry drainage channels in the Pampa del Tamarugal demonstrate that water has had a significant influence on geomorphological features during the Quanternary (Borgel 1973). Heavy surface runoff of water from the Andes during the *Invierno Boliviano* (i.e., summer precipitation) still occurs at irregular intervals. Brüggen (1936) hypothesized flooding in this region at intervals of 15–20 years. Surface flooding of the Pampa del Tamarugal occurred in 1819, 1823, 1852, 1859, 1878, 1884, 1903, and 1911 (Billinghurst 1886; Bollaert 1860; Bowman 1924) and more recently in 1976. Other data suggest that cycles of strong summer rain in the drainage of the Río Loa occur approximately every 70 years (CEPAL 1960). The ground water table of areas in the Pampa del Tamarugal has lowered in recent years (Borgel 1973), but it is not clear whether this results from over-utilization of current aquifer recharge or from direct use of fossil water supplies.

Although vegetation is entirely absent in most of the Pampa del Tamarugal, scattered areas support dense stands of *Prosopis tamarugo* Phil. (Fig. 16). This species is largely restricted to the Salar de Pintados and Salar de Bellavista southeast of Iquique where more than 21,000 hectares are present, 85% of which consists of plantations (Aguirre and Wrann 1985). Mature trees grow rapidly and reach up to 20 m in height and over a meter in diameter. Careful records in plantations of *Prosopis tamarugo* Phil. have found annual productivities of leaves and pods alone of up to more than 12,000 kg ha^{-1} (Elgueta and Calderon 1971; Aguirre and Wrann 1985), a remarkable figure for trees growing in an area with a mean annual precipitation of less than 1 mm yearly. While early studies suggest that *P. tamarugo* was able to take up moisture directly from the air (Sudzuki, Botti, and Acevedo 1973; Went 1975), more recent studies indicate that this species is existing as a deeply rooted phreatophyte (Mooney, Gulmon, Rundel, and Ehleringer 1980*b*; Aravena and Acevedo 1985). Hydrologic studies of the region have shown that groundwater tables occur at 5–12-m depths over the range of *P. tamarugo* at Salar de Pintadas (Castillo 1960; Tricart 1966). Increased planting of these trees in recent years may be a factor in lowering water table depths.

While *Prosopis tamarugo* is the dominant species in the Pampa del Tamarugal, a small flora of other species are also present, including *Pluchea absinthioides, Distichlis spicata, Atriplex atacamensis, Euphorbia tarapacana* Phil., *Tagetes minuta* L., *Prosopis strombulifera* (Lam.) Benth., and *P. alba* Griseb. Since only the latter two species are obvious phreatophytes, these other species may be indirectly "parasitic" in their dependence on the hydraulic lift of ground water into shallow soil horizons. *Schinus molle* L. and a variety of exotic crop plants are also widely planted in the Pampa del Tamarugal, utilizing this same shallow water pool.

Fig. 16. Natural stand of *Prosopis tamarugo* near La Tirana, Chile, in the Pampa del Tamarugal.

Fig. 17. Coastal formation of *Neoraimondia aticensis* Rauh & Backeb. and associated species near Atico, Peru.

GEOMORPHOLOGY AND VEGETATION OF THE COASTAL PERUVIAN DESERT

The vegetation of the coastal Peruvian Desert was first studied and described by Ruiz, Pavón, and Dombey between 1778 and 1788. They are responsible for describing over 70 species currently recognized from the flora. Weberbauer (1911, 1936, 1945) described the overall phytogeography of the coastal region; however, Ferreyra (1953, 1961*a*, 1983) was the first worker to complete a comprehensive inventory for the Peruvian lomas formations. Other investigators contributing descriptions of the region, at least in part, include Rauh (1958, 1985), Koepcke (1961), Ono (1982, 1986), Ogawa, Oka, and Ohga (1986), Oka and Ogawa (1984), Péfaur (1982), and Müller (1985*a, b,* 1988). The discussion presented here includes information from the aforementioned works, combined with field observations and herbarium collections (Dillon, unpubl. data).

The geomorphology of southern Peru from the Chilean border (18°24′S) to Ocoña (16°30′S) is dominated by a coastal plain, 20–30 km in width, and extensive steep coastal ridges. The narrow valleys and broken topography of this region provide little area suitable for agriculture (Robinson 1964), with the exception of groves of the Mediterranean olive (*Olea europaea* L.) that are cultivated in the transverse valleys near the ocean (Mollendo, Atico, Ocoña).

Directly north of the Peru/Chile border, vegetation is restricted to dry streambeds within the Pampa de Hospicio. This dry alluvial fan is below the fog-zone and derives moisture from the occasional flooding of the Río Caplina from interior rains. Vegetation consists of small trees and shrubs, including *Tecoma fulva* (Cav.) D. Don, *Grindelia glutinosa* (Cav.) Dunal, *Pluchea chingoyo* (H.B.K.) DC., and various halophytic herbs including *Phyla nodiflora* (L.) Greene, *Philippiamra pachyphylla* (Phil.) Kuntze, *Tiquilia paronychioides* (Phil.) A. Richardson. The broad Pampa de La Yarada northwest of Tacna extends for some 20–30 km north with a width of 10–15 km and gives way to the costal hills along the slopes of the interior mountains. These areas receive heavy fog for a distance of 40–50 km inland, and unlike the Chilean fog-zones to the south, the dominant vegetation is herbaceous, with many of these locally endemic.

It is in this region that the southernmost Peruvian *Tillandsia* formations occur, composed of pure stands of the endemic, sand epiphyte, *Tillandsia werdermannii* Harms, and occasional scattered mounds of *Tephrocactus sphaericus* (Först.) Backeb. Terrestrial species of *Tillandsia* in Peru are generally restricted to the lower and upper margins of the fog-zone (Fig. 2A), and are largely absent from the central zone of lomas formations where moisture input is maximal. This absence from the central fog-zone can likely be explained by the continuously wet conditions which prevail at such sites during the winter months. Because the stomata of *Tillandsia* species are characteristically located flush on the leaf surface between the trichome shields, which allow foliar water uptake, the presence of even a thin film of water on the leaf surface significantly reduces CO_2 exchange and thus restricts photosynthesis (Rundel 1982). For this reason, diurnal cycles of wetting and drying are usually necessary for survival of these species.

