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Vegetation in an altitudinal gradient along the Río Loa in the Atacama Desert of northern Chile

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Six sites between 0 m and 4000 m were sampled for plant and soil chemical characteristics along the Río Loa, Atacama Desert, Chile. Sites located between 0 m and 1500 m showed lower species richness, higher plant cover and higher herbaceous productivity than the upper part of the altitudinal gradient. The number of species varied non-linerly with precipitation along the altitudinal gradient. Plant cover and herbaceous productivity in the lowlands is characterized by the *Pluchea absinthioides*–*Distichlis spicata* association of anthropic origin. We propose that vegetation structure along the altitudinal gradient has been affected by past and present human activities, and climatic and edaphic factors.

Keywords: Atacama Desert; Río Loa; altitudinal gradient; vegetation; human-driven system

Introduction

The combined effect of a high pressure system located on the western Pacific Ocean, the drying effect of the cold north-flowing Humboldt Current and the rain shadow effect of the Cordillera de Los Andes intercepting precipitation from the Intertropical Covergence causes the hyperarid climate which characterizes the Atacama Desert in western South America (Arroyo *et al*., 1988). This desert is considered one of the driest deserts worldwide, with no recorded rains in some localities. The Atacama Desert is part of a major geomorphological unit, the Peruvian–Chilean Desert which forms a continuous belt for more than 3500 km from northern Perú to northern Chile (Rauh, 1985; Rundel *et al*., 1991).

The distribution of flora and vegetation in the Atacama Desert is tightly associated to three physiographic units. The first is the Cordillera de la Costa, a line of faulted cliffs which rise abruptly from a narrow coastal plain of few kilometers wide. Atmospheric conditions, influenced by a stable subtropical anticyclone, result in a mild, uniform coastal climate with scarce rainfall. The presence of a thick cover of stratus clouds below 1000 m but above 600 m is common in northern Chile. Where isolated mountains and steep coastal slopes intercept the clouds, a fog zone develops. This coastal fog allows the development of plant communities called *lomas*. The second unit is the Intermediate Depression, a relatively flat area of *c*. 200 km wide, located between the Cordillera de la Costa and Cordillera de Los Andes. This unit is extremely dry and completely devoid of plants north of 26° S, except for oases or along river courses (riparian habitats). The third unit is the Cordillera de Los Andes where four altitudinal vegetation belts have been described (Villagrán *et al*., 1981): (a) pre-Puna belt (2700–3100 m) characterized by sparse cover of small thorny shrubs and subshrubs; (b) Puna belt (3100–3800 m), the most extensive of the altitudinal belts, presenting the highest plant abundance; (c) high-Andean belt (3850–4200) characterized by tall tussock grasses (pajonales) and cushion plants; (d) subnival belt (4200–4350 m) which is the upper limit of vascular plants. The Puna belt in the II Region is termed Puna Salada (Troll, 1968) and is one of the more fragile and harsh of the Andean ecosystems, due to the combined effects of low temperatures and extreme aridity. This unit receives summer monsoonal rains from the east (invierno boliviano) (Arroyo *et al*., 1988).

The most important river in northern Chile is the Río Loa, which represents an exceptional hydrological course within the Atacama Desert. This river arises in the Cordillera de Los Andes at 21° S (over 4000 m altitude), crosses the Atacama Desert and discharges its water into the Pacific Ocean. Despite the modest amount of water that this river transports (< 10 m^3 s^{-1}) (CORFO, 1950) it is able to reach the ocean running through 130 linear km of absolute desert, representing the longest river in Chile. Several human settlements have established along the Río Loa since pre-Columbian times (Nuñez, 1971). Mining, agriculture, grazing and other human-related activities associated with the river have developed. The Río Loa sustains an important number of plant species along its course providing resources to maintain native and introduced animals. Water supplies in the Río Loa are unusually high in lithium, boron and arsenic, with the former two elements found in very high concentration in plant tissues (Rundel *et al*., 1991).

One of the most conspicuous features of the altitudinal gradient along the Río Loa is the existence of extreme aridity in the lowlands and low temperatures in the highlands. According to this, we would expect species richness along the Río Loa to be maximum at intermediate altitudes, a phenomenon observed for North American deserts (Whittaker & Niering, 1975). This hypothesis comes from the 'favorability' concept (Terborgh, 1973), in which those habitats with stressful environmental characteristics and/or extreme unpredictability have very low plant diversity. This species diversity pattern can be reinforced in this area if resource-poor and rich areas occur at the extremes of the altitudinal gradient. Habitats poor in resources would have low numbers of species because the resource supply is under the minimal threshold required by most of the species to survive. On the other side, habitats rich in resources will be rapidly dominated by a low number of competitively superior species (Tilman, 1982). Hence, a higher diversity is expected in areas with intermediate levels of resources, in which most of the species are able to coexist. This pattern of unimodal diversity has been widely reported in the literature for plant and animals (Tilman & Pacala, 1993).

Contemporary man plays an important role in modifying the landscape through altering the spatial heterogeneity and faciliting the invasion of alien plants, thus affecting the diversity and abundance of species and the secondary successions. In this context, we will analyse the effect of agriculture and grazing activities on the plant communities along the altitudinal gradient of the Río Loa. One of the more evident characteristics of the landscapes under agriculture pressure in northern Chile is the existence of a great number of small patches or stands which form a spatial and temporal mosaic with fields having different kinds of crops and age of abandonment. This mosaic of patches at the landscape level increases the spatial heterogeneity and affects plant species' diversity and the sequence of secondary succession.

The aim of this study is to describe the structure of vascular plant communities along an altitudinal gradient in the Río Loa. We use the values of mean annual precipitation and soil nutrients as a measure of resource availability along the gradient. Past and current land use will be used as an estimation of human pressure on the ecosystems. We hypothesize that precipitation, soil nutrients and human activities (agriculture and grazing) have played a role in structuring these plant communities. If precipitation and soil nutrients are important factors we could expect to find significant relationships between these factors and abundance and plant species richness along the gradient. If man affects plant assemblages we would expect that those sites located close to or within human settlements have a higher proportion of weeds relative to the total number of plant species.

