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Growth dynamics and productivity of pure and mixed *Castanea sativa* Mill. and *Pseudotsuga menziesii* (Mirb.) Franco plantations in northern Portugal

Leónia Nunes [1-2-3], **Stith T Gower** [4], **Maria L Monteiro** [5], **Domingos Lopes** [2], **Francisco C Rego** [3]

Since the late 1980's the productivity of monocultures *vs.* mixed-species forests has been the subject of studies by forest managers and ecologists. Mixed plantations have been established in different proportions to determine if mixtures could provide greater yields and more benefits than monocultures of the component species, as well as to understand if they could be an interesting economic option. An experimental design trial was set up in the north of Portugal in a replacement series with pure and mixed *Castanea sativa* Mill. and *Pseudotsuga menziesii* (Mirb.) Franco. The objective of this study was to assess growth dynamics and compare the aboveground biomass and net primary production of the two species in pure and mixed treatments in proportions 1:1 and 1:3. The growth was measured at 7, 11, 15, 17, 19, 27 and 28 years after planting and aboveground net primary production was estimated at age 28. As a component of the mixed treatments, *P. menziesii* exhibited greater height, diameter and aboveground biomass than *C. sativa*. Relative yield total indicated a higher productivity in the mixtures compared with the pure treatments. Early in the development, pure treatments and mixtures had similar aboveground biomass per hectare, but later the mixtures showed higher yield than pure treatments. The mixture productivity increase through time appears to be the result of both canopy stratification and better use of site resources. The aboveground net primary production was also higher in mixed than in the pure treatments.

Keywords: Growth, Productivity, Biomass, Mixed-species, Interactions, Replacement Series

Introduction

Mixed forest ecosystems are important to human life. Similarly to monoculture plantations, they ensure timber production but also provide other benefits through the diversification of forests products (Khanna 1997, Montagnini 2000, Redondo-Brenes & Montagnini 2006).

In the last few years, mixed stands dynamics returned into the focus of forest science (Forrester et al. 2006b, Pretzsch et al. 2013). Research in experimental mixed-species plantations has lately increased with the establishment of replicated plots of monospecific and mixed plantations at the same site, followed by extensive data collection (Amoroso & Turnblom 2006, Forrester et al. 2006b, Kelty 2006). The results of this research have given a better understanding of growth dynamics, productivity and mixtures interaction over a relatively short time period.

One of the main objectives studying mixed-species plantations is to analyze whether mixed stands can provide not only greater total yields, as opposed to monocultures of equal densities, but also other benefits that may outweigh the advantages of stand management in monocultures (Amoroso & Turnblom 2006, Kelty 2006). To a large extent, superior productivity of mixed-species stands to monocultures depends on the design and proportion of the mixture, soils, silviculture, tree species and the availability of resources (Fridley 2002, Binkley et al. 2003). According to Kelty (1992), substantial differences between species' characteristics - in terms of shade tolerance, height growth patterns, crown structure, root depth and structure - may lead to an optimal capture and use of site resources and therefore to an overall higher productivity as compared to monocultures (Binkley & Ryan 1998). Mixed stands may also experience less intense interspecific than intraspecific light competition as a consequence of differences in shade tolerance among species. Such arrangement would, in theory, maximize the use of light because of increased light interception and light-use efficiency (Kelty 1992), leading to a higher total productivity than in pure stands (Smith et al. 1997). This type of response has been found in studies by Kelty (1989), Brown (1992), DeBell et al. (1997), Man & Lieffers (1999) and Garber & Maguire (2004). Forrester et al. (2006b) mentioned that canopy stratification is a key factor to ensure the coexistence of the species until the end of the rotation. Moreover, to achieve higher productivity in mixed stands, mixed species should exhibit differences in their requirements (niches) or in the way they use site resources, and/or should positively affect the growth of each other (Vandermeer 1989). This concept of niche separation implies that if two species are too similar in their requirements they would eventually compete intensely to exclude the other, but if competition is sufficiently weak, the two species may coexist (Harper 1977).

