Oecologia (Berl.) 46, 196–200 (1980)

Oecologia

Patterns of Drought Response in Leaf-Succulent Shrubs of the Coastal Atacama Desert in Northern Chile

P.W. Rundel, J. Ehleringer[1], H.A. Mooney[2] and S.L. Gulmon[2]

Department of Ecology and Evolutionary Biology, University of California, Irvine 92717, USA
[1] Department of Biology, University of Utah, Salt Lake City, Utah 84112, USA
[2] Department of Biological Sciences, Stanford University, Stanford, California 94305, USA

Summary. Despite the extrame aridity of the coastal Atacama Desert in northern Chile, sparse communities of leaf succulent shrubs and small cacti are regularly present. While most shrub species have small succulent leaves and accumulate high concentrations of salts in their tissues, the variable rooting patterns and mixed dominance of CAM and C_3 species indicates a significant divergence in adaptive strategies. All dominant shrubs are readily surviving extended drought, but some species are much better able than others to maintain active growth and flowering. Regular flowering may not be a prerequisite for shrub population maintenance since large piles of viable seeds are present under the canopies of many species.

While the water relations of desert plants has been the subject of an extensive body of literature, few data are available on the adaptations of plants to extreme aridity in desert areas with a mean of less than 25 mm yr^{-1} precipitation. Only two desert regions of the world have such conditions. One such region of the world, the central Sahara and Arabian Deserts, lack perennial plants altogether and support only annual plants after rare events of significant rainfall (Stocker 1976). In the other region forming much of the central Atacama Desert, however, perennial vegatation may be locally abundant (Fig. 1).

The Atacama Desert of northern Chile is the driest desert region in the world. At Chañaral (lat. 26° 30′ S) the mean annual precipitation drops below 25 mm yr^{-1}, with frequent droughts extending from 2 up to 10 years without measurable precipitation. In Arica (18° 28′ S) near the Peruvian border the mean precipitation for a 44 year record is only 0.6 mm yr^{-1}. Inland valleys from the area of Chañaral north are completely free of vegetation of any type with the exception of a few small areas with ground water. Between Chanãral and Antofagasta (23° 29′ S) however, a sparse zone of vegetation is present extending as a broken band along the seaward slopes of the coast ranges. Where the escarpment of the coast ranges is abrupt and high, a well-developed vegetation zone develops at 300–800 m elevations, associated with the limits of a characteristic fog zone (Reiche 1911; Rundel and Mahu 1976; Rundel 1978). Along the coast at lower elevations where ground fog and associated moisture condensation are virtually absent, however, perennial vegetation development is still locally present. In this paper we report on the habitat distribution and water relations of the dominant vegetation in this arid coast belt between Chañaral and Antofagasta, with emphasis on patterns at Pan de Azucar, a coastal valley at latitude 26° 15′ S.

Materials and Methods

Field measurements were carried out in northern Chile in September and October, 1978. The coastal study site at Pan de Azucar is approximately 15 km inland at an elevation of 100 m. Shrub community structure of four stands at Pan de Azucar, including both bajada and wash communities, were sampled to determine the relative composition of mature individuals of each species, the percentage of shrubs of each species in good or excellent vigor, and the mean vigor class of living shrubs. Dawn and midday water potentials were measured using a pressure bomb, while osmotic potentials and water potentials of cactus tissue were determined with thermocouple psychrometer measurements.

Leaf absorptances of dominant shrubs to solar radiation in the 400–700 mm band were measured with an Ulbricht integrating sphere (23 cm dia.) in a manner similar to that described by Ehleringer and Björkman (1978). Rooting profiles of dominant shrub species were determined by field geotome excavation. Soil conductivity profiles were measured with a conductivity probe on samples of 2 g soil mixed with 3 g of distilled water. Leaf elemental analyses were carried out using neutron activation analysis, and ash contents of fresh leaf tissue were determined from samples heated in a muffle furnace for 3 hr at 500° C.

Taxonomy follows Johnston (1929, 1936) with the exception of the Cactaceae which follows Backeberg (1976).

Results

The coastal vegetation north of Chañaral is extremely sparse and variable in pattern, but is well represented by its distribution at Pan de Azucar. Here scattered vegetation occurs from the coast to nearly 20 km inland near the crest of the first coastal range at an elevation of approximately 300 m. East of this crest vegetation is totally lacking.

