

# Peatlands in northern Chile: an overview from the perspective of plant hydraulic traits for biological conservation

*Bodefales en el norte de Chile: una visión general desde la perspectiva de los rasgos hidráulicos de la vegetación a la conservación biológica*

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## ABSTRACT

In the face of the increasing natural resource demands, soil erosion and climatic variability, the management of the Andean peatlands (bofedals) and wetlands (vegas) for conservation, production or other multiple uses is an important issue. These agroecosystems are considered critical for livestock feeding in the highlands due to the presence of plant species of high digestibility, protein content and biomass. Overgrazing, human migration and drought are currently the main problems affecting the Andean peatlands. The impact of climatic variability and overgrazing on plant water relationships and their combined effects on plant growth traits may be used as an important predictive tool for ecological health and sustainable management in these Andean landscapes. The main objectives of this review were to demonstrate the need to expand knowledge of the highland peatlands, based on concepts related to sustainability (associated with the carrying capacity), and the important role of physiological monitoring of vegetation, since the different rainfall regimes present in these natural areas represent an interesting scenario to assess the impacts of climate variability.

**Key words:** desert agrosystem, peatlands, ecophysiology, northern Chile.

## RESUMEN

*Ante la creciente demanda de recursos naturales, la erosión de los suelos y la variabilidad climática, la gestión de las turberas andinas (bofedales) y vegas destinados para la conservación, producción u otros usos múltiples es un tema importante a nivel mundial. Estos agroecosistemas son considerados críticos para la alimentación del ganado en el altiplano debido a la presencia de especies vegetales de alta digestibilidad, contenido proteico y biomasa. Actualmente, el sobrepastoreo, la migración humana y la sequía son los principales problemas que afectan a las turberas andinas. En este contexto, el impacto de la variabilidad climática y el sobrepastoreo en las relaciones hídricas de las plantas y sus efectos combinados sobre los rasgos de crecimiento de las plantas aparecen como un importante instrumento predictivo para la salud ecológica y la gestión sostenible en estos paisajes andinos. Los principales objetivos de esta revisión fueron describir la necesidad de ampliar el conocimiento del estudio de las turberas altiplánicas, acerca de la base de conceptos relacionados con la sostenibilidad (asociados con la capacidad de carga) y el importante papel del monitoreo fisiológico de la vegetación, puesto que los diferentes regímenes pluviales presentes en estas zonas representan un escenario interesante para evaluar los impactos de la variabilidad climática.*

**Palabras clave:** agroecosistema desértico, turberas, ecofisiología, norte de Chile.

## Introduction

### Andean agroecosystems and environmental stresses

Arid and semiarid agroecosystems occupy approximately 45% of the global landmass, and

most of these ecosystems experience degradation, reflecting high sensitivity and vulnerability to climatic variability and human disturbances (Anderson *et al.*, 2011). Northern Chile possesses some of the most arid regions on Earth and accounts for the increased diversity of high altitude ecological landscapes. These regions are unique scenarios

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to conduct research activities based on aspects associated with ecosystem monitoring (Squeo *et al.*, 2006). There are no current initiatives to evaluate the natural heritage of the ecosystems in arid regions of northern Chile, which are experiencing a certain degree degradation, reflecting industrial and demographic growth (Oyarzún and Oyarzún, 2011).

