Bofedales: high altitude peatlands of the central Andes

Bofedales: turberas de alta montaña de los Andes centrales

FRANCISCO A. SQUEO^{1, 3, 4}, BARRY G. WARNER^{2, 3}, RAMÓN ARAVENA^{2, 3} & DIANA ESPINOZA^{1, 4}

Departamento de Biología, Facultad de Ciencias, Universidad de La Serena, Casilla 599, La Serena, Chile ² University of Waterloo, Waterloo, Ontario, Canada N2L 3G1; e-mail: bwarner@uwaterloo.ca; roaraven@uwaterloo.ca
³ Center for Advanced Studies in Arid Zones (CEAZA), Casilla 599, La Serena, Chile ⁴ Institute of Ecology and Biodiversity (IEB); * e-mail for correspondence: f_squeo@userena.cl

ABSTRACT

There is an exceptional group of alpine peatlands in the world situated in the arid grasslands of the central Andes. The peatlands in northern Chile occur in the most arid part of their range. Members of the Juncaceae are the primary peat-forming plant species. Fresh and mildly saline groundwaters originate from glaciers, snowmelt and rain are the water sources for the northern Chile peatlands. Paleoecological investigations suggest that some peatlands are recent features of the landscape having developed within the last three thousand years or less. These peatlands are unique, extremely fragile water features sensitive to climate changes and human disturbances such as regional mining activity. Much more work is required to develop scientifically based sound management and conservation programs for the rare plants and animals that live in them and to ensure the future livelihoods of the indigenous peoples who depend on them.

Key words: peatlands, arid grasslands, Altiplano, central Andes, South America.

RESUMEN

Existe un grupo excepcional de turberas (bofedales) de alta montaña en el mundo situados en la estepa árida de los Andes centrales. Los bofedales en el norte de Chile están presentes en la parte más árida de su rango. Las principales especies de plantas responsables de la formación de turba corresponden a miembros de Juncaceae. El agua fresca y medianamente salina de los bofedales proviene de agua subterránea asociada a riachuelos proveniente de glaciares, derretimiento de nieve y lluvia. Investigaciones paleoecológicas sugieren que algunos bofedales son integrantes recientes del paisaje, habiéndose desarrollado durante los últimos tres mil años o menos. Estos bofedales son entidades únicas, extremadamente frágiles por su dependencia del agua, sensibles a los cambios climáticos y vulnerables a la alteración humana tal como la actividad minera en la región. Se requiere mucho más trabajo para desarrollar programas de manejo y conservación, con sólidas bases científicas, de las plantas y animales que viven en ellos, y para asegurar la capacidad futura de pastoreo de la cual dependen los pueblos indígenas.

Palabras clave: turberas, estepa árida, Altiplano, Andes centrales, América del Sur.

INTRODUCTION

The existence of wetlands, especially peataccumulating wetlands, in arid environments seems counter intuitive. Indeed, wetlands exist in environments with low precipitation and soil moisture deficits. The wadis of southern Africa, the oases of the Middle East, and the billabongs of Australia are well known examples of arid land wetlands. Much less known, however, are the peatlands in the high Andean arid zone of the central Andes, which have been referred to as bofedales, vegas, cushion bogs, and wet grasslands. Despite hyper-aridity, intense solar radiation, high-velocity winds, hypoxia, daily frost, and a short growing season, bofedales are near the hydrological and altitudinal limits for plant life in the cold and arid grasslands of Perú, Bolivia, Chile and Argentina (Ruthsatz 1993, 2000, Squeo et al. 1994, 2006b, Villagrán & Castro 1997).

These peatlands are like no other in the world. They have been referred to as "highland bogs" (Wilcox 1986, Ruthsatz 1993), but they

are neither dominated by *Sphagnum* mosses nor are they exclusively ombrogenous, as is typical of true bogs in the Northern Hemisphere. Their only similarity to northern bogs is the microtopographic patterns of pools, lawns, and hummocks. Individual systems vary in extent from less than one hectare to in excess of 100s of hectares. Fresh and mildly saline groundwater originate from glacier streams, snowmelt and rain are the water sources of these peatlands. Members of the Juncaceae, most common species being *Oxychloe andina* and *Patosia clandestina* are the community dominants and primary peat-formers (Ruthsatz 1993, 2000, Squeo et al. 2006b).

The peatlands play a critical role in sustaining a unique diversity of rare and endemic biota in the Cordillera de los Andes. A small number of mammals and bird species, about one-third of which is threatened, depend upon the peatlands for grazing, nesting and water. Camelid species, wild vicuña (Vicugna vicugna) and guanaco (Lama guanicoe) are the most obvious mammalian inhabitants (Villagrán & Castro 1997).

Communities of native Aymara and Atacameños peoples are directly dependent upon the peatlands in this region where conditions are so severe as to almost preclude human habitation (Villagrán & Castro 1997, 2003, Villagrán et al. 1999, 2003). The peatlands are used for grazing by their domestic herds of llamas (Lama glama) and alpacas (Vicugna pacos), which are the basis of the local indigenous economy. In other areas, the living surface layer of the peatlands is stripped away to expose underlying organicrich mineral soils for cultivation. Drainage of the peatlands by hand-dug ditches to re-route water to drier areas is undertaken to encourage expansion of peatland and hence, the extent of pastureland.

