



## Soil and fine root chemistry at a tropical Andean timberline



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### ARTICLE INFO

#### Article history:

Received 11 April 2015

Received in revised form 21 August 2015

Accepted 14 October 2015

Available online 22 October 2015

#### Keywords:

Forest–grassland boundary

Land use

Peru

Stable isotopes

Topography

Treeline

### ABSTRACT

Tropical timberlines are dynamic ecotones influenced not only by climate but often also by human activity. Understanding differences in soils across these boundaries therefore requires explicit consideration of land use. We examined patterns of soil and fine root chemistry at a tropical timberline ecotone in northern Peru nearly three decades after grazing and fire reduction. Soils were collected in forest, edge, and grassland habitat on east- and west-facing slopes and evidence of recent grazing, past fire, and shrub presence was recorded in alpine grasslands. We determined concentrations and mass (to 10 cm) of base cations, phosphorus (P), and inorganic nitrogen (N) in soil, as well as total carbon (C), total N,  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$  in soils and fine roots. Calcium and magnesium concentrations and mass, and soil P and fine root N concentrations decreased from forest to grassland. Lower soil P, soil N, and fine root N concentrations were associated with enriched soil  $\delta^{15}\text{N}$ , indicating enhanced nutrient losses from edge and grassland soils. The stable carbon isotopic composition of soils and fine roots was more enriched in grassland (soil  $\delta^{13}\text{C} = -24.1\text{‰}$ ; fine root  $\delta^{13}\text{C} = -25.1\text{‰}$ ) compared to forest (soil  $\delta^{13}\text{C} = -26.1\text{‰}$ ; fine root  $\delta^{13}\text{C} = -28.2\text{‰}$ ), except where shrubs were present. In grasslands, topography appeared to influence grazing and shrub expansion; shrubs were more prevalent on the steeper west-facing slopes while cattle dung was found only on the shallower east-facing slopes. The spatially heterogeneous patterns of shrub establishment and surface soil and fine root chemistry across these forest–grassland boundaries provide evidence of legacies of grazing and burning, underscoring the need for further research on land-use legacy effects on belowground processes in tropical timberline ecosystems.

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### 1. Introduction

Tropical timberlines form part of a spatially and temporally dynamic ecotone that encompasses the transition from the upper limit of tropical montane forest to alpine grassland (Young and León, 2007). In the Andes, this forest–grassland boundary stretches thousands of kilometers from Venezuela to northern Chile and Argentina. As such, extraordinary diversity in all of the soil-forming factors—climate, organisms, relief, parent material, and time (Jenny, 1941)—characterizes this tropical timberline ecotone.

In humid and perhumid areas of this vast and variable ecotone, numerous studies document high ecosystem carbon (C) storage (Farley et al., 2013; Gibbon et al., 2010; Tonneijck et al., 2010; Zimmermann et al., 2010). Here, timberline forest and adjacent grassland ecosystems experience cool, wet, humid, and often foggy conditions (Rapp and Silman, 2012) that favor relatively high rates of net primary productivity (NPP). Recent measurements of both above- and belowground NPP

indicate that, on average, forests and grasslands at timberline produce 5.6 and 6.3 Mg C ha<sup>-1</sup> yr<sup>-1</sup>, respectively (Oliveras et al., 2014). Large amounts of this organic material may be chemically or physically protected through the formation of organomineral associations, low pH and associated high aluminum (Al) concentrations, and large proportions of micro- and mesopores that prevent microbial access to soil organic matter (SOM) (Buytaert et al., 2007; Hofstede et al., 2002; Tonneijck et al., 2010). These processes, coupled with the wet or waterlogged conditions derived from the climate, promote slow litter decomposition and, in turn, organic matter accumulation (Hofstede, 1995).

Stocks of such nutrients as nitrogen (N), sulfur (S), potassium (K), calcium (Ca), and magnesium (Mg) in soils and roots are also often higher at timberline than at lower elevations (Soethe et al., 2007, 2008), though a considerable fraction of these nutrients may not be available to plants (Hofstede, 1995). In Andean grasslands, especially those on volcanic ash soils, adsorption of phosphorus (P) by Al and iron (Fe) oxides results in low overall P availability (Buytaert et al., 2006; Farley and Kelly, 2004). In contrast, some studies indicate increasing soil P and decreasing soil N availability in forests at or near timberline (Fisher et al., 2013; Graefe et al., 2010; Hertel and Wesche, 2008; Soethe et al., 2008). Where nutrients are available, low soil pH and elevated precipitation contribute to leaching losses (Heitkamp et al., 2014).

