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Interannual variability in competitive effects in mixed and monospecific forests of Mediterranean stone pine

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ABSTRACT

The management of species composition and competition are two of the main adaptive options that forest managers propose to cope with the expected negative impacts of climate change on forest growth in the Mediterranean basin. Species mixture can improve the resistance and resilience of forest ecosystems to face up global change. However, it seems likely that global change will modify mixed stands dynamics. Thus, studying inter-tree relationships on an annual basis is key to understanding ecosystem dynamics in the region. The aim of this paper was to evaluate the effects of tree species composition and competition on *Pinus pinea* annual secondary growth in mixed vs. monospecific stands over a period of 15 years with contrasting climatic conditions. We obtained basal area growth data from tree ring measurement on cores and cross section slices from 372 trees of *P. pinea* L., *Juniperus thurifera* L., *Quercus ilex* subsp. *ballota* (Desf.)) Samp. and *Quercus faginea* Lam., in the Spanish Northern plateau, approximately half of which were in monospecific stands and half in mixed stands. We analysed the effect of intra and interspecific competition on *P. pinea* secondary growth comparing the performance of several distance dependent competition indexes through linear mixed models. These competition indices were calculated for all trees within each plot for each year of study. The results showed competitive reduction and tree growth amelioration in mixed vs. monospecific stands of *P. pinea* indicating a spatial and temporal niche separation between species and size-symmetric effects for interspecific competition. Size-asymmetric results obtained for competition within pines indicated that the largest individuals obtain the majority of the contested resources suppressing the growth of their smaller pine neighbours. Intraspecific interactions were more negative than interspecific interactions. And we finally provide evidence of a growth enhancement in mixed vs. monospecific stands in water stressed years indicating that the promotion of mixtures in *P. pinea* stands is a powerful management tool to buffer the effects of climate change in the region.

1. Introduction

The management of species composition and competition are two of the main adaptive options that forest managers can propose in the face of expected negative effects of global change on forest dynamics (Lindner and Calama, 2013). While competition is one of the main factors that limit tree growth in forest ecosystems, numerous studies point out that the effects of competition on growth are different in mixed and monospecific stands (e.g. Pretzsch et al., 2013; Río et al., 2014b). Studies in different bioclimatic regions have reported benefits in growth and productivity from interspecific interactions in mixed stands compared to monospecific stands (Forrester, 2014; Perot and Picard, 2012). Advantages from different tree associations may include: increases in resource supply due to increased leaf nutrient content and leaf litter decomposition (Jonard et al., 2008); improved soil nutrient mineralization and better use of available water due to root stratification, soil chemistry and mycorrhiza (Brown, 1992; Rincón et al., 1999); or between species facilitation through hydraulic lift (Dawson, 1993).

Recent publications comparing growth or productivity in mixed vs. monospecific stands have also found that within species competition is stronger than between species competition (Forrester et al., 2011; Perot and Picard, 2012). This confirms that tree diversity may enhance growth and guarantee stability through species complementarity (Loreau et al., 2001; McCann, 2000). Positive interactions between species or inter-specific differences in the requirement and use of the resources are two of the possible mechanisms leading to this niche complementarity. The spatio-temporal variability of resource availability and other environmental conditions results in dynamic relationships within and between species

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(Forrester et al., 2011). These relationships are likely to change with life stage and plant age due to the dynamic nature of nutrient, water and carbon cycles, and light availability during stand development (Forrester et al., 2011); and may also change on an annual basis with complementary effects predominating in low-growth years and competition in high-growth years (Río et al., 2014b).

It is widely accepted that species mixture can improve resistance and resilience of some forest ecosystems (Landeau and Landmann, 2008; Legay et al., 2008) but not others (Grossiord et al., 2014). However, it seems likely that global change will modify mixed stands dynamics; thus, studying the different growth responses of tree species that grow together to different levels of stocking, degree of mixture and climate conditions remains a challenge. Different approaches have been proposed to analyse and compare growth in monospecific and mixed stands, including "replacement" experiments, where the proportion of each species varies while total density remains constant (Garber and Maguire, 2004), data from large-scale forest inventories (Río and Sterba, 2009) and modelling approaches. Single-tree growth models are a powerful tool to evaluate competition processes and have been previously used to explore the interactions between forest tree species (Perot and Picard, 2012; Río et al., 2014a). Among the different type of single tree models, empirical distance dependent models, including distance dependent competition indices as fixed effects (Contreras et al., 2011; Ledermann and Stage, 2001), have proved to accurately describe between and within species competition processes and to be good predictors of tree growth (Radtke et al., 2003).