Materials and methods

Study sites

Six sites were selected along the valley of the Río Loa, II Region, Chile. These, in ascending order from sea level to the Cordillera de Los Andes are (Fig. 1): (1) Desembocadura Río Loa (21°25′27″ S, 70°02′54″ W): river mouth at 39 m altitude. Here the water of the river is discharged into the sea. The water flow is very low and divided into several narrow streams of a few meters wide. The bottom of the valley is a *c*. 200-m wide basin. The site is located about 500 m east of the north−south highway. The dominant woody species are *Prosopis tamurugo* and *Atriplex madariagae*. There has been no precipitation ever recorded. (2) Quillagua (21°40′50″ S, 69°31′31″ W): small village of about 300 people at 733 m altitude. The main income activity of people is irrigated farming of alfalfa which was much more intense at the past, but has been decreasing during the last decades because of the deterioration in water quality of the Río Loa. Wood-cutting for making charcoal is another important activity of the people. The main woody species are *Prosopis alba*, *Atriplex atacamensis* and *Geoffroea decorticans*. Mean annual precipitation is 0·1 ± 0·09 mm (mean ± 1 SE) and occurs in winter. (3) Chacance (22°23′43″ S, 69°31′40″ W): a camp area at 1268 m altitude, 15 km east of Maria Elena town. This place is used as a bathing area by local people. The dominant woody species are *Prosopis alba* and *Atriplex atacamensis*. Mean annual precipitation is 0·3 ± 0·2 mm and occurs in winter. (4) Chiu-Chiu (22°18′01″ S, 68°38′26″ W): site located at 2534 m altitude, 10 km west of the Chiu-Chiu town. In this site, a large fraction of the land bordering the Río Loa is cultivated with alfalfa (*Medicago sativa*) and vegetables (carrots, lettuce, celery, garlic and others). A common practice in the area is to burn the herbaceous grass *Distichlis spicata* and the fox-tail *Cortaderia atacamensis* to open land for agriculture. Very few woody shrubs were observed. Mean annual precipitation is 5·4 ± 2·4 mm and occurs in summer. (5) Río Salado (22°16′37″ S, 68°12′59″ W): this site is in the Puna belt of the Cordillera de Los Andes (Villagrán *et al*., 1981) at 3108 m alitude. The dominant vegetation is a sparse cover of small thorny shrubs such as *Chuquiraga atacamensis* and *Fabiana densa*. Mean annual precipitation is 62·3 ± 13·5 mm and occurs in summer. (6) Arroyo Coya (22°25′58″ S, 68°08′32″ W): this site is also in the Puna belt of the Cordillera de Los Andes at 3782 m altitude. Here the dominant species are the *tolas Parastrephia lucida*