This paper focuses on the *Oxychloe* and *Patosia*-dominated peatlands in the most arid part of their range in Chile. We assess the state of current knowledge and focus on identifying factors contributing to their existence and character. Such information is needed for management and conservation programs because there is growing pressure on water and associated biological resources in this region. Potential conflict exists between industrial development and protection of these fragile

natural resources (Messerli et al. 1993). Stone (1992) asserted that fragmented and oversimplified views of fragile Andean ecosystems have led to mismanagement. The dynamics of peatlands and their connection with water sources is not well understood. Nor is it clear what the relationships are with climate. However, legislation to protect these fragile ecosystems is recognized by local governing bodies on water use in regions such as Tarapacá and Antofagasta in Chile where exploitation of water must have regard for peatlands and for their groundwater recharge areas (Dirección General de Aguas, Gobierno de Chile 1996).

There are examples of severely degraded and vanishing peatlands in northern Chile (Squeo et al. 1989, 1993, 1998, 2001, Arroyo et al. 1993, Villagrán & Castro 1997). Earle et al. (2003) suggested that degradation was associated with autoregulation processes, however, questions remain as to whether there may be external linkages with changes in regional precipitation or groundwater extraction for lowland agriculture, urbanization, and mining? Are other factors, such as a decrease in regional precipitation in recent decades responsible for peatland deterioration in this already waterstressed region? What is the connection between climate and the regional hydrological and biotic resources? Is it possible that peatlands deterioration is part of the natural autogenic aging process of these sensitive ecosystems?

Where do these peatlands occur?

Bofedales are primarily restricted to the low Alpine and sub-Alpine belts of the central Andes at elevations between 3,200 to near 5,000 m in the north and central part of their range and at elevations greater than 2800 m at their southern limit (Fig. 1 and 2). The grassland and steppe straddle the volcanic and igneous rocks of the precordillera and western cordillera ranges of the high Andes. The most distinctive geological feature in this region is the Altiplano, a large flat plateau formed by Mesozoic and Cenozoic sedimentary deposits, especially thick volcanic ashes laid down in late Cenozoic times (Charrier 1997). The Altiplano is among the highest plateaus in the world. Glaciers descended onto the Altiplano from the surrounding mountain peaks and covered it with ice during Quaternary time. Large water bodies inundated the Altiplano during ice-free periods and eventually receded by the Late Quaternary (Clayton & Clapperton 1997). Aeolian sand plains and dunes and wind-swept gravel and cobble plains characterize the modern landscape. Most of the basins in the Altiplano are endorreic and are characterized by the occurrence of salt lakes

and shallow open water wetlands (locally referred to as salares). Mechanical weathering is intense, but the cold climate, aridity and lack of leaching, high relief and the continual downward movement of mineral matter, detritus and water prevent the development of mature soils and well-established plant communities (Wilcox 1986, Veit 1996, Abraham et al. 2000).

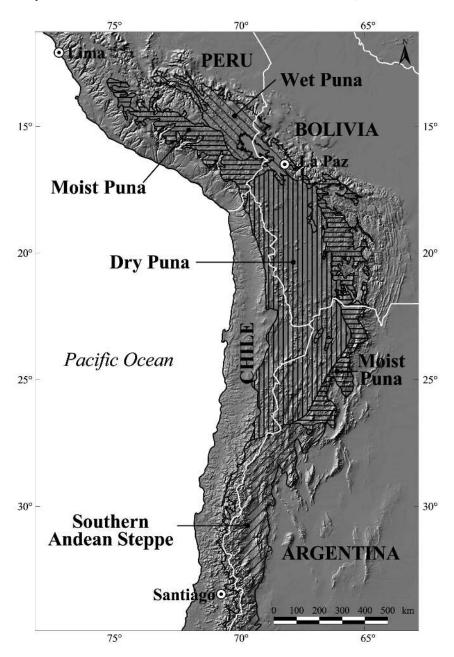


Fig. 1: Map showing the primary ecoregions of the central Andes (after Olson et al. 2001, WWF 2001).

Ubicación de las ecorregiones primarias de los Andes centrales (según Olson et al. 2001, WWF 2001).

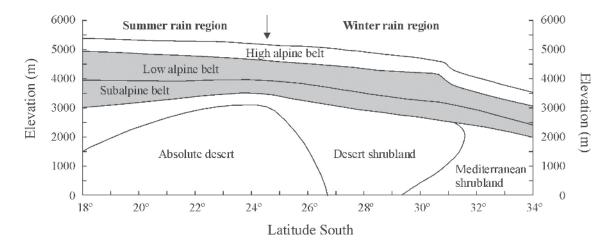


Fig. 2: Diagram illustrating the distribution of major ecozones in the western part of the central Andes between 18° and 34° S in Chile (after Squeo et al. 1994, Arroyo et al. 1997, 2004). Peatlands are confined in the low Alpine and the subalpine belts.

Diagrama ilustrando la distribución de las mayores ecozonas en la vertiente occidental de los Andes centrales entre los 18º y 34º S en Chile (según Squeo et al. 1994, Arroyo et al. 1997, 2004). Bofedales están confinados a los pisos Andino Inferior y Sudandino.

