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Tillandsia landbeckii in the coastal Atacama Desert of northern Chile

Tillandsia landbeckii en la costa del desierto de Atacama del norte de Chile

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ABSTRACT

The crest of the Cordillera de la Costa inland from Iquique supports a unique Chilean loma communities or tillandsiales of an epiphytic bromeliads growing on sand. These communities, similar to tillandsiales of the loma formations of coastal Peru, contain only a single vascular plant species, *Tillandsia landbeckii*. This terrestrial epiphyte obtains all of its moisture and nutrition from the absorption of fog moisture through specialized leaf scales, and furthermore utilizes CAM metabolism as a physiological adaptation to its arid habitat. The distribution of *Tillandsia landbeckii* is highly localized to steep, southwest-facing slopes at 930-1 050 m elevation. Here it grows in lens-shaped mounds forming bands across the slopes. Mean canopy cover of these large mounds was 24% over a broad study area, and reached to nearly 50% locally at higher elevations. Mean community biomass was 715 kg ha-1 overall, and reached 1 460 kg ha^{-1} on upper slopes. The development of individual tillandsia mounds represents a dynamic process of colonization, growth and development, and eventual senescence. The highly specific habitat relationships of *Tillandsia landbeckii* and its dependence on fog moisture inputs from the camanchaca suggest that these communities may serve as sensitive indicators of climate change in northern Chile. Existing areas of tillandsia dieback suggest increasing aridity and reduction of the intensity of the camanchaca in this century, consistent with floristic evidence from other sources.

Key words: *Tillandsia*, Atacama Desert, epiphytes, climate change, camanchaca.

RESUMEN

Hacia el interior de Iquique, en la cima de la Cordillera de la Costa, se mantienen comunidades chilenas únicas de loma o tillandsiales, de bromelias epifíticas que crece en arena. Estas comunidades, similares a tillandsiales en las formaciones de loma de la costa peruana, posee sólo una especie correspondiendo a una planta vascular, *Tillandsia landbeckii*. Esta epífita terrestre obtiene toda su humedad de la neblina a través de hojas escamosas especializadas, y además utiliza un metabolismo CAM como una adaptación fisiológica al medio ambiente árido. La distribución de *Tillandsia landbeckii* es hacia el sudoeste es altamente localizada y escarpada extendiéndose sobre pendientes de 930 - 1050 m de elevación. Aquí crece en montículos ondulados formando bandas a través de las lomas. La cobertura media de estos grandes montículos es de 24% sobre el área estudiada, y alcanzó casi un 50% a mayores elevaciones. La biomasa media total de la comunidad fue de 715 Kg ha, y alcanzó a unos 1 460 Kg ha en elevaciones superiores. El desarrollo de montículos individuales de tillandsia representa un proceso dinámico de colonización, crecimiento y desarrollo, y la eventual senescencia de la especie. Las relaciones altamente específicas en el hábitat de *Tillandsia landbeckii* y su dependencia con la humedad de la neblina impuesta por la camanchaca, sugiere que estas comunidades pueden servir como indicadores sensibles a cambios climáticos en el norte de Chile. La presencia de áreas en la que existió tillandsia sugiere un incremento en la aridez y una reducción en la intensidad de la camanchaca en este siglo, lo que se confirma con la evidencia florística de otros sectores del norte de Chile.

Palabras clave: *Tillandsia*, desierto de Atacama, epifitos, cambio de clima, camanchaca.

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INTRODUCTION

The Atacama and Peruvian Deserts along the west coast of South America support a highly restricted flora and low plant cover due to the hyperarid environmental conditions which characterize this region. Much of the floristic diversity of these deserts is associated with a narrow fog belt at 300-800 m elevation along the immediate coast where fogs known as the camanchaca form frequently during the year due to the effects of the cold offshore Humboldt Current. This fog zone produces fertile loma communities with well developed plant cover and surprising biodiversity (Ferreya 1953, Rundel & Mahu 1976, Rundel et al. 1991).