The absence of terrestrial *Tillandsia* species from the Atacama Desert south of Iquique is not clearly understood, but it likely relates to the absence of favorable microclimate conditions. The high aerosol content of water droplets in the coastal fog of the Peruvian lomas formations would favor *Tillandsia* growth, in contrast to the humid air with a lower aerosol water content in northern Chile. Epiphytic *Tillandsia geissei* Phil., while infrequent in the fog-zone around Paposo, are not found in the other coastal communities of the Atacama Desert. *Tillandsia usneoides* (L.) L., not represented in the coastal communities of the Atacama Desert, is a locally abundant epiphyte in humid forest communities in central and southern Chile (Rundel 1978).

To the northeast of Tacna, slightly rolling hillsides near Sama Grande and Sama Morro (200–672 m) support a flora first inventoried by Ferreyra (1961*a*). Rich herbaceous communities develop in response to sufficient fog or rare, aperiodic rains. During the strong El Niño event of 1982–83, dense mixed communities of annuals and herbaceous perennials developed, including *Nolana spathulata* Ruiz & Pavón, *N. arenicola* Johnst., *N. gracillima* (Johnst.) Johnst., *Portulaca pilosissima* Hook., *Calandrinia paniculata* (Ruiz & Pavón) DC., *Cristaria multifida* Cav., *Eragrostis weberbaueri* Pilger, *Argylia radiata, Leptoglossis darcyana* Hunziker & Stubis, *Allionia incarnata* L., *Tiquilia litoralis, Palaua dissecta* Benth., *P. pusilla* Ulbr., *Caesalpinia* (*Hoffmanseggia*) *prostrata* (Lag.) Macbr., *Mirabilis elegans* (Choisy) Heimerl, and *Monnina weberbaueri* Chodat. Woody species included *Ephedra americana* Humb. & Bonpl., *Encelia canescens,* and the suffrutescent *Chenopodium petiolare* H.B.K., *Nolana confinis* (Johnst.) Johnst., *N. lycioides* Johnst., and *Senna brongniartii* (Gaud.) Irwin & Barneby. The endemic cactus *Islaya* has its southernmost species, *I. krainziana* Ritter, in this region.

Occasionally vegetation develops in areas where runoff gathers from localized storms within the interior. These small communities consist of a mixture of normally montane species whose seeds were possibly carried in with the runoff water including *Ambrosia artemisiodes* Meyen, *Lycopersicon peruviana* (L.) Mill., and desert species such as *Nolana pallidula* Johnst., *Suaeda divaricata* Moq., *Sesuvium portulcastrum* L., and *Philippiamra pachyphylla.* In some areas, *Solanum multifidum* Lam. exists in large, nearly pure, populations. The vegetation of this plain provides some forage for goat and cattle grazing and, during the exceptional year of 1983, both corn and wheat were cultivated within this region. The pattern of dominance by herbaceous species is broken in the coastal Lomas de Mostazal near the port of Ilo (17°50′S). Rich herbaceous communities, similar to those described above, frequently cover the entire ground surface, but in addition a shrub community dominated by *Croton alnifolius* Lam. and *Grindelia glutinosa* is found. During 1983, vast numbers of individuals of *Palaua weberbaueri* Ulbr., *P. dissecta, Urocarpidium peruvianum* (L.) Krap., *Nolana pallidula,* and *N. spathulata* were present. East of these formations, large colonies of *Tillandsia purpurea* Ruiz & Pavón cover the sand dunes.

To the north of the Tacna-Ilo area, extensive lomas reappear at Mejia (17°07′S) with approximately 75 species recorded. Here lomas vegetation occurs sporadically on low sandy hills up to 600 m and more extensively on the higher hills further inland to 1000 m. Along the coast, perennial halophytic species such as *Nolana adansonii* (Feuillée) Johnst., *N. thinophila* Johnst. and *Tiquilia conspicua* (Johnst.) A. Richardson are common along the beaches. On slopes between 200 and 600 m, a herbaceous community including *Cristaria multifida, Palaua velutina* Ulbr. & Hill, *Portulaca pilosissima, Weberbauerella brongniartioides* Ulbr., *Caesalpinia* (*Hoffmanseggia*) *prostrata,* and *Eragrostis peruviana* (Jacq.) Trin. At elevations above 600 m ocassional cacti are encountered, including *Neoraimondia arequipensis* (Meyen) Backeb. and the night blooming *Haageocereus australis* Backeb. Near 800–1000 m, nearly continuous grasses and perennial herbs occupy the slopes, including several rare species, such as, *Centaurium lomae* (Gilg) Fabris, *Microcala quadrangularis* (Lam.) Griseb., and *Sisyrinchium micrantha* Cav. Woody species include the small tree, *Caesalpinia spinosa* (Mol.) Kuntze, a montane species common to lomas formations of central Peru. Some 20 km to the northern interior, the Lomas de Cachendo (17°00'S) receive sufficient fog to develop a small community including *Palaua dissecta, Eragrostis peruviana, Oxalis megalorhiza* Jacq., and occasionally *Neoraimondia arequipensis.*

The Lomas de Mollendo (16°55'S), 20 km north of Mejia, support a large and diverse flora of nearly 100 species of flowering plants (Péfaur 1982). The community extends from 150 to 1100 m within a narrow quebrada. On the slopes near the ocean, frequent species include, *Frankenia chilensis, Spergularia congestifolia* Johnst., *Verbena (Glandularia) clavata* Ruiz & Pavón, *Grindelia glutinosa, Loasa urens* Jacq., and the narrow endemic *Viguiera weberbaueri* S. F. Blake. At higher elevations numerous woody species including *Carica candicans* A. Gray, *Calliandra prostrata* Benth., *Heliotropium arborescens* L., *Gaya pilosa* K. Schum., *Lycium stenophyllum, Alonsoa meridionalis* (L.F.) Kuntze, *Nolana pilosa* Johnst., *Mentzelia cordifolia* Urban & Gilg, *Monnina weberbaueri,* and *Hyptis sidifolia* (L'Her.) Briq. Annuals and perennials include, *Alstroemeria paupercula* Phil., *Lupinus mollendoensis* Ulbr., *Caesalpinia (Hoffmanseggia) miranda* (Sandw.) Macbr., *Polyachyrus annuus* Johnst., and *Ophryosporus hoppii* (B. L. Rob.) King & H. Rob. Vegetation ceases near 1100 m, well above the fog-zone. To the east, toward the Andean Cordillera, stretches the hyperarid Pampa del Sacramento, an area of extensive sand dunes virtually devoid of vegetation (Barclay 1917; Finkel 1959). Similar formations are also found immediately to the north (Gay 1962).

