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THE EFFECT OF WATER TABLE LEVELS AND SHORT-TERM DITCH RESTORATION ON MOUNTAIN PEATLAND CARBON CYCLING IN THE CORDILLERA BLANCA, PERU

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THE EFFECT OF WATER TABLE LEVELS AND SHORT-TERM DITCH RESTORATION ON MOUNTAIN PEATLAND CARBON CYCLING IN THE CORDILLERA BLANCA, PERU

By

Ana Maria Planas Clarke

A THESIS

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This thesis has been approved in partial fulfillment of the requirements for the Degree of MASTER OF SCIENCE in Applied Ecology.

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Preface

The journal article which is included as the main body of this manuscript is planned for submission in the near future and was written by Ana Maria Planas Clarke.

Data collection and processing were done by Planas, as well as figures and tables.

Rod Chimner provided the experimental design and editing advice and assistance.

John Hribljan provided gas flux measurement training, constructed the gas chambers and offered valuable advice on technical issues on the field.

Erik Lilleskov provided significant insights to the project design as well as essential editing assistance.

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Abstract

Tropical mountain peatlands are abundant in the Andes but are under intense grazing pressure and subject to climate change, both of which alter hydrologic conditions. Therefore, our first objective was to assess how carbon dioxide (CO_2) and methane (CH_4) fluxes change across a hydrological gradient in a mountain peatland in Huascaran National Park, Peru. Our second objective was to evaluate how short-term carbon cycling is changed after rewetting from ditch blocking. CO_2 and CH_4 effluxes were measured using the static chamber method. Net ecosystem exchange in the reference and the unrestored areas were on average 1.07 ± 0.06, and 0.76 ± 0.11 g CO_2 m^{-2} hr^{-1}. Although this is a groundwater fed peatland, we found that drained areas responded more to seasonal precipitation. Unexpectedly, ecosystem respiration in the unrestored treatment increased as water table rose in the rainy season. CH_4 emissions were 2.76 ± 1.06 mg CH_4 m^{-2} day^{-1} on average. However, at water table levels below -10 cm, CH_4 fluxes were zero. Although establishing the effect of restoration was complicated in this study by the timing of the wet season, our results indicate that rewetting increased Net Ecosystem Exchange and the ability to store carbon to near reference conditions.

1 CHAPTER ONE

1.1.   Introduction

Peatlands are wetlands that have accumulated thick layers of organic matter. The majority of peatlands globally are found in low-elevation areas, primarily in boreal and tropical regions (Clymo 1987: Maltby & Proctor, 1996). However, peatlands are also common in many mountain ranges, including the Andes (Cooper et al. 2012). Peatlands are common throughout the Andes, occurring in several climate zones including (1) the northern *páramo* ecoregion (wet year round) of Colombia, Venezuela, and Ecuador, usually above 3,500 m (Samaniego et al. 1998; Chimner and Karberg 2008; Hribljan et al. 2016), (2) high elevation (3000 - 4,800 m) mesic *jalca* ecoregion of northern Peru, where they are locally known as "bofedales" (Cooper et al. 2010), and (3) the very high (4400–4800 m) and arid *puna* ecoregion that extends from southern Peru through Bolivia (Cooper et al. 2015; Hribljan et al. 2015) to northern Chile and Argentina (Earle et al. 2003; Preston et al. 2003).

In contrast to *Sphagnum*-dominated northern peatlands, many Andean mountain peatlands are dominated by vascular plants with a cushion life form (Cooper et al. 2010). Many common cushion plant species are in the family Juncaceae, and other species are in the families Plantaginaceae and Asteraceae (Cooper et al. 2010; Benavides 2014; Salvador et al. 2014). Cushion plants have a dense, low-statured growth form with long taproots or buried stems with adventitious roots (Cooper et al. 2015). The cushion plant growth form has undergone convergent evolution in several regions as an adaption to

arctic and alpine environments (Billings and Mooney 1968). The compact growth form can trap heat and warm plants up to ~15° C above the surrounding air temperature and increase vegetation canopy humidity by reducing wind shear and evapotranspiration. In addition, their deep roots can acquire deep soil moisture and increase access to nutrients buried in decomposing tissues as the cushions grow upward. The aerenchymatous tissue of the roots can also transport gases from the surface to deep layers of peat and vice versa. The physiological and morphological characteristics of cushion plants are vastly different from common sedges and *Sphagnum* moss species that dominate most boreal and temperate peatlands (Earle et al. 2003; Fritz et al. 2011; Salvador et al. 2014).

Biological processes in peatlands generally have been found to be strongly controlled by water table levels (Chimner and Cooper 2003b; Page et al. 2009; Silvola et al. 2010; Gatis et al. 2016; Chimner et al. 2017). The water table is a physical barrier to oxygen diffusion from the atmosphere into the peat, limiting microbial activity and slowing decomposition rates (Maltby and Proctor 1996, Oechel, W. et al. 1998). A declining water table increases the volume of oxic soil and increases CO_2 production, while decreasing anaerobically produced CH_4 (Mooret and Knowles 1989; Bubier et al. 1995; Liblik et al. 1997; Nykänen et al. 1998; Silvola et al. 2010)

However, the relationship between water table level and carbon cycling is modified by vegetation type. For instance, *Sphagnum* mosses do not have roots and are sensitive to changes in water tables (Turetsky 2002; Bubier et al. 2003; Vasander and Kettunen 2006). A first study done in a cushion dominated peatland in the Ecuadorian páramo revealed that disturbances by cattle are detrimental to greenhouse gas benefits

from mountain peatlands (Sanchez et al. 2017), however no studies have been done focusing on changes in hydrology. Since cushion plants have such different morphology and rooting strategies than plants in northern peatlands, it is unclear how cushion plant peatlands respond to changing water table levels.