Two plant communities can be recognized at Pan de Azucar and adjacent coastal areas, a low cactus "garden" community and a leaf succulent shrub community. The cactus "gardens" consist of virtual monospecific stands of low globular stems of *Copiapoa* on dry bajada slopes. At Pan de Azucar the dominant is *C. cinerea* var. *columna-alba* (= *C. columna-abla* Ritter) which

0029-8549/80/0046/0196/$01.00

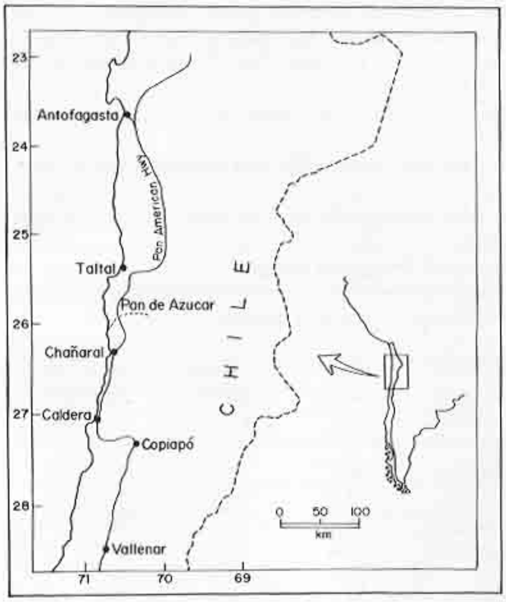

Fig. 1. Location of Pan de Azucar and adjacent sites in the Atacama Desert in northern Chile

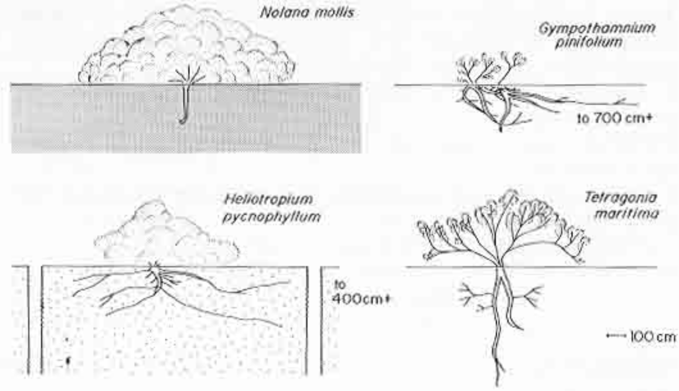

Fig. 2. Rooting patterns of dominant shrub species at Pan de Azucar. Stippled areas indicate relative densities of very fine roots. See text for discussion

forms dense local stands with an average of two plants per square meter. Individual mature plants reach 40 cm or more in height and 20 cm in diameter. Between Taltal and Paposo (Fig. 1) *Copiapoa haseltoniana* (= *C. cinerea* ssp. *haseltoniana*) forms very extensive stands over the broad coastal plain (see Rundel and Mahu 1976; Mooney et al. 1977). *Copiapoa* stands at both Pan de Azucar and Paposo reach their greatest density at about 100 m elevation and virtually or completely drop out along the immediate coast.

Slightly less xeric bajada slopes and washes along the coast where some sheet flow would be present from upslope arroyos during rare precipitation events support an open shrub community stongly dominated by low, semi-woody species with succulent leaves. Five shrub species are particularly important at Pan de Azucar: *Nolana mollis* (Nolanaceae), *Gypothamnium pinifolium* (Compositae), *Heliotropium pycnophyllum* (Boraginaceae), *Tetragonia maritima* (Aizoaceae) and *Eremocharis fruticosa* (Umbelliferae). While a variety of other species may be present, overall diversity is low and total plant coverage rarely exceeds 1–2%.

All of the above dominant shrubs at Pan de Azucar are leaf succulents. The small succulent leaves of these species are typically ovate to linear in shape with little leaves 1.5–3.0 mm in width (Table 1). The oval leaves of *Tetragonia maritima* and long pinnately dissected leaves of *Polyachrus fuscus* are broader and flattened, but still succulent. *Heliotropium* and *Gypothamnium* are somewhat less succulent than other species. The leaves are whorled in most species so that leaf angles are somewhat variable. Mean leaf angle varies from 23–79° (Table 1). Leaves of most species have leaf absorptances ranging from 74–84%. Two notable exceptions are *Nolana incana* which has a value of 68% and *Encelia canescens* which has a value of 46%. Leaves of both species are covered by thick white pubescence.