Vegetation cover is sparse with less than 22 % surface cover in the Subalpine belt and less than 0.5 % surface cover in the High Alpine belt (Fig. 2, Arroyo et al. 1988, Squeo et al. 1992, 1994). Grasses of genera such as Agrostis, Calamagrostis, Festuca, Paspalum and Stipa are the distinctive elements of the vegetation. Other plants with prostrate and roseate life forms include Hypochoeris, Lachemilla, Pyncophyllum, Azorella, and Aciachne. Xerophilous shrubs such as Adesmia, Baccharis, Fabiana, and Senecio are typical at lower elevations of the grasslands and grassy steppe zones. Halophyte communities with Atriplex atacamensis, Distichlis humilis, Muhlenbergia fastigiata, Senecio pampae, Suaeda foliosa, and Tessaria absinthioides1 occur around the salares.

The grassland and steppe vegetation communities are locally referred to as Puna, which can be subdivided into three distinct ecoregions, based primarily on precipitation and moisture trends (Fig. 1, Olson et al. 2001, WWF 2001). The central Andean "wet puna" extends from south-central Peru to central and western part of Bolivia between 3,800 and 4,200 m of altitude on the east side of the

Andean cordillera. Much of the precipitation falls in summer from easterlies associated with the Bolivian High Pressure System over the Amazon basin. Average annual precipitation is 500-700 mm (Vuille & Amman 1997, Garreaud et al. 2003). A "moist puna" zone is present in southern Peru and extends in western Bolivia to northwest Argentina over a wide altitudinal range of up to 6,600 m of altitude and receives between 250 and 500 mm of precipitation per year mostly in the summer. The "dry" puna zone covers the largest area of the three ecoregions and stretches from approximately 17-27° S in southwest Bolivia, northeast Argentina and northern Chile, immediately east of the Atacama desert, one of the most arid deserts in the world. Dry puna is characterized by the harshest environmental conditions with respect to aridity. The northern part of the dry Puna is in the summer rain region (Vuille & Keimig 2004). South of the Arid Diagonal at 24-25° S (Abraham et al. 2000), the dry Puna is in the winter rain region, which is influenced by the Southeast Pacific anticyclone carrying moisture off the Pacific Ocean to the west side of the Andes in winter. Average annual precipitation rarely exceeds 250 mm of precipitation, almost exclusively received as snow. The precipitation is seasonal with about eight months of complete aridity during the

¹ Plant taxonomy in this paper follows Marticorena & Quezada (1985), Marticorena & Rodríguez (1995), Marticorena et al. (1998, 2001).

main growing season. Values as high as 400 mm have been noted in the north and as low as 50 mm at 24-25° S, increasing again to the southern limit (Arroyo et al. 1988). Southern Andean steppe is the natural continuity of the Andean vegetation south of the dry Puna. It is located in north-central Chile and west-central Argentina. Precipitation is more abundant (over 250 mm) and falls mostly as snow during the winter (Squeo et al. 1994).

Peatlands in northern Chile

The peatlands are found from about 18°30' S in northern Chile at the southern limits of the moist Puna ecoregion, across the dry Puna where most of the peatlands occur, to about 31° S at their southern limit in the southern Andean steppe ecoregion (Fig. 1, Squeo et al. 2001). They appear as green oases in valley bottoms, shallow basins and other low areas of relief in this otherwise poorly vegetated and arid landscape (Arroyo et al. 1988, Villagrán & Castro 2003).

The climate is characterized as subtropical semi-arid desert (Miller 1976). Conditions in Chile are slightly wetter in the north of this area, and become progressively more arid to the Arid Diagonal at 24-25° S. Low atmospheric pressure, low air densities and minimal atmospheric humidity are typical of this high altitude region. In the north, rainfall is received mostly during the summer (December-March) when the regional easterlies bring moisture over the Andes from the Amazon basin. Local convective thunderstorms are most common in late afternoon as a result of the intense surface heating by solar radiation (Aceituno 1997). There is virtually no precipitation during the summer over the dry Puna between 24-25° S (Arroyo et al. 1988, 2000). Abraham et al. Potential evapotranspiration is about 1,000 mm year-1, exceeding precipitation by a factor of five (Hastenrath & Kutzbach 1985, Risacher et al. 1999). Most of the precipitation in the region is received as snowfall during the winter. However, a larger amount of snowfall is actually lost by sublimation (Vuille & Amman 1997). Runoff from snowmelt and permanent glaciers is abundant and brief during the spring, except in areas where glacier meltwaters flow year round.

Air temperatures are low with wide diurnal variations resulting from intense surface heating associated with strong solar radiation and the intense radiative cooling during the night. In high Andes at 30° S, the maximum and minimum extreme temperatures occur in January (18.7 °C, -0.4 °C) and July (8.3 °C, -14.5 °C), respectively. The minimum monthly temperature of around -5 °C during spring (end of November) is a limiting factor that controls the beginning of the growing season in this part of Chile (Squeo et al. 2006a, 2006b). The length of time with and magnitude of freezing temperatures increases with increasing altitude (Squeo et al. 1996).