CH_4 emissions in peatlands are also strongly modified by vegetation type, with graminoids (e.g., sedges and rushes) having been found to enhance rates of CH_4 emissions because labile root exudates increase CH_4 production (Vasander and Kettunen 2006) and vascular aerenchymatous tissue (air channels in roots) increases CH_4 transport when O_2 flux through roots is insufficient to support high methanotroph (CH_4 -oxidizing bacteria) activity (Schütz et al. 1990; Shannon and White 1994; Chanton 2005). However, in the few studies that have been carried out in intact cushion peatlands, cushion plant peatlands have been found to have very low CH_4 flux rates, which has been attributed to high oxidation by cushion plant roots (Fritz et al. 2011; Dullo et al. 2017; Sanchez et al. 2017).

Mountain peatlands in the Andes have undergone hydrologic changes from both climate change and pastoral activities. Climate change can be one causal agent of hydrologic change, as exemplified by rapid Andean deglaciation in recent decades (Bradley et al. 2006). Even though the consequences of climate change are somewhat uncertain, it is expected that precipitation patterns will change in the Andean region, and that temperatures will increase, drying the peatlands (Chimner and Cooper 2003b; Cooper et al. 2015). In addition to climate change, many Andean mountain peatlands are being manipulated for grazing. Local communities have been farming sheep and cattle

for over 200 years, and to facilitate grazing they often build ditches to drain the peatlands. This has changed the distribution of the natural vegetation communities as well as their ecological functions (Millones 1982).

Peatland hydrologic restoration could be a good strategy to reverse degradation due to ditching in the Andes (Chimner et al. 2017). It could potentially return the water table to natural levels and regain the C sink function of the ecosystem (Page et al. 2009; Luan et al. 2018). There are two main techniques to restore hydrology in drained peatlands, ditch-filling or ditch-blocking Chimner et al. (2017). Filling ditches is a good long-term technique, but can be difficult due to lack of suitable fill material and cost of filling. Blocking ditches is a more common method because it is often easier and less expensive than filling ditches (Chimner et al. 2017). However, it is unclear if this method will be effective in the sloping peatlands with incised channels sometimes found in the central Peruvian Andes.

Because there is little fundamental information on carbon cycling in hydrologically intact cushion peatlands, and even less is known about how cushion plant peatlands in the Andes respond to drainage or restoration, our goals of this study are to examine two questions: 1) how does carbon cycling vary along a water table gradient caused by ditching, and 2) how does carbon cycling change in the short-term (months to a year) after ditch restoration in a cushion plant peatland. We hypothesized that changes in water table will affect CO_2 fluxes, by increasing ecosystem respiration (ER) at lower water table levels, and increasing net ecosystem exchange (NEE) at higher water table levels. We also hypothesized that CH4 emissions will increase with high water table

levels in the cushion plant dominated areas. In terms of the restoration, we hypothesized that rewetting the area will bring the CO_2 fluxes rates closer to those in the reference areas.

1.2.   Methods

1.2.1. Study Sites

The study occurred in Huascaran National Park (HNP), in the Ancash region in the central Andes of Peru (Figure 1). The park has an area of 340,000 ha and covers an elevation range of 2,500 to 6,768 masl. HNP contains approximately 660 glaciers and 300 lagoons of glacial origin. Its glaciers feed the main hydrological basins in north-central Peru. The mean annual precipitation of nearby Huaraz (elevation 3050 masl) is 632 mm and the mean annual temperature is 13.5 °C. The wet season occurs typically between October and April and has a mean temperature of 13.8 °C and mean precipitation of 83 mm per month. The dry season occurs between May and September and has a mean temperature and precipitation of 13.1°C and 10.4 mm per month respectively (climate-data.org).

Many areas inside the park are currently under pressure, mainly because of climate change and overgrazing (Byers 2000). One consequence of climate change is that melting glaciers are increasing lakes in size and volume, becoming a potential risk for flooding the main city of Huaraz (Vilímek et al. 2005). Overgrazing reduces the natural plant cover, erodes the soil, and destabilizes the water and carbon cycle. For

these reasons, park authorities are implementing management strategies to avoid disasters and recuperate ecosystems like bofedales using restoration.

The research occurred in two groundwater fed peatlands in the Tambillos region. Site 1 occurred in a small valley-bottom cushion fen peatland of approximately 4 ha located near the top of the watershed (~4400 masl: S 9° 41' 14.51", W 77° 14' 54.25" Figure 1) and is used as a reference location as it has no ditching disturbances. Due to the location of the peatland, it appears that it also has had little or no grazing impacts. Peat depth in this peatland is ~415 cm and has a basal date of 8,365 yr. BP (Hribljan et al. unpublished data). Specific conductivity averaged 180 uS cm^{-1} and the pH was 5.8.