Considering the extreme aridity at Pan de Azucar, midday water potentials of the four dominant leaf succulent shrubs were not extraordinarily low. The water potentials of the most actively growing individuals of all four species were greater than −3.0 MPa (Table 2). Water potentials decreased steadily as shrub condition became poorer in four vigor classes ranging from excellent to dormant (see Table 2). The extreme water potential measured was −5.99 MPa in a virtually leafless *Heliotropium*. Dawn water potentials were −1.8 to −2.2 MPa. *Copiapoa* had a midday water potential of −1.24 MPa as determined by thermocouple psychrometry.

Tissue osmotic potentials of the dominant shrub species were relatively high, ranging from −2.3 MPa in *Gypothamnium* to −3.3 MPa in *Tetragonia*. The osmotic potential of *Copiapoa* was −1.3 MPa (Table 2).

A differential tolerance of drought stress among shrubs can be seen by comparing the relative density of all living shrubs with that of shrubs in good or excellent vigor during the period of

Table 1. Leaf Characteristics of dominant perennial plants at Pan de Azucar

Species	Family	Leaf type	Leaf width (mm)	Leaf angle (°)	Leaf absorptance
Nolana mollis	Nolanaceae	succulent	2.0	58.8	0.779
Gypothamnium pinifolium	Compositae	semi-succulent	1.5	64.1	0.827
Heliotropium pycnophyllum	Boraginaceae	semi-succulent	3.0	—	0.841
Tetragonia maritima	Aizoaceae	succulent	6.9	22.8	0.768
Eremocharis fruticosa	Umbelliferae	succulent	2.0	36.0	—
Polyachyrus fuscus	~~Valerianaceae~~ Compositae	succulent, dissected	6.8	79.2	0.743
Senecio almediae	Compositae	semi-succulent, dissected	2.3	54.8	0.750
Nolana incana	Nolanaceae	succulent	1.8	—	0.679
Ophyosporus triangularis	Compositae	semi-succulent	2.9	38.0	—
Encelia canescens	Compositae	entire, pubescent	18.5	54.2	0.457

Table 2. Water relations of dominant shrub species at Pan de Azucar, 14 September to 2 October 1978. All values are in MPa, with shrub sample sizes in parentheses. Vigor classes are as follows:
4 = Excellent condition, with little dead foliage and current or probable future flowering.
3 = Good condition, with some dead foliage but current or probable future flowering.
2 = Poor condition, with considerable dead and dying foliage and little probability of flowering.
1 = Virtually dormant, with little green foliage.

	Mid-day $\bar{x}$ ψxylem	Mid-day Range of ψxylem	ψs	Dawn $\bar{x}$ ψxylem
Nolana mollis				
Class 4	2.31 (1)		2.60 (4)	1.83 (4)
Gypothamnium pinifolium				
Class 4	2.46 (3)	2.38–2.52		
Class 3	3.05 (9)	2.72–3.23	2.32 (4)	2.18 (2)
Class 2	3.43 (8)	3.30–3.81		
Class 1	4.05 (3)	3.74–4.32		
Heliotropium pycnophyllum				
Class 4	2.91 (2)	2.89–2.93		
Class 3	3.48 (3)	3.43–3.54	3.05 (3)	
Class 2	3.80 (3)	3.74–3.87		
Class 1	5.01 (5)	4.08–5.99		
Tetragonia maritima				
Class 4	2.93 (10)	2.72–3.06	3.30 (4)	2.09 (3)
Class 3	3.31 (6)	3.12–3.54		
Class 2	3.77 (6)	3.47–4.15		
Copiapoa cinerea var. *columna-alba*	1.24 (4)		1.34 (4)	

our field work (Table 3). Although *Gypothamnium* was the dominant species with over 40% of all plants sampled, it comprised only 11% of the vigorous shrubs. *Nolana mollis* was suffering less from drought conditions with 25% of the total shurbs but two-thirds of the vigorous individuals. *Heliotropium*, like *Gypothamnium*, showed indications of drought stress. Shrubs in poor condition did not appear to be dying, however, but instead were dropping their foliage and becoming dormant.