Lomas south of the city of Camaná (16°35'S) are well developed with nearly 80 species of flowering species recorded. The loose sandy soils on the gentle slopes of the hills are bathed by fog and form a primarily herbaceous community from 20 to 800 m. The most common is *Eragrostis peruviana,* a species which formed large, pure communities in 1983. Other common herbaceous species include, *Tiquilia paronychioides, Pasithea coerulea* (Ruiz & Pavón) D. Don, *Atriplex rotundifolia* (Moq.) Moq., *Geranium limae* Kunth, *Cenchrus humilis* Hitchc., *Astragalus triflorus* (DC.) A. Gray, *Loasa urens, Cristaria multifida,* and the narrow endemics, *Loxanthocereus camanaensis* Rauh & Backeb., *Palaua camanensis* Ferreyra & Chanco, *P. trisepala* Hochr., and *Nolana cerrateana* Ferreyra.

North of Camaná, the maritime slopes of an arm of the Andes extend near the coast, and break up the coastal plain. The Lomas de Ocoña (16°30'S), and Atico (16°14'S), have lower levels of diversity with approximately 80 and 15 species recorded respectively. These formations have sparsely distributed shrubs, such as, *Ephedra americana, Coursetia weberbaueri* Harms, *Alternanthera pubiflora* (Benth.) Kuntze, and herbaceous species including *Nolana spathulata, N. pallida, N. mariarosae* Ferreyra, and *Sesuvium portulacastrum* South of Atico (Fig. 17), a sizable population of *Neoraimondia aticensis* Rauh & Backeb. occurs near the ocean, with *Heliotropium krauseanum* Fedde, *Calandrinia paniculata* and the endemics *Loxanthocereus aticensis* Rauh & Backeb., *Eremocharis ferreyrae* Mathias & Constance, *Domeykoa amplexicaulis* (Wolff) Mathias & Constance, *Helogyne hutchinsonii* King & H. Rob., *Nolana aticoana* Ferreyra, and *Mathewsia peruviana* O. Schulz.

The Lomas de Chala (15°53'S) and Atiquipa (15°48'S) in the northern part of the Department of Arequipa form a fairly continuous formation broken only by a broad and dry river channel. These were studied intensively by many of the early Peruvian botanists because of their rich diversity. No fewer than 120 species have been recorded from Atiquipa, including *Arcytophyllum thymifolia* (Ruiz &

Pavón) Standl., *Calceolaria ajugoides* Kranzl., *Galvezia fruticosa* Gmel., *Encelia canescens, Islaya paucispina* Rauh & Backeb., *Senna brongniartii, Heterosperma ferreyrii* H. Rob., *Nolana inflata* Ruiz & Pavón, *Croton alnifolius, Heliotropium pilosum* Ruiz & Pavón, and *Senecio smithianus* Cabr. This marks the northern most station for the predominantly Chilean *Argylia radiata* (L.) D. Don.

Inland to the northeast of Chala, the Lomas de Cháparra (Taimara) contain dense populations of *Grindelia glutinosa* and *Nicotiana paniculata* L. Relict stands of small trees to 5 m tall occupy ravines at upper elevations and include *Maytenus octogona* (L'Her.) DC., *Caesalpinia spinosa,* and the rare and endangered endemic, *Myricanthes ferreyrae* (McVaugh) McVaugh. The latter species has been reduced to a few hundred individuals at a handful of local sites.

North of Chala and Atiquipa, a broad coastal plain is again present extending north to Cañete (13°05'S). North of the port city of Lomas, the Lomas de Jahuay are found on windy flats at 300–900 m. The area has 60 species recorded, including several southern Peruvian endemics, such as, *Nolana plicata* Johnst., *Modiolastrum sandemanii* (Sand.) Hill & Fryxell, *Coursetia weberbaureri, Malesherbia angustisecta* Harms, *Nolana tomentella* Ferreyra, and *Ambrosia dentata* (Cabr.) Dillon.

Lomas vegetation is not well developed around Nazca, but extensive riparian forests of *Prosopis chilensis* (Mol.) Stuntz and *Acacia macracantha* Willd. are present in river channels from near the coast up to 2000 m (ONERN 1971*c*). Other important riparian species include *Salix humboldtiana* Willd. and *Arundo donax* L., as well as a variety of low shrubs and herbaceous plants. Approximately 12 km south of the city of Nazca, a small population of *Bulnesia retama* (Gilles) Griseb. represents an unusual disjunction from populations in central Argentina (Weberbauer 1939).

Ground water supplies of the coastal desert region of southern Peru appear to represent fossil water introduced during pluvial periods of the Pleistocene. Geological and meteorological conditions provide strong evidence against the possibility that these groundwaters are being replenished by gravity flow from aquifers exposed high in the Andes. The foothills of the Andes in this region are largely composed of heavily faulted granites and andesites with no permeable formations appropriate for transporting water up to 100 km to the coast. Precipitation is extremely low and irregular. Contemporary additions of significant water supplies must be limited to flash floods in river channels occurring with rare heavy rains associated with the El Niño phenomenon (Goudie and Wilkinson 1977).

Steep coastal ridges with a series of marine terraces are present from south of Ica to the Paracas Peninsula near Pisco (Craig and Psuty 1968). Inland from these ridges the coastal plain lies largely below 300 m, although individual terraces occur up to 700 m (Robinson 1964). The sparse vegetation of the Lomas de Amara (14°42'S) and adjacent communities near Ica and Pisco have been described by Craig and Psuty (1968) and by a series of Peruvian government reports (ONERN 1971*a, b*). The most diverse lomas communities existing at intermediate elevations consist of a few shrubs, principally *Encelia canescens,* in a matrix of *Tillandsia purpurea* and *T. latifolia* Meyen forming narrow horizontal stripes across the slopes (Velande 1949). Windblown fine sand and silt accumulate in the lee of each stripe, enhancing the terraced appearance of the community (Masuzawa 1982). The biotic origin of these stripes has been discussed by Broggi

(1957), but Lustig (1968) attributes them to soil creep and slumping. Densities and biomass of *T. latifolia* lomas formations have been described by Masuzawa (1982, 1986).