Vegetation cover plays an instrumental role in the formation and equilibrium of agroforestry systems in deserts and other areas prone to water stress, as plants play important ecological roles in maintaining water reservoirs and reducing soil erosion. Additionally, plants form part of the diets of domesticated camelids, goats and sheep. In the Andean agroecosystems of the Arica, Parinacota and Tarapaca regions in northern Chile plant species are particularly important, as these organisms provide a native system that contributes to the ecological and socioeconomic stability of Andean farmers in natural areas, called “bofedals” (peatlands), with high plant and animal biodiversity. These regions have experienced increased emigration of human inhabitants in recent decades, primarily reflecting the lack of socioeconomic development and opportunities oriented to the management of bofedals (CIREN, 2013). Few initiatives have been developed to improve the profitability of livestock production in these areas, and innovative projects that incorporate the sustainable use of natural resources in the Andean peatlands are scarce (Anderson *et al.*, 2011). It should be considered that natural Andean ecosystems are currently in a changing environment that needs to be considered in management and conservation options. In the current climate change scenario it is necessary to include the analysis of ecophysiological and conservation processes in the design of adaptation measures in the Atacama Desert peatlands system. The objectives of this report are (i) to review information collected from scientific studies regarding the current status of northern Chile peatlands, and (ii) to highlight these natural scenarios as appropriate areas for the study of plant hydraulic variables, in order to model future impacts of climate change in the Chilean highland.

### **Bofedals as research models**

As outlined above, some of the plant species present in Altiplano, particularly in azonal ecosystems called bofedals and vegas (peatlands), are among the most vulnerable areas and have been subjected to

degradation pressure (Holmgren *et al.*, 2006). The vegetation in bofedal agroecosystems is typically perennial, small (with the presence of grasses no taller than 1 m), and compacted, conferring protection from frosts, strong winds and the dry atmosphere. The rainy season in this high Andean plateau occurs between November and March and is known as the “Bolivian winter”, while the dry season occurs mainly in autumn and winter months (Quispe, 2003). Bofedals are critical regions for livestock feeding in the highlands, reflecting the presence of plant species of high digestibility, protein content and dense biomass (approx. 0.45 kg dry matter/m<sup>2</sup>; Alzérreca *et al.*, 1998). The main “indicator species” of bofedal systems –preferred by the domestic herbivores– are grasses of the genus *Deyeuxia*, shrubs such as *Parastrephia*, and *Polylepis*, a tree that primarily inhabits the highest altitudes above sea level throughout the world (Meza and Díaz, 2014). *Polylepis* individuals in areas with heavy grazing are most affected in terms of seedling survival and height growth of the size classes most accessible to livestock, retarding or preventing the natural recovery of *Polylepis* forests (Hoch and Korner, 2005).

The effects of overgrazing have been poorly studied in peatlands; however, previous studies have presented an interesting focus for discussion. In semiarid zones, Wang *et al.* (2014) reported that overgrazing reduces soil fertility, mainly nutrient dynamics, and induces changes in soil chemical properties as a result of pasture degradation, which consequently affects vegetation. Additional problems in bofedal agroecosystems include the incorporation of new water sources of anthropogenic origin and the modification of the existing watercourses, which together with overgrazing directly affect the natural regeneration of these areas, eventually leading to degradation (Quispe, 2003; Squeo *et al.*, 2006). Nonetheless, positive effects of grazing on bofedals have been described in Andean areas in Bolivia, as grazing is directly associated with an increase in plant cover, favoring seed dispersion through endozoochory (Alzérreca *et al.*, 1998). Studies on the effects of overgrazing on vegetation in northern Chile are incipient and divergent. Several studies have indicated that the reduction of vegetation cover and increased soil erosion are direct effects of overgrazing (Faúndez and Ahumada, 2001), while other studies support the hypothesis that climatic variability could impact land degradation (Meza and Díaz, 2014).