Site 2 is a peatland complex of approximately 7 ha located ~500 m down-valley from site 1 at ~4200 masl (S 9° 41' 21.80", W 77° 14' 18.40", Figure 1). The peatland complex slopes down into and along the valley bottom and is bordered by a road on the one side (Fig 1). Peat depth in this peatland is ~400 cm and has a basal date of 9,340 yr. BP (Hribljan et al. unpublished data). Specific conductivity averaged 112 uS cm^{-1} and the pH averaged 5.9. Local communities built ditches near the road to drain part of the peatland. Although the ditch construction date is unknown, local residents confirm that they have been there for over 10 years. Ditch sizes ranged between 30 – 50 m length, and 50 – 100 cm depth. Other parts of the peatland complex had low levels of grazing and receive groundwater inputs from the slopes on the side of the valley opposite of the road and ditches, so were hydrologically unaltered. We used two locations in these relatively undisturbed areas as additional reference locations (*reference*). Three additional locations were sampled along the length of the ditch before and after restoration

(*rewetted*). One sampling location was located in a ditched area near the road that was not restored (*unrestored*).

Measurements began in June 2015 and occurred monthly until August 2016, then occurred one more time in December 2016. Sampling occurred for 5 months before any restoration occurred, during the dry season of 2015. In October 2015, at the beginning of the wet season, the peatland was restored by the Mountain Institute, Michigan Technological University, and local community members. Ditch restoration involved blocking the ditch with 22 wooden check dams (Figure 3). The size of the check dams ranged from 1-4 m wide, and 0.4 – 1.5 m high. Measurements continued after restoration until August 2016 and again in December 2016.

1.2.2. Water table levels

At each of the seven locations we installed a polyvinyl chloride (PVC) well to measure the water table. The wells were 6.3 cm in diameter and 1 to 2 m long. All wells were perforated, covered with a fine mesh, and capped to exclude infiltration from rain. Three wells were placed in the reference areas, three in the rewetted area, and the last one was installed in the unrestored area (Fig. 2). Water table depths were measured manually once a month for 17 months, from June 2015 until August 2016, and then again in December 2016 and May 2017.

1.2.3. CO₂ flux measurements

Daytime net cosystem exchange (NEE), ecosystem respiration (ER), and (by difference) gross primary productivity (GPP) were measured once a month starting in June 2015 until August 2016 and again in December 2016 using a chamber-based method (Hutchinson and Mosier 1981) and a PP Systems EGM-4 infrared gas analyzer (IRGA; PP Systems, Amesbury, USA)). The cylindrical chamber was custom made using clear acrylic (diameter 40.6 cm, height 59 cm, volume 76,383cm^3) (Sanchez et al. 2017). It was equipped with a detachable lid, a fan and a vent valve. Before conducting the experiment, four PVC collars (diameter 40.6 cm, height 10 cm, and wall thickness 0.5 cm) with a sharpened lower edge were inserted ~5 cm into the peat at ~ 1 to 3 m distance from each groundwater monitoring well as a fixed base for the chamber measurements.

To measure NEE, the clear chamber was placed carefully on the collar, without damaging the vegetation inside, and the collar-chamber joint was sealed using a cylindrical cut section of rubber tire inner tubing. With the fan on and the lid off, the chamber was flushed before each measurement, and then closed and sealed to conduct the measurements. NEE had a negative sign when GPP was higher than ER, meaning ecosystem uptake. The measurements were taken over a 124 seconds period. The same method was used to capture ER, except we placed a lightproof white cloth cover over the chamber to prevent light from entering the chamber. All measurements took place between 10:00 and 16:00, and collars were measured in random order to avoid any systematic bias.

We measured several environmental parameters during flux measurements including water table level, time of the measurement, air temperature, soil temperature, relative humidity, barometric pressure using a barometer, and photosynthetically active radiation (PAR) using a PAR sensor. Some of these measurements, such as time of measurement, relative humidity, and barometric pressure were already recorded by the IRGA, however, we measured them as a back up to confirm that the equipment was working properly. PP Systems soil temperature probe (STP) was inserted into the soil next to the chamber at 5 cm during the light measurements and at 20 cm depth during the dark measurements, while an additional small temperature probe was also inserted into the soil, at the same depths as PP Systems STP, to compare values.

1.2.4. Light curve experiment

We developed a light response experiment to understand if the light compensation point (LCP) differs along the water table gradient. To develop light response curves, we used shade cloths of different mesh sizes to reduce light. This experiment followed the methods of (Whiting et al. 1992; Bubier et al. 1998), using a clear chamber, an IRGA, and shade cloths that provided 100%, 90%, 80%, 70%, 60%, 50%, 40% and 30% shade.

The measurements took place in May and June 2016, from 9:00 to 13:00 when wells were in direct sunlight and the sky was clear. We used the chamber-based methods described above. Six collars were measured: three in the rewetted area, two in the reference area, and one in the unrestored area. As with the regular NEE and ER measurements, we also included other environmental variables and observations. The

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measurements were done alternating shade cloths from low light to high light levels, sometimes starting and other times ending with 100%/0% shade pair, otherwise in the order: 90%, 30%, 80%, 40%, 70%, 50%, 60% shade.

