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Thirsty peaks: Drought events drive keystone shrub decline in an oceanic island mountain



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ABSTRACT

Oceanic islands ecosystems are among the most endangered in the world, as the effects of ongoing climate change may potentially combine with other pre-existing drivers of plant population decline. In the Canary Islands, nitrogen-fixing Teide broom (Spartocytisus supranubius) is a keystone species in the Teide National Park high mountain ecosystem. However, recruitment failure due to introduced herbivores and dieback episodes are decimating its populations. We explored the role of climate as a potential driver of Teide broom mortality. We analyzed annual rings of Teide broom to reconstruct the impact of climate on secondary growth, intrinsic water use efficiency (iWUE) and mortality, and to explore the potential for growth rates and levels of resilience to act as indicators of mortality risk. We found that higher precipitation from October to February improved Teide broom secondary growth, whereas iWUE increased with high July-August temperatures. Extreme drought events in 2001 and 2012 strongly reduced secondary growth and resulted in subsequent plant death. Individuals that subsequently died had lower growth rates, poorer capacity for growth recovery after drought events and marginally higher iWUE than those which survived. More frequent recurrence of extreme drought events in the future would increase the frequency of dieback episodes, and the combination of a decline in mature individuals and lower recruitment rates due to exotic herbivore pressure would mean an uncertain future for the Teide broom. Our results indicate how global change may impact keystone species in protected areas and highlight the need for urgent implementation of proactive conservation policies.

1. Introduction

High mountains in oceanic islands are Noah's Arks of biodiversity. The ecological barrier created by their two-fold isolation has fueled evolutionary processes (Steinbauer et al., 2012), leading to a disproportionately large number of endemic taxa in relation to their extent (Cronk, 1997; Kreft et al., 2008; Steinbauer et al., 2012). At the same time, the combination of geographical isolation, small populations and reduced distribution ranges makes these ecosystems particularly susceptible to species extinction (Martín, 2009). Higher historical incidence of extinctions in island ecosystems has already been documented (Diamond et al., 1989); of 80 plant species extinctions documented in the last 400 years, around 50 were from island ecosystems (Sax and Gaines, 2008). Continuation of the ecological heritage of island mountains is considered to be globally threatened by the combination of human activity and invasive species, and this is exacerbated by climate change (Caujapé-Castells et al., 2010; Ferreira et al., 2016;

Harter et al., 2015; Triantis et al., 2010).

Tenerife is the largest and highest island of the Canary archipelago. Located in the Atlantic Ocean 300 km away from the African continent, the island is a large volcanic outcrop that peaks in the 3718 m high Teide volcano, which towers over the island just 15 km from the shoreline. Such a steep altitudinal gradient creates a rough orography that is only interrupted on the southern Teide slopes, where a relatively flat area creates an extensive high mountain environment at over 2000 m altitude, where an original biota has evolved. The singularity of this high mountain ecosystem has long been recognized (von Humboldt and Bonpland, 1807) and led to the designation of this area as a National Park in 1954. Since them, Teide has become one of the most visited National Parks in the world, with > 4 million visitors in 2016.

The nitrogen-fixing Teide broom (*Spartocytisus supranubius* (L. f.) Christ *ex* G. Kunkel, Fabaceae) is the keystone species in this ecosystem. Traditional land management involved the intensive use of Teide broom as fodder and fuel, which reduced its abundance until the

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suppression of traditional pastoral activities following designation of the National Park, which prompted a recovery of Teide broom population levels (Elena and Rodríguez, 2005; Kyncl et al., 2006). However, this positive trend ceased in the 1980s due to the onset of dieback episodes, combined with massive recruitment failure following an increase in abundance of the rabbit (*Oryctolagus cuniculus* L.), a non-native herbivore that had been introduced from continental Europe (Garzón-Machado et al., 2010). Measures for controlling rabbits in such a large area (Teide National Park occupies nearly 19.000 ha) have proved insufficient to contain the expansion of the species and its detrimental impact on native flora, and large exclosures are now being planned to promote Teide broom recruitment.

Even within exclosures, however, strong dieback episodes are a major concern for National Park managers. Dieback episodes began at the end of 1980s in the southern part of the Park; they have since extended across the whole of the National Park, but continue to be most intense in the south. These events are characterized by plant wilting that eventually leads to the death of affected individuals, with decaying plants being attacked by different species of pathogenic fungi and phytophagous insects (Lorenzo et al., 1991). Even if the primary factors triggering dieback episodes remain unclear, the onset of this phenomenon in the southern/drier edge of the species' range hints at the possibility that drought stress might be a contributory factor. This hypothesis is supported by evidence that high drought stress levels are a primary cause of dieback episodes for numerous woody species in arid and semiarid environments (Allen and Breshears, 1998; Liu et al., 2013; Marqués et al., 2016; McDowell, 2011). This may be a critical issue in the study area which is experiencing a warming rate (0.14 \pm 0.07 °C per decade) closer to the rates experienced in nearby continental regions than to the mean of Canary Islands archipelago (Martín et al., 2012).

