Disentangling the effects of competition and climate on individual tree growth: A retrospective and dynamic approach in Scots pine

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ABSTRACT

Understanding the relative contributions of competition and climate on individual tree growth is critical to project realistic forest dynamics under projected climate scenarios. Furthermore, present competition levels may reflect legacies of past use. Here, we analyze the effects of climate, site conditions and competition on radial growth in three Scots pine stands located along an altitudinal gradient in central Spain. Current stand structure and retrospective analyses of radial growth (basal area increment, BAI) were used to model changes in tree growth as a function of a spatially-explicit competition index (CI) and climate. Linear mixed-effects models were employed to model BAI and to quantify the growth responses to climate of trees under low and high competition levels. Competition effects on growth were steady over time regardless of tree age. High competition levels negatively affected growth since negative exponential functions characterized the CI–BAI relationships. Tree growth sensitivity to climate increased with decreasing competition intensity. Growth at high elevations was mainly limited by low winter temperatures, whereas warm spring enhanced growth at middle elevations and warm late summer temperatures constrained growth at low elevation. Growth responsiveness to climate is enhanced under low competition levels. Overall, current competition is a more relevant driver of recent growth than climate. Proactive forest management should be adopted to reduce the vulnerability of Scots pine forests currently subjected to higher competition levels and warmer and drier conditions.

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1. Introduction

Competition is a key process driving forest dynamics (Coomes and Allen, 2007; Kunstler et al., 2011). Trees of different sizes and canopy status compete differently for water and light (Orwig and Abrams, 1997), particularly when growth becomes limited by these resources (Tilman, 1988). Thus, trees may have different growth responses to climate, depending on the stand structural attributes (Andersen et al., 2008). It is known that changes in stand structure, climate and local site conditions alter tree growth and, as a result, forest dynamics (Lebourgeois et al., 2014). Thus, the

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growth rates of neighboring trees may vary markedly across monospecific forests with contrasting ages and structures (e.g., Hara, 1984; He and Duncan, 2000). This variation in growth rates in turn influences stand dynamics, driving size structure and spatial pattern diversification (Gómez-Aparicio and Canham, 2008; Castagneri et al., 2012; Fraver et al., 2014). Understanding the relative contributions of stand structure and climate on growth should be essential to achieve accurately estimations of forest dynamics, as well as to assess forest vulnerability under a climate change scenario (Lindner et al., 2010).

Past forest dynamics, including disturbances and management, affects current individual tree growth responses to climate through legacies determining present stand structure (Farrell et al., 2000; Rozas, 2014). Accordingly, competition has usually been characterized at the stand or plot levels through summary indicators such as density or basal area. However, competition and climate–growth sensitivity are tree-level processes that should be explicitly taken into account at the individual scale where selection operates (Carrer, 2011; Rozas, 2014). In addition, the specific case of long-living organisms such as trees, the social status and climate sensitivity demand a representative time span (Lebourgeois et al., 2014).

During the last decade, numerous studies have highlighted how competition interacts with growth responses to climate in different tree species and forest biomes (e.g., Weber et al., 2008; Ruiz-Benito et al., 2013; Madrigal-González and Zavala, 2014). Competition for nutrients, water and light is known to limit tree growth, and this effect has been estimated using competition indices (Daniels et al., 1986; Holmes and Read, 1991; Biging and Dobbertin, 1992; Kunstler et al., 2011). For instance, contrasting responses to climate between dominant and suppressed trees have been frequently reported within the same stand (Cherubini et al., 1998; Castagneri et al., 2008; Linares et al., 2010). However, tree competition estimates usually provide only a static picture based on the current stand structure (Burton, 1993), while dynamic competition estimates and related climate–growth responses remain poorly understood (but see Weber et al., 2008; Dorman et al., 2015). We argue that this temporal component of competition is supported by at least two aspects influencing tree growth. First, competition depends on the phenotypic plasticity of crown and root systems over time, which influences the access to resources such as light, water and soil nutrients (García, 2014). Second, the uses of these resources also determine how competition proceeds through time. For instance, in drought-prone areas trees compete for water, thus reducing the amount of water available for their neighbors. Following this rationale, those trees able to cope with intense drought stress might maintain higher growth rates, inhibiting growth of neighboring trees through shading (Craine and Dybzinski, 2013).

