



Giant rosette plant morphology as an indicator of recent fire history in Andean páramo grasslands



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ABSTRACT

High-altitude Andean páramo grasslands are fire-dependent systems but reconstructing recent fire history is difficult using conventional approaches. From Venezuela to Ecuador, páramos are usually dominated by giant rosette plants of the genus *Espeletia*. This study assesses *Espeletia*'s potential as an indicator of recent fire history. Their peculiar morphology is an adaptation to the mountain environment. Fire removes dead leaves which sheathe the single stem, but they begin to reaccumulate after the fire. It is this reaccumulation of leaves, plus post-fire mortality rates, that might indicate recent fire history. Adult mortality during the first two years after the fire varied according to fire intensity, from 8% (low intensity) to 56% (very high intensity), and was low in the absence of fire (2.5%). Growth rates were much faster at 3600 m (14.8 cm y^{-1}) than at 4100 m (1.6 cm y^{-1}), and so was leaf turnover (94 compared with 50 leaves y^{-1}). Taller plants grew faster than shorter ones. Dead leaf cover on the stems successfully predicted time since fire in four sites of known fire age. *Espeletia* does represent a useful indicator of fire history but requires calibration to account for local growth rates. At lower altitudes, *Espeletia* plants could provide information in fires during the previous 20 y, and longer periods at higher altitudes (where plants grow more slowly and live longer). It is a relatively cheap method that could be used to support a wide range of wider studies where recent fire history is influential. A protocol for calibrating the use of *Espeletia* as an indicator is proposed.

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1. Introduction

High-altitude páramo grasslands form a chain along the Andes Mountains from Venezuela and Colombia, through Ecuador, to northern Perú and occupy a total of around 35,000 km² (Hofstede et al., 2003). Páramos also exist in the mountains of Costa Rica (Kappelle and Horn, 2005). For mountain grassland, Andean páramo is relatively biodiverse, with around 5000 plant species or 10–20% of Andean floral richness (Rangel Ch, 2000). Furthermore, as much as 60% of páramo plant species are endemic to this ecosystem (Luteyn, 1999). The páramos provide water for people, agriculture and industry at lower altitudes and the soils are rich in organic material, storing large amounts of carbon (Hofstede et al., 2003).

These páramos are fire-dependent systems (Horn and Kappelle, 2009). Mounting evidence suggests that extensive grasslands and fires did exist before the arrival of humans (Di Pasquale et al., 2008), but that a significant increase in fire frequency after their arrival

has been responsible for an increase in the extent of páramos at the expense of forest cover, especially at lower altitudes (Laegaard, 1992; White, 2013).

What is absolutely clear is that local fire regimes determine the detail of biodiversity composition and ecological dynamics in modern páramo grasslands. Differential fire mortalities of growth forms, enhanced recruitment of some species after fires, and fire-induced changes to species interactions like competition for light have all been demonstrated for páramo plants within landscape-scale fire mosaics in Ecuador (Laegaard, 1992; Ramsay, 1999; Ramsay and Oxley, 1996, 1997; Sklenář and Ramsay, 2001), with some evidence of consequences on populations of páramo animals (Suárez and Toral, 1996). In addition, páramo fires have been shown to affect soils and hydrology (Buytaert et al., 2006; Harden, 2006; Poulard et al., 2001) and agricultural production (Hofstede, 1995; Ramsay and Oxley, 2001).

Therefore, any plan aimed at protecting biodiversity and managing natural resources in the páramo must take account of fires. Normally, management plans for protected páramo areas prohibit fires because they are assumed, anecdotally, to be damaging to páramo soils, hydrology and biodiversity. Such dictats are often not enforced and, even where they are, can result in significant fires

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when they do occur (Keating, 2007). They also ignore the role fire might play in maintaining the ecological context that many such plans aim to protect.

Understanding the nature of the local fire regime is key to understanding the impact of burning on biodiversity, ecosystem services and landscape. Unfortunately, the complexity of fire regimes makes them difficult to understand. Páramo fire frequency and intensity change according to fuel availability, wind direction, slope, vegetation composition and structure, climatic conditions and human intervention—resulting in complex landscape mosaics (Horn and Kappelle, 2009; Keating, 2007; Ramsay, 1999). The unpredictability of wildfire events means that most studies of the effects of fire are carried out retrospectively, once a fire has occurred, and comparisons with pre-fire conditions are impossible. Only a few manipulative studies using experimental or prescribed fire in the páramo have been carried out (Keating, 1998; Ramsay and Oxley, 1996), too few to understand the effects of the diverse combination of fire events that characterize the páramos.

The time needed for recovery of páramo vegetation, soils and hydrology after fire is an essential component of any effective management plan. One way to determine recovery time is to monitor plots through time after a fire until recovery has been achieved, but such studies take time and involve long-term commitment of resources to accomplish—none have been published to date for páramo ecosystems. Alternatively, *ad hoc* post-fire investigations can provide valuable information about recovery after fire, but often fail because detailed information about fire history in the páramo zone is lacking (Horn and Kappelle, 2009). Remoteness and rugged topography mean observational records are limited. In other fire-dominated systems, satellite imagery and/or air photography can provide useful historical insights into fire regimes. Unfortunately, significant cloud cover makes this difficult for páramo studies.

Some means to determine time since fire at a landscape scale would be extremely valuable in promoting the understanding of fire dynamics and ecosystem response in the páramo (Horn and Kappelle, 2009). Ecological indicators offer one possible source of information. The absence of some fire-sensitive species may offer crude indicators of fire prevalence (e.g., Bromley, 1971), but do not provide enough information for detailed investigations. In Costa Rican páramos, the annual rings of some shrubs allow past fires to be dated (Williamson et al., 1986), but this approach does not transfer to more equatorial páramos where shrubs do not have annual growth rings. In Ecuador, patches of same-age *Puya* giant rosette plants have been proposed to estimate time since fire: pulses of recruitment occur soon after fires and the steady growth rate of the rosettes allow the time of recruitment of the cohort to be estimated up to the 28–30 y lifespan of these plants (García-Meneses and Ramsay, 2014). However, one drawback of this method is that the recruitment pulse may take place within a window of several years, resulting in a similar margin of error of that length.

Another giant rosette offers the prospect of estimating time since fire with more precision. *Espeletia* plants are characteristic of páramos from Venezuela to the north of Ecuador (Luteyn, 1999). They have a peculiar morphology, shared with several other tropical mountain plants around the world where the growth form has evolved independently (Smith, 1994). The typical morphology of an *Espeletia* plant is depicted in Fig. 1: a rosette of leaves sits on a tall stem which retains its dead leaves (known as marcescence). The morphology is a response to the particular demands of the high-altitude tropical climate (Carlquist, 1994; Goldstein and Meinzer, 1983). The important point here is that a central reservoir in the tall stem, insulated by the dead leaves, provides a supply of unfrozen water to the leaves in the early morning when the soil water is potentially still too cold to be of use. The marcescent leaves are retained throughout the life of the plant, with the aid of phenolic

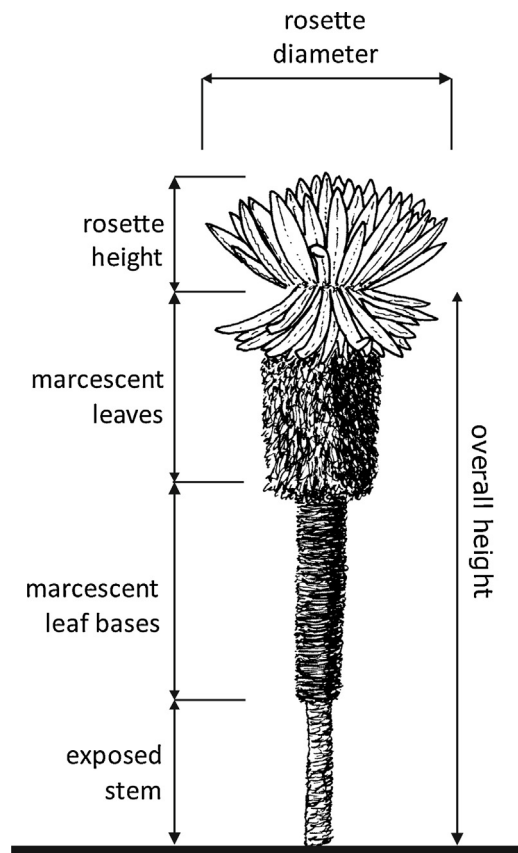


Fig. 1. Morphological components of a burned *Espeletia* plant. Sometimes, marcescent leaf bases and exposed stem show more complex patterns than the simple (but common) pattern shown here. The plant represented here would measure around 2 m in height.

compounds that resist decay, and some old plants may still retain leaf remains more than 100 y old (Acosta-Solís, 1984). Fire removes the leaf blades of the marcescent leaves, leaving behind the dense leaf bases which sheathe the stem (these may also be removed by repeated fires). Assuming the plant survives the fire, the living rosette on top of the plant regrows and the new leaves eventually become marcescent, building up a new section of stem clothed in dead leaves. Thus, the stem cover of marcescent dead leaves might be an indicator of time since fire, if the plants have a reliable growth rate regardless of fire. Interestingly, the relationship has been used in reverse, estimating *Espeletia* growth rate by means of a known fire date (Verweij, 1995).

This study presents growth rates for one species, *Espeletia pycnophylla* subsp. *angelensis*, in burned and unburned situations in northern Ecuador, and considers mortality rates in a range of fire intensities. Using the measured growth rates and the morphology of burned *Espeletia* plants in places with known fire history, the reliability of time-since-fire estimates using this method are assessed. Finally, the applicability of this indicator to widespread use in the northern páramos is discussed.

2. Methods

2.1. Study sites

The study was carried out within one páramo grassland area in Carchi Province, Ecuador, incorporating Volcán Chiles (at altitudes 3600–4100 m) and El Ángel (in the buffer zone for the Reserva Ecológica El Ángel at altitudes 3600–3700 m).

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