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Growth and organic carbon production in peatlands dominated by *Distichia muscoides*, Bolivia, South America

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Abstract

Little is known about the growth or production of alpine cushion plant communities in the southern hemisphere, even though they dominate many high elevation peat-accumulating ecosystems in this region. We measured the growth and organic carbon production in four *Distichia muscoides* cushion plant–dominated peatlands in the tropical Andes of Bolivia, South America. Height growth was measured using the modified crank wire system. Cores were collected at the end of the 18-month study period to determine the biomass and organic carbon production rate. Bulk density averaged 0.081 g cm^{-3}. Total height increase ranged from 0.96 to 5.37 cm yr^{-1}, indicating very rapid growth. Most growth occurred during the austral summer wet season. Mean organic carbon production for the four sites ranged from 1.5 to 4.0 kg C m^{-2} yr^{-1} and is among the most rapid rates of potential peat accumulation known for high elevation or high latitude ecosystems on Earth.

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Introduction

An understanding of plant growth and production is essential for quantifying forage availability for grazing animals, as well as carbon inputs to peatlands (Asada et al., 2003). In most high-mountain, boreal and austral regions of the world, annual aboveground production can be quantified by clipping herbaceous plants at the ground surface at the end of the growing season to quantify aboveground standing crop and organic matter production (Walker et al., 1994). However, clipping cannot be used to assess plant growth and production in ecosystems dominated by bryophytes (Gunnarsson, 2005), lichens, or cushion plants (Gunnarsson and Rydin, 2000), because they do not die back to the ground each year. In tropical regions, the growing season may extend over the entire year and no single harvest approximates annual growth or production. Therefore, quantifying production in tropical grasslands requires multiple clippings per year (Long et al., 1989).

High mountain peatlands in the central Andes of South America, locally termed *bofedales*, are dominated by vascular plants, many of which have a cushion growth form. Many bofedales have perennially high water tables and thick peat bodies (Earle et al., 2003; Cooper et al., 2010). The cushion-forming species *Distichia muscoides* Nees & Meyen dominates many high elevation bofedales in Chile (Squeo et al., 2006), Peru (Skrzypek et al., 2011; Salvador et al., 2014), Ecuador (Chimner and Karberg, 2008), and Colombia (Benavides et al., 2013). This species has densely packed short green shoots and forms a hard and relatively flat surface, with leaves and shoots being only millimeters long. Clipping this species to estimate plant production has many problems because the cushions are very dense, the plants are evergreen and growth may be continuous throughout the year. In the drier puna region of the central Andes, bryophytes, grasses, and sedges form a minor component of the vegetation, and *Distichia muscoides* and other cushion plant species dominate organic matter production. The carbon dynamics of these Andean cushion plant–dominated ecosystems are poorly understood.

Bofedales provide critical forage production for grazing native domestic (llama and alpaca) and wild (guanaco and vicuña) camelids, as well as livestock species introduced from Europe during the colonial period (particularly sheep and cattle) (Buttolph and Coppock, 2004; Benavides and Vitt, 2014; Barros et al., 2014). These animals utilize bofedales because the evergreen plants provide year-round forage, especially in comparison with the semi-desert bunch grasses that dominate uplands in the dry puna region of the central Andes. There is also concern that the water supply for bofedales is meltwater from glaciers (Benavides et al., 2013), and as glaciers diminish bofedale plant production could diminish, creating significant limitations on pastoral agriculture. Pastoralists depend on the natural production of bofedales as a critical forage source and have been mountain herders for several millennia (Baied and Wheeler, 1993; Browman, 1989). Maintaining herds across the puna region in the coming decades is challenged by the sustainability of bofedales given both climate change and grazing pressures.

Climate in the tropical and subtropical Andes is changing rapidly, with drying and warming conditions, especially at higher elevations (Bradley et al., 2006; Vuille et al., 2008). Air temperature is rising rapidly, and a 21st century warming of 4.5–5.0 °C is predicted for the Andean altiplano (Vuille et al., 2008). Climate models also predict a stronger effect of global warming in mountain than lowland regions, and some areas are expected to experience longer or stronger dry seasons (Buytaert et al., 2010). These conditions could reduce water availability for bofedale plants and influence the production and survival of *Distichia muscoides* and other species.