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Although vegetation may have profound effects on soil chemistry, direct comparisons of forest and grassland soils at tropical timberlines have produced some surprising results. For example, at two sites in southern Peru, soil C stocks and soil nutrient concentrations did not differ across the treeline (Heitkamp et al., 2014; Zimmermann et al., 2010). Comparison of páramo grassland and native forest soils in Ecuador revealed no differences in soil N concentrations or pools (Chacón et al., 2009; Hofstede et al., 2002). Working at the molecular level, Nierop et al. (2007) found that SOM composition varied little between forest and páramo soils and could not explain observable contrasts in soil profile development. There is, however, evidence that vegetation type at tropical timberlines can alter surface soil chemistry through effects on canopy nutrient fluxes (Ponette-González et al., 2010, 2014), litter quantity and quality (Coûteaux et al., 2002; Pérez, 1992), soil moisture and acidity (Farley and Kelly, 2004; Harden et al., 2013; Hofstede et al., 2002), vertical nutrient redistribution (Jobbágy and Jackson, 2004), and weathering (Heitkamp et al., 2014).

In addition to differences in vegetation, human populations have long occupied, utilized, and managed tropical alpine puna and páramo grasslands (Kessler, 2002; Wesche et al., 2000)—in some cases intensively and for thousands of years (Harden, 2006; Horn and Kappelle, 2009; Urrego et al., 2011; White, 2013). Widespread throughout the Andes, the coupled practices of burning and grazing reduce above-ground biomass and vegetation cover through trampling, consumption, and combustion, frequently resulting in the stimulation of root growth and exudation (Hofstede, 1995). These land-use practices also alter nutrient cycling directly through nutrient additions. For example, by accelerating N mineralization and nitrification and releasing P, Ca, Mg, and K stored in biomass, fires increase available N and base cations in the short term (Certini, 2005; Wan et al., 2001). Nutrients consumed by grazers are returned to the soil in the more labile forms of urine and feces (Haynes and Williams, 1993). Grazing and burning also influence soil nutrient availability indirectly through effects on the factors that control decomposition, including soil temperature, moisture, and the quantity and quality of litter (Thomas and Asakawa, 1993).

Fire and grazing result in nutrient loss as well. Nutrients are volatilized during fire and from urea, and those deposited to soil in ash or dung can be lost via wind or water erosion (Certini, 2005; Cingolani et al., 2013). As a result, repeated grazing and burning in tropical landscapes may lead to declining soil base cations, N, and P (Hamer et al., 2013), increasing potential for nutrient limitation over the long term (Davidson et al., 2004).

While there is growing interest in the importance of land use and vegetation to soil characteristics at Andean tropical timberlines, much of the recent research focuses on soil C storage. However, less is known in these systems about other dimensions of nutrient availability and cycling, and the influence that land use might have on variation in soil and plant nutrient and isotopic patterns across forest–grassland transitions and the effects of roots and soils on each other (Nierop and Jansen, 2009). Research on Andean timberline soils is also limited in geographical scope, with few studies available for the northern Peruvian Andes.

In this study, we investigated patterns of soil and fine root chemistry across a tropical forest–grassland transition at a Peruvian Andean timberline nearly three decades after the implementation of grazing reduction and fire exclusion policies. Base cations, inorganic N pools, and extractable P in soil, as well as total C and N in soils and fine roots were examined. We employed stable C and N isotopes to evaluate longer-term changes in vegetation and N cycling, respectively: natural abundance of  $\delta^{13}\text{C}$  can be used to detect shifts in vegetation between plants with  $\text{C}_3$  and  $\text{C}_4$  photosynthetic pathways because of differences in the carbon signature of  $\text{C}_3$  (−34‰ to −23‰) and  $\text{C}_4$  plants (−17‰ to −10‰; Cerling, 1999), while the natural abundance of  $\delta^{15}\text{N}$  is commonly used as an integrator of N cycling (Robinson, 2001). Plant and soil  $\delta^{15}\text{N}$  tend to be enriched in systems where N losses exceed N inputs, and vice versa.

