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Original Article

# The facultative bimodal growth pattern in *Quercus ilex* – A simple model to predict sub-seasonal and inter-annual growth

Filipe Campelo[a,*], Emilia Gutiérrez[b], Montserrat Ribas[b], Raúl Sánchez-Salguero[c,d], Cristina Nabais[a], J. Julio Camarero[c]

[a] Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, Calçada Martim de Freitas, 3000-456 Coimbra, Portugal
[b] Dept. Biologia Evolutiva, Ecologia i Ciències Ambientals, Univ. Barcelona, Av. Diagonal 643, 08028 Barcelona, Spain
[c] Instituto Pirenaico de Ecología (IPE-CSIC), 50192 Zaragoza, Spain
[d] Dept. Sistemas Físicos, Químicos y Naturales, Univ. Pablo de Olavide, Crta de Utrera, Km. 1, 41013 Sevilla, Spain

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ABSTRACT

In Mediterranean climates, bimodal growth patterns, corresponding to two peaks in radial increment during favorable seasons, have been described in several tree species. However, we lack a better mechanistic understanding of bimodality and its potential responses to the predicted warming and aridification trends. Filling this research gap is important since growth duration affects the capacity of trees to form wood and uptake carbon. Here we used an 11-year (1994–2004) long record of dendrometer data of the Mediterranean Holm oak (*Quercus ilex*) and compared how climate related to radial increment in trees from the south- and the north-facing slopes. We also related climate variables to tree-ring width and the production of intra-annual density fluctuations (IADFs), which reflects bimodality. In this paper, we introduce a model called VS-Lite2 to simulate tree-growth dynamics, which is a modified version of the process-based Vaganov-Shashkin Lite model. The VS-Lite2 model adequately reproduced the bimodal intra-annual pattern of radial growth, IADFs, and annual tree growth. Trees from the south-oriented slope grew more, produced more IADFs and showed a more marked bimodal pattern than trees from the north-facing slope. These differences agree with the observation that late-summer drought constrained growth. Therefore, radial-growth models should consider plastic bimodality and micro-environmental conditions in areas subjected to seasonal droughts.

## 1. Introduction

The drought-prone Mediterranean Basin lies in a transitional area between more temperate conditions northwards and more arid conditions southwards, and it is forecasted that more arid conditions will become more intense and widespread there (Giorgi and Lionello, 2008). This aridification trend is translated into more frequent, severe, and sustained droughts which cause productivity reductions, growth decline, canopy dieback and mortality episodes in conifers (Camarero et al., 2015b; Sánchez-Salguero et al., 2012; Sarris et al., 2007), and hardwood (mainly oaks) species (Camarero et al., 2016, 2015a; Carnicer et al., 2011; Colangelo et al., 2017; Nardini et al., 2013). Moreover, such climate changes could alter the length of the growing season, which is a major driver of wood formation and carbon uptake in these forests (Lempereur et al., 2015). Therefore, we need a better understanding how Mediterranean forests respond to favorable wet-cool climate conditions and withstand drought. For instance, growth bimodality (a pattern with two growth peaks) could allow some species to benefit from favorable conditions before (spring) or after (autumn) the summer drought (Camarero et al., 2010b). These two growing seasons are very different for most Mediterranean tree species since most primary growth (e.g., shoot expansion, leaf formation) occurs before the beginning of summer drought, though in mild coastal areas leaf formation is frequent after summer (second flush), whereas fruit enlargement and bud formation are the main phenological processes occurring in autumn and winter (Camarero et al., 2015a, 2010a, 2010b; Gratani, 1996; Montserrat-Martí et al., 2009).

Evergreen Mediterranean tree species face summer drought by keeping their leaves and peaking carbon uptake and growth in two favorable seasons (spring and autumn) (Granda et al., 2014; Gutiérrez et al., 2011; Mitrakos, 1980). However, the variability within the Mediterranean climate causes different radial-growth patterns since humid and mild conditions (prevailing in coastal sites) favor growth through a longer growing season and lead to higher growth rates and a more marked bimodality (Gutiérrez et al., 2011; Nabais et al., 2014), while dry and continental conditions (prevailing in inland sites) would

* Corresponding author.
*E-mail address:* fcampelo@uc.pt (F. Campelo).