The four dominant shrub species in our study area at Pan de Azucar show quite divergent patterns of rooting (Fig. 2). In *Nolana mollis* there is a single main tap root, 20 mm in diameter at the soil surface which extends downwind for approximately 50 cm with no major branching. An extensive network of fine rootlets passes through the entire soil profile for a radius of 100 cm from the center of the shrub and to a depth of 40 cm. These fine rootlets average 0.35 mm in diameter. At the time of our sampling, all of these fine rootlets were dead below the upper 2 cm of soil but above this level live root hairs were present (verified by SEM examination of field-fixed tissues).

In *Gypothamnium pinifolium* the root system is much more massive and variable in structure. The root biomass of the small shrub excavated was greater than the above-ground biomass, but since this species readily resprouts from its root crown, it is difficult to know if this pattern is typical. Multiple major roots curl both laterally and downward from the root crown, branching repeatedly into secondary roots. Most fine roots were found in the upper 10 cm of soil. While the depth of rooting is very shallow, individual roots may extend laterally 5–10 m or more from the root crown.

Table 3. Community structure of perennial plants (excluding cacti) in four sampled stands at Pan de Azucar, including 487 individuals. Vigorous shrubs are considered those in Vigor Class 3 and 4. Vigor classes are as follows:
4 = Excellent condition, with little dead foliage and current or probable future flowering.
3 = Good condition, with some dead foliage, but current or future probable flowering.
2 = Poor condition, with considerable dead or dying foliage and little probability of flowering.
1 = Virtually dormant, with little green foliage.

	Relative density		
	All shrubs (%)	Healthy shrubs (%)	Mean shrub vigor class (1–4 scale)
Gypothamnium pinifolium	40.5	11.0	1.5
Nolana mollis	25.3	66.3	3.2
Heliotropium pycnophyllum	21.1	4.3	1.3
Tetragonia maritima	6.8	6.1	2.1
Nolana incana	1.6	2.4	2.6
Eremocharis fruticosa	1.6	4.3	2.8
Polyachyrus fuscus	1.0	2.4	2.8
Ophyosporus triangularis	0.8	1.2	2.2
Deuterocohnia crysantha	0.6	0.0	1.3
Encelia canescens	0.4	0.6	2.0
Senecio almediae	0.2	0.6	3.0
Cynanchum viride	0.2	0.0	2.0
Euphorbia lactiflua	0.2	0.6	3.0

The root system of *Heliotropium pycnophyllum* is intermediate in many ways between *Nolana* and *Gypothamnium*. A short thick tap root in *Heliotropium* branches into numerous secondary roots which extend laterally to short distance beyond the canopy. These laterals in turn give rise to an open network of fine roots 1–2 mm in diameter which in turn produce very fine feeder roots from 6–60 cm depth in the profile and extending laterally up to 400 cm from the center of the canopy. The density of these feeder roots, all dead during our excavation, was much less than that of the fine rootlets of *Nolana*.

The rooting pattern of *Tetragonia maritima* is phreatophytic in structure. A branched tap root extends straight downward to depths beyond the range of our excavation. At 60 cm depth the tap root was still one cm in diameter. Few lateral roots are present and none of these extend beyond the canopy. Fine feeder roots are present to a depth of 40 cm, but the density of these is very low except in the 10–20 cm level.

Characteristic white to gray ash piles are present under the canopies of all of the dominant shrubs at Pan de Azucar. These salts build up as a result of gradual decomposition of old leaves and organic debris beneath the canopies. Accumulated ash piles under dead shrubs may be 50 mm or more in depth and remain for years.