Much less well known however, are the tillandsiales formed of simple communities of epiphytic *Tillandsia*. Tillandsiales are best described from central and southern Peru where they form distinctive gray bands along the lower or upper margins of the typical loma communities (Ferreya 1953, Rauh 1966, Rundel & Dillon 1997). While it may seem contradictory to speak of a terrestrial epiphyte, the dominant species of *Tillandsia* in these communities are entirely rootless, growing unattached to the sandy soil surface. These species absorb fog moisture and nutrients through specialized scales on the surface of their leaves, and use Crassulacean acid metabolism (CAM) as a physiological adaptation to their arid environment (Benzing 1980, Rundel 1982, Rundel & Dillon 1997).

Tillandsiales are invariably simple in structure, generally with a single species of *Tillandsia dominant*. Any one of several species may fill this role in Peru, including *T. purpurea* Ruiz & Pav., *T. latifolia* Meyen, *T. capillaris* Ruiz & Pav., and *T. werdermanii* Harme (Dillon 1991, Rundel & Dillon 1997). Although tillandsia lomas are rare in Chile, they do form a characteristic formation in the high coastal range east of Iquique. Here a single species, *T. landbeckii* Phil., thrives under extreme conditions which are beyond the tolerance limits of any other vascular plant species (Figure 1). The deceptive lack of complexity in these communities *of Tillandsia landbeckii* and their isolation belies the potential significance of such tillandsia lomas as biological indicators of potential global change. These are truly vascular plants living at the edge. This remarkable growth form, and the obligate relationship of survival of *T. landbeckii* to fog moisture inputs from the camanchaca gives this community a special importance in understanding and monitoring the regularly of climatic conditions along the coastal Atacama Desert in northern Chile. In this paper we describe the ecological relationships of *T. landbeckii* and suggests the value of long-term future studies of this community.

MATERIALS AND METHODS

Field studies of *Tillandsia landbeckii* were carried out in April 1991 in tillandsia lomas near the crest of the Cordillera de la Costa east of Iquique, along Highway 65 between Iquique and Pozo Almonte. Here *T. landbeckii* grows abundantly in bands across the hillsides on southwest-facing slopes at 930-1050 m elevation (Figure 1).

Iquique has a long record of climatic data because of its importance as a shipping port for nitrate and other minerals. Rainfall records began in 1899 (Almeyda 1950), and have continued up until the present with only scattered missing records. Irregular climatic data are also available for Refresco and Canchones, two stations in the Pampa del Tamarugal 30-40 km east of our study site.

Vertical patterns of coverage and banding by colonies or mounds of Tillandsia landbeckii were sampled by line transects running parallel with the fall of the slope from the upper limit of mounds near the crest of the hill at 1 025 m elevation to 950 m elevation near the lower margin of occurrence for the species. The intercept of each band of *T. landbeckii* and interband distance was measured along the transect to the nearest 10 cm. Two horizontal transects of 100 m length were run across the slope at 1 010 m and 985 m elevation, the zones of greatest and medium tillandsia cover, to estimate mean community coverage.

The biomass of living *Tillandsia landbeckii* was estimated from the collection of all