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favor more unimodal patterns characterized by a spring peak and a shorter growing season (Camarero et al., 2010b). In theory, a bimodal growth pattern would occur in response to wet and mild spring and autumn conditions allowing stem wood formation during those favorable seasons. Nevertheless, such bimodality is still understudied and we lack information on long-term and intra-annual growth patterns of most Mediterranean tree species.

In most Mediterranean tree species, high evapotranspiration rates induced by warm temperatures during summer are associated with a quiescent phase of cambial activity, while sporadic rainfall events may trigger growth and the formation of intra-annual density fluctuations (hereafter IADFs) or "false rings" (Battipaglia et al., 2016; Campelo et al., 2009, 2007a; Cherubini et al., 2003; De Micco et al., 2016). Therefore, following the intra-annual stem radial growth is crucial to understand the plasticity of wood formation in response to water restrictions. Also, there are still very few long-term studies providing a mechanistic view of these intra-annual growth dynamics as related to climate conditions (cf. Gutiérrez et al., 2011). Combining field observations with mechanistic models may provide greater insight on how widespread is the bimodal growth pattern across Mediterranean tree species. This is a critical step to better predict the responses of these species and forests to the forecasted climate warming and potentially dryer conditions.

Process-based growth models as the Vaganov-Shashkin model (hereafter V-S model) have been successfully used to simulate tree-ring growth of conifers as a function of climate in boreal zones (Evans et al., 2006; Vaganov et al., 2006, 2011), where growth follows a clear unimodal pattern during a short growing season (e.g., Yang et al., 2017). The V-S model has never been used to study the intra- or inter-annual growth dynamics of angiosperms under Mediterranean climate. The V-S model has revealed two peaks of growth in *Pinus halepensis*, a Mediterranean pine species, in response to wet and cool conditions in spring and autumn (Touchan et al., 2012), indicating a potential bimodal growth pattern (Camarero et al., 2010b). However, such simulations considered as input data tree-ring width and climate variables (e.g., solar radiation, air temperature, soil moisture) but lacked a more realistic view of the fitted growth parameters. We argue that such models should be based on field observations which provide long-term records of intra-annual growth patterns and allow quantifying relevant growth parameters (e.g., Gutiérrez et al., 2011). Dendrometers provide measurements of intra-annual radial increment, once reversible shrinking-swelling dynamics of stems are taken into account (Deslauriers et al., 2007; Oberhuber and Gruber, 2010; Sheil, 2003; Zweifel et al., 2016, 2001; Zweifel and Häsler, 2001). In Mediterranean tree species such as Holm oak (*Quercus ilex*), dendrometer data revealed that radial-growth data (rates, duration) and water availability are better predictors of forest productivity than carbon supply (Lempereur et al., 2017, 2015). However, to characterize the bimodal growth pattern it is required to identify when the maximum growth rates are attained in spring and autumn, in addition to the estimation of the growing-season length. Holm oak is a suitable species to study bimodal growth patterns due to: (i) its relevance and wide geographic distribution across the Mediterranean Basin (Barbero et al., 1992), (ii) its plastic phenological growth responses to climate (Campelo et al., 2009, 2010; Castro-Díez and Montserrat-Martí, 1998; Corcuera et al., 2004; Gea-Izquierdo et al., 2009; Martín et al., 2014; Montserrat-Martí et al., 2009; Nabais et al., 1999), and (iii) the fact that it presents two major peaks of growth, photosynthetic activity and carbon gain in spring and autumn coinciding with the main growth phases (Corcuera et al., 2005; Gratani, 2000, 1996; Gratani et al., 2008; Liphschitz and Lev-Yadun, 1986).