1.2.5. CH$_4$ flux measurements

We collected CH$_4$ samples from two collars at each well for three months. CH$_4$ sample collection took place at the end of the wet season in May, at the middle of the dry season in July, and at the end of the dry season in August 2016. We prepared field CH$_4$ standards in the MTU wetlands lab before going to Peru in order to test for any effects of sample transport. We filled nine 10 ml exetainers with 10 ppm CH$_4$ standard and another nine 10 ml exetainers with 100 ppm CH$_4$ standards, and sealed them with silicone caulk.

We used two closed CH$_4$ chambers (diameter 40.6 cm, height 31 cm, volume 40,133cm^3) to collect gas samples (Hutchinson and Mosier 1981; Sanchez et al. 2017). CH$_4$ chambers were placed on the same collars installed for CO$_2$ measurements. Each chamber was equipped with a narrow vent tube (to minimize pressure differentials) and a fan. Samples were collected every fifteen minutes for a period of 45 minutes per collar using a 60 ml syringe and needle. Gas samples were taken from the chamber's port without pumping the syringe to minimize changes in pressure inside the chamber. Prior to affixing the chamber, a sample of ambient air was taken over the vegetation of each collar to use later to correct fluxes. Ambient barometric pressure, humidity, temperature, dew point, soil moisture and soil temperature from a temperature probe inside the collar were recorded at the beginning and end of each measurement. We injected ~20 ml of gas

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in the exetainers to keep the vial pressurized. The syringe was flushed a 2-3 times before

taking the next sample. Both chambers were used concurrently on neighboring collars.

CH_4 samples were analyzed in the laboratory using a flame ionization detector (FID)

installed in a gas chromatograph (Varian CP- 3800, Palo Alto, CA, USA). We calculated

a headspace correction to account for the gas dilution when taken samples from the

chamber. The difference between the gas concentration with and without the headspace

correction was negligible (0.02% on average). We used the ideal gas law equation to

estimate CH_4 fluxes:

$$F_{CH_4} = \frac{\Delta C}{\Delta t} \times \frac{P}{1013} \times \frac{273}{273+T} \times \frac{16.043\,kg}{22.4414\,m^3} \times \frac{Vc}{Ac} \times \frac{mol}{10^6\mu mol} \times \frac{86400s}{day} \times \frac{10^6 mg}{kg} \qquad \text{Eq. 1.}$$

Where: F_{CH_4} is the CH_4 efflux (mg m^{-2} d^{-1}), $\Delta C/\Delta t$ is the change in CH_4 with time (μmol

mol^{-1} s^{-1}), P is the barometric pressure (atm), T is the air temperature at soil surface (°C),

16.043 kg/22.4414 m^3 are molar volume and ideal gas constants, Vc is the volume of the

chamber when placed on top of the collar (m^3), and Ac is the area of the chamber (m^2).

1.2.6. Vegetation survey

We took pictures of each collar at the beginning, middle and end of the study

period to look at plant communities and changes in plant growth. Each collar was

examined visually to determine the plant communities inside of them. We visually

estimated the percent cover of the cushion plants, non-cushion plants, as well as the

percent bare ground for each collar. Then, we averaged the four collars around each well

to estimate percent cushion plant cover, non-cushion plant cover, and bare ground cover

around the well. We estimated the cushion plants contour and the percent cover of the non-cushion plants growing on top of them; therefore, it allows over 100% cover measurements.

We also estimated cushion plant production to relate with C fluxes. To estimate cushion plant production, we used the modified cranked wire method (Clymo 1970; Gunnarsson and Rydin 2000; Cooper et al. 2015). This method consists of 20 cm long metal wires with bristles installed in the cushion plants inside the collars. Every wire was inserted carefully in the cushions allowing 5 cm to extend vertically above the ground surface. Wires were installed on February 2016 and growth was measured in May, August and December 2016. In December 2016, we took 6 core samples of cushion plants near the collars in the reference area and 15 in the rewetted area. Cores were taken without altering their density and volume. Each core was 2 cm in diameter and 8 cm in length and included the live vegetation. We cut them into four 2 cm increment subsamples to relate organic carbon (OC) content with height gain. Samples were oven dried at 65 °C to a constant weight, then combusted in a muffle furnace to calculate OM content of each sample. Next, we followed the method described in Cooper et al. (2015) to estimate organic carbon (OC) production. To estimate production in plots with cranked wires but lacking core samples, we estimated a linear regression of height growth vs biomass for the cored plots, and used the average bulk density of the same cushion plant species in the same treatment to estimate biomass production.

1.3.   Results

1.3.1. Water table

Water table levels in the reference areas were relatively stable throughout the year, with a mean of -4.6 ± 0.35 cm depth during the wet season, and -7.6 ± 0.6 cm depth in the dry season (Fig. 5). The unrestored area had a mean water table level of -108.5 ± 3.13 cm depth in the wet season, and -154 ± 4.23 cm depth in the dry season. The rewetted area had an average of -53.8 ± 8.3 cm depth during the early wet season before the restoration, and an average of -6.1 ± 2.2 cm depth after the restoration for the same season. During the dry season, the rewetted area had an average of -69.4 ± 7.3 cm depth before the restoration and -38 ± 11.3 cm depth after the restoration.