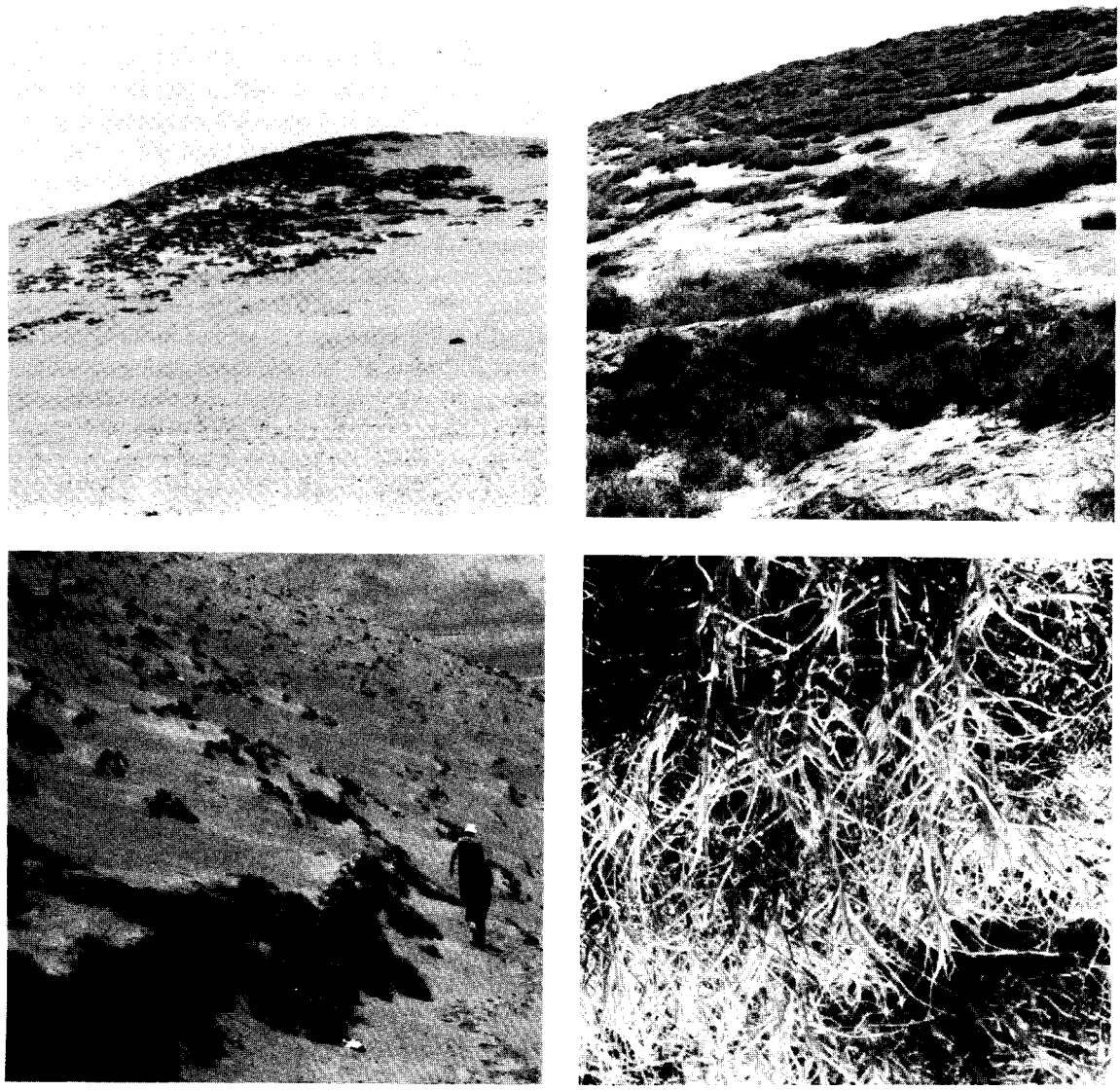

Fig. 1: Tillandsia landbeckii lomas near the crest of the Cordillera de la Costa west of Iquique: 1a. Dark bands of *Tillandsia landbeckii* on upper southwest-facing slopes; 1b. Patterns of mound growth on the upper slopes in an area of high plant cover; 1c. Scattered distribution of smaller mounds lower on the slope; 1d. Branching morphology of *Tillandsia landbeckii.*

Tillandsia landbeckii en las lomas cercanas a la cima de la Cordillera de la Costa al oeste de Iquique : 1a. Bandas oscuras de *Tillandsia landbeckii* en la parte alta de la pendiente hacia el sudoeste ; 1b. Patrones de crecimiento de un montículo en pendientes altas en un área cubierta alta de plantas; 1c. Distribución diseminada de pequeños montículos en la parte baja de la pendiente; 1d. Rama morfológica de *Tillandsia landbeckii.*

living material from two 50 x 50 cm areas on what determined to be representative mounds. Larger sample sizes were not taken because of concern for damage to this potentially endangered species. Total stand biomass was estimated from the product of mean cover values and biomass per unit area.