Peatlands types in northern Chile

Three main groups of peatlands can be recognized based on their overall shape, hydrogeological setting and dominant source of waters (Fig. 3). The first group is sloping peatlands that occur along steep valley bottoms and streams (Fig. 3A and 3B). These sloping peatlands can be a few kilometers long and only a few 10s of meters wide. Groundwater discharge from local flow systems seems to be the dominant source of water with some input of water from direct snowmelt and surface feeder streams (J.C. Aravena, unpublished data). Waters near the surface of these sloping peatlands have high pH between 8-9 and low conductivity 1-2 µS cm⁻¹ (Iriarte et al. 1998) but low pH waters have also found in peatlands in areas near ore deposits.

The second group, referred to as basin peatlands, tends to be wider with a flat surface and includes those developed behind end moraines and in cirque basins, shallow depressions and other low areas of relief (Fig. 3C and 3D). They can be up to a few hundred meters wide and can have some slope relief but are not as steep as the sloping peatlands. Glacier streams originating from higher elevations and groundwater discharge associated with regional groundwater flow systems, together create a complex hydrology for these peatlands. In the Andean steppe ecoregion, there appears to be a strong relationship between plant communities and salinity. The water associated with Distichia muschoides communities ranges between 19 and 713 µS cm⁻¹, which are linked to springs

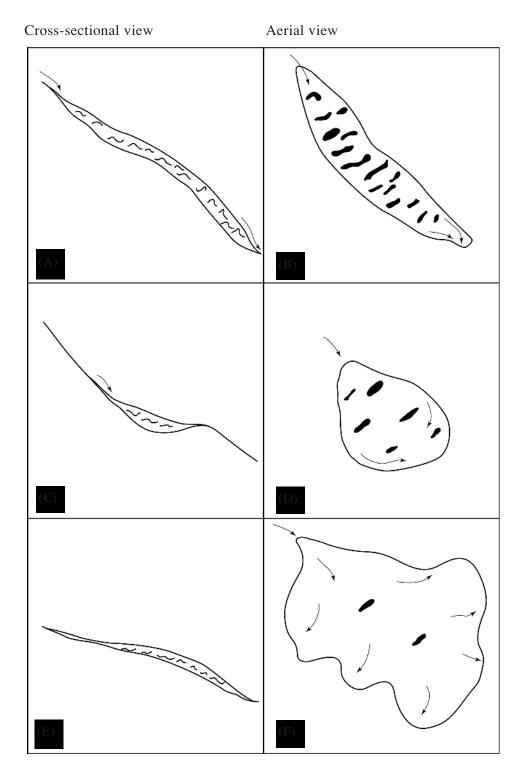


Fig. 3: Sketches of cross-sectional (A, C, E) and plan views (B, D, F) of the types of general peat landform types in the high Andes of northern Chile based on geomorphological setting and hydrological conditions: (A, B) sloping peatland, (C, D) basin peatland, and (E, F) flat peatland. Arrows indicate water flow directions.

Esquemas de secciones verticales (A, C, E) y vistas superficiales (B, D, F) de los tipos de bofedales presentes en los Andes altos del norte de Chile basado en la geomorfología y condiciones hidrológicas: (A, B) bofedal de ladera, (C, D) bofedal de quebrada, y (E, F) bofedal plano. Las flechas indican las direcciones del flujo del agua.

and small streams that do not accumulate salts during the dry season. The *Oxychloe andina* communities are associated with more saline conditions with conductivity values between 22 and 2,620 µS cm⁻¹ and mixed *Oxychloe andina-Deschampsia caespitosa* communities grow in water with conductivity values as high as 2300 µS cm⁻¹ (Espinoza, unpublished data).

The last group, are flat peatlands, which are large and expansive (Fig. 3E and 3F) covering wide areas. These peatlands complexes include natural systems and peatland areas created and restored by human actions. The local inhabitants cut networks of shallow channels to divert water in and around pre-existing natural peatlands, which initialize peatland formation and overall peat landform expansion. Surface waters largely dominate the restored parts of these systems. The main characteristics of a typical bofedal in Chile are showed in Table 1.

Vegetation

The peatland vegetation contrasts sharply with surrounding terrestrial communities by having plant cover usually greater than 70 % and high plant productivity (biomass over 1,000 g m⁻²) (Squeo et al. 1993, 1994, 2006b). Three distinct vegetation communities are characteristic of these peatlands in Chile (Villagrán et al. 1983, Arroyo et al. 1988, Ruthsatz 2000, Villagrán & Castro 2003). Cushion plants of the Juncaceae, mainly *Oxychloe andina* and *Patosia clandestina* and scattered *Distichia muscoides*

and D. filamentosa, dominate the lawn and hummock communities. Open water pools are second major community where Potamogeton strictus, Myriophyllum quitense and Ranunculus sp. grow in the dark dissolved organic carbon-rich waters. A third characteristic community is more typical of peatlands in the Southern Andean Steppe ecoregion. Members of the Poaceae, primarily Deschampsia caespitosa and Deyeuxia velutina are dominants with species of the Cyperaceae, such as Carex spp. and Eleocharis and other Juncaceae including Juncus spp. are more secondary representatives. All three of these communities may grade into one another forming mixed communities.