Although the soils are non-saline, all of these succulent-leaved shrubs concentrate salts in ash piles. A typical conductivity profile from the center of the canopy outward from *Nolana mollis* indicates a concentration decrease of 60 times for the upper 2 cm of soil (Table 4). At a depth of 10–12 cm in the soil profile, the concentration gradient is much less steep. In a sample of eleven canopies of *Nolana* the range of conductivity values for the 0–2 cm soil horizon under the canopy ranged from 0.142–0.665 meq (NaCl) g^{-1} soil. No correlation of shrub size and conductivity level was present; high conductivity was related to the presence

Table 4. Conductivity profiles under canopies of dominant shrubs at Pan de Azucar. All values are in m-equiv. g^{-1} fresh weight. Mean moisture content of soil is approximately 5%

	Center of Canopy		Edge of Canopy		Outside Canopy	
	0–2	10–12	0–2	10–12	0–2	10–12
Nolana mollis	0.300	0.057	0.262	0.074	0.005	0.012
Gypothamnium pinifolium	0.118	0.133	0.094	0.024	0.004	0.004
Heliotropium pycnophyllum	0.068	0.044	0.062	0.015	0.006	
Tetragonia maritima	0.022	0.011	0.045	0.024	0.008	0.010
Eremocharis fruticosa	0.109					

Table 5. Leaf content of mineral ions and ash content for dominant shrubs at Pan de Azucar. All values in % dry weight, with standard deviations shown in parentheses

	Chlorine (%)	Sodium (%)	Calcium (%)	Magnesium (%)	Potassium (%)	Ash content (%)
Nolana mollis	12.25 (0.50)	6.17 (0.30)	2.03 (0.22)	1.80 (0.45)	0.91 (1.03)	34.0
Gypothamnium pinifolium	1.36 (0.06)	1.04 (0.06)	1.28 (0.08)	0.20 (0.08)	2.22 (0.59)	9.8
Heliotropium pycnophyllum	4.23 (0.180)	4.26 (0.22)	6.14 (0.39)	1.07 (0.27)	1.40 (0.89)	44.8
Tetragonia maritima	6.09 (0.25)	8.90 (0.44)	1.53 (0.17)	2.82 (0.63)	– (0.98)	34.2
Eremocharis fruticosa	3.79 (0.16)	1.31 (0.07)	7.03 (0.37)	0.64 (0.16)	1.15 (0.63)	23.2

of a buildup of a significant litter layer of organic matter. Samples of pure white ash from decomposed shrubs gave values of 0.514–0.665 meq (NaCl) g^{-1} soil.

Lesser but still significant degrees of salt conventration are present beneath the canopies of *Gypothamnium*, *Heliotropium*, *Tetragonia* and *Eremocharis*. The variability of concentration beneath canopies of these species was not sampled, but we expect that it is similarly variable in relation to soil organic matter accumulation. Both *Heliotropium* and *Tetragonia* accumulate significant ash piles, while *Gypothamnium* and *Eremocharis* do not do so to the same extent. With the low regional precipitation, the sites of former occurrence of ash-accumulating species are marked for years after all organic matter has disappeared by distinct white rings of piles of ash.

The observed buildup of salts in the soil profiles beneath canopies of the dominant leaf succulent shrubs results from the decomposition of leaf material rich in salts. The ash content of fresh leaves of these species is remarkably high, even for halophytic species. With the exception of *Gypothamnium*, all of the dominant leaf succulent species have ash contents above 20% dry weight, with values of 45% for *Heliotropium* (Table 5).

Neutron activation analyses of leaf tissue for the four dominant species indicate that the most significant elemental constituents of the leaf salts are chlorine, sodium and calcium, although both magnesium and potassium are also in high concentrations (Table 5). Sodium and chlorine together comprise over 18% of the dry weight of *Nolana mollis*. Both *Heliotropium* and *Eremocharis* have significantly higher concentrations of calcium than sodium. Only *Gypothamnium*, the least succulent species, has a moderately low salt content.

Discussion

Despite the extremely low rainfall of the coastal Atacama Desert and apparent lack of relative humidities above about 80% in the coastal zone of Pan de Azucar (see Rundel et al. 1980), a variety of shrub species are remarkably successful in surviving under these stressful conditions. The dominant shrub species of Pan de Azucar all share a common characteristic of small succulent leaves, but their patterns of adaptive response to drought are quite different. *Nolana mollis*, *Tetragonia maritima* and *N. incana* have carbon isotope ratios which indicate a possibility of flexible utilization of crassulacean acid metabolism (CAM) (Mooney et al. 1974, 1980). All of the other important shrub species, with somewhat less succulent leaves, appear to utilize C_3 metabolism. A mixed dominance of CAM and C_3 species is paralleled in the coastal fog belt of the Namib Desert of southwestern Africa (Mooney et al. 1977) and in portions of the fog-influenced Vizcaino Desert in central Baja California (Shreve, 1951).