Above the lomas communities, *Neoraimondia arequipensis* forms a characteristic belt of columnar cacti, although its density is low. As at Nazca to the south, extensive stands of *Acacia macracantha, Prosopis chilensis,* and other phreatophytes are present along the channels of the Ríos Ica and Pisco. Scattered stands of cultivated date palms suggest a dependable supply of ground water. Marshy soils are present below the fog-zone along the coast, with saline areas dominated by *Distichlis spicata* and freshwater sites supporting stands of *Scirpus.* Weakly developed dunes adjacent to the coast are frequently stabilized by *Distichlis* and *Sesuvium portulacastrum,* a succulent halophyte. *Distichlis* is a particularly effective stabilizer since its roots extend several meters in depth to trap shallow ground water tables (Craig and Psuty 1968).

Between Pisco and Lima, the coastal plain disappears and the coastal geomorphology is dominated by the foothills of the Cordillera Occidental of the Andes. The ridges of these foothills separate the numerous river valleys which drain the Andes in this area. Geological evidence suggests past land subsidence in this region, with broad valley floors restricted to a few small coastal areas (Robinson 1964). The city of Lima is situated at the edge of deposits of one such valley where the Ríos Rimac and Chillón merge.

South of Lima, the Lomas de Lurín (12°17′S), Atocongo (12°08′S), and Amancaes (12°01′S) all support communities of varying diversity with recorded numbers of 30, 80, and 50 species respectively. The common woody elements include *Senna incarnata* (Benth.) Irwin & Barneby, *Heliotropium arborescens, Carica candicans.* Several primarily Andean species are recorded in this region, including *Passiflora suberosa* L., *Tourrettia lappacea* L'Her.) Willd., *Stevia melissifolia* (Lam.) Schultz-Bip., *Philoglossa peruviana* DC., *Ophryosporus floribundus* (DC.) King & H. Rob., *Stenomesson coccineum* (Ruiz & Pavón) Herb., *Begonia geranifolia* Hook., and *Pelexia matucanensis* (Kranzl.) Schltr. Several typical lomas species are also present including *Encelia canescens, Trixis paradoxa* Cass., *Drymaria paposana* Phil., *Centaurium lomae, Vicia lomensis* Macbr., *Palaua malvifolia* Cav., *Urocarpidium peruvianum, Nolana gayana* (Gaud.) Johnst., and *N. humifusa* (Gouan.) Johnst.

Three of the guano islands lying offshore of the central Peruvian coast (San Lorenzo, San Gallan, and Veijas) extend high enough to support sparse lomas communities. Johnston (1931) recorded only 19 species of vascular plants on these islands, including one endemic, *Nolana insularis* (Johnst.) Johnst. (Johnston 1936; Ferreyra 1961*b*).

In the immediate Lima area, a number of lomas formations have been severely disturbed or eliminated due to the population expansion of the last 60 years. The Lomas de Chorrillos, Cajamarquilla, Cerro Agustino, Manzano, among others, have been effected. From Lima northward, frequency and amplitude of precipitation increases significantly and lomas communities increase dramatically in diversity. Floristically these communities show greater subtropical affinities than those to the south. The Lomas de Pasamayo (11°38′S) occupies the upper limit of a large bluff affronting the ocean at nearly 500 m. This small herbaceous community includes *Loasa urens, Solanum multifidum, Palaua moschata* Cav., *Erigeron leptorhizon* DC., *Acmella alba* (L'Her.) Jansen, *Nolana gayana, Nolana humifusa, Verbena litoralis* H.B.K., and *Cryptantha limensis* (A. DC.) Johnst.

Directly north, the Lomas de Chancay and Iguanil (Granado) comprise a rich fertile zone between 160 and 400 m (Ferreyra 1953). True succulents are less common in this zone where a diverse group of herbaceous species and shrubby perennials are dominant, including *Begonia octopetala* L'Her., *Tinantia erecta* (Jacq.) Schlecht., *Stachys peruviana* Dombey, *Mirabilis prostrata* (Ruiz & Pavón) Heimerl, *Sicyos baderoa* Hook. & Arn., *Philoglossa peruviana,* and *Hyptis sidifolia* (L'Her.) Briq.

Perhaps the most famous lomas formation in Peru is the Lomas de Lachay (Fig. 18, 19), approximately 60 km north of Lima. This site was declared a National Reserve in 1977 and is protected and managed by the Peruvian Government. These lomas were described in both detail and glowing adjectives by Ruiz in the late 18th century (see Jaramillo-Arango 1952). Ferreyra (1953) described two distinctive lomas zones at this locality. The lower zone from 100 to 300 m is dominated by a cryptogamic community of *Nostoc commune* Vauch. and a diverse array of foliose and fruticose lichens. Herbaceous and semiwoody vascular plants are less common. The perennial vegetation becomes much richer above 300 m, where distinctive communities occur on hillsides, or rocky slopes in canyons. Hillside communities are dominated by conspicuous associations of *Croton ruizianus* Muell., *Loasa urens, Nicotiana paniculata* L., *Acmella alba, Senecio abadianus* DC., *Galinsoga caligensis* Canne, *Urocarpidium peruvianum, Hebecladus umbellatus* (Ruiz & Pavón) Miers., and *Solanum montanum* L. Dry rocky slopes support stands of terrestrial bromeliads, *Tillandsia latifolia* and *Puya ferruginea* (Ruiz & Pavón) L. B. Smith, and a considerable coverage of lichens. Moist microsites (Fig. 19) on these slopes support a very different flora with many herbaceous perennials, including *Commelina fasciculata* Ruiz & Pavón, *Astrephia chaerophylloides* (J. E. Sm.) DC., *Triodanis perfoliata* (L.) Nieuwl. var. *biflora* (Ruiz & Pavón) Bradley, *Tropaeolum minus* L., *Oxalis megalorhiza, Begonia octopetala, Bowlesia palmata* Ruiz & Pavón, *Spananthe paniculata* Jacq., *Tourrettia lappacea* (L'Her.) Willd., *Cyclanthera mathewsii* Arn. in Hook., *Ophryosporus peruvianus* (Gmel.) King & H. Rob., *Calandrinia alba* (Ruiz & Pavón) DC., *C. ruizii* Macbr., and *Exodeconus prostratus* (L'Her.) Raf. Canyons and valleys in the lomas zone are characterized by relatively dense stands of small trees, notably *Caesalpinia spinosa, Capparis prisca* Macbr., *Senna birostris* (Vogel) Irwin & Barneby, and *Carica candicans.* A remarkable feature of these small woods are the dense accumulation of epiphytes of all types, with mosses, lichens, ferns, *Peperomia hillii* Trel., *Calceolaria pinnata* L., and *Begonia geranifolia,* common on branches and trunks of the low trees.