The peatland vegetation is controlled by four main interacting ecological factors: (a) water quantity and seasonal availability, especially during dry periods, (b) favourable ambient temperatures and occurrence of frost events that control the duration of the growing season, (c) water pH, availability of nutrients (mainly, N, P, K, Ca and Mg), and exposure to toxic elements such as As, B, Fe, and Al in the water, and (d) biotic factors such as seed dispersion by animals, grazing and human impacts (Villagrán et al. 1983, Ruthsatz 1993, 2000, Villagrán & Castro 2003, Squeo et al. 2006b). Our ongoing work is characterizing the different peatlands communities over their geographic range to understand more fully the ecological linkages between a variety of ecological parameters and the plant

TABLE 1

Characteristics of typical bofedales in Chile. These characteristics may not apply to bofedales that have been modified or disturbed by humans

Características de los bofedales típicos de Chile. Estas características podrían no ser aplicables a bofedales que han sido modificados o alterados por el hombre

Characteristic	Description
Geologic/physiographic setting	Situated on flat terrain, in sloping valley bottoms and shallow broad basins
Peatland landform	Flat or slightly raised centre
Hydrology	Predominantly groundwater, and some stream/river influence, snow melt
Water table position	At or slightly below the surface
Water pH	typically pH 7-8
Dominant vegetation	Dominated by members of Juncaceae (i.e., Oxychloe andina, Patosia clandestina), with some Gramineae and other herbaceous species
Soil composition	Poorly decomposed Juncaceae peat

communities. Our research approach includes tracing the history of past plant communities and peatland development, and understanding the rate and magnitude of changes in plant communities and their relationships with past hydrological conditions, actual water sources used by plants, and plant productivity and water availability (Squeo et al. 1993, 2006b, Earle et al. 2003).

Age and development

Even though these peatlands are unique in the world because of their geographic and environmental settings and the unusual vegetation cover dominated by compact colonies of Juncaceae, they are like other peat landforms in their structure and ability to form peat. They possess the typical diplotelmic soil structure with a near surface oxygen-rich layer and a deeper oxygen-poor zone. The preserved record in the peat lends itself well to using paleoecological methods to trace the age, time of origin, and developmental sequence leading to present day conditions. Unfortunately, there have been few such studies (Earle et al. 2003, Rech et al. 2003).

A paleoecological investigation of a sloping peatland developed in a stream channel in the Nevado Tres Cruces National Park near the southern limit of the dry Puna zone at 4,300 m of altitude. showed the peatland was unexpectedly young, dynamic and sensitive to environmental changes (Earle et al. 2003). A transect of cores along the longitudinal axis of the peatland revealed up to 3.6 m of peat, organic muck and inorganic sediments below the surface. Organic matter began to accumulate around 1,000 years ago. An important question revolves around the delay in onset of peat accumulation given that the area is known to have been ice-free during the Holocene. Earle et al. (2003) proposed that given the mid-Holocene climate is thought to have been dry (Grosjean et al. 1997, Grosjean 2001), the peatland started to develop after a change to more wet conditions during the late Holocene. The intercalation of limnic and sand and gravel sediments in the early phases at the study site reveals a complex history of low and high energy surface flow through the valley. It seems the peat-forming Oxychloe andina started to develop only after modern climate

conditions (slightly drier) became established and water supplies and the energy of surface flow diminished in the narrow valley and hydrological conditions became more quiescent. It is also possible that intrinsic processes such as rapid peat growth in low energy stretches of the valley contributed to the establishment of the present *O. andina* dominated wetland. Internal factors are also in large part responsible for peat degradation currently underway at the Nevado Tres Cruces peatland site (Earle et al. 2003).

We can confirm that onset of modern-day peatland development has been within the last century or two elsewhere in Chile, near the southern limit of bofedales (Warner et al. unpublished results). Cores from a basin peatland in the Río Tres Quebradas (29º16' S, 70'04' W) valley impounded behind an end moraine produced ages of around 6,600 years old, however, the Oxychloe communities began to spread out across the basin about 1,200 years ago. It appears that peatlands in this part of Chile are relatively recent features too, and do not represent old ecosystems formed during the early Holocene as is usually assumed for peatlands with thick accumulations of peat such as the Sphagnum-dominated systems in the south of Chile (Arroyo et al. 2005) or elsewhere in the northern hemisphere. Much more needs to be learned about how such water-dependant features can form and are maintained in such arid environments. In another of the few examples where peatlands have been radiocarbon dated, we have found a complex stratigraphy of peat, sand and gravel, clay, and marl deposits up to 15 m in thickness under a basin peatland in Collacaqua (20°00' S, 68°45' W), near the centre of the dry Puna zone (Warner & Aravena, unpublished results). A radiocarbon date of 8,600 yrs BP was obtained on the bottom of the section, but it seems the Oxychloe peat of the modern-day peatland started to accumulate around 3,000 BP and became well established about 1,400 years ago, which is comparable to the record at the Nevado Tres Cruces site about 800 km to the south.

The presence of old wetlands deposits formed at various times during the Holocene has been documented by Grosjean et al. (1997) and Rech et al. (2002, 2003) in the Salar de Atacama basin. Grosjean et al. (1997) postulated that the middle Holocene wetlands,

initiated during dry regional conditions, were due to a rise in the local water table caused by damming of the river canyon downstream of the wetlands. Rech et al. (2003) obtained a wide range of dates in the same river canyon studied previously by Grosjean and postulated that the wetlands were formed during high water table conditions produced during a period of wet regional conditions. These contrasting interpretations (Grosjean 2001) highlight the need for further studies to evaluate if the groundwater regime that made possible the existence of these Holocene wetlands was representative of a local groundwater flow system or the regional groundwater flow system. Recent evidence based on ¹⁸O and ²H data obtained in rivers and wetlands at different altitudes in the high part of the Huasco valley seem to show that sloping wetlands found near the rivers are associated with a local flow systems (Aravena et al. unpublished results). However, it is more likely that the large wetlands found at the foot of the Andes representative of the types found around the high altitude salares are fed by regional groundwater flow systems.