Subsamples of *Tillandsia* biomass were analyzed for macronutrients, cations, and trace elements using an arc-emission spectroscopy system in the Laboratory of Structural Biology and Molecular Medicine at UCLA. Pooled subsamples of soil from areas between the *tillandsia* mounds were

extracted in distilled water and this solution analyzed for macronutrients, cations and trace elements using inductively coupled plasma spectroscopy at UCLA.

The natural distribution of *Tillandsia landbeckii* was determined from field observations during multiple field expeditions in northern Chile made between 1978 and 1994. Data were also taken from Loma-Flor (M. O. Dillon, unpublished), an electronic data base containing detailed collection data and herbarium records for coastal loma species.

RESULTS

Biogeographic distribution

Tillandsia landbeckii is placed in the subgenus *Diaphoranthema* and is closely related to three other *Tillandsia* species which may occur in loma communities (Smith 1977, Dillon 1991, Till 1992a). These are the widespread *T. usneoides* (L.) L. and *T. recurvata* L. and *T. capillaris* Ruiz & Pav. which may form extensive monocultures growing on soil in the lomas of central and southern Peru.

The range of *Tillandsia landbeckii* is still poorly known. The literature suggests that it occurs from San Gallan Island (13° 50' S) in central Peru (Smith 1977) to La Serena in central Chile (30° 40' S). There has been confusion in the past, however, between *T. landbeckii* and the closely related *T. capillaris*. Such difficulties could possibly explain disjunct Peruvian reports of *T. landbeckii* and a record of *T. capillaris* from near Coquimbo (30° S), well south of its typical range. While most of the reported range of *T. landbeckii* lies at the upper margin of the coastal fog zone, Till (1992b) has recently described two new subspecies from the west slopes of the Andean Cordillera at about 2500 m in southern Peru.

The occurrence of *Tillandsia landbeckii* in Chile today is strongly centered in the Cordillera de la Costa west of Iquique where this species is extensive and conspicuous in occurrence. To the north, we have examined small populations along the northern margin of the Pampa de Camarones (19°S) at about 1000 m elevation. These populations occur on the relatively flat surface of the pampa where they form small scattered mounds. These mounds are irregular in shape and poorly formed compared to the much more robust growth mounds of *T. landbeckii* east of Iquique. This suggests that growing conditions here in the Pampa de Camarones are marginal for survival. There are single collection records for *T. landbeckii* at Paposo and Cerro Perales near Taltal (25° S). We have not encountered this species at either of these sites in our field studies, indicating at the very least that *T. landbeckii* is rare.

The occurrence of *Tillandsia landbeckii* in the Cordillera de la Costa east of Iquique is highly correlated with specific elevations and slope exposures. All of the populations that we examined occurred from 930-1 050 m elevation on southwest-facing slopes or on the margins of other slope faces where regular southwest winds off of the Pacific Ocean provide inputs of fog moisture. Coastal fogs near Iquique, however, are relatively light at best, and thus far different than the camanchaca characteristic of Paposo to the south or the gaura of the Peruvian lomas to the north (Rundel et al. 1991). Fog moisture input is strongest and most frequent during the winter and relatively light or absent in summer.

Growth form

The characteristic growth pattern of *Tillandsia landbeckii* are mounds distributed as horizontally extended bands across the plain of the slope in their habitat (Figure 1). These bands were typically 20-40 cm in width, and 2-4 m in length across the slope. Careful examination of the growth structure of individual bands revealed a lens-like pattern of radiating growth, with the youngest vegetative tissues formed across a steep face of each band on the downslope side. These faces were slightly bowed outward at their center, and commonly reached 30-60 cm in height.