The knowledge on advantages/disadvantages of mixed *vs.* pure stands with respect to productivity decisively influences the forest manager decision in support or against tree species poly-culture (Olsthoorn et al. 1999). However, sound knowledge about mixing effects even for the most common tree species combinations is rather rare and scattered. Furthermore, it is difficult to accurately predict success of mixed-species combinations and sites especially with regard to growth dynamics (Forrester et al. 2005, 2006b,

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✉ (1) Escola Superior Agrária, Instituto Politécnico de Viseu (ISPV), Estrada de Nelas, Quinta da Alagoa, 3500-606 Viseu (Portugal); (2) CITAB, Universidade de Trás-os-Montes e Alto Douro (UTAD), Apartado 1013, 5000-911 Vila Real (Portugal); (3) CEABN, Instituto Superior de Agronomia, Tapada da Ajuda, 1349-017 Lisboa (Portugal); (4) Department of Forestry, 1630 Linden Drive, University of Wisconsin, Madison, 53706 Wisconsin (USA); (5) CIMO, Instituto Politécnico de Bragança (IPB), Escola Superior Agrária, Bragança (Portugal)

@ Leónia Nunes (leonianunes@gmail.com)

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Amoroso & Turnblom 2006, Pretzsch 2013).

Several studies have focused on the effects of a valuable timber species growing in mixture with a nitrogen-fixing species to investigate facilitative interactions (increased nutrient availability) between the species and resultant stand-level productivity (Binkley 1983, Bauhus et al. 2000, Forrester et al. 2005, 2006b, Laclau et al. 2008, Patrício et al. 2010). Complementary use of resources have also been analyzed (Forrester et al. 2004, Forrester et al. 2006a). If facilitation and complementary or competitive reduction in species' resource requirements occur simultaneously, a higher productivity is obtained by the combination of interactions among species (Forrester et al. 2004, Kelty 2006, Pretzsch et al. 2010). More total light interception has also been measured in mixtures (Bauhus et al. 2004, Le Maire et al. 2013). Furthermore, the effect of competition between species has been analyzed to identify the key constraint (Newton & Cole 2008). Additional improvements in mixed-species plantations compared with monocultures have been reported, such as nutrient cycling (Forrester et al. 2006c), foliar nutrients (Brown 1992, Richards et al. 2010, Nunes et al. 2011), soil fertility (Montagnini 2000), biomass production (Binkley & Ryan 1998, Binkley et al. 2003, Forrester et al. 2004) and carbon sequestration (Kaye et al. 2000, Resh et al. 2002, Forrester et al. 2006a).

Mixed forests in northern Portugal are an important source of timber, but little is known about their productivity. Some non-native species have been used for their establishment, though information on their yield is currently lacking. It is therefore important for this region to carry out studies on the productivity of mixed-species, to evaluate stand biomass production and compare the results with monocultures of the component species, in order to guide local farmers' decisions on their plantations.

Pseudotsuga menziesii (Mirb.) Franco is a shade-intolerant, non-native tree species introduced in Portugal in the XIX century, when it was first planted at Sintra (Gomes & Raposo 1939). It has been used in plantations on mountainous areas of central and northern Portugal, showing high adaptability, fast growth, and a high potential for timber production (Louro & Cabrita 1989, Luís 1989).

Castanea sativa Mill. is native to Portugal where is known since the Miocenic period and cultivated since Roman times (Luís & Monteiro 1998), and has important economic, cultural and ecological functions in northern Portugal (Maia 1988). It covers an area of 34 087 ha (AFN 2010), mainly spread over northeastern Portugal, with the largest production area located in the Trás-os-Montes region, which represents almost 85% of the total Portuguese coverage (Gomes-Laranjo et al. 2009).

Because *C. sativa* has a good adaptation to the shade, it can be planted in mixed-species stands as an understory level with shade-intolerant species such as *P. menziesii*, which tends to occupy the upper part of the canopy (Oliver & Larson 1996).

The objectives of this study were: (1) to assess differences in growth dynamics between *C. sativa* and *P. menziesii* in both pure and mixed-species plantations in a replacement series experiment; (2) to compare on site species biomass and aboveground net primary production; and (3) to estimate specific leaf area of pure and mixed plantations. Results were expected to give a better understanding of the development of these species growing in the same site, thus sharing soil and climatic conditions. The study intended also to evaluate if specific interactions intervening between *C. sativa* and *P. menziesii* would increase the overall stand productivity.

Material and methods

Experimental site

The study was carried out at an experimental site established on private land located at Bemlhevai, Bragança district (41° 24' N, 7° 6' W), with an elevation of 710 m a.s.l. and almost flat (2°). The ecological zone is submontano SA X SM, between 400 and 700 m (Albuquerque 1954). The soil is litholic non-humic from serecitic schist.

The climate in this region is a transition between continental and Mediterranean. The annual precipitation is 690 mm (± 8.8), of which 60% falls from October to February, and the mean annual temperature is 12.5 °C (± 1.8 - Ruas 1997).

The experiment is a replacement series design using two trees species, *Castanea sativa* