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Changes in structural heterogeneity and stand productivity by mixing Scots pine and Maritime pine

José Riofrío[a,*], Miren del Río[a,b], Hans Pretzsch[c], Felipe Bravo[a,d]

[a] Sustainable Forest Management Research Institute, University of Valladolid & INIA, Av. Madrid 44, Palencia 34004, Spain
[b] Department of Silviculture and Forest Management, INIA, Forest Research Centre, Ctra. A Coruña, km 7.5, Madrid 28040, Spain
[c] Chair for Forest Growth and Yield Science, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, D-85354 Freising, Germany
[d] Departamento de Producción Vegetal y Recursos Forestales, E.T.S de Ingenierías Agrarias, Universidad de Valladolid, Palencia, Spain

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ABSTRACT

Mixed-species stands have been studied extensively due to their potentially superior productivity, multi-functionality benefits and high ecological value compared to pure stands. The higher structural heterogeneity in mixed stands that can emerge from species interactions could be linked to the relationship between species diversity and ecosystem functions. We tested whether changes in stand structure also occur in mixtures of species with similar traits and whether they explain over-yielding patterns. Based on research with 12 triplets of Scots pine (*Pinus sylvestris* L.) and Maritime pine (*Pinus pinaster* Ait.) in the northern Iberian Peninsula (Spain), we provide evidence that species mixing increased structural heterogeneity and may induce over-yielding in mixed-species stands compared to monospecific stands. In this mixture of two light-demanding species, we observed that (i) stand composition influenced the inter-specific crown allometric variation, (ii) structural heterogeneity in mixed stands was caused by both specie-specific traits and species interactions, and (iii) intraspecific and interspecific differences in both crown size plasticity and size-distribution differentiation were associated with the increased relative productivity of mixed stands. We detected that crown complementarity and vertical stratification in the canopy space is a crucial mechanism for enhancing ecosystem productivity in light-demanding species and could be related to light interception and light-use. This work improves our understanding of emerging properties in mixed stands and introduces considerations for properly scaling and tracing mixing effects at individual tree, size distribution and stand levels.

1. Introduction

Mixed-species forests are becoming more prominent in forest management due to increasing evidence of their greater potential to supply ecological and socio-economic goods and services, with respect to monospecific forests. A plausible comparison between mixed stands with neighboring pure stands makes it possible to detect positive or negative mixture effects. Combining tree- and stand-level analysis may help to determine which mixing effects are most important for forest functioning (Forrester and Pretzsch, 2015). Each organizational level provides special insights that are not attainable at the levels above or below. Additionally, research into size structure dynamics can link findings at individual tree and stand levels and thus contribute to tracing the effects of species mixing (Pretzsch and Schütze, 2016)

Stand structure is usually described in terms of stand density, size distribution, horizontal and vertical tree distribution patterns, or combinations of several attributes (Gadow et al., 2012; McElhinny et al., 2005). Mixing species with complementary structural and functional traits may enhance structural complexity above and below ground, which can increase stand productivity and resource efficiency compared to monocultures (Dănescu et al., 2016; Pretzsch, 2014; Pretzsch and Schütze, 2016). However, negative or non-significant effects have also been reported for structural diversity-productivity relationships (Bourdier et al., 2016).

Structural attributes such as crown morphology and the resulting canopy structure are pivotal drivers of stand dynamics, which may be key determinants of productivity and a broad range of ecosystem services (Gadow et al., 2012). This applies to mixed-species stands where inter- and intra-specific interactions may increase structural heterogeneity (Pretzsch, 2014). Interspecific differences in morphological and physiological traits among coexisting species may enhance complementary mechanisms, such as the filling of canopy space, accumulating leaf area index (LAI), light capture and light use efficiency, all of which can contribute to explaining greater productivity in more diverse

* Corresponding author.
E-mail address: jgriofrio@hotmail.com (J. Riofrío).

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forests (Jucker et al., 2015; Larocque et al., 2012; Pretzsch, 2014; Toïgo et al., 2017; Williams et al., 2017). Recent studies have also uncovered evidence that intraspecific differences in allometric scaling of tree crowns in mixed stands were dependent on the competitive environment and competitive species composition in the stand (Forrester et al., 2017b; Pretzsch, 2014), which are directly related to canopy structure. In some mixtures, even small differences in species structural traits can trigger positive interspecific interactions through complementarity or competition reduction mechanisms (Jucker et al., 2014), but the role of differences in species-specific traits in mixed stands functioning is still non-well understood.

When mixed-species stands are more productive than monocultures, higher light absorption is often suggested as a cause. However, few studies have quantified this effect and even fewer have examined light-related interactions (Forrester et al., 2017a). A key question is whether differences in structural attributes between mixed and pure stands result from a merely '*additive effect*', i.e. the combination of the different species-specific morphological traits in a mixed stand, or if species interactions trigger species traits that surpass their behavior in pure stands, modifying outcomes such as productivity, stability, and resistance, in a *'multiplicative effect'* (Forrester and Pretzsch, 2015; Pretzsch, 2014). Multiplicative effects are highly relevant for understanding changes in forest functioning and for modelling and predicting mixed-stand dynamics and productivity (Forrester et al., 2017a; Pretzsch et al., 2016).