Despite a habitat with an aridity so extreme that no other vascular plants are able to survive, *Tillandsia landbeckii* is remar-

kably successful. The mean coverage of living mounds of this species over our study area was 24%. This coverage showed a strong pattern of elevational association. Coverage down the slope in ten meter sections of the transect peaked at 37% at about 1 020 m elevation near the top of the transect, and declined steadily below this point (Figure 2). A 100 m transect run horizontally across the slope at 1 010 m elevation in the area of greatest tillandsia abundance found 49% cover by living plants. A similar transect run at 985 m in the center of the tillandsia zone showed 24% cover. Near the lower margin of tillandsia occurrence at 950-975 m elevation there was only about 10% cover. No tillandsias occurred below 930 m on the slope at our site.

The median width of living vegetative tissue across the bands of *Tillandsia landbeckii* was 30-40 cm, but the frequency of tillandsia band widths present showed a prominent decline toward narrower bands moving from upper to lower positions on the slope (Figure 3). The median band width was 40 cm in the upper quarter of the transect (1 000-1 025 m) where coverage was greatest, 30 cm width in the next quarter (975-1 000 m), and continuing to decline to only 10 cm width in the lowest quarter (925-950 m). Reduced total cover by tillandsia with lower elevation on the slope was due in part to these smaller mounds, but also to a lower frequency of the mounds themselves. Our vertical transect encountered a band of a tillandsia mound every 1.5 m on the upper quarter of the slope, but this frequency declined to 1.8, 2.2, and 3.0 m, respectively with lower quarters of the transect.

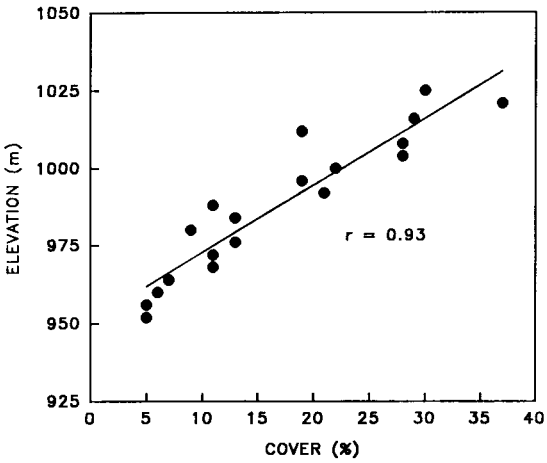

Fig. 2: Mean cover by living *Tillandsia landbeckii* in 10 m units along a transect running downslope from the upper limit of growth at 1 025 m elevation to 950 m elevation near the lower margin of tillandsia occurrence in the Cordillera de la Costa east of Iquique.

Cobertura media de *Tillandsia landbeckii* en unidades de 10 m a lo largo de una transecta bajando la pendiente desde el límite superior de crecimiento a 1 025 m de elevación hasta 950 m de elevación cercano al margen más bajo de presencia de tillandsia en la Cordillera de la Costa al este de Iquique.

Biomass and nutrient content

The mean dry weight biomass of mounds of *Tillandsia landbeckii* was 298 g m^{-2}. With a mean cover of 24 % on the slope, this would provide a community biomass estimate of 715 kg ha^{-1}. The central zone of highest abundance of *T. landbeckii* had approximately 1460 kg ha^{-1} biomass. These are surprisingly high biomass levels for such an extreme environment.

The fine soils around the tillandsia mounds showed moderately high concentrations of both calcium and sodium, reflecting mineral origin from maritime fogs which bathe this area irregularly. Boron was a trace element present in high concentrations (38 μg g^{-1}). Plant cation concentrations were not unusually high in these cations, but did show moderately high levels of boron (58.5 μg g^{-1}) copper (65.2 μg g^{-1}), and molybdenum (1.0 μg g^{-1}). The presence of the latter two elements almost certainly indicates dust deposition on the outer surface of the foliage of these rootless plants.

DISCUSSION

Excavations around individual mounds suggest a dynamic pattern of colonial development of *Tillandsia landbeckii* from a single point of origin. The radiative growth of each lens-like mound can be readily traced back to a focal point where we hypothesize that a single colonial plant became established. In most cases a small area of rock outcrop was associated with the focal point, perhaps as a critical point of colonization.

