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The Phytogeography and Ecology of the Coastal Atacama and Peruvian Deserts

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THE PHYTOGEOGRAPHY AND ECOLOGY OF THE COASTAL
ATACAMA AND PERUVIAN DESERTS1

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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.

Chilean Atacama

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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 com-
munities with floristic affinities to desert regions to the north. Although La Serena

Fig. 1. Geographic features, including lomas localities referred to in text, within the Atacama and Peruvian Deserts.
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 a dozen days in the past 30 years when more

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).
On the other hand, marks the region where the influence of the specific anticyclone is a year-ward movement of air that is actively blocked by the high pressure. As a result of these conditions, only 29 mm at Copiapó to 29 mm at Copiapó to 100 mm at Antofagasta and 50 mm at Punta Angosta.

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.

Miller (1976) reported that the past 30 years when more 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.

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

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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 34 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).
Aliso receive torrential virtually unknown precipitations for a 24-
d 10 mm respectively storms and El Niño phenomenon is discussed precipitation falling in Other El Niño years, a northern Chile. The ation levels in central ent of 1983 produced Peru, and a relatively rains further south e fogs appear to have ring conditions in the marine air is confined air above. The mean at Quintero in central at fog-zones of stratus hundreds of kilometers y apparent in satellite less than 250 m thick, n. This pattern is quite and central Chile where ne) is relatively stable, version, the lowest few al have surprisingly d-level fog. Antofagasta per year, while Iquique aison La Serena at the r year and Valparaíso in al fogs also occur along moisture contents of the ed volume of moisture fog per week over a 16-
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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 in the heart of a large area of well-developed fog, Chañaral (20°27′S, 69°33′W), is a coastal town where the temperature amplitude during the night was near 8°C. Paposo had an average temperature of 15°C. Pan de Azúcar had a temperature of 21°C, and Cerro Moreno had a temperature of 16°C. The temperature amplitude was near 8°C at Paposo and above 33°C at Pan de Azúcar.

Diurnal patterns showed three elevation levels: coastal (Pan de Azúcar and Cerro Moreno), fog belt (Paposo) and inland valley (Canchones). The diurnal pattern at Paposo was almost continuous, with high humidity levels during the day and low levels in the evening. Diurnal patterns were intermediate. It is worth noting that the relative humidity was near 80%, despite the cold temperatures. Peruvian coastal fog fog is a unique phenomenon that affects this region.

Differences in the microclimate between coastal plains and Maule valley were significant. Chañaral is a coastal town that has a very humid microclimate due to the presence of coastal fog. The maule valley, on the other hand, has a drier microclimate due to the absence of coastal fog. This difference in microclimate affects the vegetation and the overall environment in the region.
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 m² 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, with 46 mm per year in that year (Gou.}
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Figure 7: Latitudinal gradients of mean January maximum temperature, mean July minimum temperature and mean January relative humidity through the Atacama and Peruvian Deserts.

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In South America is conditions were present. mm per year and Lima, 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 Antuzes 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 Talca 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 Vícuña 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

La Serena to the Border

Along the coast a relatively high coastal matorral occurs. It include: Trichocereus polyphylla Hook. & A. Puya chilensis Mol. phyllum Hook. & A. and N. sedifolia Poe. Johnston & Tetra are present when

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Peruvian Deserts (Dillon, unpubl. data), including field collections and herbarium 
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 steno-
L. (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, Balsamocarpus 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, Argyria radiata (L.) D. Don, Bulnesia chilensis, Encelia canescens Lam., Frankenia chilensis Roem. & Schult., Caesalpinia angulata (Hook. & Arn.) Baillon, Polyachryis fuscus (Meyen) Walpers, P. poepigii (Less.) Less., Nolina 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/l, 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., Carpodrurus 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 Rios 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).
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. pycnothyllum Phil., Oxalis gigantea, Ophryosporus triangularis Meyen, Ephedra andina C. A. Mey., Euphorbia lactiflora 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 Juss., Nolana aplocaryoides (Gaud.) Johnst., and Tiquilia littoralis (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 Pedmerales 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 limited areas in the N.E. Br., Distichlis spp., Argyrolobium fuscus (Mey. ex. Miers) Miers, and N. divaricata are commonly found in the dunes. Some species found in these coastal dunes are also found inland, but in limited areas or with limited water availability. The coastal strand and dune formations of the littoral belt from the Río Copiapó to Chanaral 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. pycnothyllum Phil., Oxalis gigantea, Ophryosporus triangularis Meyen, Ephedra andina C. A. Mey., Euphorbia lactiflora 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 Juss., Nolana aplocaryoides (Gaud.) Johnst., and Tiquilia littoralis (Phil.) A. Richardson.