Research on interactions in mixed forests is often based on net effects due to the difficulty to isolate effects of from different mechanisms that influence interspecific interactions (Pretzsch and Schütze, 2009). However, growth and productivity at the stand level results from numerous interactions operating at the individual tree level, and therefore depends on the arrangement or distribution of competitive neighborhoods across a stand (Forrester and Pretzsch, 2015; Pretzsch et al., 2015b). In this study, we explored net mixing effects on productivity and stand structure in mixed forests composed of Scots pine (*Pinus sylvestris* L.) and Maritime pine (*Pinus pinaster* Ait.) in the Northern Iberian Range in Spain. These two main forest species in Spain grow in pure and mixed stands, either naturally or derived from species selection for afforestation. Riofrío et al., (2017b) identified large-scale positive interactions between these species when they coexist in mixtures, and suggested that light competition is the main driver limiting growth. These species show similar crown architecture (Poorter et al., 2012) and slight differences in shade tolerance (Gaudio et al., 2011; Sánchez-Gómez et al., 2006), thus slight or null mixing effects could be expected.

The main objective of this study was to analyze the mixture effects by comparing mixed stands with neighboring pure stands at three organizational levels – individual tree, tree size distribution, and stand – in order to infer possible complementarity mechanisms between these pine species with similar traits. Our hypothesis is that small differences in structural and functional traits between the two species under study and species interactions can induce changes in above-ground species allometries, crown dominance and stand structural traits. This would result in vertically structured canopies or crown complementarity among species in mixtures, that are related with the way light is distributed among trees. Changes in structural heterogeneity may be a mechanism that produces mixture effects on productivity in Mediterranean mixed-pine forests. To assess this hypothesis, we asked the follow working questions:

- Are tree crown allometric relationships affected by neighboring species composition?
- To what extent does mixing modify structural attributes at the stand and species levels compared to pure stands?
- How does volume production of mixed-species stands differ from that of neighboring pure stands?
- Are mixing effects on stand productivity related to structural heterogeneity?

2. Materials and methods

2.1. Field site and study design

The study was conducted in the Mediterranean mixed pine forests of Scots pine (*Pinus sylvestris* L.) and Maritime pine (*Pinus pinaster* Ait.) that cover approximately 50,000 ha in the Northern Iberian Range. This forest cover is divided in even-aged sections and compartments. The main objective is timber production, however, in recent years, other ecosystem services have gained great importance (Aldea et al., 2014). To achieve this objective, an even-aged management consisting of strip clear-cutting with soil movement and planted or sowing when necessary. Thinnings are common and not limited to self-financed interventions. In the study area mean annual temperature was 9.0 °C, mean annual precipitation ranged from 715 to 888 mm, elevation ranged from 1090 to 1277 m a.s.l. Soils were acidic brown earths (pH 3.9–5.4) with sandy loam to sandy texture, low cation exchange capacity (2.4–18.1 $cmol_C\ kg^{-1}$) and medium to lower water-retention capacity (1.5–18 $g\ cm^{-2}$) (Lopez Marcos et al., 2017).

A total of 36 plots, grouped into 12 triplets of mixed plots (*PS,PT*) and their corresponding pure plots of Scots pine (*PS*) and Maritime pine (*PT*) were established in 2014–2015 (Fig. S1). Plots within triplets had similar site conditions, age and density and belonged to the same management compartments where the same silviculture regime had been applied (Table S1); facilitating a pair-wise plausible comparison of mixed versus pure stands. The stands were approximately full stocked, stocked above 60% relative to or even exceed the maximum density, and none of the plots had been thinned for at least 10 years. In most of the triplets, both species were in the same age phase comparing monoculture and mixed-species stands, ranging from mature (45–50 years) to old stands (120–140 years). Site quality at age 100 years indicated moderate to low growth conditions according to specific curves of pure stands (Bravo-Oviedo et al., 2007; Rojo and Montero, 1996). Some variations in stand age and site conditions were tolerated among triplets in order to cover stand variability in the study area.

Each triplet consisted of three circular plots of 15 m radius, including one pure plot of Scots pine, one pure plot of Maritime pine and one mixed plot that contained both species. Mixed plots had varying individual tree mixtures and the mixing proportion between species had a combination of at least 75–25% of the total basal area. Pure plots were located within 1 km of the mixed plots. Pure plots stands were considered only when total basal area of the target species was higher than 90% and were used as reference to evaluate mixing effects on stand structure, growth and yield.

All stems > 7.5 cm in diameter were inventoried, positioned ('*x, y*' coordinates) and measured the diameter at breast height (*d*). For each tree total height (*h*) and height to crown base (*hcb,* base of the crown's lowest primary branch) were measured using a vertex hypsometer. A crown class was assigned to each tree (dominant, co-dominant, dominated and suppressed). Dendrometric variables at the tree and stand level were calculated from stand measurements (Table 1). All data treatment, calculations and analyses were performed in R (R Develomment Core Team, 2015); the specific packages used are mentioned in each section.

Increment cores at stem height of 1.30 m were taken from most trees, covering at least the last 15 years, and avoiding dead or suppressed trees. A total of 736 from Scots pine and 693 from Maritime pine trees in mixed and pure plots were sampling. All cores were mounted, sanded till tree-ring boundaries were clearly visible and scanned at 1800 ppi image resolution. For each cored tree, tree ring widths (mm $year^{-1}$) were dated and measured from the scanned images using the *'measuRing'* package (Lara et al., 2015). The quality of cross-dating and synchronization of the growth series were assessed using the *'dplR'* package (Bunn, 2010).