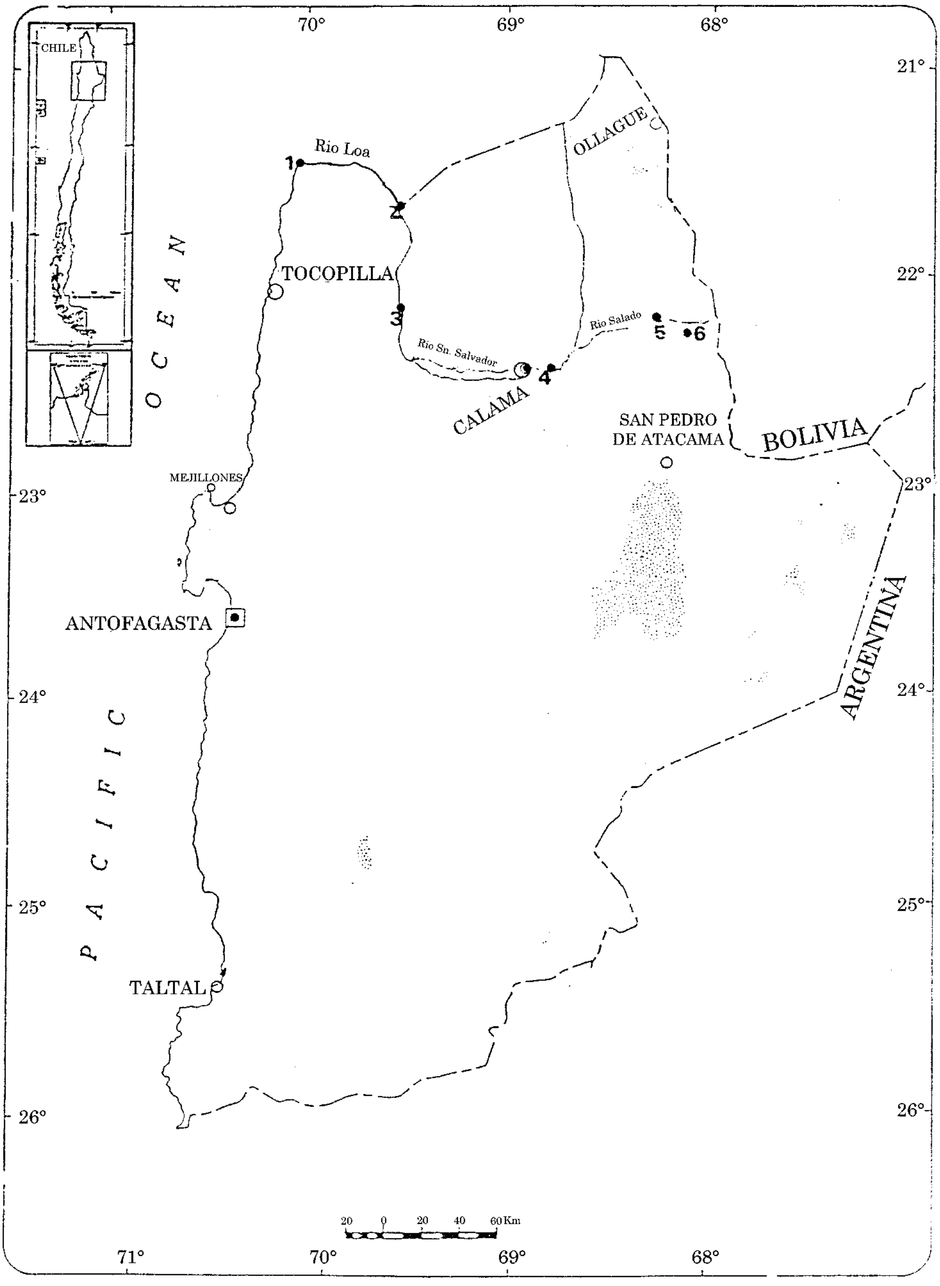

Figure 1. Map showing the study sites along the Río Loa, Atacama Desert, Chile. 1 = Desembocadura Río Loa; 2 = Quillagua; 3 = Chacance; 4 = Chiu-Chiu; 5 = Río Salado; 6 = Arroyo Coya.

and *Parastrephia quadrangularis* forming a shrubland locally known as *tolar*. Mean annual precipitation is 141·6 ± 8·8 mm and occurs in summer.

None of the sites receive significant water from the coastal fogs, and the two highest sites likely receive additional water from snowfall, but no data is available.

Survey of vascular plant species

In each site all vascular plants in an area of *c*. 2 km^2 were collected for taxonomical determination at the Herbaria of the Universidad de La Serena and Universidad de Conceptción. The nomenclature of plant species follows Marticorena (1990) and Marticorena & Quezada (1985), except for Cactaceae which follows Hoffmann (1989), the genera *Baccharis* (Reiche, 1905), *Lilaeopsis* (Squeo *et al*., 1994) and *Lycium* (Bernardello, 1986).

Plant sampling

Plant sampling in Desembocadura Río Loa, Quillagua and Chacance was done during August 1996 (late winter), whereas Chiu-Chiu, Río Salado and Arroyo Coya were sampled during November 1996 (spring). To determine tree, shrub and perennial herbaceous cover, four parallel lines (each 75 m long) located 15 m apart were used in two stands for each site; each line had 150 points at 50-cm intervals. Plant cover was determined using the point intercept technique (Bonham, 1990).

Soil sampling

In each of the three lowland sites (Desembocadura Río Loa, Quillagua and Chacance) a soil sample from the top 10 cm (*c*. 1 kg) was taken from under the canopy of three randomly chosen *Prosopis* trees. Three soil samples were taken in the open at least 5 m away from the *Prosopis* canopy. Because in the other three sites *Prosopis* was too scarce or absent, three soil samples were taken in each stand. Hence, six soil samples were collected in each site. Since soils underneath tree canopies have usually higher nutrient contents, data reported here for the three lowland sites correspond to the soil samples taken in the open only. The samples were transported to the laboratory for chemical analysis. The pH was determined in a 1:5 (w/v) suspension of soil in water. Organic matter was calculated from organic carbon estimated by oxidization with dichromate in the presence of H_2SO_4, without application of external heat. Electrical conductivity was determined by a saturated-paste method. Available nitrogen was extracted with 2 M KCl. Available phosphorus was extracted with a 0·5 M $NaHCO_3$ solution at pH 8·5 (Olsen's method). Available potassium was extracted with 2 M ammonium acetate at pH 7·0. Calcium and magnesium levels were determined by atomic adsorption spectrophotometry and via humid calcination with a nitropercloric mixture. Available arsenic, boron and lithium were extracted by a saturated-paste method and then determined by atomic adsorption spectrophotometry. Soil texture was determined by the Bouyoucos' densimeter method (see Dewis & Freitas (1984) for a detailed description of the soil chemical analyses mentioned above).

Standing crop of herbaceous layer

Distichlis spicata is a perennial grass species which is present, except for Arroyo Coya, along the transect studied and is one of the more abundant herbaceous species. The other species have a narrower distribution, either restricted to low or highlands, or patchly distributed. Hence, we considered that *D. spicata* could be a good indicator of standing crop of the herbaceous layer along the Río Loa transect. For Arroyo Coya we sampled the grass *Deyeuxia breviaristata* instead of *D. spicata*. In each site, we randomly placed four 30 cm × 30 cm quadrat frames in patches of *D. spicata* or *D.*

Table 1. *Soil texture along the altitudinal gradient of the Río Loa II Region, Chile. Values are means (±1 SE)*

Site	Textural class	Sand (%)	Silt (%)	Clay (%)
Desembocadura	Sandy loam	79·07 (0·97)	4·62 (0·76)	16·31 (0·75)
Quillagua	Sandy loam	77·67 (2·89)	6·95 (2·08)	15·37 (1·21)
Chacance	Sandy loam	73·64 (3·76)	8·63 (2·16)	17·70 (2·18)
Chiu-Chiu	Sandy loam	80·64 (0·86)	5·59 (0·85)	13·77 (0·95)
Río Salado	Loamy sand	84·20 (0·52)	5·25 (0·33)	10·53 (0·35)
Arroyo Coya	Loamy sand	81·55 (1·63)	5·23 (0·38)	13·22 (1·33)

breviaristata (Arroyo Coya). Plants inside the quadrats were harvested at ground level and deposited in paper bags. Plants were then oven-dried at 50°C for 72 h in the laboratory; the dry material was then weighed to the nearest mg on a Sartorius scale. To estimate the actual standing crop, the values of dry matter were multiplied by the cover of the species in each site.