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**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 limited areas in the rocky hills surrounding the valley. These rocky hills are Marine erosion has scoured these rocky hills and have restricted the formation of sand dunes. The sand dunes that do exist are limited in area due to the gentle slope of the hills. The coastal strand and dune formations of the littoral belt from the Río Copiapó to Chanaral 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. pycnothyllum Phil., Oxalis gigantea, Ophryosporus triangularis Meyen, Ephedra andina C. A. Mey., Euphorbia lactiflora 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 Juss., Nolana aplocaryoides (Gaud.) Johnst., and Tiquilia littoralis (Phil.) A. Richardson.

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**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. Philipp’s first collecting efforts in Chile (1853–54), culminating in the *Florula Atacamensis* (1860). This is, therefore, the type locality for nearly 200 of Philipp’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 Díaz (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* (Poep. & Endl.) Moq., *Atriplex taltalisensis* Johnston, *Berberis littoralis* Phil., *Adesmia viscidissima* Johnst., *Croton chilensis* Müll. Arg., *Haplopappus deserticola* Phil., *Stevia hyssopifolia* Phil., *Guiterrezia taltalisensis* Phil., *Senecio almeidai* Phil., *Monttea chilensis* Gay, *Nicotiana solanifolia* Walp., *Teucrum nudicaule* Hook. and *Balbisia peduncularis* (Lindl.) D. Don. This region is a center of diversity for family Nolanaeae (Fig. 9), with several species typically occurring sympatrically. Frequently encountered species include, *Nolana mollis* (Phil.) Johnst., *N. salso­loidies* (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 in 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., *Corula coronopifolia* L., *Baccharis juncea* (Lehm.) Desf., *Scirpus cernus* Vahl, *Limonium plumosum* (Phil.) Kunze, *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, Guimon, 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, Guimon, Ehleringer, and Rundel 1980a). Other salt accumulators in-
The flora of this region of Chile (1853-54), crowds the type locality during the last century with F. San Roman L. Darapsky (1889). (just south of Chanaáed in northern Chile coastal escarpment and These quebradas are periods. The greatest as, from their mouths quebradas increase in fog at 900-1000 m. further to the south, dry all the species en area as well. Important Anisomeria littoralis littoralis Phil., Ades- plopappus deserticola enecio almeidae Phil., Gypothamnium nudicaule Hook. center of diversity for occurring sympatrically. Phil.) Johnst., N. saflo- Johnst., N. leptophylla soides. thin the lower reaches the surface. Where the of highly saline water, adas occur within this ypes and typically arid sources include, Cressa folia L., Baccharis jun- nosum (Phil.) Kuntze, and Zanichellia palus- can reach exceptional el, Ehleringer, Guzman, are marked with white (10). The foliar content (Rundel et al. 1980), the most common species of high-lived perennial shrubs in with salt glands and saturated atmospheres or salt accumulators in-clude Gypothamnium pinifolium, Heliotropium pycnothyllum, Tetragonia mar- tima 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. haseitoniana Backeb. (Mooney, Weisser, and Gulmon 1977; Gulmon, Rundel, Ehleringer, and Mooney 1979; Ehleringer, Mooney, Guzman, and Rundel 1980). Small subter- ranean cacti, such as Neochilenia malleolata (Ritter) Backeb., are also present (Weisser 1967a, 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, Oxy­ phyllum ulcinium Phil., Euphorbia lactiflua, Tetragonia maritima, and Ere­ mocharis 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).
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 iquiqueensis* 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 *Trichocereus 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* and *Chae...
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
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 dominants change (Fig. 13). While *Euphorbia lactiflora* 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., *Nolina stenophylla* Johnst., *N. villosa*, *N. sedifolia*, and *N. peruviana*. Some shrub species such as *Gyposhamnium 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 coastal slopes and coastal plain is scattered individually. Within Quebrada...
coastal slopes along the Pacific Ocean becomes increasingly sparse. The slopes and coastal plain around Antofagasta 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 (Follemann 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, Arsythamnia 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 (Follemann 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 fringe cover 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. columnana 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), Mathewia 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 Rio 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 principal port cities of kilometers from high in lithium, concentration in other areas as well as human health problems and other areas. Pluchea absinthica, Distichlis spicata, E. nuta L., Prosopis st. latter two species are "parasitic" in their soil horizons. Schir planted in the Pam...
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impressive fluvial deposits and dry drainage channels in the Pampa del Tamarugal suggest that water has had a significant influence on geomorphologic features during the Quaternary (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 Rio 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 Acvedo 1973; Went 1975), more recent studies indicate that this species is existing as a deeply rooted phreatophyte (Mooney, Gulmon, Rundel, and Ehleringer 1980b; Aravena and Acvedo 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.
GEOMORPHOLOGY AND VEGETATION OF THE COASTAL PERUVIAN DESERT