In this paper, we quantify *Distichia muscoides* growth and production using the cranked wire method (Clymo, 1970) modified by adding bristles (Gunnarsson and Rydin, 2000) to stabilize wires in the soil (hereafter called wires). The cranked wire method has been widely used in boreal communities and austral communities dominated by *Sphagnum* spp. (Asada et al., 2003; Gunnarsson and Rydin, 2000); however, this appears to be the first use of this technique

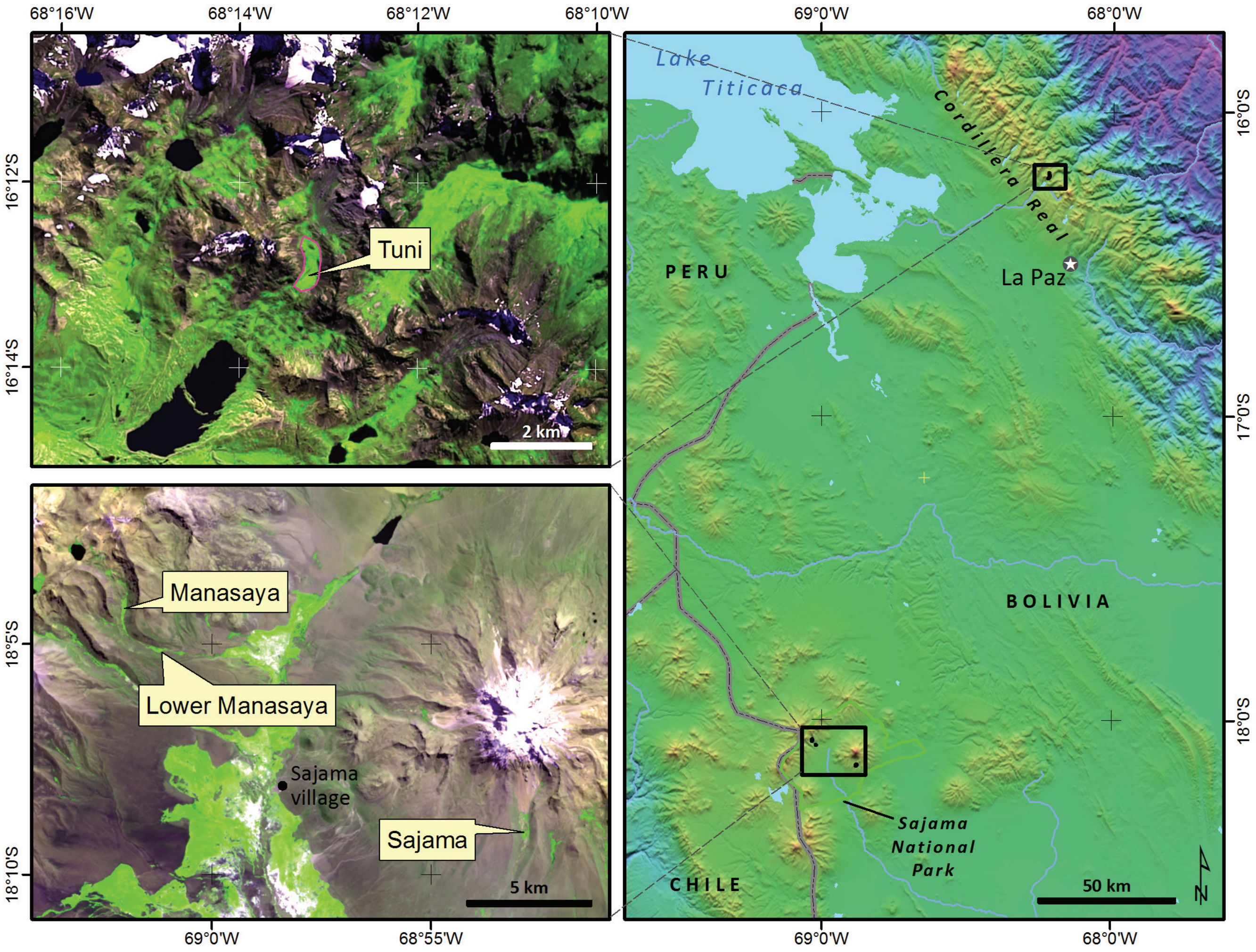

FIGURE 1. **Map showing locations of study sites Manasaya, Lower Manasaya, Sajama, and Tuni in Bolivia. Detail maps (left) are false-color Landsat 8 images, with the NIR band displayed in green to accentuate vegetation. The Tuni site is outlined to clearly demarcate its extent. Overview map (right) displays a colorized shaded relief elevation image, using data from the NASA Shuttle Radar Topography Mission.**

to quantify the growth of vascular plants. This method allows the continuous growth of the hard and dense cushions to be measured. Most cushion-dominated bofedales are snow covered for only days at a time during the winter and persistent snowpack rarely occurs. Limitations of the moss wire approach include animals pulling wires from the ground, or stepping on and bending them over. Also, the ground surface is rarely perfectly flat, and the method used to measure the distance from the wire to the ground must be standardized.

We use data collected over two austral summers and one winter to address the following questions: (1) what is the annual height growth of *Distichia muscoides* cushions, (2) does height increase vary significantly along a depth to water table gradient, and (3) what is annual organic carbon (OC) storage for *Distichia*-dominated cushions? These data are critical for assessing annual growth, forage production, and the potential for short- and long-term OC storage.