The most successful species at Pan de Azucar, *Nolana mollis*, is frequent both on rocky bajadas and in sandy washes. The detailed water relations of this species, described in detail by Mooney et al. (1980), is unique among all of these species in allowing it to utilize water vapor from humid but unsaturated air to maintain favorable conditions for growth under extreme drought. The extensively-branched fine root system under *Nolana* is adapted to utilizing small amounts of water in the surface layers of soil as well as soil moisture following rare precipitation.

Tetragonia maritima tolerates drought better than either *Gypothamnium* or *Heliotropium* (Table 3). It is most characteristic of sandy washes where its deep tap root may aid in capturing ephemeral ground water supplies.

Gypothamnium pinifolium, the most abundant species at Pan de Azucar, is dominant on rock bajadas but is much less frequent in sandy washes. The broad, shallow branching of the root system of this species provides a large area of soil for water absorption. Even under the drought conditions we encountered in 1978, healthy individuals of *Gypothamnium* were apparently finding available water since their water potentials recovered considerably at dawn from midday values (Table 2).

Heliotropium pycnopyllum is widespread in both bajada and wash habitats. Its root system appears to combine the extensively-branched fine root system of *Nolana* with a broader extent to tap more soil volume. Virtually leafless individuals of *Heliotropium* had the lowest water potential of any species class sampled but the water potentials of more healthy classes were comparable to those of other shrub species (Table 2).

In contrast to the shrub species, *Copiapoa* and other Cactaceae at Pan de Azucar and similar areas along the coast appear to utilize CAM throughout the year (Mooney et al., 1974). These species, characteristic of more xeric bajada slopes than the shrub communties, are local in distribution but occur in remarkably dense stands. Difficulty of establishment rather than competition for water appears to be the limiting factor in determining population densities (Gulmon et al. 1979). The northern orientation of the inclined heads of *Copiapoa* are an important aspect of their environmental adaptations (Mooney et al. 1977; Ehleringer et al. 1980).

While soils at Pan de Azucar are not saline, the extreme concentration of salts in tissues of the dominant is remarkable. Although the ash content of halophytic species is commonly extremely high, reaching levels of 15–30% dry weight (Walter and Stadelmann 1974), we know of no higher values than those of the coastal shrub species in northern Chile. Three of the four dominant species at Pan de Azucar have a leaf ash content in excess of 30% dry weight, and we measured 48% ash content in a *Nolana* species from Cerro Moreno near Antofagasta. The leaf contents of major cations and anions at Pan de Azucar are comparable to those reported for Spanish and Great Basin halophytes (Moore et al. 1972).

Despite these high concentration of leaf cations the osmotic potentials of the Pan de Azucar shrubs are not as low as would be expected for desert halophytes. Moore et al. (1972) found osmotic potentials of *Atriplex confertiflora* during the growing season to range from −4.0 to −7.4 MPa and Walter (1939) reported osmotic potentials less than −5.0 MPa in halophytes from the Karoo, South Africa. The midday osmotic potentials in shrubs at Pan de Azucar range from −2.3 to −3.3 MPa, values equivalent to those reported for xeromorphic perennial shrubs in Arizona (Walter and Stadelmann 1974). *Copiapoa cinerea* var. *columna-alba* with an ash content of 14% has a midday osmotic potential of −1.3 MPa, consistent with values of Cactaceae from Arizona (Walter and Stadelmann 1974).

The establishment of shrub seedlings at Pan de Azucar must be a rare event coinciding with several successive years of favorable precipitation. Limited flowering in many species in drought years may not seriously influence their reproductive potential. Large accumulations of seeds are present under the canopies of many species, particularly *Nolana mollis*, *Gypothamnium*, *Heliotropium* and *N. incana*. Seed predators appear to be virturally absent from this habitat, perhaps reflecting an unpalatibility in the abundant seeds. Although rodents are present in favorable sites in northern Chile (Meserve and Glanz 1978), none were captured in 120 trap-nights at Pan de Azucar and no evidence of their presence was seen. Two species of ants are common, *Conomurma goetschi* and *Campanotus morosus* but neither is granivorous. Only nectar-feeding and foliage-gleaning birds were observed.