Future of peatlands and management

The peatland in the Nevado Tres Cruces National Park exhibits obvious degradation on its downslope end (Earle et al. 2003). The stratigraphic analyses and dating suggest that the peatland played an increasing role in water retention as the Oxychloe andina vegetation expanded and accumulated peat under it. The porous nature and extremely compact growth of the vegetation impeded drainage and evaporation probably contributed to retention of large volumes of water, mostly during spring runoff. It is thought that further vegetation growth and peat accumulation would reduce flows and evaporative water losses over time and likely reduced through flow to the lower extremities of the peatland. Earle et al. (2003) have shown that autoregulation processes played a significant role in growth and degradation of bofedales and it has to be taken into account in studies dealing with the assessment of human impact or climate in the development of bofedales.

What is the future of peatlands elsewhere in this water-stressed region, especially in light of precipitation decreasing to nearly 50 % of what it was 100 years ago in north-central Chile? Global climatic models (GCM) suggest that precipitation will continue to decrease at the same rate over the next 50 years. We know that plant species in the peatlands ecosystems are long-lived species (a minimum of 20-50 years; Squeo et al. 1996a, 2006a). Radiocarbon dating of peat records reveal that instead of being ancient ecosystems that originated immediately after deglaciation, peatlands are extremely young features arising when local hydrological and geological factors come together to favour establishment. Are the peatlands relicts of ancient ecosystems or are they temporary ecosystems that come and go as local water availability conditions change? In the present scenario of reduced precipitation, the sloping peatlands associated with discharge of local groundwater flow system will be much more sensitive to water availability than the wetlands associated with regional groundwater flow systems.

One important observation is emerging that may help to explain the climatic sensitivity of these peatlands in northern Chile. In the southern Andean steppe, measurements of plant biomass production from year to year show changes in response to water availability and length of the growing season that are directly controlled by El Niño Southern Oscillation (ENSO) phenomena (Squeo et al. 2006a, 2006b). In the winter rain region, El Niño (rainy) years increase water availability but reduce the growing season due to higher accumulation of snow over the peatlands which results in lower plant productivity. Maximum plant productivity occurs in the summer immediately following an El Niño summer, when water availability remains high and the length of growing season remains the same. We can, therefore, expect that primary productivity in these peatlands, and hence capacity to form and accumulate peat will decrease after several successive La Niña (dry) years because of an expected decrease in water availability. A series of successive La Niña years, would therefore contribute to peatland degradation. However, winter rain has been declining during the last century in Chile, while summer rains are globally increasing (Houghton et al. 2001). There may be an opposite trend in the quantity of precipitation and response of the bofedales

vegetation depending on El Niño/La Niña north of the Arid Diagonal.

If autoregulation processes of the local hydrological cycle also are contributing to degradation of parts of the peatlands system too, we can expect to see major decline in extent and accelerated deterioration of the delicate peatlands ecosystems south of the Arid Diagonal in the central Andes of Chile and Argentina. Much more studies are required to further understand the relationship between water sources (regional versus local groundwater flow systems) and plant productivity in bofedales. This information is crucial for the long term management of these fragile ecosystems in a future scenario of decreasing precipitation and increasing water demand by the mining and agriculture sectors.

ACKNOWLEDGEMENTS

Financial support from the National Commission for Scientific and Technical Research of Chile (CONICYT) and the Natural Sciences and Engineering Research Council of Canada (NSERC) is gratefully acknowledged.

LITERATURE CITED

- ABRAHAM EM, K GARLEFF, H LIEBRICHT, AC REGAIRAZ, F SCHÄBITZ, FA SQUEO, H STINGL, H VEIT, & C VILLAGRÁN (2000). Geomorphology and paleoecology of the arid diagonal in Southern South America. Zeitschrift für Angewandte Geologie: Sonderheft SH 1: 55-61.
- ACEITUNO P (1997) Aspectos generales del clima en el Altiplano sudamericano. In: González C (ed) El Altiplano: Ciencia y Conciencia en los Andes: 63-69. Vicerrectoría Académica y Estudiantil, Universidad de Chile, Santiago.
- ARROYO MTK, FA SQUEO, J ARMESTO & C VILLAGRÁN (1988) Effects of aridity on plant diversity in the northern chilean Andes: results of a natural experiment. Annals of the Missouri Botanical Garden 75: 55-78.
- ARROYO MTK, JJ ARMESTO, FA SQUEO & JR GUTIÉRREZ (1993) Global change: flora and vegetation of Chile. In: Mooney H, E Fuentes & B Kronberg (eds) Earth system responses to global change: contrast between North and South America: 239-263. Academic Press, New York, New York, USA.
- ARROYO MTK, FA SQUEO, H VEIT, L CAVIEDES, P LEÓN & E BELMONTE (1997) Flora and vegetation of Northern Chilean Andes. In: González C (ed) El altiplano: ciencia y conciencia en los Andes: 167-178. Universidad de Chile, Santiago.