Here we develop and describe a multi-parameter model (VS-Lite2), based on the VS-Lite model (a simplified version of the V-S model) which was originally formulated for conifers (Vaganov et al., 2006). We used the VS-Lite2 to simulate monthly stem radial increment of Holm oak using an 11-year long dataset (1994–2004) of dendrometer data as related to climate data (mean temperature and precipitation). We compare the intra- and inter-annual radial-growth patterns of trees growing in the south- and north-facing slopes to test the effects of their different thermal regimes on growth patterns. We also used the frequency of IADFs as a proxy of bimodal growth since these anatomical structures are formed during autumn months, often in response to rainfall, and not during the main spring growing-period (Campelo et al., 2007a, De Micco et al., 2016).

Since shoot elongation and leaf expansion in Holm oak mainly occur in spring, while a new flush can occur in late-summer or early autumn in response to rainfall, especially at coastal sites (Gratani, 1996; Montserrat-Martí et al., 2009), we also expect a bimodal pattern for intra-annual radial growth rates in *Q. ilex*. We hypothesize that growth rates would peak in spring and autumn when precipitation is high and temperatures and evapotranspiration rates are lower than in summer. Lastly, we expect that trees from the warm-dry S-oriented slope would present higher growth rates and a more marked bimodal pattern characterized by summer quiescence than trees from the cool-wet N-oriented slope. Therefore, trees from the S-oriented slope should be characterized by a longer growing season with a more marked bimodal pattern and, consequently, produce more IADFs.

## 2. Materials and methods

### 2.1. Study area and tree species

The study area is located in an interior valley of the Garraf karstic mountains (41.33°N, 1.83°E, 300 m a.s.l., Fig. 1), near Barcelona, northeastern Spain. The Garraf forest experiences Mediterranean climate and it is dominated by *Quercus ilex* and *Pinus halepensis*. Two contrasting north- (N) and south-facing (S) slopes were investigated to understand seasonal changes in tree growth. There are differences in the vegetation type and communities between slopes. In the S-slope, *Quercus coccifera* dominates with scattered *P. halepensis* and *Q. ilex* trees. In the N-slope, *Q. ilex* is the dominant tree species (Gutiérrez et al., 2011). Most of the trees and large shrubs are multi-stemmed as a result of the firewood gathering carried out until the 1970s. All individuals used in this study are multi-stemmed trees and were 21 years old in 2004, meaning that trees in this coppice stand resprouted in 1983 after the 1982 fire (Campelo et al., 2007a).

The soil in the study site is shallow with a low water-holding capacity that was developed from Cretaceous limestones (Gutiérrez et al., 2011). To evaluate the impact of climatic conditions on stem radial increment and to develop the mechanistic growth model, historical monthly climate data for the period 1984–2004 were obtained from the nearest weather station (Begues; 41.29°N, 1.91°E); located 8 km away from the study site. According to these records, the average total annual precipitation is 662 mm, and the average annual temperature is 13.6 °C (Fig. 1b) with a maximum mean monthly temperature of 21.1 °C (July), and a minimum of 5.1 °C (January). Most of the annual precipitation occurs in autumn (33% was recorded between September and November) and spring (25% was recorded between March and May), while drought occurs from June to August (Fig. 1b). During the study period, several droughts (e.g., 1994–1995, 1998) affected the study area (Fig. 1c).

### 2.2. Dendrometer measurements, radial increment, and tree-ring width data

Ten multi-stemmed *Q. ilex* trees were randomly selected on an even-aged stand (Campelo et al., 2007a; Gutiérrez et al., 2011). Five trees were located on the South-facing slope and the other five trees were on the North-facing slope at a similar elevation. The initial diameter at breast height (measured at 1.3 m) of the selected trees in the N- and on the S-slope was 4.4 ± 2.0 and 4.7 ± 1.4 cm, respectively.

Variations in stem girth of *Q. ilex* were measured using stainless-steel band dendrometers (Agricultural Electronics Co., Tucson, USA). On July 1993, band dendrometers were installed on the largest stem of