Study Areas

We worked in four bofedales in the Cordillera Real and Cordillera Occidental in Bolivia, South America (Fig. 1, Table 1). All four bofedales are ground water fed, peat-accumulating fens (Cooper et al., 2010), and all have at least 5.5 m of peat accumulation. Most bofedales in our study region are dominated by *Distichia muscoides* (Fig. 2) (hereafter called *Distichia*) and *Oxychloe andina* Phil. (hereafter called *Oxychloe*) (Table 1). We chose to work on *Distichia* because of its regional importance. In each bofedal we installed a grid of monitoring wells to quantify water table depth. We chose 12 *Distichia*-dominated stands located near monitoring wells for our analyses.

Study sites in the Cordillera Occidental are located in Sajama National Park, the first national park of Bolivia, established in 1939. The sampling sites are named Manasaya and lower Manasaya, as they belong to pasture zones of the Manasaya community. These sites are located 9 km northwest of the village of Sajama. Our third bofedal site, named Sajama, is located at the southern base of Nevado Sajama, the highest peak in Bolivia at 6542 m, 9 km southeast of the main village in the park. Our fourth study area is near the community of Tuni, and mountain of Tuni-Condoriri, situated in the Cordillera Real, 30 km northeast of La Paz. This bofedal site is located above the main reservoir that provides water to La Paz and El Alto. All study sites occur at elevations exceeding 4450 m (Table 1, Fig. 1), with surrounding peaks exceeding 6000 m in both ranges.

Climatically, the region is marked by seasonal precipitation with a single wet season and 70% of precipitation falling from

TABLE 1

Site characteristics for the four study bofedales (high mountain peatlands). Mean elevation, pH, and electrical conductivity (EC in uS) of groundwater in monitoring wells.