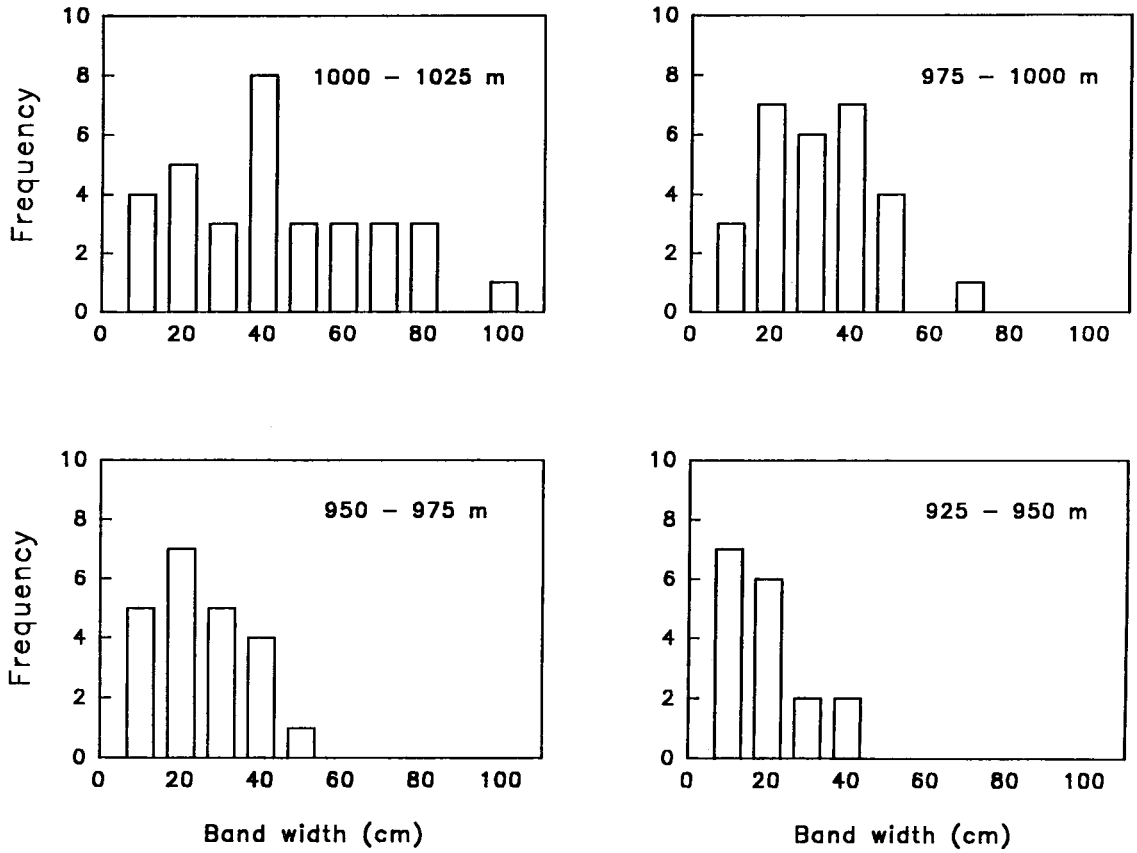

Fig. 3: Frequency of width distributions for bands of *Tillandsia landbeckii* intercepted within 50 m units along a transect running downslope from the upper limit of growth at 1 025 m elevation to 925 m elevation below the lower margin of *tillandsia* occurrence.

Frecuencia en las distribuciones del ancho de las bandas de *Tillandsia landbeckii* interceptadas alrededor de unidades de 50 m a lo largo de una transecta que desciende desde el límite superior de crecimiento a 1 025 m de elevación hasta 925 m de elevación bajo el margen inferior en la presencia de *tillandsia*.