The vegetation of the coastal Peruvian Desert was first studied and described by Ruiz, Pavón, and Dombe between 1778 and 1788. They are responsible for describing over 70 species currently recognized from the flora. Weberbauer (1911, 1936, 1943) and Ferreyra (1952) provided an inventory for the flora, and the descriptions of Ono (1961), Ono (1961), Péfaur (1982), and information from the herbarium are used here.

The geomorphology of Coña (16°30'S) is characterized by steep coastal ridges that provide little protection to the coastal groves of the Pampa del Tarnaruga.

Directly north of Coña, beds within the coastal plain provide little protection to the groves of the Pampa del Tarnaruga, with a width of 150 m. Interior mountains inland, and unlike the Pampa, the flora is herbaceous, with few trees.

It is in this region that the climate is composed of periodic fogs during July and August, described by Harms, and occasionally in November. Terrestrial species adapted to the humid air and upper margins of lomas fall within the central fog-zone of the Pampa del Tarnaruga, which prevail at the upper limits of Tillandsia species. During periods when fog is heavy, the trichome shingles on the trichome of Tillandsia geissei in the film of water on the leaves, which restricts photosynthesis and drying are assumed.

The absence of a persistent moisture gradient in the fog of the Peruvian Desert is not evident in the humid air of the fog of the Peruvian Desert, which prevails in the central fog-zone of the Pampa del Tarnaruga. Tillandsia geissei is found in the other coastal desert in Chile (Rundel 1982), and it is a locally abundant species.
1936, 1945) described the overall phytogeography of the coastal region; however, Ferreyra (1953, 1961a, 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), Koepecke (1961), Ono (1982, 1986), Ogawa, Oka, and Ohga (1986), Oka and Ogawa (1984), Péfar (1982), and Müller (1985a, 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, Plucheia chingoyo (H.B.K.) DC., and various halophytic herbs including Phyla nodiflora (L.) Greene, Philippia parviflora (Phil.) Kunze, 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 coastal 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 (Forst.) 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 CO₂ exchange and thus restricts photosynthesis (Rundell 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 (1961a). Rich herbaceous communities develop in response to sufficient fog or rare, aperiodic rains. During the strong El Niño event of 1982–83, dense communities of annuals and herbaceous perennials developed, including Nolana spathulata Ruiz & Pavón, N. arenicola Johnst., N. gracilima (Johnst.) Johnst., Portulaca pilosissima Hook., Calandrinia paniculata (Ruiz & Pavón) DC., Cristaria multifida Cav., Eragrostis weberbaueri Pilger, Argelia radiata, Leptoglossis darcyana Hunziker & Stubis, Allionia incarnata L., Tiquilia litoralis, Palawa dissecta Bentham., P. pusilla Ulbr., Caesalpinia (Hoffmansegga) prostrata (Lag.) Macbr., Mirabilis elegans (Choisy) Heimerl, and Monnina weberbaueri Chodat. Woody species included Ephedra americana Humb. & Bonpl., Encelia canescentes, 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., Suarea divaricata Moq., Sesuvium portulcastrum L., and Philippiamra pachypylla. 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 Palawa 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 (Feuillee) Johnst., N. thompsonii 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, Palawa velutina Ulbr. & Hill, Portulaca pilosissima, Weberbauerella brongniartoides Ulbr., Caesalpinia (Hoffmansegga) prostrata, and Eragrostis peruviana (Jacq.) Trin. At elevations above 600 m occasional 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 micranthum 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 exterior, the Lomas community extends northward to 17°10'S