Site	Elevation (m)	pH	EC
Manasaya	4490	6.24	289.0
Lower Manasaya	4534	5.85	259.2
Sajama	4590	5.48	36.4
Tuni Condoriri	4680	6.05	82.1

December to February (Garreaud et al., 2003; Vuille et al., 2000). Total annual precipitation is higher in the Cordillera Real than the Cordillera Occidental. At Tuni, in the Cordillera Real, most rainfall is produced by deep convection, with moisture build-up from the eastern slopes and Amazon basin. Tuni records an average temperature of 4.6 °C and average annual precipitation of 700 mm (EPSAS, 2009). Long-term meteorological instrumentation is lacking for Sajama, but available data indicate an average annual temperature of 4.6 °C and mean annual precipitation of 321 mm (maximum 430 mm and minimum 60 mm) (Beck et al., 2010). These data resonate with a relatively long-term data set (1950–2006) from nearby Charaña (located 110 km NNW of Sajama), which has average annual precipitation of 300 mm (SENAMHI, 2007).

FIGURE 2. *Distichia muscoides* cushions in upper Manasaya study area, Bolivia.

The sites had water tables near the soil surface for at least part of the year, and some areas had a water table within 20 cm of the soil surface for the entire study period. However, a few sites had water table declines to 50 or even 100 cm below the soil surface for weeks or months during long rainless periods during the study period.

Methods

In each stand 14–22 wires were installed in October 2012 in two parallel rows of 7–11 wires spaced 25 cm apart (Appendix 1). Each wire was 15 cm long, with the lower 2 cm having bristles, and installed with the bristles approximately 7 cm deep in the cushion, and 6–8 cm of wire extending vertically above the ground surface. The height of each wire was measured at the time of installation, and repeated in April 2013, September 2013, and March 2014. The periods from October 2012 to April 2013 and September 2013 to March 2014 span austral summers, which is the rainy period, and April 2013 to September 2013 the austral winter, which typically has long rainless periods.

In March 2014, blocks of *Distichia* cushions 30 × 30 cm in surface area and approximately 30 cm deep were collected for analysis without disturbing their density or volume. A serrated knife was used to cut rectangular cores, each with a surface area of approximately 9 cm^2, and 1, 2, 3, 4, and in some sites 5, 6, and 7 cm long from each block of *Distichia*. Each core included the live vegetation. The volume of each sample was measured at the time of collection by carefully measuring all dimensions of the core. Samples were oven dried to a constant weight at 105 °C for 24 h, weighed, and the entire sample burned in a muffle furnace at 550 °C for 7 h. The remaining sample was weighted to determine the organic matter (OM) content of the sample. Samples averaged 90.2% OM. We converted all OM samples to OC using the following formula (Chimner et al., unpublished data):

$$\%OC = 0.53 * \%OM\text{: } R^2 = 0.92. \tag{1}$$

Bulk density (g OC cm^{-3}) was calculated for all analyzed cores. Then the relationship of peat core length to OC production for each study stand was analyzed using linear regression. For stands lacking sampled cores, the linear regression for the nearest stand was used to determine the relationship between peat core length and OC. Organic carbon was linearly related to height gain measured using the wires over the study period (%OC = 2605 × height – 2824, $R^2 = 0.93$). OC gain for each time period was related to height increase using the linear relationships. A few stands had height gains greater than 7 cm, and their OC gain was estimated using regression analysis relating peat thickness to total OC (Total OC = 3139.1 * height – 4239.1; $R^2 = 0.87$).

We also examined the relationship between annual height growth and annual OC accumulation to the mean standard deviation and annual maximum depth to groundwater using multiple linear regression analysis. We log transformed annual height and annual OC gain for analyses. All analyses were completed in R v. 3.0.2 (R Core Development Team, 2013).

Results

A height increase of more than 1 cm occurred for *Distichia* each summer, for most study stands (Fig. 3). Growth during the