We suggest a dynamic cycle of development where slow plant growth from this initial point expands outward toward the direction of fog moisture input (Figure 4). As new vegetative tissues are added to the exposed face of the colony, the older stems behind senesce and die. Although decomposition is slow in this arid environment, the dead organic materials behind the living face of the lens-like mound break down, and windblown sand fills this hollow to form a sandy top to the mound. Excavations of this area revealed cyclical profiles of organic matter and windblown sands over multiple cycles. Through time the front face of the mound continues to expand laterally, increasing its length and width. The steep slope of the habitat, however, means that continued outward growth of the mound increases the vertical profile of the front face of the mound. The eventual extension of this height to 50 cm or more appears to result in structural instability, leading to the collapse of the living face of the mound and death to the colony. Gaps on the slope are thus formed in this manner, providing openings for the colonization cycle to be repeated.

Much more study would be needed to fully understand the dynamics of mound development and its biological nature. Each individual mound may well be formed by cloned ramats from a single colonizing genet. We do not know if secondary colonization by new individuals is occu-

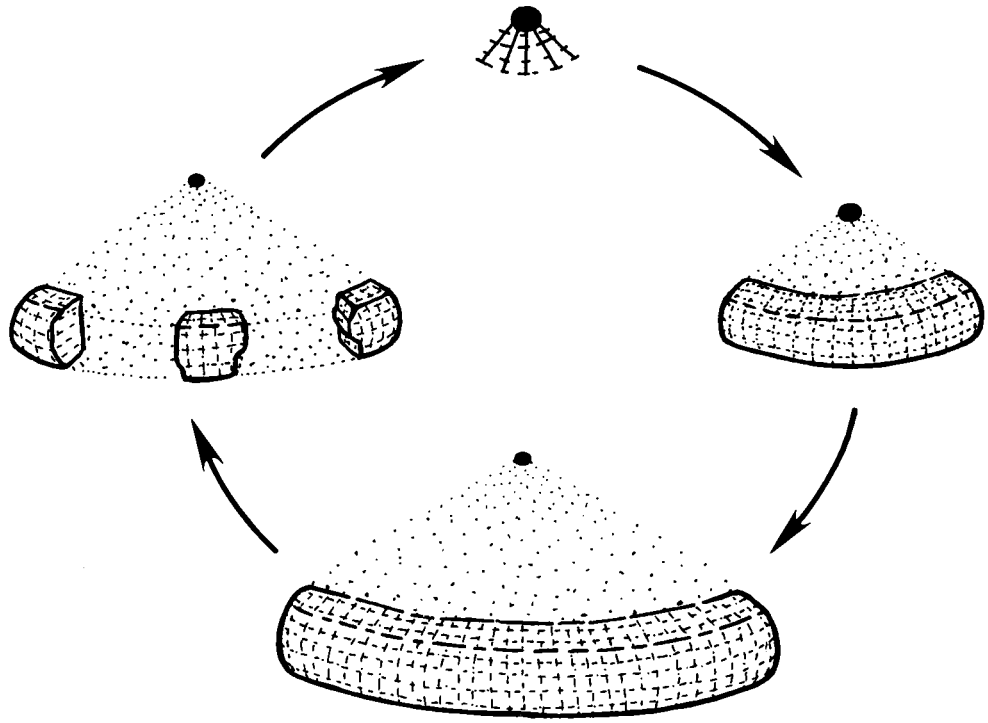

Fig. 4: Hypothetical growth dynamics of mounds of *Tillandsia landbeckii.* See text for discussion.

Dinámicas de crecimiento hipotéticas de los montículos *Tillandsia landbeckii.* Vea el texto para la discusión.

rring. Furthermore, we can only guess at the time frame for cycles of mound development and senescence. We surmise that this cycle is one of at least decades, but such estimates are conjectural without specific long-term studies. Despite the extreme environmental conditions of a loma habitat, epiphytic terrestrial *Tillandsia purpurea* in tillandsiales of Peru are known to have surprisingly high rates of growth (Alvim & Uzeda in Walter 1971, Walter & Breckle 1984).