Results

Chemical characteristics of soil samples

Soil texture of the four lower sites (0–2500 m) is sandy loam, while in the two higher sites (over 3000 m) the soil texture is loamy sand (Table 1). Sites below 1500 m had on average less than 80% sand whereas the sites above 2500 m had over 80% sand. The mean ± 1 SE for the elements analysed in the soil samples collected in the study sites are shown in Table 2. Concentrations of Ca and Mg follow a similar decreasing trend up the gradient. The soil samples of the four lower sites have one order of magnitude more Ca and Mg than the soil samples of the two higher sites. The highest values for both Ca and Mg are found in the soil samples of Chiu-Chiu. Boron follows a similar trend to Ca and Mg with very high concentrations in Quillagua and Chiu-Chiu (over 100 p.p.m.), two orders of magnitude higher than the values found for the soil samples of the higher sites. Electrical conductivity (soil salinity) decreases with altitude ($F_{(1,4)} = 12{\cdot}7$; $p < 0{\cdot}05$; $r^2 = 0{\cdot}76$). The pH (7–8) goes from neutral to moderately basic except for the soils of Arroyo Coya (pH = 5·1). Organic matter is highest in the soil of the intermediate sites (Chancance and Chiu-Chiu) and lowest at both ends of the altitudinal gradient. Nitrogen and phosphorous peaked in the soils of Chacance and Chiu-Chiu, respectively, decreasing at both ends of the gradient. The levels of K are extremely high in the four lower sites (over 1000 p.p.m.), and one order of magnitude over the values in the two higher sites, thus decreasing with altitude ($F_{(1,4)} = 12{\cdot}2$; $p < 0{\cdot}05$; $r^2 = 0{\cdot}75$). Similarly, Li decreases with altitude ($F_{(1,4)} = 10{\cdot}7$; $p < 0{\cdot}05$; $r^2 = 0{\cdot}73$) with a difference of two orders of magnitude between the ends of the gradient. While the soils of Arroyo Coya and Río Salado have As concentrations below 50 μg kg^{-1}, in Quillagua it is over 3000 μg kg^{-1}. Hence, salinity, lithium, boron and arsenic concentrations increase down the altitudinal gradient.

Flora

A total of 69 vascular plant species were recorded along the climatic (altitudinal) gradient of the Río Loa (Table 3). The highest number of taxa was found in the sites

Table 2. *Chemical characteristics of soils along the altitudinal gradient of the Río Loa, II Region, Chile. Values are means (±1 SE)*

Sites	pH (%)	EC (mS/cm)	OM (%)	Ca (cmol(+) kg^{-1})	Mg (cmol(+) kg^{-1})	N (p.p.m.)	P (p.p.m.)	K (p.p.m.)	B (p.p.m.)	Li (mg kg^{-1})	As ($\mu g\ kg^{-1}$)
Desembocadura	8·07	72·87	0·97	22·58	11·22	7·33	11.00	1241.0	79.11	15.74	414.93
	(0·09)	(18·13)	(0·19)	(1·06)	(4·35)	(1·86)	(0·58)	(419·8)	(37·95)	(6·62)	(142·24)
Quillagua	7·77	65·73	1·53	28·65	7·91	18·00	40·00	1487·3	190·53	19·01	3313·6
	(0·19)	(23·98)	(0·12)	(3·79)	(2·35)	(3·21)	(4·36)	(390·6)	(69·60)	(3·73)	(1161·6)
Chacance	7·23	26·63	2·13	22·33	6·18	65·33	36·00	1254·3	35·84	4·76	623·63
	(0·33)	(15·71)	(1·53)	(2·36)	(4·05)	(35·03)	(16·56)	(635·3)	(21·36)	(3·28)	(229·26)
Chiu-Chiu	7·87	46·17	4·23	30·52	13·86	17·17	46·83	1015·5	106·35	8·26	802·55
	(0·16)	(18·84)	(0·62)	(3·92)	(3·92)	(2·02)	(19·22)	(307·9)	(41·80)	(3·32)	(418·83)
Río Salado	7·10	0·95	0·60	4·39	0·80	17·00	14·17	191·67	1·87	0·11	38·22
	(0·09)	(0·28)	(0·05)	(0·27)	(0·04)	(6·18)	(3·71)	(21·41)	(0·88)	(0·05)	(13·83)
Arroyo Coya	5·12	1·70	1·02	3·58	0·99	16·83	24·33	158·17	1·03	0·10	2·12
	(0·15)	(0·73)	(0·16)	(0·43)	(0·10)	(3·94)	(4·05)	(15·37)	(0·14)	(0·07)	(0·44)

over 3000 m reaching the maximum value at 3108 m (Río Salado). The lowest number of species was found at 1268 m (Chacance) (Fig. 2). Plant species richness tends to increase with altitude; however this trend is marginally significant (Pearson's $r = 0{\cdot}74$; $p = 0{\cdot}094$). The number of introduced and weedy species is relatively constant along the gradient (Fig. 2). However, if we consider the ratio of weeds: total number of species, the greater ratios are found in the lower four sites reaching the maximum value in Chiu-Chiu, the site most affected by agriculture activities.

Families with a higher number of species along the Río Loa are the Asteraceae, Gramineae, Cactaeae, Papilionaceae and Salonaceae (Table 3). *Pluchea absinthioides* and *Baccharis petiolata* (Asteraceae), and the perennial grass *Distichlis spicata* are the species with the widest distribution along the gradient, being present from 0 m up to 3782 m (Table 3). The families Mimosaceae and Chenopodiaceae are present in the four lowland sites (below 3000 m), but they are represented by only one genus, *Prosopis* and *Atriplex*, respectively. The families Cactaceae and Solanaceae, in turn, are present in the highlands over 3000 m.

In regard to life-forms, trees are present from sea level up to 2530 m altitude, disappearing completely at higher altitudes. Low temperatures at high altitudes would limit the presence of trees. Succulent plants are present in the two higher sites (over 3000 m) but mainly in the Río Salado. Cushion plants were found only in Arroyo Coya (3782 m). This life-form is typical of highlands in the Cordillera de Los Andes because it is well adapted to cold environments (Arroyo *et al*., 1988). Shrubs and perennial herbs are represented all along the altitudinal transect, while annual herbs were found only in the two higher sites. However, absence of annual plants in the lowland sites is related to the season in which the survey was done.

The number of species shows a quadratic relationship with annual precipitation ($F_{(2,3)} = 17{\cdot}16$; $p = 0{\cdot}023$; $r^2 = 0{\cdot}92$) (Fig. 3). In general, species richness showed a negative correlation with all the variables characterizing the chemical composition of soils, but only attained marginal significance for K (Pearson's $r = -0{\cdot}78$, $p = 0{\cdot}065$).