### Importance of plant hydraulic adaptations in drought-prone ecosystems

Xylem hydraulic variables are the most important physiological parameters for plants living in hyper-arid zones, as these variables provide insight into plant adaptations to extreme water stress conditions and habitats with increased climate variability. For example, seasonal analyses of plant water conductivity and xylem cavitation episodes in xeric plant ecosystems are useful parameters to investigate the role of abiotic factors such as precipitation variability and frost (Blum, 2011). Recently measurement of variables such as hydraulic conductivity, xylem features and water efficiency in desert plants has been shown to be a useful strategy to increase the current understanding of growth and reproductive traits under natural conditions (Cochard *et al.*, 2013). Altiplano agroecosystems are an interesting natural scenario for studies on plant adaptation to extreme conditions, as the mean annual precipitation and temperature gradients vary during the year depending on the latitudinal and longitudinal location. These abiotic factors, i.e. temperature and water availability, play important roles in physiological processes that drive reproductive parameters and xylem features among populations (León and Squeo, 2004). For example, Caquena bofedal is located in the Arica and Parinacota region (Table 1), with a mean annual precipitation of 300 mm year<sup>-1</sup> (with peaks of 800 mm year<sup>-1</sup> and years with only 100 mm) and approximately 200 days of frost per year, while Enquelga bofedal in the Tarapacá region has a mean precipitation of 122.5 mm year<sup>-1</sup> and approximately 160 days of frost per year (CIREN, 2013; Meza and Díaz, 2014). These environmental differences might reflect phenotypic plasticity variations in the physiology of the same plant species in response to different precipitation and abiotic conditions. Carvajal *et al.* (2015) showed that *Encelia canescens* populations

–a species adapted to arid climates– have different strategies to cope with variable precipitation under natural conditions; plants from the driest habitats showed adjustments in the root-to-shoot ratio of water, while plants growing in the wettest areas did not show adjustments in root-to-shoot ratios, but rather showed reduced biomass. As outlined above, rates of plant development processes are regulated by temperature, suggesting another interesting problem reflecting the effect of low temperatures on the percent loss of conductivity (PLC). According to Gleason *et al.* (2016), water, hence by analogy xylem sap, is exceptionally vulnerable to cavitation (increasing PLC) at low temperatures in the range of 0–5 °C. However, in contrast, Ritman *et al.* (1988) indicated that in vascular plants sap is less vulnerable to cavitation at temperatures above the freezing point, highlighting potential species-specific responses.

According to Fitter and Hay (2002), the flow of water along a cylindrical pipe (down a constant gradient of hydrostatic pressure between its ends at a constant temperature) is proportional to the square of the radius of the pipe. Theoretically, long and wide xylem vessels would provide more efficient water flow but would also be more vulnerable to cavitation than short and narrow vessels (Ritman *et al.*, 1988). In angiosperms, vulnerability to stress-induced xylem cavitation reflects many different factors, including conduit diameter pit membrane pore size, pit membrane flexibility and ion-mediated changes in the sap solute concentration (Cochard *et al.* 2013). At the ecological level, an increased frequency of cavitation might decrease the leaf *plastochron* (the period between the initiation of successive leaves in the shoot meristem) and leaf *phyllochron* (the period between the appearance of successive leaves) of desert plants (Rosenthal *et al.*, 2010). However, several gaps remain in the current knowledge of the morphological traits that can be used to assess the ecological stress tolerance of arid species.

Table 1. General data on the main bofedal areas in the XV and I regions.

Area	Meters Above Sea Level	Region	Mean annual days with frost	Mean monthly temperature (°C)	Mean annual precipitation (mm)	Type
Caquena (Lauca National Park)	4289	XV	202	9.9	322	Grazing
Taipuma (Lauca National Park)	4119	XV	205	9.8	322	Peatland without grazing
Enquelga (Isluga National Park)	3688	I	161	8.6	122.5	Grazing
Isluga river (Isluga National Park)	3701	I	162	8.5	126.9	Peatland without grazing

Because the onset of vessel cavitation is typically correlated with stomatal closure, these parameters (i.e., xylem conductivity, relative water content at the turgor loss point and stomatal conductance) can be used to evaluate species' fitness under stress conditions (Tognetti *et al.*, 1998). Turgor loss in cells is an indicator of plant water stress, directly impacting hormonal stimuli, cell metabolism and whole plant performance (Ritman *et al.*, 1988). This parameter plays a key role in the control of stomatal function, thus the strategies of populations more tolerant to variations in the water supply under field conditions can be identified. Indeed, stomata can be regulated based on the level of abiotic stress through partial closing, benefiting carbon fixation under stress conditions and increasing the efficiency of xylem water transport (Lawlor and Tezara 2009). Traditionally, gas exchange variables such as leaf cuticular transpiration ( $E_c$ ) and stomatal conductance ( $g_s$ ) have been strongly correlated with xylem hydraulic flow (Cochard *et al.*, 2013). In addition, non-stomatal limitations on photosynthesis and growth also occur during periods of abiotic stress.  $E_c$  rates provide an estimate of the water lost during transpiration when the stomata were closed, therefore facilitating the assessment of leaf epidermis permeability (Fernández *et al.*, 2015).