Climate in the Mediterranean basin is characterized by a great interannual variability (Pugnaire et al., 2000) that conditions vegetation growth and diversity. Mediterranean forests have higher diversity levels than temperate European forests due to a higher species richness in the understory (Legay et al., 2008). Despite the importance of Mediterranean mixed forests as hotspots of specific diversity, the dynamics, production and management of these mixed forests are scarcely known. In addition, the Mediterranean basin is considered one of the most vulnerable regions under climate change scenarios, and evidence of processes of growth decline, tree decay and dieback, species shift and replacement, and changes in phenology have already been detected as a response to severe drought induced stresses (Peñuelas and Filella, 2001; Sánchez-Salguero et al., 2012).

Pinus pinea L. (Mediterranean stone pine) is a widespread tree species in European Mediterranean forests occurring across an area of 400,000 ha in Spain (Montero et al., 2008). Its management plays an important role in the local economy for the production of pine nuts and wood (Calama et al., 2012). Although it is well adapted to the current Mediterranean environmental conditions, the climate in the Mediterranean basin is expected to get hotter and drier, especially in the summer season (Lindner and Calama, 2013), inducing a decline in growth in Mediterranean forests (Peñuelas et al., 2001; Sánchez-Salguero et al., 2012) which may severely affect *P. pinea*'s distribution in the Iberian Peninsula (Benito Garzón et al., 2008).

The aim of the present study was to evaluate the effects of tree species composition and competition on *P. pinea* secondary growth in monospecific and in mixed stands in a series of 15 years with contrasting climatic conditions. The specific objectives of this analysis were to (a) compare the growth pattern response of *P. pinea* to intra and interspecific competition by fitting individual distance dependent tree models; and (b) assess the pattern of interannual variability in competition between and within species associated with climatic fluctuations. Our first hypothesis is that the effect of competition on growth is different in monospecific vs. mixed *P. pinea* stands as shown in other studies (Pretzsch et al., 2013; Río et al., 2014b). In accordance with the principle of "niche complementarity" we further expect to find differences in competition between and within species (Loreau et al., 2001). Based on the same principle, our third hypothesis is that intra-specific interactions will be more competitive than inter-specific interactions (Forrester, 2014; Pretzsch, 2014) due to inter-specific differences in crown and root architecture and intra-specific differences due to inter-specific interactions. Finally, we expect that the effects of competition in dry and wet years will not be the same in monospecific and mixed stands with a growth enhancement in mixed vs. monospecific stands on driest years (Pugnaire et al., 2000).

2. Material and methods

2.1. Data collection and processing

2.1.1. Study area

The study area is located in the limestone plain areas in the east of the province of Valladolid (Spain), within the geographical region of the Spanish Northern Plateau, defined by the river Duero basin. "Limestone areas" is a specific natural unit within the existing general ecological stratification of the region, based on soil, climate, rock and orographic attributes (Gordo, 2004). Altitude ranges from 800 to 890 m, the average annual precipitation is highly variable (between 220 and 630 mm) and the mean annual temperature is 11 °C. The area has a Mediterranean continental climate with a characteristic dry summer period during which mean monthly precipitation is 21 mm. The main types of soils found in the area are alfisols, entisols and inceptisols, with an average water holding capacity (WHC) of 248 mm/m.

2.1.2. Composition

In the province of Valladolid, *P. pinea* occupies 74,000 ha (29,000 ha are monospecific stands, 33,000 are mixed stands with other conifers and 12,000 ha are mixed stands with hardwoods). Mixed stands with hardwoods represent the most diverse and complex forest systems in the region and are mainly located in limestone plain areas. In these stands *P. pinea* grows with *Quercus ilex* subsp. *ballota* (Desf.)) Samp. and *Q. faginea* subsp. *faginea* Lam., *J. thurifera* L. and *Pinus pinaster* Aiton. The present study will focus on these more complex admixtures, which are considered to reach the maximum level of specific diversity within the region (Madrigal, 2014).

2.1.3. Stand management

From the end of the 19th century to mid-1970s the management of *P. pinea* forests in the Spanish Northern Plateau tried to maximize timber production while maintaining a secondary pine nut production. To attain this aim, *P. pinea* stands were transformed into monospecific even-aged high stocking stands by applying clearcuts by strips followed by direct seeding (Gordo, 1999; Montero et al., 2008). Other codominant species, like *Quercus* species, were either removed from these stands, or intensively coppiced for fuelwood. This type of silviculture was carried out in public forests until the 1980s, when high prices of edible pine nuts in the international markets set nut production as the main management objective. When nut production is the main objective, thinnings must aim for low densities to encourage crown development, avoid crown overlapping and promote individual cone production (Calama et al., 2008). Traditional nut oriented management focuses on these low density stands, proposing high intensity thinnings and shelterwood system regeneration methods. These practices have resulted in large open gaps where *P. pinea* has regeneration problems (Manso et al., 2012), but where other species are nowadays naturally recruited.