Annual growth rings in the secondary xylem provide a valuable proxy to enable reconstruction of growth history and mortality dynamics, and to improve our knowledge about the role of climatic trends and climatic extremes on plant growth and survival (Speer, 2012). The presence of well-resolved annual growth rings in the wood of Teide broom (Kyncl et al., 2006) allows a retrospective analysis of growth patterns and mortality events in this species, in order to determine the importance of water availability and extreme drought events in triggering dieback episodes. In this study we compared the responses to climate shown in the growth rings of living and dead plants in the northern/wet and southern/dry edges of the species distribution in the National Park.

We performed a range of analyses to gain a better understanding of the factors driving Teide broom dieback. Firstly, we determined the effect of climate on secondary growth and intrinsic water use efficiency (iWUE). We then analyzed (a) whether plant mortality was associated with extreme drought events, (b) whether growth rates and iWUE varied between individuals that survived and died, and between wet and dry edge populations, and (c) whether resilience to drought events could serve as an early indicator of predisposition to die.

2. Materials and methods

2.1. Study area

The study area is located at 2055–2340 m a.s.l. in Teide National Park, Tenerife, Canary Islands, Spain (Fig. 1). The climate varies from semiarid continental subalpine in the North to arid in the South, with strong daily variations of temperature. Monthly time series of precipitation and temperature were recorded in the Izaña meteorological station, located within the northern edge of the study area at 2373 m a.s.l. (Fig. 2). Annual mean temperature for the 1961–2015 period is 10.3 °C, the coldest month being January (mean daily minimum temperature of 1.3 °C) and the warmest month July (mean daily maximum temperature of 22.9 °C). Average annual precipitation is 330 mm with a

drought period of six months from May to September. Temperature increases and precipitation decreases towards the southern half of the National Park (Bustos and Delgado, 2000).

Poorly developed soils of volcanic origin dominate in the study area, mainly consisting of volcanic scoria with acidic pH, poor water retention capacity and low organic carbon and nitrogen contents (Rodríguez et al., 2014). Teide broom is the dominant species of a singular vegetation community which includes a variety of plants adapted to dry alpine conditions and numerous endemic species of Tenerife and the Canary Islands (Fernández-Palacios and de Nicolás, 1995).

2.2. Study species

Spartocytisus supranubius is a multibranched leguminous shrub endemic to the highest Canary Islands, i.e. Tenerife and La Palma (Fig. 2). This species inhabits mountain areas at elevations from 1400 to 3250 m, with its largest population occurring within the Teide National Park. It can reach 4 m in height and > 10 m in crown diameter with some degree of clonal growth (Kyncl et al., 2006). Diameter growth occurs from the end of April to mid-July (González-Rodríguez et al., 2017). Secondary xylem is semi-ring porous (Fig. 2) with distinct annual rings (Kyncl et al., 2006).

2.3. Sampling design and chronology elaboration

In June 2016, 15 living and 15 dead individuals were sampled from six sites across the Teide National Park (Fig. 1). Three of the sites were in the northern part of the National Park, where adult broom mortality is lower, and three sites were in the southern part, where broom dieback is more intense and death rates higher (Fig. S1). At least one core was extracted from branches of living Teide brooms in areas with active secondary growth, as close as possible to the central stem collar in order to capture individual age. A second core was taken from 5 trees per site for analysis of stable isotope content in the secondary xylem. A stem cross section was obtained with a chainsaw from dead Teide brooms, as close to the plant base as possible. From each stem cross section, we selected the radius with highest growth rate and obtained a complete section of this radius from pith to bark. Comparing cross-sections and branch cores may induce some bias in the result due to different growth rates. Nevertheless, both growth patterns were highly correlated, and no difference in mean growth rates were found before extreme drought events. Cores and sections were dried and both were surfaced with a sliding microtome (Gärtner and Nievergelt, 2010) to observe the cellular structure of the secondary xylem. After visual cross-dating, treering widths were measured to the nearest 0.001 mm using a slidingstage micrometer (Velmex Inc., Bloomfield, NY, US) interfaced with a computer. Individual tree-ring series were statistically compared with a master living trees chronology using the COFECHA program and checked for dating accuracy (Grissino-Mayer, 2001).

Individual ring-width series for living and dead plants were standardized and averaged separately for each group to assess state (living/ dead) and location (north/south) differences in tree-ring width and climatic response. For standardization, raw series were fitted to a spline function that retained 50% of the variance in the original series over periods of 32 years, which was flexible enough to reduce the non-climatic variance by preserving high-frequency climatic information (Cook and Peters, 1981). The residuals obtained by dividing each raw ring width by its fitted spline values were prewhitened by autoregressive modeling, giving dimensionless indices that represent independent records of annual growth for each measured series. Growth indices for each group were averaged on an annual basis into a chronology using a biweight robust mean. Ring-width series were detrended, standardized and averaged with the ARSTAN computer program (Cook and Holmes, 1996). First order autocorrelation (AC1), mean sensitivity (msx), mean inter-tree correlation (rbt), signal-to-noise ratio (SNR) and expressed population signal (EPS) were calculated to

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