1.3.2. Vegetation survey and plant productivity

We found 28 plant species in total, including cushion plants, graminoids, mosses, and other vascular plants. Reference and rewetted areas had the greatest number of species, and the unrestored area was less diverse (Table 1). We identified three species of cushion plants (*Distichia muscoides* Nees & Meyen*, Distichia* sp., and *Oreobolus obtusangulus* Gaudich), graminoids including sedges (*Carex* sp.), herbaceous (*Lachemilla* sp.), grasses (*Calamagrostis* sp.), and mosses (*Sphagnum* spp.). We categorized them into two vegetation types for the purposes of this study: cushion plants and non-cushion plants (Table 2).

Plant community composition changed across the water table gradient. The reference area had only ~ 3% of bare ground and the highest percent cover of cushion plants (64.6%), including both *Distichia* species as well as *Oreobolus*. We found an almost even percent cover of *Oreobolus obtusangulus* and non-cushion plants in the rewetted area (47.9% and 45.8% respectively), as well as 20% bare ground. The non-cushion plants found were mostly sedges (*Carex sp.*) and grasses (*Calamagrostis sp.*). Lastly, we found a non-cushion plant community in the unrestored area, dominated by a trailing herb that is common in disturbed areas (*Lachemilla orbiculata* Ruiz & Pav) and an invasive grass *(Agrostis breviculmis* Hitchc) with approximately 97% plant cover and ~3% bare ground.

Cushion plants in the reference area had higher plant production than in the rewetted area ($p = 0.0054$), with a mean plant growth of 0.463 ± 0.11 g C m^{-2} hr^{-1} in the reference area and 0.064 ± 0.016 g C m^{-2} hr^{-1} in the rewetted area. Within the reference area, *Distichia* and *Oreobolus* had no significant difference in growth ($p = 0.308$), *Distichia* had a mean growth of 0.639 ± 0.21 g C m^{-2} hr^{-1} and Oreobulus 0.362 ± 0.13 g C m^{-2} hr^{-1}. *Oreobolus* in the reference site had a greater production than in the rewetted area ($p = 0.028$), with a mean plant growth of 0.064 ± 0.016 g C m^{-2} hr^{-1} in the rewetted area and 0.362 ± 0.13 g C m^{-2} hr^{-1} in the reference area.

1.3.3. CO$_2$ fluxes

CO$_2$ fluxes varied by season and among treatments (Fig. 6, Table 3). We use the sign convention in which negative values signify ecosystem release of CO$_2$, and positive

values signify ecosystem uptake of CO_2. During the wet season, NEE was higher than in the dry season in all treatments (Table 3). ER was stable in the reference sites, and decreased slightly in the rewetted areas during the wet season. ER in the unrestored area had a very different behavior than other treatments, increasing greatly during the wet season. GPP tended to increase during the wet season in the unrestored and reference areas, however, it remained stable in the rewetted area. The greatest ER and GPP fluxes were registered in the unrestored area during both the wet and dry season (Table 3). ER and GPP were greater in the reference area than in the rewetted area for both seasons.

Throughout the study period, all treatments had a mean daytime CO_2 uptake by the ecosystem (i.e., positive NEE), except for two months in the unrestored area. The reference areas had the greatest ecosystem uptake of 1.07 ± 0.06 g CO_2 m^{-2} hr^{-1}, followed by the rewetted area with 0.86 ± 0.04 g CO_2 m^{-2} hr^{-1}, and lastly the unrestored area with 0.76 ± 0.11 g CO_2 m^{-2} hr^{-1}. In the rewetted area, NEE increased when water table levels were closer to the soil surface, approaching the reference area values (Fig. 7A).

We did simple regression analysis between water table depth and fluxes for each month, and found that the correlation between ER and water table is significant for several months in the wet season, but not the dry season (Table 4). We plotted the slope of ER:WT over time (Fig. 8) and noticed that as the dry season progressed, the slope of this relationship decreased.

Because these are instantaneous measurements, without considering nighttime respiration, we developed a GPP:ER ratio plot in order to have a better estimate of what a

24-hour basis carbon balance will look like. A value of 2 for the ratio is considered to be a *rough* approximation of a zero net carbon balance on a 24 hour bases. As expected, water table had a strong positive relationship with the GPP:ER ratio. Carbon balance becomes more positive as water table increases, especially in the rewetted area (Figure 9). Within the reference treatment, we found high variation in the GPP:ER ratio, and the rewetted treatment shows a similar behavior when water table level is above ~20 cm depth. The unrestored area did not show a significant increase in its carbon balance with changes in water table.

1.3.4. Light response curves

For the pooled data from all dates, light levels were a strong predictor of NEE, explaining over 30% of the variation in rates, with rates saturating (95% of maximum) at ~1900 and an overall light compensation point of ~300 μmol CO_2 m^{-2} s^{-1} (Fig 10A). We couldn't estimate a light saturation point (LSP) from the light response curve experiments, because we did not have enough points at the high end of the curve (Figure 10B); however, we could estimate the light compensation point (LCP) using the NEE values for each collar. We found that LCP was lowest in the reference and rewetted areas with higher water table levels, while the unrestored area with lower water table levels had the highest light compensation point (Figure 11).