The impact of fog condensation on plant water relations has been studied in some detail by Ellenberg (1959) in the rich communities of the Lomas de Lachay. Condensation of moisture from the atmosphere in the upper lomas zone at Lachay is sufficient to support growth of woody shrubs and trees. The vegetation itself provides a key factor in influencing the amount of condensation which occurs through the action of fog drip. Woody plants extending above the ground provide a large surface area to intercept wind-blown fog and allow moisture condensation to occur. Measurements of fog drip under plantations of *Casuarina* and *Eucalyptus* at Lachay from 1944 to 1954 found a mean of 488 mm yr^{-1} and 676 mm yr^{-1},

Fig. 18. Dense population of *Loasa urens* on the lower slopes of the Lomas de Lachay, with the ocean in the background. Tree trunks are introduced species of *Casuarina* and *Eucalyptus*.

respectively (Ellenberg 1959). Over the same period a control rain gauge in the open recorded a mean of only 168 mm yr^{-1}. Similar patterns of heavy fog drip have been reported under trees in other fog areas of the world.

Fog drip at Lachay is sufficient to produce clear seasonal patterns of soil moisture content. In 1957, the winter fogs began in June (later than normal in this dry year), soil moisture content increased steadily and extended to greater depths. By September, available moisture extended to a depth of 150 cm in the soil profile under open plantations of *Eucalyptus*. In many years soil moisture is readily available at 100 cm depth through the summer months (Ellenberg 1959). When no vegetation is present, little condensation of atmospheric moisture occurs and soil moisture levels remain low. During 1957, bare areas at Lachay absorbed soil moisture only to a depth of 10 cm. Soils beneath stands of herbaceous vegetation developed a moist zone to a depth of 50 cm. Ellenberg (1959) found that patterns of root distribution in the sandy soils beneath different plant communities at Lachay corresponded well with the penetration of water. Buried seed pools in these lomas provide a reservoir of herb populations in years when fog moisture is too little to promote germination (Ohga 1982, 1986).


19

Fig. 19. Mid-elevation formation (ca. 500 m) at the Lomas de Lachay with *Begonia octopetala* in the foreground.

North of Lachay, the frequency and size of lomas formations drops steadily. Luxuriant lomas vegetation is well developed, however, within the Lomas de Lupín (10°33′S), and to a lesser extent at Casma (9°28′S) and Chimbote (9°04′S) with approximately 50, 25, and 10 flowering plant species recorded respectively. As at Lachay, the lower lomas zone is dominated by cryptogamic coverage (Ferreyra 1953). North of Chimbote a series of small discrete mountains occur within the coastal plain. Each has vegetation present between 200 and 600 m elevation and include the Lomas de Virú (8°19′S), Cerro Negro (8°18′S), Cerro Chiputur (8°10′S), Cerro Cabras (8°03′S), and Cerro Prieto (7°59′S). These formations have been extensively collected and described by Sagástegui, Mostacero, and López (1988) and contain approximately 95, 25, 100, 45, 25 species of flowering plants respectively. The vegetation is a mixture of shrubs and herbaceous species that appears to be a subset of the assemblages of the next two formations.

Some 20 kilometers northwest of Trujillo, Cerro Campana (7°58′S) and Cerro Cabezón (7°54′S) are the northernmost extension of well-developed lomas vegetation. On the lower sandy slopes below 200 m occurs a *Tillandsia* zone with *T. latifolia, T. purpurea, T. recurvata* L., *T. usneoides, T. disticha* H.B.K. and a mixture of cacti such as *Pseudoespostoa melanostele* (Vpl.) Backeb., *Haageocereus decumbens* (Vpl.) Backeb., *Melocactus trujilloensis* Rauh & Backeb., and prostrate shrubs, including *Heliotropium angiospermum* Murray, *Chamaesyce lasiocarpha* (Kl.) Arthur, *Tiquilia paranychioides,* and *Alternanthera halimifolia* (Lam.) Standl. Arborescent species include *Maytenus octogona, Capparis scabrida* H.B.K., *Trixis paradoxa, Cercidium praecox* (Ruiz & Pavón) Harms, *Acacia huarango* Macbr., *Encelia canescens, Cryptocarpus pyriformis* H.B.K., and *Grabowskia boerhaviifolia* (L.F.) Schlecht. Above 400 m, moisture conditions are more favorable and a diverse community of shrubs and herbaceous perennials occurs (Fig. 20), including *Lycianthes lycioides* (L.) Hassl., *Cardiospermum corindum* L., *Passiflora suberosa, Oxalis megalorhiza, Dicliptera peruviana* (Lam.) Juss., *Sacrostemma solanoides* (H.B.K.) Dcne., *Stenomesson flavum* (Ruiz & Pavón) Herb., *Chionopappus benthamii* S. F. Blake, *Nolana humifusa, Begonia geranifolia, B. octopetala, Calandrinia alba, C. lingulata* (Ruiz & Pavón) DC., *C. ruizii, Tropaeolum peltophorum* Benth., *Calceolaria pinnata, Philoglossa peruviana, P. purpureodisca* H. Rob., and *Verbesina saubinetioides* S. F. Blake. Several species not usually found within coastal desert environments are represented by sizable numbers, including *Tillandsia multiflora* Benth. (Fig. 21), *Puya ferruginea* (Ruiz & Pavón) L. B. Smith, *Hypericum uliginosum* H.B.K., *Pelexia matucanensis, Peperomia dolabriformis* H.B.K., and *Valeriana pinnatifida* Ruiz & Pavón. One of the endemics in this formation is *Pitcairnia lopezii* L. B. Smith, the only member of this large Neotropical genus to occur in the lomas formations. Other endemics include *Senecio truxillensis* Cabr., *Apodanthera ferreyrana* M. Crov., *Matelea alicae* Morillo, and *Solanum mochiquense* Ochoa (Sagástegui et al. 1988).

It appears that Cerro Reque (6°52′S), near Chiclayo marks the last outpost for a few common Peruvian lomas species, such as *Caesalpinia* (*Hoffmanseggia*) *prostrata, Tiquilia dichotoma* (Ruiz & Pavón) A. Richardson; however, this area does not receive sufficient moisture to develop each year as do the formations to the south.