- ARROYO MTK, FA SQUEO, L CAVIERES, & C MARTICORENA (2004) Chilenische Anden. In: Burga CA, F Kötzli & G Grabherr (eds) Gebirge der Erde: Landschaft, Klima, Pflanzenwelt: 210-219. Eugen Ulmer Gmb and Co., Stuttgart, Germany.
- ARROYO MTK, P PLISCOFF, M MIHOC & M KALIN-ARROYO (2005) The magellanic moorland. In: Fraser LH & PA Keddy (eds) The World's larger wetlands: ecology and conservation: 424-445. Cambridge University Press, Cambridge, United Kingdom.
- CHARRIER R (1997) Ciencias de la tierra y recursos mineros y energéticos en el Altiplano Chileno. In: González C (ed) El Altiplano: Ciencia y Conciencia en los Andes: 5-14. Universidad de Chile, Santiago.
- CLAYTON JD & CM CLAPPERTON (1997) Broad synchrony of a late-glacial advance and the highstand of palaeolake Tauca in the Bolivian Altiplano. Journal of Quaternary Science 12: 169-182
- DIRECCIÓN GENERAL DE AGUAS (1996) Delimitación de acuíferos de vegas y bofedales de las regiones de Tarapacá y Antofagasta. Dirección General de Aguas, Ministerio de Obras Públicas, Gobierno de Chile, Santiago, Chile. 169pp.
- EARLE L, BG WARNER & R ARAVENA (2003) Rapid development of an unusual peat-accumulating ecosystem in the Chilean Altiplano. Quaternary Research 59: 2-11.
- GARREAUD R, M VUILLE & AC CLEMENT (2003) The climate of the Altiplano: observed current conditions and mechanisms of past changes. Palaeogeography, Palaeoclimatology, Palaeoecology 194: 5-22.
- GROSJEAN M (2001) Mid-Holocene climate in the southcentral Andes: humid or dry? Science 292: 2391.
- GROSJEAN M, BL VALERO-GARCÉS, MA GEYH, B MESSERLI, U SCHOTTERER, H. SCHRIER, & K KELTS (1997) Mid- and late-Holocene limnogeology of Laguna del Negro Francisco, northern Chile, and its paleoclimatic implications. Holocene 7:151-159.
- HASTENRATH S & J KUTZBACH (1985) Late Pleistocene climate and water budget of the South American Altiplano. Quaternary Research 24:249-
- HOUGHTON JT, Y DING, DJ GRIGGS, M NOGUER, PJ VAN DER LINDEN, X DAI, K MASKELL & CA JOHNSON (2001) Climate change 2001: the scientific basis, contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press, Cambridge, United Kingdom. 881 pp.
- IRIARTE S, I UGALDE & M VENEGAS (1998)
 Hidrogeología de la cuenca Laguna del Negro
 Francisco (Región de Atacama). Servicio Nacional
 de Geología y Minería, Ministerio de Economía,
 Gobierno de Chile, documento de trabajo 10,
 Santiago, Chile.
- MARTICORENA C & M QUEZADA (1985) Catálogo de la flora vascular de Chile. Gayana Botánica 42: 1-155.
- MARTICORENA C & R RODRÍGUEZ (1995) Flora de Chile. Ediciones de la Universidad de Concepción, Concepción, Chile. 351pp.
- MARTICORENA C, O MATTHEI, R RODRÍGUEZ, MTK ARROYO, M MUÑOZ, FA SQUEO & G ARANCIO (1998) Catálogo florístico de la Región de Antofagasta. Gayana Botánica (Chile) 55: 23-83.
- MARTICORENA C, FA SQUEO, G ARANCIO & M