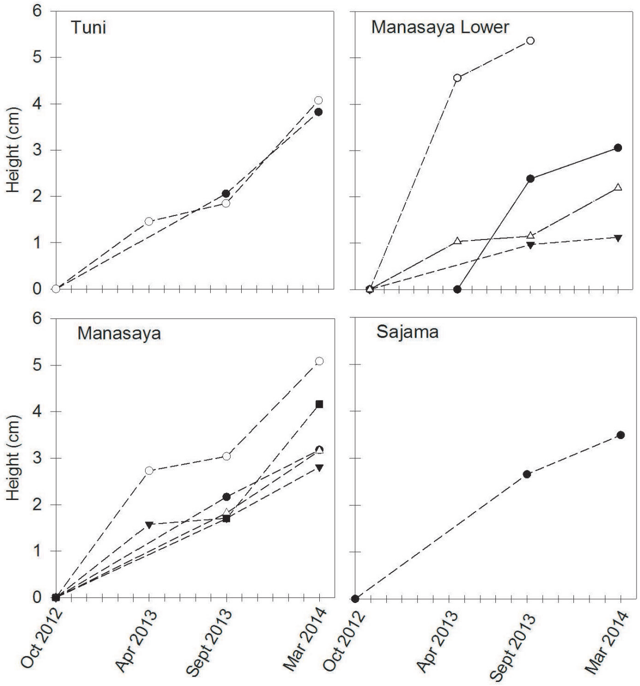

FIGURE 3. Height growth from October 2012 to April 2013, September 2013, and March 2014 for each moss wire site in the four study areas. Each symbol and line represents measurement from one site.

winter was slower, less than 1 cm for all stands. Over the study period, a total height increase of 2–6 cm was measured for most stands (Fig. 4). Stand D11, in an area with very stable groundwater levels, grew more than 5 cm in the first year, but the cushion surface overtopped the wires, which were engulfed and the plot could not be relocated the second summer. In contrast, total growth at stand D12 during the second summer was only a few millimeters, and the *Distichia* appeared to have died due to drought conditions by summer's end. The water table at this site was within 40 cm of the ground surface for several months each year, but during the second half of our study period the water table was more than 80 cm below the ground surface for many months, and there were long periods when it was deeper than 100 cm.

Bulk density of all cores averaged 0.081 g cm^{-3} (standard deviation = 0.023 g cm^{-3}), with a range of 0.135 to 0.044 g cm^{-3}. Mean net OC production for the period October 2012 through September 2013 ranged from 1.5 to >4.0 kg m^{-2} for the four bofedales, but was much less during the growing season of September 2013 to March 2014 (Fig. 5). Height gain was positively correlated with water table depth (WTD) (Fig. 6). The best model describing height gain explained 44% of the variance (log Annual Height Gain = 1.20 + 0.041 avgWTD, $p = 0.012$, $R^2 = 0.44$). OC production was positively correlated to measured groundwater depth (log kg carbon accumulation per year = 1.597 + 0.073 avgWTD, $p = 0.02246$, $R^2 = 0.36$) with great OC production in sites with more shallow water tables.

Discussion

The rate of *Distichia muscoides* height increase in the study areas is comparable to or higher than growth rates for *Sphagnum* spp. and other mosses in boreal (Gunnarsson, 2005; Bauer et al., 2007) and coastal temperate peatlands (Asada et al., 2003) in the northern hemisphere. Growth rates of *Distichia muscoides* reported for Colombia averaged 1–2 cm yr^{-1}, with a maximum of 3 cm yr^{-1} (Benavides et al., 2013). The data presented here and in Benavides et al. (2013) indicate that current and recent rates of OM and OC production in *Distichia muscoides*–dominated Andean bofedales are much faster than peatlands in other mountain or boreal regions. For example, *Sphagnum* peatlands worldwide have an average gain of 0.259 kg OM m^{-2} yr^{-1} (Gunnarsson, 2005), and OM is approximately 50% of OC. Chimner and Cooper (2003) reported 0.217 kg OC m^{-2} yr^{-1} for peatlands in the Colorado Rocky Mountains. Benavides et al. (2013) reported recent accumulations of 0.48 kg OM m^{-2} yr^{-1} over the past 25 years, and 1.40 kg OM m^{-2} yr^{-1} for the past 10 years in Colombia. These values also are for OM, not OC, and would be at the lowest end of the OC production rates we measured in Bolivia, which ranged from 0.5 to 12.7 kg OC m^{-2} yr^{-1} for the one full year measured.