The Lomas have a diverse flora of community extending inland near the ocean, consisting of Eragrostis gestifolia Johnst. and Loasa urticaeoides (Jacq.), and occurring in the sandy part of the beach. At higher elevations, Calliandra procera and Lycium stenopetalum are common. Scorpiurus stenoplumulosus (L'Her.) Briq., Lupinus mollis, Hieracium lacatulum, Polycarpon, & H. Rob. Vegetation is very similar toward the Andes, as described in the eastern area of extensive lomas research by Ferreyra & Chaves (1959).

Lomas south of Mejia include 80 species of flowering plants of the hills are 20 to 800 m. The vegetation is dominated by large, pure communities of Tiquilia paronychialis and Tiquilia tundifolia (Moq.) Trin. and a variety of endemic species, Loxa, Sola, Neoraimondia, and Nolina. Ferreyra & Chaves (1959) describe the Department of Ilo as having a sable population of sea otters, with Haageocereus australis Backeb. The Lomas of Ilo are a broad and dry early Peruvian community in the Department of Ilo.
The endemic cactus in this region, *Tillandsia purpurea*, and the suffrutescent *Sesuvium portulacastrum*, both in with the runoff from localized areas of high rainfall, are typical of the coastal Lomas de Chala (15°53'S) and Atiquipa (15°48'S) in the northern part of the Lomas south of the city of Camana (16°35'S), are well developed with nearly 80 species of flowering plants 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 paronychiioides, Pasitheca coerula* (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 camuwaensis* 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 puhiflora* (Benth.) Kuntze, and herbaceous species including *Nolana spathulata, N. palida*, *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 *Arctophyllum thymifolia* (Ruiz &
Pavón) Standl., Calceolaria ajugoides Kranzl., Galvezia frutcosa Gmel., Encelia canescens, Islaya paucispina Rauh & Backeb., Senna brongniartii, Heterosperma ferreyrii H. Rob., Nolana inflata Ruiz & Pavón, Croton alnolius, Heliotropium pilosum Ruiz & Pavón, and Senecio smithianus Cabr. This marks the northern most station for the predominantly Chilean Argyria 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 occur on 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., Modiolastrium sandemannii (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 Wildl. are present in river channels from near the coast up to 2000 m (ONERN 1971c). 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 Buinesia 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 1971a, 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 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 it is not clear how the distinctive striae form.

The ridges of the Pacífic coast north of Chala and Atiquipa, and inland to the northeast of Chala, are marked by a series of marine terraces occurring with 2000 m. Windblown fine sand and silt accumulate in these islands, which are separated from the mainland by the broad coastal plain extending from north of Chala to the Lomas de Jahuay, a broad coastal plain 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., Modiolastrium sandemannii (Sand.) Hill & Fryxell, Coursetia weberbaureri, Malesherbia angustisecta Harms, Nolana tomentella Ferreyra, and Ambrosia dentata (Cabr.) Dillon.

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(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 character-
istic belt of columnar cacti, although its density is low. As at Nazca to the south,
sextensive stands of Acacia macracantha, Prosopis chilensis, and other phreato-
phytes are present along the channels of the Rios Ica and Pisco. Scattered stands
of cultivated date palms suggest a dependable supply of ground water. Marthy
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 effec-
tive 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 geomor-
phology 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
Rios Rimac and Chillón merge.

South of Lima, the Lomas de Lurín (12°17’S), Atocongo (12°08’S), and Amanc-
eaes (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
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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., Ophrysosporus 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 1961b).