Using these indicators, we hypothesized that concentrations of base cations, N, and P in soil and of N in fine roots would be lower in grassland compared to forest because long-term grazing and burning often result in losses of these elements (Davidson et al., 2004). Further, we hypothesized that both soil and fine root  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  would be enriched in edge and grassland compared to forest because grassland grazing and burning promote: 1) establishment of  $\text{C}_4$  grasses; and 2) hydrologic and gaseous losses that typically lead to an enrichment of soil and plant  $\delta^{15}\text{N}$  (Pardo and Nadelhoffer, 2010).

## 2. Materials and methods

### 2.1. Study region

Río Abiseo National Park (7°45'S and 77°15'W) lies along the eastern slopes of Peru's Cordillera Oriental within the Andean–Amazon basin (Fig. 1, inset). The timberline ecotone is a relatively narrow belt between 3200 and 3800 m (Young, 1993a). This study was conducted above the upper altitudinal limit of continuous montane rainforest in the southern region of the park. Long-term observations of climate at this site do not exist but available data indicate mean annual temperature is likely between 6 and 10 °C (Young, 1992). According to satellite-derived rainfall estimates for 2003–2008, annual rainfall ranges from ca. 1000–1500 mm (CPC MORPhing technique; Joyce et al., 2004) with two distinct periods: a wetter period from October to April and a drier period from May to September. In addition, orographic fog forms throughout the year as a result of west-flowing air masses originating in the Amazon basin.

During the Pleistocene, glaciers in Río Abiseo National Park extended down to 3000 m, covering what is presently the timberline ecotone (Rodbell, 1993). Deglaciation began ~13.3 ka and cirques were ice free by at least  $10.3 \pm 0.6$  ka (uncalibrated  $^{14}\text{C}$  dates; Rodbell, 1993). A layer of loess ranging in thickness from 25 to 54 cm was deposited across the landscape following deglaciation (Miller et al., 1993). Today, the lower limit of glaciation is demarcated by a clear boundary between north–south trending U-shaped valleys above ~3000 m and steep-sided V-shaped valleys below.

The present study was conducted in one of the glaciated U-shaped valleys between 3391 and 4067 m elevation (Fig. 1). Although knowledge of the park's geology is limited, bedrock along side slopes of the study valley and of cobbles from till is lithologically similar; both are composed of andesite, dacite, and rhyolite porphyries, are dominated by plagioclase, and have low abundance of amphiboles and pyroxenes (R. Ferring, *personal communication*). Detailed soil mapping has not been done, but soils have histic and nearly histic epipedons; soils are black to dark brown and wet with generally greater than 16% C and low bulk density. Full soil pits were not dug at the sites, so it is unknown whether there are any diagnostic sub-surface horizons, but exposures throughout the valley suggest that mineral soils in till parent material extend to at least 1 m depth in grassland areas.

Vegetation in the timberline ecotone is a mosaic of tropical alpine grassland and montane rainforest. Inhabited by the Chachapoya peoples during precolonial times (Church and von Hagen, 2008), this montane rainforest extends up to 3200 m on valley floors and to 3450 m on valley sides, intermixing with grasslands between 3200 and 3800 m. In some valleys, small (<5 ha) isolated forest patches dot the landscape. These forest canopies and their edges have one to two orders of magnitude more woody plant species than equivalent timberline forests in temperate areas (that is, 10–100 species rather than 1–3 species; Young and León, 2007). Within forest patches, common tree genera include *Polylepis*, *Weinmannia*, *Clethra*, and *Myrsine*, while at forest edges shrubs of the genera *Baccharis*, *Brachyotum*, and *Miconia* are abundant. The native  $\text{C}_3$  tussock grasses *Calamagrostis*, *Cortaderia*, and *Festuca* dominate tropical alpine grasslands (Young, 1993a). Before park establishment in 1983, Andean herders burned these grasslands every one to

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