The biomass of *Tillandsia landbeckii* measured in our study is similar to that reported for pure stands of *T. latifolia* in Peru. Masuzawa (1982) found mean stand biomass ranging from 1 255-1 616 kg ha^{-1} in two sites in central Peru, but small smaller biomass in other stands to the south where mean plant size and density were both lower. This species, despite its similar habitat, has a very different growth form than *T. landbeckii*, with distinctive individual rosettes which averaged about 41 g in dry weight in healthy stands (Masuzawa 1986). Both vegetative and sexual reproduction is important in the ecological success of stands of *T. latifolia.*

The highly specific and local habitat of *Tillandsia landbeckii* in an area of such extreme aridity suggests that its distribution will be highly sensitive to even small changes in environmental conditions. Increased rainfall or fog moisture inputs would be expected to increase biomass and cover of *T. landbeckii,* and perhaps allow other species to colonize these lomas, while reduced moisture availability would restrict their occurrence and vigor.

Our observations in recent years near Iquique suggest to us that a decline in abundance is taking place, albeit gradually. While much of the area of *T. landbeckii* shows vigorous growth, careful examination of the tillandsia lomas above Iquique revealed locally extensive areas of dead mounds, with no indication of recolonization.

Such a dieback around the periphery of these tillandsia lomas parallels a clear decline in the health and abundance of the arborescent cactus *Eulychnia iquiquensis* in the lower hills above Iquique (Espinoza

1993, Rundel et al. 1995). Furthermore, much of the sparse flora that was present earlier in this century around Iquique on the lower slopes of the Cordillera de la Costa appears to have now disappeared, and a similar pattern of declining plant diversity and cover appears to be taking place all along the coast of northern Chile (Rundel & Dillon, unpublished data).

Another plant group dependent on atmospheric moisture for its growth, the lichens, apparently grew luxuriantly on slopes and epiphytically on cacti above Iquique in the last century. Charles Darwin (1835) described abundant growth of *Cladonia* sp. (=*Niebla tigrina* (Follm.) Rund. & Bowl.) on the slopes above Iquique, and Reiche (1907) mentions epiphytic growth of six more species on cacti. Lichens are virtually absent from Iquique today.

The mean annual rainfall for Iquique over the nearly 100 years of climatic records is less than 2 mm (Rundel, unpublished data). Even this low amount, which makes Iquique one of the most arid cities in the world, obscures the significance of the irregularity of rainfall. Much of the rainfall for this century fell between 1920 and 1940 when a series of regular years with rain and strong El Niño conditions brought rains in 16 of 21 years and an average of more than 3.3 mm per year. The El Niño conditions of 1940 brought 20.0 mm of rain, nearly three times that falling in any other year on record. The past half century has been unusually dry along the coast of northern Chile, with Iquique receiving a mean annual rainfall of less than 1 mm over this period (Rundel et al. 1996). Periods of 60 months or more without rain have occurred several times in the historical record.

The relationship between rainfall and fog moisture input from the camanchaca are not clearly understood, but there appears in our experience to be a connection, albeit a loose one. Thus we hypothesize that declining levels of precipitation have been associated with reduced fog moisture input as well. Such a condition would be consistent with the observations by Follmann (1995) of sharp declines in the abundance and diversity of epiphytic lichen populations along the coast of Chile over the past few decades. The causes of reduced precipitation is not clearly established, but may relate to a lower frequency of strong El Niño conditions that promote rainfall along the coast of northern Chile (Quinn et al. 1989, Ortlieb & Macharé 1993). We know too little about these conditions to address this issue appropriately, but the camanchaca may well be tied to similar patterns of ocean currents that are related to El Niño/Southern Oscillation (ENSO) cycles.

We propose that the lomas of *Tillandsia landbeckii* near Iquique deserve special attention as sensitive bioindicators of regional climatic dynamics. Permanent transects and mapped populations of this species could provide sensitive indicators of changing patterns of broad scale fog moisture conditions related to ENSO cycles or slowly changing global climates. Changes in rainfall patterns and fog moisture inputs should be monitored by quantitative growth studies at both the community and population level.

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