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 precipi-
tation 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 Domby, 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 Yauch. 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 calicensis Canne, Urocarpidium peruvianum, Hebecladus umbellatus (Ruiz & Pavón) Miers., and Solanum monanum 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 megaiorhiza, Begonia octopetala, Bowlesia palmate Ruiz & Pavón, Spananthe paniculata Jacq., Tourrettia lappacea (L'Her.) Wild., Cyclanthera mathewsi Arn. in Hook., Ophrysopsis peruvianus (Gmel.) King & H. Rob., Calendria alba (Ruiz & Pavón) DC., C. ruizii Macbr., and Euxodeconus prostratus (L'Her.) Raf. Canyons and valleys in the lomas zone are characterized by relatively dense stands of small trees, notably Caesalpinia spinosa, Capparis procera Macbr., Senna bissora (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 hili Trel., Calceolaria pinnata L., and Begonia geranioides, 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\(^{-1}\), respectively (Ellenberg, open recorded have been rep...
The Lomas de Lachay has been declared a National Huashian Government. Ruiz and Pavón in the description by Ruiz (1953) described two zones: from 100 to 300 m is rich in succulents and shrubby species and above 300 m, rich in woody vascular plants. Flora rich above 300 m, rich in dry rocky slopes in canyons. species of Croton ruiziana, Senecio ababavanum, Hebecladusinter., Tinantia erecta (Ruiz & Pavón) DC., and Hyptis sidifolia have been studied in the Lomas de Lachay.

The vegetation itself has been studied in the Lomas zone at Lachay. The vegetation itself and the condensation which occurs on the ground provide moisture for 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).
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 (Ferreya 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 Sagastegui, 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. dicticha H.B.K. and a mixture of cacti such as Pseudepipogon melanostele (Vpl.) Backeb., Haageocereus decumbens (Vpl.) Backeb., Melocactus trujilloensis Rauh & Backeb., and prostrate shrubs, including Heliotropium angiospermum Murray, Chamaesyce lasiocarpa ( KL.) Arthur, Tiquilia paranaeiformis, and Alternanthera halimifolia (Lam.) Standl. Arborescent species include Maytenus ocygona, Capparis scabrida H.B.K., Trixis paradoxa, Cecidium praeox (Ruiz & Pavón) Harms, Acacia huarango Macbr., Encelia canescens, Cryptocarpus pyriformis H.B.K., and Grabowskia borhaviifolia (L.F.) Schlecht. Above 400 m, moisture conditions are more favorable and a diverse community, including Lycium suberosa, Calycolpus solanoides (operculus benthami) H. M. B., Calandrinia lophophora H. Rob., and a few flowering species, including Ti. Babcock, Dolabraformis, and Helianthea. The northern extreme of this large Neotropical flora are found in the northern coastal plain region has been identified above 800 m, but cacti include species found in all of Peru.

Although the coastal plain in southern Peru is free of vegetation, the coastal plain in northern Peru is not. Instead of the evergreen xerophytic flora of the Desert, Salaverry and Cerro Campana have been extensively collected and described by Sagastegui, Mostacero, and López (1988). Ecological conditions are more favorable and vegetation is more diverse. Much of the coastal plain in northern Peru is free of vegetation, but cacti include species found in southern Peru, but not in northern Peru. Instead, the coastal plain has an evergreen xerophytic flora, similar to that of the Desert.
a diverse community of shrubs and herbaceous perennials occurs (Fig. 20), including Lyciaches lycioides (L.) Hassl., Cardiospermum corinum L., Passiflora suberosa, Oxalis megalorhiza, Dicliptera peruviana (Lam.) Juss., Sacrostemma solanoides (H.B.K.) Dcne., Stenomessona flavum (Ruiz & Pavón) Herb., Chionopappus benthamii S. F. Blake, Nolana humifusa, Begonia geraifolia, B. octopetala, Calandra alba, C. lingulata (Ruiz & Pavón) DC., C. ruizii, Tropaeolum petrophorum Benth., Calceolaria pinnata, Philoglossa peruviana, P. purpureodiscus H. Rob., and Verbesina saubinetoides 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 (Sagastegui 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 cactus 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 Sibbitol and Erickson (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
the hill and at its base (H.B.K. The slope at the base of the hill and at its immediate cog was described as corridors (Weberbauer 1950) which were at the sea, and Clisea germinans (L.) H.B.K. mangle L. (R.

of the Tumbez

Geomorphically, standing favorable portions of the Tumbez have been described as 20 km south of Tumbez. At 55 m in near-dune-sized barchan and tiny dunelets are present. The windward face of these paronychioides.

apparently subsided at a precipitation average of 800 mm of water. Simon described these dunelets due to the Pur-Pur dune. There are agricultural lane along the arms of the Pur-Pur.