- MUÑOZ (2001) Catálogo de la flora de la IV Región. In: Squeo FA, G Arancio & JR Gutiérrez (eds) Libro rojo de la flora nativa de la Región de Coquimbo y de los sitios prioritarios para su conservación: 105-142. Ediciones de la Universidad de La Serena, La Serena, Chile.
- MESSERLI B, M GROSJEAN, G BONANI, A BURGI, MA GEYH, K GRAF, K RAMSEYER, H ROMERO, U SCHOTTERER, H SCHREUER & M VUILLE (1993) Climate change and natural resource dynamics of the Atacama Altiplano during the last 18,000 years: a preliminary synthesis. Mountain Research and Development 13: 117-127.
- MILLER A (1976) The climate of Chile. In: Schwerdtfeger W (ed) Climate of Central and South America: 113-129. Elsevier Scientific Publishing Co., Amsterdam, The Netherlands.
- OLSON DM, E DINERSTEIN, ED WIKRAMANAYAKE, ND BURGESS, GVN POWELL, EC UNDERWOOD, JA D'AMICO, I ITOUA, HE STRAND, JC MORRISON, CJ LOUCKS, TF ALLNUTT, TH RICKETTS, Y KURA, JF LAMOREUX, WW WETENGEL, P HEDAO & KR KASSEM (2001) Terrestrial ecoregions of the world: a new map of life on earth. Bioscience 51: 933-938.
- RECH JA, JS PIGATI, J QUADE & JL BETANCOURT (2003) Re-evaluation of mid-Holocene deposits at Quebrada Purifica, northern Chile. Palaeogeography, Palaeoclimatology, Palaeoecology 194: 207-222.
- RECH JA, J QUADE & JL BETANCOURT (2002) Late Quaternary paleohydrology of the central Atacama desert (lat 22° -24°), Chile. Geological Society of America Bulletin 114: 334-348.
- RISARCHER F, H ALONSO & C SALAZAR (1999)
 Geoquímica de aguas en cuencas cerradas: I, II y III
 región, Chile. Dirección General de Aguas Universidad Católica del Norte Institut de
 Recherche Pour le Developpement. 89pp.
- RUTHSATZ B (1993) Flora and ecological conditions of high Andean peatlands of Chile between 18°00' (Arica) and 40°30' (Osorno) south latitude. Phytocoenologia 25: 185-234.
- RUTHSATZ B (2000) Die Hartpolstermoore der Hochanden und ihre Artenviefalt. Ber. D. Reinh.-Tüxen-Ges. 12: 351-371.
- SQUEO FA, J CEPEDA-PIZARRO & JE NOVOA (1989) Estudio del impacto minero sobre la flora y fauna andina: ejemplo de la relación empresa-universidad. Anales del Tercer Encuentro Científico sobre el Medio Ambiente (Chile) 1: 405-413.
- SQUEO FA, H VEIT, G ARANCIO, JR GUTIÉRREZ, MTK ARROYO & N OLIVARES (1993) Spatial heterogeneity of high mountain vegetation in the andean desert zone of Chile (30° S). Mountain Research and Development 13: 203-209.
- SQUEO FA, R OSORIO & G ARANCIO (1994) Flora de los Andes de Coquimbo: cordillera de Doña Ana. Ediciones de la Universidad de La Serena, La Serena, Chile. 176 pp.
- SQUEO FA, CE RADA, ME GARCÍA, AL PONCE, AL ROJAS & A AZÓCAR (1996) Cold resistance mechanisms in high desert Andean plants. Oecologia 105: 552-555.

- SQUEO FA, LA CAVIERES, G ARANCIO, JE NOVOA, O MATTHEI, C MARTICORENA, R RODRÍGUEZ, MTK ARROYO & M MUÑOZ (1998) Biodiversidad de la flora vascular en la Región de Antofagasta, Chile. Revista Chilena de Historia Natural 71: 571-591.
- SQUEO FA, Y TRACOL, D LÓPEZ, JR GUTIÉRREZ, AM CÓRDOVA & JR EHLERINGER (2006a) ENSO effects on primary productivity in Southern Atacama desert. Advances in Geosciences 6: 273-277.
- SQUEO FA, E IBACACHE, BG WARNER, D ESPINOZA, R ARAVENA & JR GUTIÉRREZ (2006b) Productividad y diversidad florística de la Vega Los Tambos, Cordillera de Doña Ana: variabilidad interanual, herbivoría y nivel freático. In: Cepeda J (ed) Geoecología de la Alta Montaña del Valle del Elqui: 333-362. Ediciones Universidad de La Serena, La Serena, Chile.
- STONE PB (1992) The state of the world's mountains: a global report. Zed Books Ltd., London, United Kinwdom. 391 pp.
- VEIT H (1996) Southern westerlies during the Holocene deduced from geomorphological and pedological studies in the Norte Chico, northern Chile (27-33°
 S). Palaeogeography, Palaeoclimatology, Palaeoecology 123: 107-119.
- Palaeoecology 123: 107-119.

 VILLAGRÁN C & V CASTRO (1997) Etnobotánica y manejo ganadero de las vegas, bofedales y quebradas en el Loa superior, Andes de Antofagasta, Segunda Región, Chile. Chungará (Chile) 29: 275-304.
- VILLAGRÁN C & V CASTRO (2003) Ciencia indígena de los Andes del norte de Chile. Editorial Universitaria, Santiago, Chile. 362 pp.
- VILLAGRÁN C, MTK ARROYO & C MARTICORENA (1983) Efectos de la desertización en la distribución de la flora andina de Chile. Revista Chilena de Historia Natural 56: 137-157.
- VILLAGRÁN C, V CASTRO, G SÁNCHEZ, F HINOJOSA & C LATORRE (1999) La tradición altiplánica: estudio etnobotánico en los Andes de Iquique, Primera Región, Chile. Chungará (Chile) 13: 81-186.
- VILLAGRÁN C, M ROMO & V CASTRO (2003) Etnobotánica del sur de los Andes de la Primera Región de Chile: un enlace entre las culturas altiplánicas y las de quebradas altas del Loa superior. Chungará (Chile) 35: 73-124.
- VUILLE M & F KEIMIG (2004) Interanual variability of summertime convective cloudiness and precipitation in the central Andes derived from ISCCP-B3 data. Journal of Climate 17: 3334-3348.
- VUILLE M & C AMMANN (1997) Regional snowfall patterns in the high, arid Andes. Climatic Change 36: 413-423.
- WILCOX BP, MK WOOD, JT TROMBLE, & TJ WARD (1986) Grassland communities and soils on a high elevation grassland of central Peru. Phytologia 61: 231-250.
- WWF (2001) Terrestrial biorealms: Neotropical. World Wildlife Fund, Glanz, Switzerland. (http://www.worldwildlife.org/wildworld/profiles)