Northern Peru

Coastal geomorphology changes abruptly north of Casma (9°28′S) near Puerto Salaverry and the foothill dominated coast of central Peru gives way to a broad coastal plain extending north to the Ecuadorian border. Although some of this region has been geologically uplifted (Robinson 1964), only a few areas have elevations above 1000 m. The gently sloping valleys of the southern part of the coastal plain from Trujillo north provides some of the richest agricultural land in all of Peru.

Although the coastal fog-zone only extends from 0 to 500(800) m in northern Peru (Rauh 1958), the low topography provides a broad arid zone, much of it free of vegetation. Low shrubs dominate the sparse vegetation cover below 100 m, but cacti increase in importance with greater elevation. Unlike central and southern Peru, an interior desert at intermediate elevations is absent from northern Peru. Instead summer precipitation influences occur as low as 500(800) m forming an evergreen savanna woodland. The flora of these woodlands is very much less xerophytic than that of any part of the true Atacama or Peruvian Deserts.

Much of the northern coastal plain of Peru is covered by the semiarid Sechura Desert with extensive areas of flat sandy plains and active dunes (Fig. 22). The geomorphology of this region was described by Silbitol and Ericksen (1953), Kinzl (1958), and Broggi (1961). Large expanses of these sandy areas support little or no vegetation, however, *Parkinsonia aculeata* L. and the narrow endemic *Alternanthera peruviana* (Moq.) Suesseng. are common. A brief description of vegetation in the area of Cerro Illescas along the coast near Bayóvar (5°50′S) has been given by Ferreyra (1979) and Huey (1979). Flat sandy terrain is relatively bare of vegetation but low hummocky dunes are stabilized by *Capparis scabrida* H.B.K. (Fig. 23), a species illustrated by Weberbauer (1911). Coarse alluvial sands, near

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21

Fig. 20. Mid-elevation, seaward slope at Cerro Campana (ca. 500 m) with *Pseudoespostoa melanostele, Pitcairnia lopezii, Puya ferruginea,* and diverse perennial herb cover.

Fig. 21. Mid-elevation, seaward slope at Cerro Campana supporting a dense population of the tank bromeliad, *Tillandsia multiflora.*

the hill and at its base, have a mixed dominance of *C. scabrida* and *C. avicennifolia* H.B.K. The slopes of the hill support only scattered *C. scabrida*. Dunes along the immediate coast are stabilized by *Distichlis spicata* and *Cryptocarpus pyriformis* (Weberbauer 1911). North of 6°S, the prevailing current turns west to the open sea, and Clüsener and Breckle (1987) report small coastal stands of *Avicennia germinans* (L.) Gaertn. at 5°30'S near the mouth of the Río Piura and *Rhizophora mangle* L. (*R. harrisonii* Leechm., auth.) at 3°44'S near Bocapán. The vegetation of the Tumbez region was also described by Ferreyra (1957).

Geomorphic features of dune structure may be extremely important in providing favorable microhabitats for vascular plant survival in the extremely arid portions of the Sechura Desert. One remarkable example of this phenomenon has been described from the Pur-Pur dune, a large barchan near the Virú Valley, 40 km south of Trujillo (Simons 1956). This striking dune is 750–850 m in width and 55 m in maximum height. Its discontinuous arms are formed from small dune-sized barchans which extend several thousand meters. Large numbers of tiny dunelets are clustered along the arm barchans, most less than 20 cm in height. The windward tip of each of these dunelets is anchored by an individual of *Tiquilia paronychioides.* These small plants with very shallow roots and trailing branches apparently subsist on moisture concentrated in the adjacent dunelets. The regional precipitation averages only about 2 mm annually, providing a very poor source of water. Simons (1956) suggested that fog and spray collect preferentially in these dunelets due to movements of large amounts of humid air over the arms of the Pur-Pur dune. The widening of the pattern of *Tiquilia* dunelets move downwind along the arms is attributed to increasing air turbulence in these areas.

River valleys flowing through the southern Sechura Desert are largely irrigated agricultural land today but these once supported riparian communities with thickets of *Acacia macracantha, Salix humboldtiana, Schinus molle* L., *Sapindus saponaria* L., *Muntingia calabura* L., and a variety of woody and semiwoody shrubs (Weberbauer 1911; Ferreyra 1983). Inland from the Sechura Desert along the coastal plain of northern Peru, semidesert vegetation is well developed on slopes between the ranges of the Andes. Weberbauer (1911) and Ferreyra (1979, 1983) described this vegetation, with dwarf trees of *Eriotheca discolor* (H.B.K.) Robyns, *Bursera graveolens* (H.B.K.) Tr. & Pl., *Acacia huarango,* a variety of columnar cacti, and terrestrial bromeliads. The phytogeographical significance of these woodlands has been discussed by Ferreyra (1960) and Simpson (1975).

DESERT FORMATION AND PROBABLE AGE

Unlike many desert areas in the world, the hyperaridity of the Atacama and southern Peruvian Deserts appears to be very old. Climates similar to those that prevail today have existed, at least regionally, since the Middle Miocene. This was related both to the establishment of the ancestral Humboldt Current, as an increase in the upwelling intensity of the Antarctic ice cap began 13–15 million years ago, and to an uplift of the central Andes Cordillera to at least half of its present height at this same time (Alpers and Brimhall 1988). While direct data on the paleoclimatic history of the Atacama and Peruvian Deserts are largely lacking, there is strong geological evidence that the desert climates of northern Chile and southern Peru have been generally arid since at least the Late Eocene (Brüggen 1950; Galli-Olivier 1967; Mortimer 1973; Mortimer and Saric 1975).


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Fig. 22. *Alternanthera peruviana* acts to stabilize sand dunes along the coast 96 km north of Trujillo, Peru, with scattered *Parkinsonia aculeata* in the background.

Fig. 23. Dunes stabilized by *Capparis scabrida* near San Pedro de Lloc, between Trujillo and Chiclayo, Peru.

Depositional sediments and evaporite deposits suggest that intermittent periods of relatively high rainfall occurred in the Oligocene and Miocene (Alpers and Brimhall 1988). However, conditions of hyperaridity have largely prevailed for the last 13–15 million years as evidenced by absence of erosion evident in the stratigraphic record (Mortimer, Farrar, and Saric 1974; Baker 1977; Mortimer

1980; Alpers and Brimhall 1988). The Pampa del Tamarugal stopped accumulating sediments some time after the close of Middle Miocene, marking the beginning of extreme climate desiccation (Mortimer and Saric 1975).