Differences in OC production rates may in part be due to the methods used. Benavides et al. (2013) used ^{210}Pb chronologies that integrate a longer multiyear time frame, including more decompo-

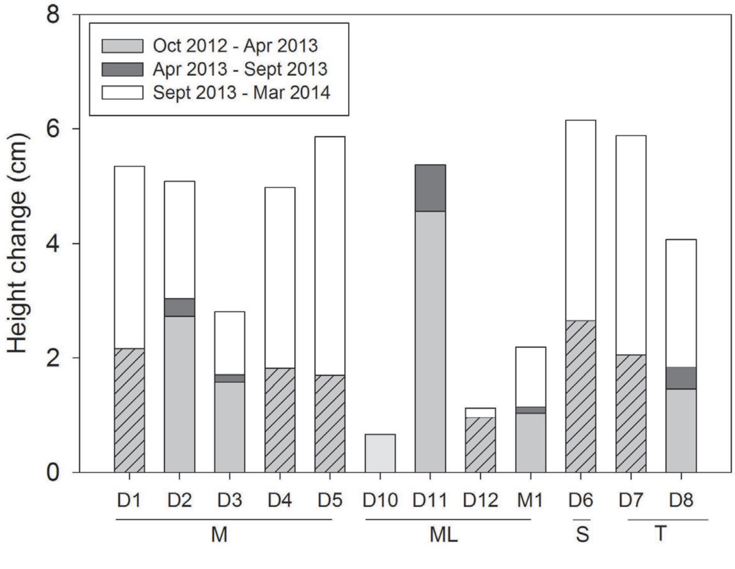

FIGURE 4. Height change (cm) for the periods October 2012–April 2013 (solid gray bar), April 2013–September 2013 (solid dark gray bar), and September 2013–March 2014 (white bar) for all study sites. Hatched areas are height change from October 2012–September 2013 (hatched gray bar) for sites that were not measured in April 2013. M = Manasaya, ML = Lower Manasaya, S = Sajama, T = Tuni. Height at each site is represented by its site code.

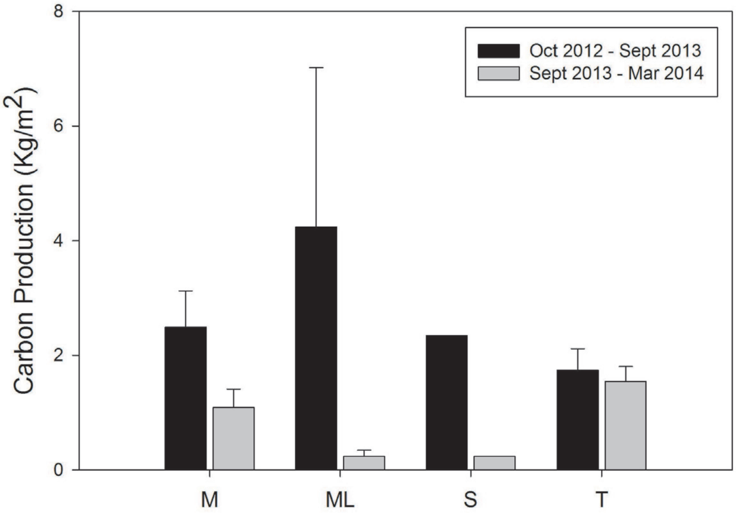

FIGURE 5. Mean organic carbon production for the four study sites Manasaya (M), Lower Manasaya (ML), Sajama (S), and Tuni (T) for the year October 2012–September 2013.

sition, while we directly measured annual height changes and OC production using the modified crank wire method.

The very high rates of cushion plant growth we measured may help explain the very rapid rates of peat accumulation reported for *Oxychloe andina*–dominated bofedales in the puna of northern Chile (Earle et al., 2003; Squeo et al., 2006). Long-term rates of OC accumulation in their studies ranged from 0.070 to 0.292 kg OC m^{-2} yr^{-1}, and peat bodies 1–3 m thick with basal calibrated ^{14}C ages up to 1761 ± 133 yr B.P. (Earle et al., 2003). Peat bodies in our study area exceed 5 m thick in many areas, and due to the rapid rates of accumulation this peat accumulation may only represent the late Holocene (Chimner et al., unpublished data).