Standing crop of the herbaceous layer

There is a significant decrease in standing crop of *Distichlis spicata* with altitude ($F_{(1,3)} = 9{\cdot}5$; $p = 0{\cdot}0538$; $r^2 = 0{\cdot}76$), at a rate of 6·8 g 100 m^{-1}, and it is almost absent above 3200 m. This species is replaced by the perennial grass *Deyeuxia breviaristata* in the upper site (Fig. 4). Species richness tends to be negatively correlated with standing crop of the herbaceous layer, however this trend is marginally significant (Pearson's $r = -0{\cdot}76$, $p = 0{\cdot}080$).

Plant cover

Total plant cover is higher in the four lower sites (over 50%), while in the two higher sites the cover is lower than 40% (Fig. 5). In the four lower sites the dominant species are the perennial grass *Distichlis spicata*, which reaches its maximum cover in Quillagua, and the herbaceous subshrub *Pluchea absinthioides*, with maximum cover in Chacance (Table 4). Other subdominant species are *Atriplex madariagae* in Desembocadura Río Loa, *Atriplex atacamensis* in Quillagua and Chacance, and the exotic juncus *Scirpus californicus* in Chiu-Chiu. *Atriplex* species reach large dimensions in the three lower sites. For instance, in Desembocadura Río Loa, *Atriplex madariagae* is $0{\cdot}98 \pm 0{\cdot}13$ m (mean ± 1 SE) in height and $3{\cdot}22 \pm 0{\cdot}32$ m in diameter; in Quillagua *Atriplex atacamensis* is $2{\cdot}18 \pm 0{\cdot}30$ m in height and $9{\cdot}10 \pm 0{\cdot}49$ m in diameter; and in Chacance *A. atacamensis* is $2{\cdot}72 \pm 0{\cdot}09$ m in height and $7{\cdot}66 \pm 0{\cdot}80$ m in diameter. In Río

Table 3. *Recorded species along the altitudinal gradient of the Río Loa, II Region, Chile (+ indicates presence)*

Species	Family	Desem-bocadura (39 m)	Quillagua (733 m)	Chacance (1268 m)	Chiu-Chiu (2534 m)	Río Salado (3108 m)	Arroyo Coya (3782 m)
Trees							
Geoffroea decorticans (Gill. ex H. et. A.) Burk	Papilionaceae		+				
Prosopis alba Griseb.	Mimosaceae		+	+	+		
Prosopis tamarugo Phil.	Mimosaceae	+					
Schinus molle L.	Anacardiaceae				+		
Succulents							
Echinopsis atacamensis (Phil.) Fried. et Rowl.	Cactaceae					+	
Echinopsis uebelmanniana (Lembcke et Back.) A. Hoffmann	Cactaceae					+	
Eriosyce sp.	Cactaceae					+	
Neoporteria aricensis (Ritter) Don. et Rowl.	Cactaceae					+	
Opuntia conoidea (Back.) A. Hoffmann	Cactaceae					+	
Opuntia ignescens Vaupel	Cactaceae					+	+
Oreocereus leucotrichus (Phil.) Wagenknecht	Cactaceae					+	
Cushions							
Azorella compacta Phil.	Umbelliferae						+
Oxychloe andina Phil.	Juncaceae						+
Urbania pappigera Phil.	Verbenaceae						+
Shrubs							
Acantholippia tarapacana Botta	Verbenaceae					+	
Adesmia atacamensis Phil.	Papilionaceae					+	
Adesmia spinosissima Meyen ex Vogel	Papilionaceae						+
Arundo donax L.	Poaceae		+				
Atriplex atacamensis Phil.	Chenopodiaceae		+	+	+		
Atriplex madariagae Phil.	Chenopodiaceae	+					
Baccharis petiolata D.C.	Asteraceae	+	+	+	+		

Table 3. *(continued)*

Species	Family	Desem-bocadura (39 m)	Quillagua (733 m)	Chacance (1268 m)	Chiu-Chiu (2534 m)	Río Salado (3108 m)	Arroyo Arroyo (3782 m)
Baccharis sp.	Asteraceae				+		
Baccharis tola Phil. spp. *altiplanica*	Asteraceae					+	
Chuquiraga atacamensis O.K.	Asteraceae					+	
Diplostephium meyenii Wedd.	Asteraceae				+		
Ephedra multiflora Phil. ex Stapf	Ephedraceae					+	
Fabiana densa Remy	Solanaceae					+	
Fabiana denudata Miers	Solanaceae					+	
Haplopappus rigidus Phil.	Asteraceae				+		
Lycium humile Phil.	Solanaceae					+	
Lycium stenophyllum Remy	Solanaceae				+		
Mulinum crassifolium Phil.	Umbelliferae						+
Parastrephia quadrangularis (Meyen) Cabr.	Asteraceae					+	
Parastrephia lucida (Meyen) Cabr.	Asteraceae					+	
Perezia atacamensis (Phil.) Reiche	Asteraceae					+	
Pluchea absinthioides (H. et. A.) DC.	Asteraceae	+	+	+	+	+	
Nolana peruviana (Gaud.) Johnst.	Nolanaceae	+					
Unknown	Verbenaceae					+	
Annual herbs							
Cistanthe sp.	Portulacaceae				+		
Polypogon australis Brongn	Poaceae					+	
Sisymbrium sp.	Brassicaceae					+	
Urtica trichantha (Wedd.) Acev. ex Navas	Urticaceae						+
Perennial herbs							
Arenaria rivularis Phil.	Caryophyllaceae						+
Baccharis juncea (Lehm.) Desf.	Asteraceae	+	+	+	+	+	
Bromus catharticus Valh	Poaceae				+		
Caiophora superba Phil.	Loasaceae					+	

