Agricultural and Forest Meteorology 217 (2016) 35–45

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Phenological shifts in climatic response of secondary growth allow *Juniperus sabina* L. to cope with altitudinal and temporal climate variability

Alberto Arzac[a], Ana I. García-Cervigón[b], Sergio M. Vicente-Serrano[c], Javier Loidi[a], José M. Olano[b,*]

[a] Departamento de Biología Vegetal y Ecología, Facultad de Ciencia y Tecnología, Universidad del País Vasco, Barrio Sarriena s/n, Leioa E-48940, Spain
[b] Área de Botánica, Departamento de Ciencias Agroforestales, EU de Ingenierías Agrarias, Universidad de Valladolid, Campus Duques de Soria, Soria E-42004, Spain
[c] Instituto Pirenaico de Ecología, Consejo Superior de Investigaciones Científicas, Avda Montañana 1005, Zaragoza E-50059, Spain

ARTICLE INFO

Article history:
Received 8 September 2015
Received in revised form 9 November 2015
Accepted 14 November 2015
Available online 6 December 2015

Keywords:
Altitudinal gradient
Global warming
Juniperus sabina
Mediterranean high mountains
Shrubs
Tree rings

ABSTRACT

The long-term persistence of Mediterranean high mountain flora is challenged by global warming. Understanding plant responses to different climatic drivers along altitudinal gradients is necessary in order to predict the response of Mediterranean mountain systems to the ongoing increase in drought intensity and severity. We selected the prostrate shrub *Juniperus sabina* L. as a model species and explored its growth response to climatic variability over the last six decades through dendrochronological methods at four sites along a 750 m altitudinal gradient. Secondary growth was maximal at lower altitudes, where growing seasons are longer. Water availability was the main factor controlling secondary growth variability along the whole gradient, although the timing and strength of climatic variables affecting growth shifted with altitude. Earlier and stronger signals were detected in lower sites, where a combination with late summer signals suggested the existence of a second growth pulse in response to longer growing seasons. *J. sabina* adjusted its secondary growth to the changing climatic conditions by shifting the timing of its climatic response to favorable climatic windows, with earlier responses to spring rainfall in lower sites and an expanded growing season at the highest site during the second half of the study period. Our results show that at least some Mediterranean plants can grow faster at the drier edge of their range even under intense climate pressure, indicating that the response to drought stress may be highly idiosyncratic. The plastic nature of *J. sabina* secondary growth combined with its role as a nurse plant in Mediterranean mountains may be key to maintaining the high diversity levels of these particular ecosystems.

1. Introduction

Mediterranean mountains are a global hot spot of plant biodiversity (Médail and Quézel, 1997). Isolation and a singular climatic combination of low winter temperatures and summer drought stress have shaped a highly endemic flora (Médail and Diadema, 2009) whose persistence is threatened by current global climate change (Pauli et al., 2012). Projections of above average warming for the Western Mediterranean (Giorgi and Lionello, 2008) pose a serious potential threat for plant species persistence, especially since the low altitude of mountains constrains the possibilities for altitudinal ascent as a way to keep within the same climatic envelopes (Jump and Peñuelas, 2005; Walther et al., 2005). One the one hand, most of these mountains are relatively low (usually below 2500 m), providing little space for altitudinal displacement. Furthermore, both niche models and different empirical evidences suggest that under the current climate change scenario the altitudinal ascent that is occurring in other European mountains may not suffice to provide adequate conditions for Mediterranean high mountain plants (Olano et al., 2013; Pauli et al., 2012; Thuiller et al., 2005). Understanding plant responses to different climatic drivers along altitudinal gradients, and the mechanisms underlying these responses, is thus particularly relevant to predict the response of Mediterranean mountain systems in this context of global biodiversity loss.

Climatic factors constraining plant growth in temperate and boreal environments shift along altitudinal gradients, moving from water shortage at lower altitudes to temperature limitation

* Corresponding author. Tel.: +34 975129485.
E-mail address: jmolano@agro.uva.es (J.M. Olano).

http://dx.doi.org/10.1016/j.agrformet.2015.11.011

at higher altitudes (Babst et al., 2013). However, under certain environments, precipitation may constrain growth all along the altitudinal gradient (Yang et al., 2013), even at the timberline (Galván et al., 2015; Liang et al., 2014). This is the case in Mediterranean mountains (Babst et al., 2013), at least in drier locations (Linares and Tíscar, 2010). Actually, water availability has been shown to be the most critical climatic factor controlling Mediterranean plant performance (Lebourgeois et al., 2012; Martín-Benito et al., 2010; Pasho et al., 2011a). The fact that water availability determines plant performance along the whole altitudinal gradient (Olano et al., 2013) may be essential to our understanding the differential behavior of Mediterranean mountain flora to climatic change.

Water shortage affects secondary growth at multiple scales, impacting both xylogenesis and resource acquisition (García-Cervigón et al., 2015; Olano et al., 2013). Drought decreases the cambial division rate, reduces cell expansion and constrains secondary wall formation, which eventually may arrest secondary growth (Camarero et al., 2010; Olano et al., 2014). The combination of water shortages with rising temperatures may exacerbate the impact on plant water budgets, by increasing evapotranspirative demand (Christensen et al., 2007; Vicente-Serrano et al., 2014a). At the same time, this combination may trigger more frequent and severe drought episodes in the Mediterranean (Vicente-Serrano et al., 2014b), which could ultimately reduce growth rates and increase mortality events (Camarero et al., 2015). In addition, decreasing temperatures along altitudinal gradients lead to lower growth rates due to shorter optimal periods for cambial activity (Gričar et al., 2014; King et al., 2013; Prislan et al., 2013), limiting the ability of plants to invest reserves in secondary growth with increasing altitude. In alpine environments, secondary growth shows higher sensitivity to temperature than photosynthesis (Körner, 2003), and limitations in the ability to invest available photosynthates in secondary growth may lead to an excess in carbon reserves (Hoch et al., 2002). However, low water availability may negatively impact photosynthetic capacity, decreasing the carbon pools available for growth (Galiano et al., 2011). As a consequence, the impact of climatic variables on carbon reserve levels and their relation with plant growth in Mediterranean mountains is still unclear.