Cushion plant–dominated peatlands high in the Andes appear to have among the most rapid rates of net primary production and OC production of any known peat-accumulating ecosystem. This likely results from a combination of a nearly 12 month growing season due to the location near the equator, the high insolation rates in the dry climate of the Andean puna, the persistent inflow of groundwater that provides a constant source of water for growth, the neutral to slightly acid water with pH near 6.5, and high ion concentrations of water flowing from watersheds composed of volcanic and sedimentary rocks, and the cold and anoxic soils that limit decomposition. The OC production rates reported here should also be considered minimum rates, as grazing by llama and alpaca occur at least seasonally on all of our study sites. Our stand with the fastest rate of height and carbon gain, D11, overtopped its wires and was lost. Therefore, its rapid growth rate is not included in the second summer mean OC production for Lower Manasaya.

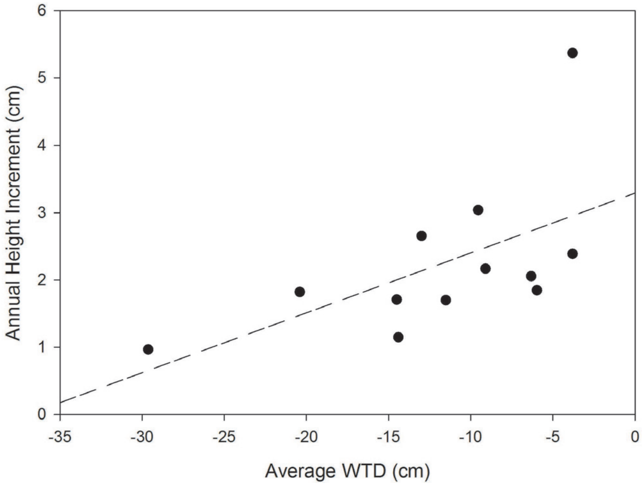

FIGURE 6. Relationship between Annual Height Increment (cm) and average water table depth (WTD) over the study period (October 2012–March 2014).

Since the 1930s, a persistent negative trend in precipitation for the Bolivian Altiplano, including the region of our study sites, has been documented using tree ring width series from *Polylepis tarapacana* (Morales et al., 2012). At our study sites, we recorded dramatic variance of up to 100 cm in the depth to water table in some portions of the study bofedales. For example, depth to water table in our well 12, located in Lower Manasaya, declined to more than 100 cm below the soil surface and remained deep for several months even during the wet season, from October to December 2012, April to May 2013, September to December 2013, and March 2014. This deep and persistent water table appears to have disconnected *Distichia* plants from their groundwater source resulting in plant mortality in some areas. Most *Distichia* stands had water tables within 20 cm of the soil surface for most of the study period, with the water table periodically declining to 40 cm deep. These stands support dense and vigorous cushions.

The methods presented here provide an important approach for seasonal, annual, and long-term studies of cushion plants and should be widely employed to provide critical information for monitoring the effects of climate changes on bofedal condition, and forage production under a range of grazing regimes. They are also important for measuring long-term OC production in a region that has sustained very high rates of peat accumulation for several millennia.

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APPENDIX

Table A1

Number of moss wires installed in each stand at the start of the experiment (Oct 2012) and the number that could be found and measured at the end of the experiment.

Stand	Site	Start	End
D1	Manasaya	14	7
D2	Manasaya	14	8
D3	Manasaya	14	14
D4	Manasaya	14	14
D5	Manasaya	8	6
D6	Sajama	14	12
D7	Tuni	14	12
D8	Tuni	14	7
D10	Lower Manasaya	22	22
D11	Lower Manasaya	22	17
M1	Lower Manasaya	20	14
D12	Lower Manasaya	22	21