1.3.5. CH₄ fluxes

We measured very low CH_4 fluxes overall, averaging 2.76 ± 1.06 mg CH_4 m^{-2} day^{-1} across all dates and treatments (Figure 12). However, there appears to be a water table threshold at approximately -10 cm above which CH_4 fluxes increase. Below -10 cm water table depth, the average CH_4 flux is -0.07 ± 0.784 mg CH_4 m^{-2} day^{-1} and above -10 cm water table depth, the average CH_4 flux is 5.58 ± 9.18 mg CH_4 m^{-2} day^{-1}.

1.4.   Discussion

1.4.1. Hydrologically undisturbed sites

Even though there are large differences in precipitation amounts between the wet and dry seasons, the water table levels in the reference sites were stable. Average water table levels in the wet season were 4.6 cm below the soil surface and only dropped to an average of 7.6 cm below the soil surface during the dry season. The stable water table levels, in combination with a moderately high pH ~ 5.8 and specific conductivity of 146 μS cm^{-1} indicates that these are groundwater fed peatlands, or fens. Fens are the most common peatland type in mountains with bogs being limited to very high rainfall areas (Cooper et al. 2012). These results are similar to other studies that have found that undisturbed mountain fens have perennially stable water table levels (Cooper et al. 2012).

Our CO_2 values are the first measured in a mountain peatland in the Puna ecosystem. The reference CO_2 flux averages for NEE, GPP, and ER values were NEE, 1.05 g CO_2 m^{-2} hr^{-1}, 1.82 g CO_2 m^{-2} hr^{-1}, -0.76 g CO_2 m^{-2} hr^{-1}, respectively. Our values

are slightly greater than reference conditions measured in an Ecuadoran Paramo cushion plant fen where Sánchez et al. (2017) measured an average NEE, GPP, and ER rate of 0.69 g CO_2 m^{-2} hr^{-1}, 1.35 g CO_2 m^{-2} hr^{-1}, -0.66 g CO_2 m^{-2} hr^{-1}, respectively. Such differences might be caused by the difference in climatic conditions and vegetation communities. However, our values are lower compared to mountain sedge fens in Colorado. The Colorado sedge fens had greater NEE and GPP (1.74 g CO_2 m^{-2} hr^{-1} and 2.85 g CO_2 m^{-2} hr^{-1}), but lower ER (-0.63 g CO_2 m^{-2} hr^{-1}) (Schimelpfenig et al. 2014). The CO_2 values are also very similar to *Sphagnum* moss poor fen in Michigan that had an average NEE, GPP, and ER rate of 1.05 g CO_2 m^{-2} hr^{-1}, 1.82 g CO_2 m^{-2} hr^{-1}, -0.75 g CO_2 m^{-2} hr^{-1}, respectively (Ballantyne et al. 2014). Although our GPP values are lower than those found for sedge fens, the growing season for temperate peatlands lasts for about 7 months, whereas plants in the tropics grow all year long, making them productive all year.

CH_4 emissions increased with high water table levels, confirming our hypothesis. CH_4 emissions in the wet undisturbed areas were very low (7.06 ± 3.42 mg CH_4 m^{-2} day^{-1}), comparable to what Sánchez et al. (2017) found in a cushion peatland in Ecuador (8.1 ± 1.17 mg CH_4 m^{-2} day^{-1}). These rates are lower than those reported for northern temperate and boreal peatlands (Turetsky et al. 2014; Abdalla et al. 2016; Strack et al. 2016) (Figure 13), but higher than another study conducted by Fritz et al. (2011) in a cushion peatland in Patagonia where they found zero CH_4 emissions. Low CH_4 fluxes might be explained by vegetation communities present in the area, especially cushion

plants and sedges, which have deep roots that transport oxygen deep in the soil, making it available to oxidize the CH_4 produced by Archaea (Fritz et al. 2011).

1.4.2. Response to water table drawdown

Carbon cycling in the very dry unrestored area responded differently to water table levels compared to the reference and rewetted areas. Although NEE was relatively unresponsive to water table in all treatments, the slope of the water table- CO_2 flux relationship in the unrestored treatment differed from the other two in both GPP and ER. These differences might be related to the divergence in plant communities, specifically the absence of the cushion plants in the unrestored treatment. Surprisingly, ER in the unrestored treatment had a negative relationship to water table depth, possibly because dry season drought suppressed plant and microbial respiration. Although this phenomenon has not been explored previously in mountain peatlands, a study conducted in a forested peatland in Alaska discovered that microbial activities decreased up to 50% after a prolonged drought (Allison and Treseder 2008).

Our findings indicate that the reference sites have a more positive carbon balance than the unrestored treatment, as indicated by the GPP:ER ratio and the light compensation point analysis. Although our results are based on daytime flux rates, we expect that the low GPP:ER ratios of the unrestored area might indicate that this area is a net carbon source when considered on a 24-hour basis.

Although the effect of restoration was complicated in this study by the timing of the wet season, our results indicate that rewetting increased NEE and the ability to store carbon to near reference conditions. This was also found in Colorado mountain fens that were restored as NEE increased from -1.3 to -2.2 g CO_2 m^{-2} hr^{-1} after ditch plugs were installed (Schimelpfenig et al. 2014). This indicates that hydrologic restoration in the Andes have the potential to reinstate carbon cycling to more reference conditions.