Drought conditions like those we studied in the spring of 1978 are not unusual in the coastal Atacama Desert of northern Chile, where periods of up to 10 years may occur between rains. To be successful in this area species must be able to efficiently utilize the infrequent precipitation and tolerate long drought periods. *Nolana mollis* is unique among the species studied in its maintenance of vigorous shrub growth and flowering during extend drought. However, all of the dominant species successfully survive extented drought although shrubs become virtually leafless and dormant on the driest sites. All shrubs are able to resprout successfully from ground level, but the length of dormancy over which these species may survive is not known. *Deuterocohnia crysantha*, a terrestrial bromedliad, is the only common species at Pan de Azucar which is surviving poorly. The basis for extensive death of species all along the coastal region from Chañaral north to Paposo is not clear since more extensive drought periods have occurred in the last two decades than that present during our study.

Acknowledgements. We thank Gloria Montenegro and the staff of the Laboratorio de Botánica of the Universidad Católica in Santiago for their considerable help, and the University of California – Universidad de Chile Convenio Program for logistic support. The assistance of Vincent Guinn and C. Chu in providing analyses is gratefully acknowledged. We thank Gordon Marsh for help in ant identifications. Research funds were provided by the National Science Foundation (PWR), the National Geographic Society and National Science Foundation (H.A.M. and S.L.G.) and the Department of Biology, University of Utah (J.E.).

References

Backeberg C (1976) Cactus Lexicon, Poole Dorset Blanford Press

Ehleringer J, Björkman O (1978) A comparison of photosynthetic characteristics of *Encelia* species of possessing glabrous and pubescent leaves. Plant Physiol 62:185–190

Ehleringer J, Mooney HA, Gulmon SL, Rundel PW (in review) Orientation and its consequences for *Copiapoa* (Cactaceae) in the Atacama Desert. Oecologia (Berl)

Gulmon SL, Rundel PW, Ehleringer J, Mooney HA (1979) Spatial relations and competition in a Chilean desert cactus. Oecologia (Berl) 44:40–43

Johnston IM (1929) Papers on the flora of northern Chile. Contr Gray Herb 85:1–172

Johnston IM (1936) A Study of the Nolanaceae. Contr Gray Herb 112:1–83

Meserve PL, Glanz WE (1978) Geographical ecology of small mammals in the northern Chilean arid zone. J Biogeo 5:135–148

Mooney HA, Gulmon SL, Ehleringer J, Rundel PW (1980) Atmospheric water uptake by an Atacama Desert shrub. Science (in press).

Mooney HA, Troughton JA, Berry JA (1974) Arid climates and photosynthetic systems. Carnegie Inst Wash Yb 73:793–805

Mooney HA, Troughton JH, Berry JA (1977) Carbon isotope ratio measurements of succulent plants in southern Africa. Oecologia (Berl) 30:295–305

Mooney HA, Weisser PJ, Gulmon SL (1977) Environmental adaptations of the Atacaman Desert cactus *Copiapoa haseltoniana*. Flora 166:117–124

Moore RT, Breckle SW, Caldwell MM (1972) Mineral ion composition and osmotic relations of *Atriplex confertiflora* and *Eurotia lanata*. Oecologia (Berl) 11:67–78

Rundel PW (1978) Ecological relationships of desert fog zone lichens. Bryologist 81:277–293

Rundel PW, Mahu M (1976) Community structure and diversity of a coastal fog zone in northern Chile. Flora 165:483–505

Rundel PW, Mooney HA, Gulmon SL, Ehleringer J (in press) The coastal Atacama Desert. In: (Juvik J) (ed) The Role of Fog in Ecosystems Cambridge Univ Press Cambridge

Shreve F (1951) Vegetation of the Sonoran Desert. Carnegie Inst Wash Publ 591:1–178

Stocker O (1976) The water-photosynthesis syndrome and the geographical plant distribution in the Saharan Desert. In: Water and Plant Life (Lange O, Kappen O, Schulze E) eds Springer, Berlin-Heidelberg-New York p 506–522

Walter H (1939) Grasland, Savanne und Busch der ariden Teile Afrikas in ihrer ökologischen Bedingtheit. Jahrb Wiss Bot 87:750–860

Walter H, Stadelmann E, (1974) A new approach to the water relations of desert plants. In: Brown GW (ed) Desert Biology Vol 2 Academic Press New York p 213–310

Received March 31, 1980