River valleys are lined with agricultural land. Clusters of Acacia marnaria L., Muntingia calabura (Weberbauer 1950; Brieggen 1950; Pichon 1946) coastal plain of the Tumbez. Between the ranges, Pichon described this vegetation as Bersera graveolens, cacti, and terro.

Unlike many southern Peruvian coastal valleys, current vegetation may have been related both to an increase in the uniform 800 mm of precipitation years ago, and to more effective farming. The present height at 55 m south of Tumbez on the paleoclimate was lacking, there is not a single tree in Chile and southern Peru (Brüggen 1950; Giesecke 1950).
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 Clisener and Breckle (1987) report small coastal stands of *Avicennia germinans* (L.) Gaertn. at 5°30'S near the mouth of the Rio 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 sem woody 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).
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). Periods of episodic sedimentation at the beginning of extreme hyperarid periods may also be recorded in the stratigraphic record.

The uplift of the Andes was one critical event responsible for the formation of the modern Andes. The Andes and the rain shadow effect of the Andes resulted in a significant Earth system response to global wind and climate changes. The uplift of the Andes is thought to have influenced the formation of the modern Andes and the rain shadow effect of the Andes resulted in a significant Earth system response to global wind and climate changes.

While overall aridity has prevailed since the Middle Miocene (Alpers and Brimhall 1988), Glacial phases of relatively high rainfall occurred in the Pacific Ocean and the development of cold fronts may have affected the climate of the Pacific coast of Peru. However, the uplift of the Andes has also influenced the formation of the modern Andes and the rain shadow effect of the Andes resulted in a significant Earth system response to global wind and climate changes.

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Biological evidence from biological and palynological records such as those of Macarau, Macrae, and Mequela (1969–70) suggests that lomas forests survived up to the Late Pleistocene, but these animals may have been extirpated (Vuilleumier 1960; Barnwell and Guest 1967). Evidence from the Late Pleistocene suggests that the uplift of the Andes may have influenced the formation of the modern Andes and the rain shadow effect of the Andes resulted in a significant Earth system response to global wind and climate changes.

Because of the uplift of the Andes, the effect of soil moisture on vegetation distribution may be significant. However, the uplift of the Andes has also influenced the formation of the modern Andes and the rain shadow effect of the Andes resulted in a significant Earth system response to global wind and climate changes.

The compositional and floristic changes within lomas forests reflect a long history of evolution and adaptation to the environment. However, the uplift of the Andes has also influenced the formation of the modern Andes and the rain shadow effect of the Andes resulted in a significant Earth system response to global wind and climate changes.

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ALISO}

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; Erickson 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 (Casmiquela 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 sig-
nificance 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 1961b). 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 (Runde 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) widespread 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 (Laxanthocereus, 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 ter-
is difficult to plants, once estab-
removed, however, it in exceptional years. There is a clear which has existed since is no question that the that of the Chilean fog., Ferreyra 1961b). One flora in Peru may in northern Chile have fog formation may occur. nt coverage in fog-zone undel and Mahu 1976), lowing the rains of 1987, y high in the fog-zone at d for herbaceous species d seasonal fog moisture

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, Oxyphylhum, Dinemandra, Copiapoa, and Eulychnia. A considerable number of endemics occur within a wide range of genera, including species of Ambrosia, Argyria, Astragalus, Nolana, Calceolaria, Palaua, Cristaria, Tiquilia, Dinemandra, and Eremocharis. Müller (1985a) 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 (Arnegullin, pers. comm.) and appears to represent an allodisjunction. This type of disjunction 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, Microcdoa quadrangularis (Lam.) Griseb., Triodanis perfoliata (L.) Nieuwl., Cressa truxillensis H.B.K., Malacothrix clevelandii A. Gray, Bahia ambrosioideas 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 undoubtly 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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