The steep threshold in the water table-CH_4 relationship deviates from the pattern shown in a global analysis of CH_4 emissions from lowland peatlands (Turetsky et al. 2014). This could be because dry conditions during the CH_4 measurement period (May-August 2016) which led to drying of the surface of the peat, favoring methanotrophy over methanogenesis. Alternatively, cushion plants have deep aerenchymatous roots that transport oxygen to the deep peat and could also stimulated CH_4 oxidation. Consistent with this hypothesis, Fritz et al. (2011) found zero emissions of CH_4 at a water table depth of ~-12 cm.

1.5.   Conclusions

This is the first study to measure CO_2 and CH_4 emissions in a mountain peatland in Peru and the second one in South America, providing novel insights about these ecologically important and unexplored ecosystems.

Effects on CO_2 fluxes from water table differed across the drainage gradient. Moderately drained areas responded similarly to the reference areas when water table

levels were high, whereas the highly drained area had a strikingly different behavior, where ecosystem respiration increased as the peat went from low moisture content to wetter conditions. We suggest a 24-hour measurement study to determine whether these undisturbed ecosystems are C sources.

The low observed CH_4 emissions were consistent with what another study in the Ecuadorian Andean peatland found. Even though areas with high water table levels exhibit CH_4 emissions, values are lower than what is found in peatlands in the boreal and temperate regions. This could mean that as a CO_2 sink and small CH_4 source, these ecosystems are likely to reduce greenhouse gas from the atmosphere and have a cooling effect in the long term.

1.6.   References

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1.7.   Figures

Figure 1. Location of study site in Huascaran National Park (yellow marks), located in the central Andes of Peru.

Figure 2. Ditch in site 2 with check dams (yellow lines) and location of wells (red numbers inside white ovals) in the rewetted area, and unrestored area (well 2.10).

Figure 3. Ditched areas in paramo peatland. Two ditch sections shown before (A and B) and after (C and D) ditch blocking.

Figure 4. Peatlands study sites in Huascaran National Park, Peru. A) shows reference area at site 1. B) and C) show reference area at site 2. D) shows a ditched and degraded part near the unrestored area.

Figure 5. Average precipitation (mm/month) from four meteorological stations near the study area – Milpo, Chavin, Recuay, and Santiago Antunez de Mayolo (grey bars) – and the fluctuation in water table levels from the different treatments (lines) during the study period. Water table is averaged by treatment per month, error bars show standard error (SE). Note that the reference area is an average of both sites (1 and 2). Red arrow shows when the check dams were installed (October 2015).

Figure 6. Changes in CO_2 fluxes in the Tambillos valley during the wet and dry seasons by water table treatment. A) shows net ecosystem exchange (NEE), B) shows ecosystem respiration (ER), and C) shows gross primary production (GPP). Symbols are averages of fluxes by treatment, error bars show standard error (SE). Red arrow indicates when the restoration began.

Figure 7. Daytime CO_2 fluxes fluctuate by treatment in relation to water table: A) NEE, B) ER, and C) GPP. Means are averages of fluxes by treatment and error bars represent standard error (SE). A regression line shows the relationship between CO_2 fluxes and water table for the unrestored (red line) and rewetted (orange line) treatments.

Figure 8. Slope of WT:ER regression by date. Areas in grey correspond to the wet season, and white to the dry season.

Figure 9. Changes in instantaneous daytime GPP/ER ratio at different water table levels by treatment. Blue circles represent the averaged fluxes of the reference areas, yellow triangles the rewetted area before the restoration and the orange triangles the rewetted area after the restoration. Red diamonds represent the unrestored area. Error bars represent standard error (SE). Simple regression lines for the unrestored (red line), and rewetted (orange line) treatments.

Figure 10. Peatland net ecosystem exchange of CO_2 in response to light. A) Light response curve for net ecosystem exchange of CO_2 for all plots during the study period. B) Light response curves of each of the collars assessed in the light curve experiment for three months in the dry season.

Figure 11. Light compensation point for net ecosystem exchange of CO_2 estimated using the collars assessed in the light response curve experiment by water table at the time of measurement.

Figure 12. CH$_4$ fluxes by water table from May 2016, July 2016 and August 2016 in all treatments in a peatland carbon cycling experiment in the páramo of Peru.

Figure 13. Comparison of best fit for water table effect on CH_4 emissions in temperate and boreal peatlands (Abdalla et al. 2016; black filled circles) and cushion dominated mountain peatland in Peru by water table gradient (this study; blue filled circles).

1.8. Tables

Table 1. Average water table; species richness; percent cushion, non-cushion, and bare ground cover by well. Note that cover can sum to > 100%.