Table 3. *(continued)*

Species	Family	Desem-bocudura (39 m0	Quillagua (733 m0	Chacance (1268 m)	Chiu-Chiu (2534 m)	Río Salado (3108 m)	Arroyo Coya (3782 m)
Calceolaria stellariifolia Phil.	Scrophulariaceae						+
Carex gayana Desv.	Cyperaceae						+
Convolvulus arvensis L.	Convolvulaceae				+		
Cortaderia atacamensis (Phil.) Pilger	Poaceae				+	+	
Cotula mexicana (DC.) Cabr.	Asteraceae					+	
Cyperus sp.	Cyperaceae						+
Deyeuxia breviaristata Wedd.	Poaceae						+
Deyeuxia curvula Weed.	Poaceae						+
Distichlis spicata (L.) Greene	Poaceae	+	+	+	+	+	
Heliotropium curassavicum L.	Boraginaceae		+				
Imperata condensata Steud.	Poaceae				+		
Juncus balticus Willd.	Juncaceae				+	+	
Lilaeopsis macloviana (Gand) A. W. Hill	umbelliferae					+	
Medicago sativa L.	Papilionaceae		+		+		
Plantago lanceolata L.	Plantaginaceae				+		
Puccinellia sp.	Poaceae					+	
Pycnophyllum bryoides (Phil.) Rohrb.	Caryophyllaceae					+	+
Ranunculus cymbalaria Pursh	Ranunculaceae				+		
Scirpus californicus (C.A. Mey.) Steud.	Cyperaceae	+	+	+			
Senecio rosmarinus Phil.	Asteraceae						+
Valeriana urbanii Phil.	Valerianaceae						+
Werneria glaberrima Phil.	Asteraceae						+
Werneria pinnatifida Remy	Asteraceae						+
Number of families		6	7	5	10	14	12
Number of genera		7	10	6	16	28	16
Number of species		8	11	7	20	31	18

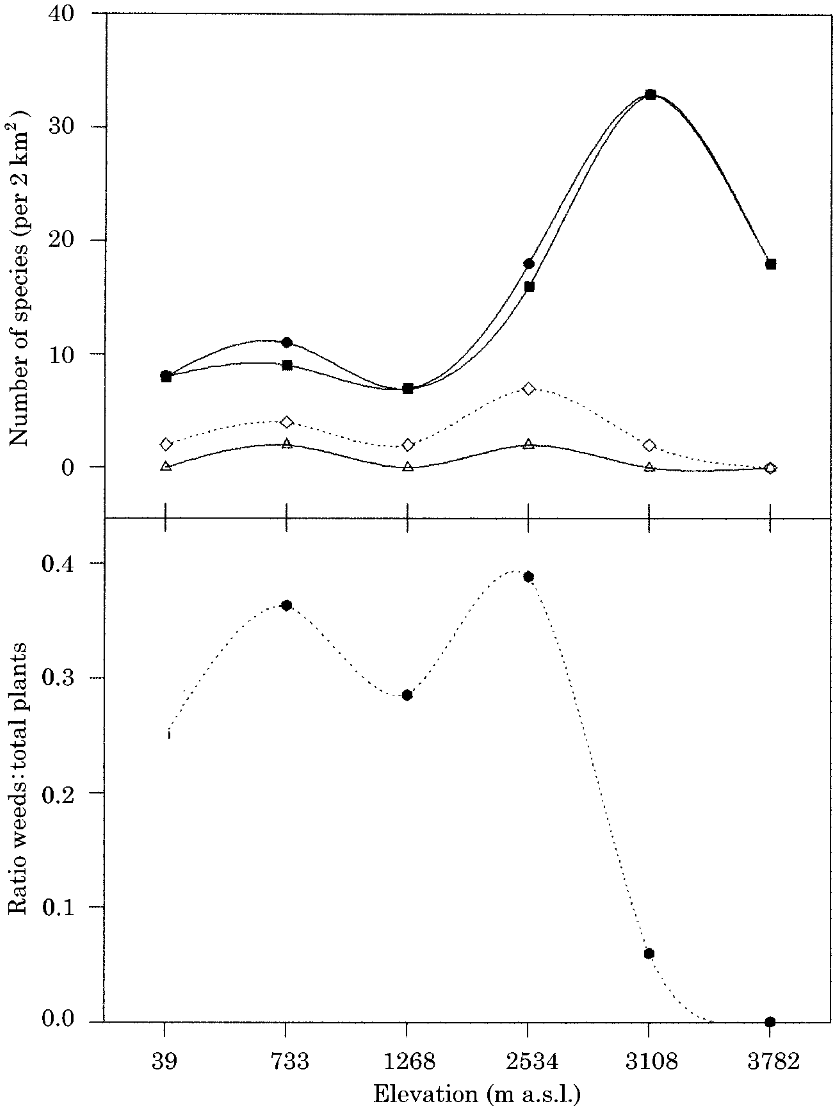

Figure 2. (a) Number of plant species {(●) = total species; (■) = natives; (△) = introduced; (◇) = weeds} and (b) the ratio of weeds to total number of plant species along the altitudinal gradient of the Río Loa, Atacama Desert, Chile.

Salado the dominant species is *Fabiana densa* (6·2% cover) and a Verbenaceae (5·7% cover), whereas in Arroyo Coya the dominant species are the *tolas Parastrephia lucida* (27·2% cover) and *Parastrephia quadrangularis* (5·6% cover). Arboreal species were found only in the three lower sites: *Prosopis tamarugo* (2·35 ± 0·17 m height) in Desembocadura Río Loa, *Prosopis alba* (14·72 ± 0·91 m height) and *Geoffroea decorticans* (4·00 ± 0·32 m height) in Quillagua, and *P. alba* (10·5 ± 0·74 m height) in Chacance.