The uplift of central Andean Cordillera during Oligocene and Early Miocene was one critical factor in the initiation of these arid conditions. The Andean Cordillera probably reached to at least 2000 to 3000 m at this time, providing a rain shadow for precipitation from the Amazon Basin and stabilizing the position of high pressure center of the southeastern Pacific anticyclone (Alpers and Brimhall 1988). Contemporaneously, the development of the Antarctic ice cap allowed formation of the transport of cold Antarctic waters along the Chile-Peru coast by the ancestral Humboldt Current, and the upwelling of deep cold waters in response to global wind and ocean circulation patterns (Tricart 1963; Paskoff 1973; Shackleton and Kennett 1975). Marine fossils provide further evidence of this development of cold water circulation (Kennett 1980; Alpers and Brimhall 1988).

While overall hyperaridity has prevailed in northern Chile and southern Peru since the Middle to Late Miocene, there is evidence of minor periods of pluvial activity in the Pliocene, Pleistocene, and Quaternary (Alpers and Brimhall 1988). Glacial phases of the Pleistocene caused pluvial modifications of pediment surfaces and nitrate deposits (Mortimer 1980; Ericksen 1981, 1983), and Late Pleistocene glaciation descended to about 4200 m in northern Chile (Hollingworth and Guest 1967; Ochsenius 1982) and lowered the snow line by 1300 m in Peru (Vuilleumier 1971). Archaeological evidence exists for more mesic climates during the Late Pleistocene and Holocene (Nuñez 1983; Lynch 1984, 1986; Alpers and Barnes 1986). Even very brief pluvial events in the Holocene may have been biologically significant (Craig 1985). Pleistocene conditions with lowered snow lines and mean temperatures 7 C lower than at present (Ahlfeld and Branisa 1960), and the formation of pluvial lakes in the Andes increased the potential for the establishment of drought-adapted plants from the Cordillera in the coastal deserts.

Biological evidence for more mesic Pleistocene conditions can be seen in paleontological findings that many large vertebrates (*Megatherium, Scelidodon, Macrau, Macrauchenia,* and *Equus*) occupied areas that are dry today (Casamequela 1969–70). A relict population of *guanacos* (*Lama guanicoe* Muller) has survived up to the present in the fog-zone of Cerro Moreno north of Antofagasta, but these animals have become dependent on lichens as a major part of their diet (Follmann 1963). Quaternary events in northern Chile have been summarized by Paskoff (1977).

FLORISTIC PATTERNS AND COMMUNITY STRUCTURE

The composition and distribution of the Peruvian and Atacama Desert floras reflect a long history of extreme aridity. The present-day distribution of plants within lomas formations can give an indication of their origins. Traditional views hold that oceanic islands have derived their floras through independent dispersal events and thus tend to have a mixture of species different from those found in neighboring mainland communities (Carlquist 1981). This premise also appears true for the lomas formations, where the flora appears to be derived from several sources and perhaps at different time periods.

Because of the interactions of plant canopies on condensation and the reverse effect of soil moisture availability on plant structure, a clear picture of the significance of soil moisture on the structure of lomas communities is difficult to determine. Where aerosol moisture content is high, woody plants, once established, should be able to maintain themselves. If they are removed, however, it may be impossible for them to reestablish themselves except in exceptional years. It is possible, therefore, that some of the prominent herbaceous lomas of central and southern Peru may once have supported woody vegetation. There is a clear pattern of human impact and grazing in these areas which has existed since precolonial times.

Despite the possible influences of disturbance, there is no question that the herbaceous flora of the Peruvian lomas is far richer than that of the Chilean fog-zones. This pattern can be seen clearly in the biogeographic distribution of herbaceous and woody species of *Nolana* (Johnston 1936; Ferreyra 1961*b*). One important factor favoring the evolution of a larger herbaceous flora in Peru may be the greater regularity of fogs. Our own field studies in northern Chile have indicated that extended drought periods with irregular fog formation may occur. Herbaceous plants which commonly provide a significant coverage in fog-zone at Paposo, even in years without significant rainfall (Rundel and Mahu 1976), were almost totally absent during the spring of 1978. Following the rains of 1987, the coverage and diversity of ephemerals was unusually high in the fog-zone at Paposo. Very sensitive germination cues must be required for herbaceous species to adapt successfully to these conditions of irregular and seasonal fog moisture and rare events of precipitation.

Current estimates (Dillon, unpubl. data) for the total number of species represented within the Peruvian lomas formations are 72 families, 284 genera, and 557 species; and total numbers within the Atacama formation are 73 families, 196 genera, and 373 species (Dillon, unpubl. data). Of the total of nearly 1000 species, only 68 species (ca. 7%) are distributed within both Peruvian and Chilean formations. Lomas species can be grouped into five broad categories: 1) wide-ranging pantropical or "weedy" species found within and outside of the lomas (see Müller 1988); 2) lomas disjuncts from adjacent Andean source populations; 3) lomas endemics (Peruvian and Chilean) with no extralomas populations, but widely distributed within the lomas; 4) narrow lomas endemics found in only one or a few lomas formations; 5) amphitropic disjuncts, primarily from arid and semiarid regions of North America.

While the entire coast of the Atacama and Peruvian Deserts is arid, a lack of topographic barriers to provide fog moisture in the region between Arica and Antofagasta produces conditions with drought too severe for most plants to survive. As a result, this area acts as an important floristic barrier, differentiating Chilean and Peruvian floras. As mentioned previously, these areas only share about 7% floristic similarity at the species level.

The region around Arica itself is clearly related floristically to Peruvian lomas areas. Many Chilean genera and species drop out at or immediately to the south of Arica. Three of the most important cactus genera of northern Chile (*Eulychnia, Copiapoa,* and *Neoporteria*) all fail to cross into Peru. Conversely, the four most important genera of coastal Peruvian cacti (*Loxanthocereus, Haageocereus, Islaya,* and *Neoraimondia*) do not occur south of Arica (Rauh 1958). Terrestrial *Tillandsia* species which are a dominant aspect of the coastal vegetation of southern Peru are of very limited distribution in the Atacama. The southernmost limit of terrestrial species is between Iquique and Tocopilla where pure stands of *Tillandsia landbeckii* occur.