Tree-ring data provide individual- and time-explicit information of competition by reconstructing growth patterns of individual trees (Weber et al., 2008; Pach and Soberka, 2011), and by quantifying the effects of climate and competition on these growth patterns (Cook, 1990). The competitive status of individual trees is affected not only by past growth changes (e.g., suppressions or releases), but also by precedent mean growth rates (Banks, 1991). The century-long exploitation of European forests further complicates the inference of past competition in these stands through the reconstruction of radial growth (Fritts, 2001). The massive migration of rural populations in Europe over the past century has favored forest encroachment. Nonetheless, the current stand structures still reflect the legacy of past human activities (Barbero et al., 1990; Chauchard et al., 2007; Gimmi et al., 2010).

The present paper addresses these issues by reconstructing and quantifying the competitive dynamics of three Scots pine (*Pinus sylvestris* L.) stands subjected to different climatic limitations along

an altitudinal gradient located in central Spain (Sánchez-Salguero et al., 2015). The stands are located in a formerly logged area which has not been intensively managed since the 1980s (Gea-Izquierdo et al., 2014). Our aim was to analyze how past forest management determines current tree-to-tree competition using growth data and assessing sensitivity of tree growth to climate. We hypothesize that the role played by regional climate as a growth constrain is modulated by the competitive conditions among neighboring trees. Specifically, we expect that trees subjected to high competition are more sensitive to drought stress, particularly at low-elevation sites.

2. Material and methods

2.1. Study area

The study was carried out along an altitudinal gradient located on the north-facing slopes of the Spanish Central Range (Valsaín Forest, Sierra de Guadarrama National Park; 40°49′N, 4°01′W, altitudinal range 1100–2125 m a.s.l.). The forest is dominated by Scots pine (*Pinus sylvestris* L.), although other tree species occur in marginal areas of the forest (*Quercus pyrenaica* Willd., *Quercus ilex* L., *Pinus nigra* Arn.). This area is located near the southernmost limits of the distribution of Scots pine. Climate is Mediterranean with marked continental influence, characterized by dry summers and cool winters (Appendix A, Fig. A1). The total annual rainfall is 1266 mm and the mean annual temperature 6.5 °C (at 1890 m a.s.l.), with December–January (mean temperature of −0.4 °C) and July–August (mean temperature of 16.5 °C) being the coldest and warmest months, respectively. The bedrock is mainly formed by granite and gneiss. Soils are shallow and usually acid being predominantly humic cambisols and leptosols at high-elevation sites (Forteza et al., 1988).

In this study, we used monthly climate data (mean, maximum, minimum temperatures and total precipitation) for the period 1985–2011, obtained from three meteorological stations located near the study sites at different elevations: Puerto de Navacerrada (40°47′N, 4°00′W, 1894 m a.s.l.), Granja de San Ildefonso (40°46′N, 4°00′W, 1191 m a.s.l.), and Segovia (40°56′N, 4°10′W, 1005 m a.s.l) and additional climatic data measured within forests (see Sánchez-Salguero et al., 2015 for details). Data were provided by the Spanish National Meteorological Agency (AEMET).

Historical evidence and dendrochronological studies show that the Valsaín forest has been intensively managed for centuries (Donés and Cabrera, 2009; Génova, 2012). The forest has been dedicated to timber production with an established management plan since 1889 (Rojo and Montero, 1996). This even-aged forest has been managed from group shelterwood system (rotation of 140 years and regeneration period of 40 years) to selective cuttings (Barbeito et al., 2011), which have been reduced in intensity and frequency until the 1980s, when a forest reserve was established. A flexible management plan was then introduced to increase the priority of recreational activities and biodiversity conservation (Montes et al., 2005).

2.2. Field sampling

In August 2012, field sampling was carried out in three Scots pine stands located at different elevations (Table 1, Fig. 1; additional information on the study area is available in Touchan et al., 2013). Since we were mainly interested on individual tree growth than on stand patterns, we chose to sample more intensively all trees located within each plot than to replicate several plots at each of the three elevations. Therefore, one square plot (40 m × 40 m) per elevation was randomly located at 1400 m near