Discussion

Plant species richness along the rainfall gradient tends to follow the humpbacked

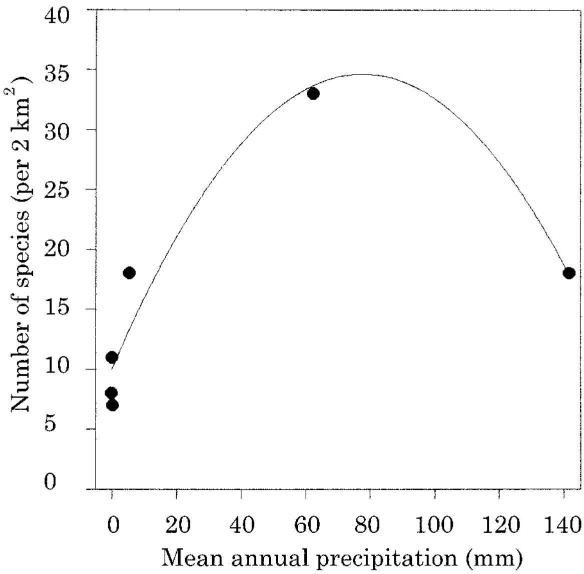

Figure 3. Relationship between the number of plant species and the mean annual precipitation in the altitudinal gradient of the Río Loa, Atacama Desert, Chile. Curve fitted is $y = 9{\cdot}97 + 0{\cdot}63x - 0{\cdot}0041x^2$.

species diversity curve proposed for plants and animals (Tilman, 1982; Tilman & Pacala, 1993). Among the factors analysed, mean annual rainfall accounts for a large part of the variation (92%) in plant species richness. A similar pattern was found by Arroyo *et al.* (1988) considering a broad biogeographical scale. The low number of species in the lower sites of the altitudinal gradient would be a consequence of the high

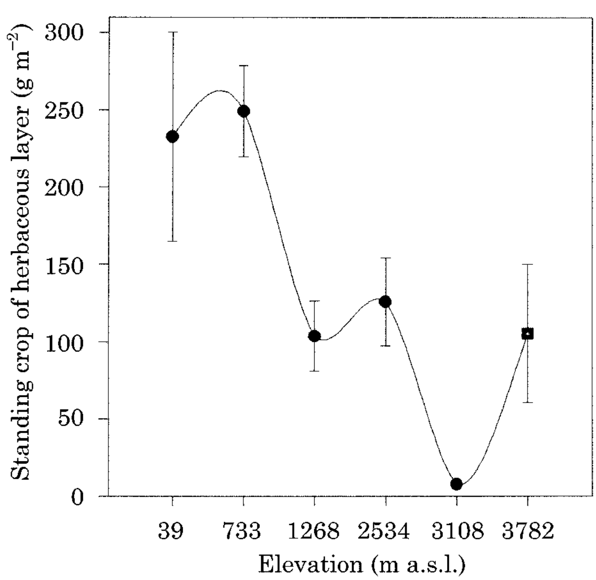

Figure 4. Net primary production of herbaceous layer (g m^{-2}) along the altitudinal gradient of the Río Loa, Atacama Desert, Chile. (●) = *Distichlis spicata*; (■) = *Deyeuxia breviaristata*.

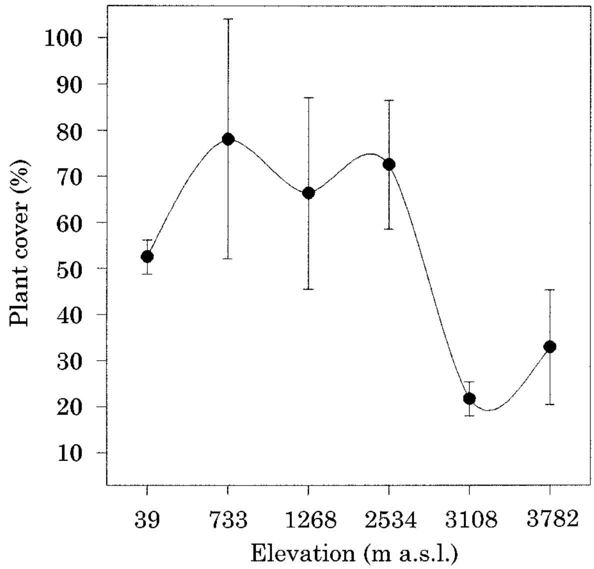

Figure 5. Plant cover (%) along the altitudinal gradient of the Río Loa, Atacama Desert, Chile.

content of toxic elements in the soil. The richest site is Río Salado, which is probably a consequence of its ecotonal characteristics. This site shares species with both low and high altitude sites, but in addition it possesses a large fraction of species (70%) restricted to it, especially cacti and shrubs. This site is located in the Puna belt, as distinguished by Villagrán *et al.* (1981), which is characterized by possessing a large number of restricted-range endemic species as a consequence of the altitudinal penetration of the Atacama Desert. The further decrease in species richness with altitude is probably a consequence of the increasingly harsh environment experienced at high elevations, with nutrient-poor soils and low temperatures. However, more sites located above 4000 m are needed in order to check for the generality of this decreasing richness pattern. The species richness does not follow the humpbacked species diversity curve when considering other variables related to resource abundance such as nutrient concentration in the soil.

Along the altitudinal gradient the sites located between 0 m and 1500 m showed a low richness of vascular plants, high plant cover and high standing crop of the herbaceous layer. This zone of the gradient is characterized by extremely low precipitation which occurs in winter, soils with high concentrations of boron, lithium and arsenic and high soil salinity. High concentrations of Li, B and As are considered toxic for several plant species (Primo-Yúfera & Carrasco-Dorrién, 1973), and Rundel *et al.* (1991) have detected high levels of Li and B in plant tissues collected along the Río Loa. Chemical characteristics of soils are probably greatly affected by agriculture activities, especially in Quillagua, because irrigation water from the Río Loa contains high levels of B, Li and As (Rundel *et al.*, 1991). Plants are restricted to the area influenced by the Río Loa; precipitation is too low to sustain plants out of this area. The most abundant species in the lower part of the gradient are *Pluchea absinthioides* and *Distichlis spicata*. Both species are considered as weeds and they are widely distributed in Chile (Matthei, 1995). This association has a wide distribution in oases and riparian habitats of the Atacama Desert (Gajardo, 1993) and is described as a plant formation which is typical of areas disturbed by man, either for agriculture or grazing activities. Riparian habitats have been shown to be favorable sites for invasion of alien plant species (e.g. Pysek & Prach, 1993; Planty-Tabacchi *et al.*, 1995). *Pluchea*