Despite the presence of the aforementioned floristic barrier in the region south of Arica, a number of species have become successfully established over the entire length of the Atacama and Peruvian Deserts, such as, *Apium* (*Ciclospermum*) *laciniatum* (DC.) Urb. in Mart., *Encelia canescens, Chenopodium petiolare, Mirabilis prostrata,* and *Loasa urens. Alstroemeria paupercula* Phil., occurs from Caldera in Chile to Chala in south-central Peru. *Pasithea coerulea* (Ruiz & Pavón) D. Don and *Fortunatia biflora* (Ruiz & Pavón) Macbr. occur from central Chile to southern Peru. A number of genera containing coastal perennials also cross the barrier, including *Alternanthera, Ophryosporus, Tetragonia, Oxalis, Calandrinia, Senna, Palaua, Tiquilia, Heliotropium, Caesalpinia, Tephrocactus, Urocarpidium.* The genus *Nolana* is distributed from central Chile to northern Peru and the Galapagos Islands, with peaks of species diversity near Paposo in Chile and Mollendo in Peru (Fig. 9). It is noteworthy that only one species, *N. lycioides,* is distributed in both Chile and Peru.

DESERT ENDEMICS AND DISJUNCTIONS

Although the great majority of Atacama and Peruvian Desert species have obvious floristic affinities with the Andean Cordillera, the level of endemism in the isolated coastal vegetation is extremely high. Two endemic families of the Andean flora, the Nolanaceae and Malesherbiaceae, are largely Atacama/Peruvian Desert groups (Solbrig 1976). Most of the important desert families, however, are widespread ones: Aizoaceae, Asteraceae, Boraginaceae, Cactaceae, Cruciferae, Leguminosae, Malvaceae, Portulacaceae, Solanaceae, and Umbelliferae. Solbrig (1976) drew a strong significance to the presence of floristic elements of the Chaco region of Argentina in the Atacama, but few of the species he mentions actually enter the coastal desert region. Most of them are found in central Chile or on the higher slopes of the Andes.

Within the entire desert flora, the greatest number of endemic genera are to be found in southern Peru between 15° and 18°S latitude, and northern Atacama formations, specifically between 24°14′ and 26°21′S latitude. These include the largely Peruvian genera, *Islaya, Weberbaueriella, Mathewsia,* and *Dictyophragmus,* and the largely Chilean, *Domeykoa, Gymnophyton, Gypothamnium, Oxyphyllum, Dinemandra, Copiapoa,* and *Eulychnia.* A considerable number of endemics occur within a wide range of genera, including species of *Ambrosia, Argylia, Astragalus, Nolana, Calceolaria, Palaua, Cristaria, Tiquilia, Dinemandra,* and *Eremocharis.* Müller (1985*a*) calculated 42% overall endemism within the Peruvian lomas formations, 62% endemism for southern Peru formations, and 22% for central Peru formations.

Conversely, the greatest number of species with principally Andean distributions with coastal disjunct populations are in northern Peru, specifically between 8° and 12°S Lat. In this region, various families with typically more mesic requirements are represented, e.g., Pteridaceae, Orchidaceae, Passifloraceae, Piperaceae, Begoniaceae. This undoubtedly reflects the more mesic geographic position of these formations within Pleistocene times.

A few North American species with amphitropic disjunct distributions are present in the lomas formations. For the most part, these are not the usual Mediterranean species commonly disjunct from California to central Chile (Constance 1963; Raven 1963, 1972). Rather, these species have their origins in the Sonoran or Mojave Deserts and their distributions are often restricted to the lomas formations. Several primarily North American genera have endemic species within the coastal deserts, including *Encelia, Viguiera,* and several species of *Tiquilia.*

One endemic shrub, *Ambrosia dentata,* has been investigated chemically (Aregullin, pers. comm.) and appears to represent an allodisjunction. This type of disjunct was defined by Turner (1972) as "two or more closely related populations (i.e., more closely related to each other than either is to yet some other taxon) that are widely separated spatially, the various elements of which have been derived through phyletic divergence from populations now *extinct.*" The ancestral stock of *A. dentata* was undoubtedly derived from the Sonoran Desert, and it shares little morphological or phytochemical relationship with its nearest geographic neighbor *A. artemisioides* (Dillon 1984; Jakupovic, Jaensch, Bohlmann, and Dillon 1988).

Other North American species are obvious autodisjuncts, defined by Turner (1972) as "two or more morphologically similar populations that are widely separated spatially, the more remote elements having become isolated through the dissemination of appropriate colonizers from some *extant* population or gene pool." These include *Nama dichotoma* (Ruiz & Pavón) Choisy, *Phyla nodiflora, Linaria canadensis* Dumont, *Microcala quadrangularis* (Lam.) Griseb., *Triodanis perfoliata* (L.) Nieuwl., *Cressa truxillensis* H.B.K., *Malacothrix clevelandii* A. Gray, *Bahia ambrosioides* Lag., *Amblyopappus pusillus* Hook. & Arn., and *Perityle emoryi* Torr., all species with distributions between North America and the Peruvian and/or Atacama Deserts. These patterns of disjunct distributions possibly reflect the long history of stable arid conditions in the southern Peru and northern Atacama Deserts. A few taxa are derived from other arid regions of the world. For example, the widespread succulents, *Carpobrotus chilensis* and *Mesembryanthemum crystallinum* L., both undoubtedly have their origins in South Africa.

CONCLUSIONS

Despite the unifying influences of extreme aridity, mild temperatures, and fog input, the structure and diversity of plant communities in the coastal Atacama and Peruvian Deserts are remarkably varied. These differences correspond well with the floristic patterns separating northern Chile from southern and central Peru. The dominance of herbaceous plant cover and the extensive development of terrestrial *Tillandsia* stands at the margins of the fog-zone in the Peruvian lomas sharply distinguishes these communities from the shrub-dominated Chilean communities. The northern Peruvian communities have undergone dramatic change during recent glacial episodes and appear to have a much more recent origin than those of southern Peru or northern Chile.

The compositional differences of the coastal South American flora have not been fully investigated but they undoubtedly relate to patterns of water use, both in terms of the amplitude and frequency of moisture availability. The habitat ecology and water relations of Atacama and Peruvian Desert plants are important subjects which are necessary for the understanding of the distribution and evolution of the flora described here.

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FOOTNOTE

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