Bartlett *et al.* (2012) established the importance of leaf water potential at turgor loss ( $\pi_{tlp}$ ), elasticity modulus ( $\epsilon$ ) and relative water content at the turgor loss point ( $RWC_{tlp}$ ) as predictive traits of drought tolerance at biome scales, where  $\epsilon$  seems to be the most sensitive parameter to predict the distribution of species in arid zones. This information could be valuable to establish potential risks and information on environmental health, to identify the lowest values of plant water relations. This has led several authors to suggest that physiological parameters could be involved in the main important productive processes in plants: fertilization and seed production. Some preliminary studies on arid species are required to measure the effect of water stress on photosynthesis and net  $CO_2$  uptake without considering the effect of environmental variables in reproductive processes (Martínez-Vilalta *et al.*, 2014).

### Target species of bofedals

The high genetic variability of *Polylepis* forests should be expressed in a series of ontogenetic strategies of each population to

adapt to each microhabitat. For example, the low temperatures at treeline restrict growth processes (meristem activities) in *Polylepis* species, and the slope exposure or soil humidity determines the distribution of this forest (Hoch and Korner, 2005). In Andean agroecosystems, the queñoa forest is an important source of forage for sheep during dry periods when Poaceae species are in dormancy. Thus different responses to abiotic conditions are expected in these populations, resulting in the high variability of seed production within and between populations.

Herb and shrub species play a vital role in the biomass for livestock in Andean bofedals. *Poaceae* species are a source of forage for cattle due to the high protein content of predominant species; *Festuca* and *Deyeuxia* species have the highest dominance in terms of biomass (Moreau and Le Toan, 2003). The population densities of *Parastrephia* shrubs are strongly associated with the density of llamas and the carrying capacity in Andean peatlands, reflecting high protein and nitrogen content in the leaves of these plants (Treydte *et al.*, 2011). The development of appropriate methods for the spatial assessment and temporal monitoring of the aboveground vegetation biomass and physiological levels is important for efficient livestock management, as these data facilitate the evaluation of the carrying capacity of bofedals and the detection of the effects of overgrazing on vegetation. Moreover, understanding how and why many desert plant species exhibit variability in reproductive parameters is of considerable ecological and evolutionary interest for agroecosystems such as bofedals. Studies on the physiology of plants growing under extreme conditions and along latitudinal climatic gradients can contribute to the increased efficiency and economic value of these species. The relationship of water to the physiological response of important species such as *Deyeuxia curvula*, *Polylepis tarapacana* and *Parastrephia* at inter-annual periods is strategically important because these data can be used to improve stress tolerance genetically and highlight the development of areas of rest in bofedals with periods of non-grazing.

### Conclusions

The effects of climate change have been evaluated by the scientific community on an

abiotic level based on global data. They have predicted that in the near future the new climate scenario will present increased temperature, decreased precipitation and social migration. However, integral studies on the effects of these variables in natural and agroforestry species of Andean ecosystems at the regional level have been generally under-studied. The most accepted hypothesis suggests that plants will develop a series of physiological and morphological changes on their own as a way to adapt efficiently to the new climate. Better understanding of the influence of climate on the growth activity and processes of Andean vegetation will help to identify tools of management in a hyper-arid ecosystem that is

currently a very difficult task. Plant hydraulics is an interesting way to represent bofedals for the study of the plant physiology of its vegetation, since the different water regimes of rainfall that the Altiplano areas possess –according to the region to be evaluated– may represent a powerful tool to analyze the future effects of climatic variability.

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