Table 4. *Recorded plant cover (%) along the altitudinal gradient of the Río Loa, II Region, Chile. Values are means (±1 SE)*

Species	Desem-bocadura (39 m)	Quillagua (733 m)	Chacance (1268 m)	Chiu-Chiu (2534 m)	Río Salado (3108 m)	Arroyo Coya (3782 m)
Trees						
Geoffroea decorticans (Gill. ex H. et. A.) Burk.		4·78 (4·78)				
Prosopis alba Griseb.		8·70 (8·70)	2·76 (2·76)			
Prosopis tamarugo Phil.	2·26 (2·26)					
Succulents						
Opuntia conoidea (Back.) A. Hoffmann					0·67 (0·00)	
Shrubs						
Atriplex atacamensis Phil.		10·62 (6·41)	7·98 (7·98)			
Atriplex madariagae Phil.	9·33 (3·17)					
Baccharis petiolata D.C.	2·17 (1·09)		0·15 (0·15)			
Chuquiraga atacamensis O.K.					3·78 (1·93)	
Ephedra multiflora Phil. ex Stapf					1·09 (0·76)	
Fabiana densa Remy					6·22 (0·84)	
Pluchea absinthioides (H. et. A.) DC.	2·08 (2·08)	36·71 (27·75)	44·10 (1·30)	26·03 (3·02)		
Parastrephia lucida (Meyen) Cabr.						27·21 (15·68)
Parastrephia quadrangularis (Meyen) Cabr.						5·62 (5·21)
Unknown					5·71 (0·67)	
Perennial herbs						
Baccharis juncea (Lehm.) Desf.		0·44 (0·44)		0·07 (0·07)		
Bromus catharticus Valh				2·29 (2·29)		
Cortaderia atacamensis (Phil.) Pilger				4·50 (4·50)		
Deyeuxia breviaristata Wedd.						0·06 (0·06)
Distichlis spicata (L.) Greene	32·52 (3·26)	16·77 (10·17)	11·35 (8·58)	24·93 (10·18)	2·27 (2·27)	
Juncus balticus Willd.					0·17 (0·17)	
Lilaeopsis macloviana (Gand) A. W. Hill					0·08 (0·08)	
Medicago sativa L.				3·54 (3·54)		
Plantago lanceolata L.				0·74 (0·74)		
Scirpus californicus (C.A. Mey.) Steud.	4·08 (3·90)			10·47 (3·00)		
Total plant cover	52·45 (3·71)	78·08 (25·98)	66·33 (20·78)	72·57 (14·01)	21·68 (3·69)	32·94 (12·50)

absinthioides is a rhizomatose perennial subshrub distributed in South America, being frequent in sandy wet soils of Bolivia, Uruguay, Argentina and Chile. In 1848 Remy cites this species for Chile (Matthei, 1995). This species is found on roadsides, on the margins of cultivated lands and on saline soils. *Distichlis spicata* is a perennial grass with gross rhizomes, widely distributed in America from the United States to Santa Cruz where it inhabits saline soils. This species is a weed in northern Chile, being present in orchard crops and roadsides (Matthei, 1995). The characteristics of these species allow them to colonize the harsh environment along the Río Loa. They cover extensive areas and their rhizomatose system probably prevents the establishment of other species.

A common practice of local people to open areas for cultivation is to burn patches of *D. spicata* and the fox-tail *Cortaderia atacamensis*. After burning, the old fields are colonized by *P. absinthioides*. In recently-burned areas *P. absinthioides* was found to be in active vegetative growth, while in nearby old stands it was flowering (pers. obs.). Those sites in or close to human settlements had the higher proportion of weeds compared to the total number of plant species. Gajardo (1993) points out that in this association it is very difficult to distinguish between original and man-induced vegetation. This is due in part to the very localized and restricted distribution of areas capable of sustaining life below 3500 m, and because human use and transformation of these areas date back to pre-Columbian times (Nuñez, 1971).

The plant community of Chiu-Chiu is more similar to the sites below 1500 than to the plant community of the higher sites, where thorny shrubs and tolas are the dominant life-forms. Chiu-Chiu is strongly influenced by the Río Loa and agricultural activities, which is reflected in the chemical characteristics of the soils. The two higher sites are more acidic and depauperate in nutrients than the soils of Chiu-Chiu. Indigenous people in the area possess a sophisticated knowledge of plants. Aldunate *et al.* (1983) report that inhabitants of the indigenous community of Toconce have uses (i.e. forage, medicinal, fuel, ritual, construction) for 89% of the 134 native plant species occurring in the surrounding area. *Pluchea absinthioides* and *D. spicata*, which are the dominant species in sites below 2500, are almost absent in the highlands. Arboreal species are present only in the lower sites, being replaced by tall columnar cacti in the highlands. The Río Loa acts as a corridor for the distribution of lowland plant species, however its influence decreases at higher altitudes. In the Cordillera de Los Andes summer precipitation is much more important than the effect of the Río Loa, and the low temperatures and the hyperarid conditions of the Atacama Desert act as an effective barrier for migration of plants from the lowlands (Villagrán *et al.*, 1981). The azonal bog vegetation makes an important contribution to species richness in the higher sites.

Higher productivity of plants in the lower part of the altitudinal gradient would be the result of several factors, namely abundant supply of water year-round from the Río Loa, warm temperatures and high levels of organic matter and nutrients in the soils. Low productivity of plants in the higher part of the altitudinal gradient is probably caused by low temperature, low rainfall and low soil nutrient levels. However, these environmental conditions would facilitate the coexistence of a greater number of plant species.

Differences in rainfall timing (winter and summer), water supply for plants (river and rainfall), water quality, temperature and differences in land use by man have probably all had a great influence in structuring the plant communities along the altitudinal gradient of the Río Loa, in addition to the rainfall gradient and the nutrient composition in soils.

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