Well #	Water table (cm) BR	Species Richness	*Distichia* sp. (% cover)	*Oreobulus obtusangulus* (% cover)	Total cushion (% cover)	Non-cushion (% cover)	Bare ground (%) cover
1.1 Reference	-3.8 ± 1.13	6	22.5	13.75 ± 8.98	36.25 ± 11.34	80 ± 13.54	10 ± 7.07
2.1 Reference	-8.3 ± 2.04	7	67.5 ± 13.15	20 ± 12.25	87.5 ± 12.24	50 ± 12.25	0
2.2 Reference	-14.0 ± 14.13	10	0	70 ± 10.8	70 ± 14.14	52.5 ± 9.46	0
2.7 Rewetted	-56.9 ± 10.26	10	0	48.75 ± 19.4	50 ± 12.87	60 ± 10.31	18.75 ± 6.57
2.4 Rewetted	-68.1 ± 9.59	7	0	45 ± 2.89	45 ± 8.61	30 ± 0	37.5 ± 2.5
2.3 Rewetted	-68.3 ± 9.57	8	0	50 ± 17.8	48.75 ± 12.54	47.5 ± 13.54	6.25 ± 1.25
2.10 Unrestored	-172.1 ± 10.33	4	0	0	0	97.5 ± 2.5	2.5 ± 2.5

Table 2. The most abundant species in all treatments (> 10% cover). The presence of each species in a well is marked with an X.

Species	Functional type	1.1 (Ref.)	2.1 (Ref.)	2.2 (Ref.)	2.3 (Rew.)	2.4 (Rew.)	2.7 (Rew.)	2.10 (Unresto.)
Distichia spp.	Cushion	X	X					
Sphagnum spp.	Moss	X	X					
Zameioscirpus sp.	Graminoid		X					
Oreobolus obtusangulus	Cushion	X	X	X	X	X	X	
Oritrophium limnophilum	Herbaceous	X	X	X	X	X	X	
Calamagrostis spp.	Graminoid	X	X	X	X	X	X	X
Plantago tubulosa	Cushion		X	X	X	X		
Carex spp.	Graminoid			X	X	X	X	
Werneria nubigena	Herbaceous			X	X	X	X	
Lachemilla spp.	Herbaceous							X
Agrostis breviculmis	Graminoid							X

Table 3. Mean ± SE daytime of CO_2 fluxes by treatment in the wet and dry season.

Season	Treatment	NEE (g CO_2 m^{-2} hr^{-1})	ER (g CO_2 m^{-2} hr^{-1})	GPP (g CO_2 m^{-2} hr^{-1})	GPP/ER
Wet	Reference	1.116 ± 0.084	-0.762 ± 0.033	1.888 ± 0.100	2.66 ± 0.121
	Rewetted	0.896 ± 0.052	-0.643 ± 0.035	1.543 ± 0.065	2.84 ± 0.151
	Unrestored	0.786 ± 0.165	-1.837 ± 0.122	2.613 ± 0.203	1.49 ± 0.103
Dry	Reference	1.022 ± 0.084	-0.761 ± 0.035	1.810 ± 0.101	2.58 ± 0.133
	Rewetted	0.813 ± 0.06	-0.658 ± 0.030	1.524 ± 0.071	2.59 ± 0.142
	Unrestored	0.719 ± 0.133	-1.469 ± 0.128	2.188 ± 0.223	1.55 ± 0.97

Table 4. R², p-values, and slopes for the CO$_2$ flux vs water table simple regressions by month. Values with the symbol (*) were significant.

CO2 fluxes	NEE			ER			GPP			GPP/ER		
Month/year	R²	P value	Slope	R²	P value	Slope	R²	P value	Slope	R²	P value	Slope
June 2015	0.375	0.196	0.003	0.421	0.098	0.003	-0.215	0.753	0.001	0.184	0.218	0.005
July 2015	0.087	0.569	-0.007	-0.247	0.924	-0.001	0.097	0.283	-0.014	0.162	0.233	-0.023
August 2015	0.183	0.187	0.002	0.005	0.357	0.001	0.014	0.345	0.002	0.395	0.077	0.008
September 2015	0.091	0.262	0.005	0.261	0.138	0.003	-0.171	0.74	0.002	0.126	0.231	0.008
October 2015	-0.107	0.545	0.002	0.904	0.006*	0.007	0.049	0.305	-0.004	0.173	0.194	0.009
November 2015	-0.198	0.924	-0.001	0.933	0.003*	0.013	0.335	0.101	-0.012	0.010	0.35	0.008
December 2015	0.052	0.301	0.008	0.739	0.008*	0.012	-0.135	0.616	-0.005	0.596	0.026*	0.016
January 2016	-0.196	0.901	0.001	0.781	0.005*	0.013	0.13	0.227	-0.012	0.232	0.154	0.01
February 2016	-0.176	0.750	-0.002	0.109	0.245	0.005	0.084	0.268	-0.007	-0.19	0.846	0.002
March 2016	0.097	0.256	-0.008	0.66	0.016*	0.01	0.416	0.07	-0.017	-0.127	0.595	0.008
April 2016	-0.006	0.371	0.005	0.924	0.000*	0.026	0.713	0.011*	-0.022	0.297	0.119	0.025
May 2016	-0.196	0.899	-0.001	0.717	0.01*	0.013	0.158	0.204	-0.013	0.146	0.214	0.015
June 2016	0.272	0.132	0.004	0.815	0.003*	0.01	0.391	0.079	-0.005	0.222	0.161	0.011
July 2016	-0.12	0.575	0.002	0.597	0.023*	0.008	0.013	0.347	-0.006	0.236	0.152	0.013
August 2016	-0.084	0.496	0.002	-0.01	0.527	-0.001	-0.065	0.462	0.003	-0.199	0.948	-0.0003
December 2016	0.584	0.028*	0.01	0.266	0.135	0.006	-0.096	0.521	0.005	0.841	0.002*	0.013