Annual growth rings in perennial plants have been used to interpret the biological response to climate (Speer, 2010). However, most of the literature on this topic has focused on tree species (Dittmar and Elling, 1999; Fonti et al., 2007; Fritts et al., 1965), with work on forbs and shrubs being more scarce (Gazol and Camarero, 2012; Olano et al., 2013; Palombo et al., 2014; von Arx et al., 2006). This knowledge gap may be particularly relevant in Mediterranean high mountains where shrubs are a critical functional component (Ojeda et al., 2000). In these systems, the large contribution of shrubs in terms of diversity and biomass is amplified by their role as nurse plants (Castro et al., 2002; Gómez-Aparicio et al., 2004; Michalet et al., 2014). Shrubs facilitate the establishment and performance of a wide array of mountain plants (García-Cervigón et al., 2013; Gómez-Aparicio et al., 2008), increasing their potential range and thereby promoting the maintenance of high biodiversity levels (Cavieres et al., 2014; Schöb et al., 2013). In addition, shrubs also preserve soil fertility by means of the reduction of erosion rates (García-Ruiz and Lana-Renault, 2011; García-Ruiz et al., 1996). In spite of this engineering role of high mountain shrubs, very little is known about their response to climatic factors along altitudinal gradients in terms of growth and carbon pools (García-Cervigón et al., 2012).

To gain knowledge of the response of Mediterranean mountain systems to global warming, we selected the prostrate shrub *Juniperus sabina* L. as a model species. *J. sabina* is a keystone species in Mediterranean mountains, creating islands of fertility with higher nutrient and humidity levels (García-Cervigón et al., 2012, 2015; Verdú and García-Fayos, 2003) and enhancing the establishment and fitness of protégée plants (García-Cervigón et al., unpublished results). We analyzed ring width and carbohydrate pools along a 750 m gradient comprising the whole altitudinal range of the species to test the following hypotheses: (a) secondary growth would be maximal at intermediate locations, since growth would be constrained by drought at the lower altitudinal limit and by drought and low temperatures at the upper altitudinal limit; (b) temperature limitation of cambial activity at the upper altitudinal limit would lead to higher carbohydrate contents due to sink limitation; (c) the effect of drought would be stronger at lower sites, where the combination with higher temperatures would increase the evapotranspirative demand; (d) the timing of climatic factors controlling secondary growth will shift with altitude, with earlier signals in lower sites; and (e) rising temperatures during the 20th century will have led to enhanced and earlier drought signals.

2. Materials and methods

2.1. Study species

J. sabina (Savin juniper) is a prostrate shrub inhabiting mountains from Western Europe to Eastern Asia (Adams et al., 2007; Wesche and Ronnenberg, 2004). It is usually less than 1 m tall, but with a large lateral extent, with individual plants covering surfaces as large as 1900 m^2 (García-Cervigón et al., 2012). It prefers calcareous substrates and has a wide altitudinal range, from 1000 to 2750 m asl, with an optimum distribution in the oromediterranen belt where it often coexists with other conifers (Mateo Sanz, 1997).

2.2. Study area

The study area was located over an altitudinal gradient of 750 m in the Javalambre mountain range (Teruel), Eastern Spain. Four sampling sites were selected along an elevation gradient, comprising the whole juniper altitudinal range in this mountain (S1: 1250 m, S2: 1400 m, S3: 1700 m and S4: 2000 m, see Fig. 1). In the lowest locality, Savin juniper co-occurs with other juniper species (*Juniperus thurifera* L., *J. phoenicea* L., *J. oxycedrus* L.). In the second locality (S2) Savin juniper occurs in open grasslands with scattered *Pinus nigra* Arnold. and *Quercus faginea* Lam. individuals. The habitat is similar in S3, but with the added presence of the more mesic *Pinus sylvestris* L. The upper site (S4) is above the tree-line and the landscape is dominated by Savin juniper (García-Cervigón et al., 2012). Parent material is predominantly limestone, leading to calcareous soils.

The climate is Mediterranean continental with a marked summer drought, although water deficit intensity decreases with altitude. Maximum temperatures combined with minimum rainfall occur between July and August and are associated with a pronounced dry period that can start as early as May at the lowest altitudes (Fig. 2A). The frost period can be extended from early October to early June at higher altitudes, whereas at lower altitudes frost duration is shorter and may range from the end of October to May (Mateo Sanz et al., 2013). Climatic data for total monthly precipitation were obtained from the neighboring weather station of Torrijas (1400 m asl), located 15 km from the study site. Monthly maximum and minimum temperatures were available from the station of Segorbe (364 m asl), located 25 km from the study site and corrected for altitude. Climate data was quality controlled and homogenised to remove any artificial non-climate noise in the series (see details in El Kenawy et al., 2013 and Vicente-Serrano et al., 2010a). Climate analysis revealed that mean temperature has increased during the period 1953–2009, in particular during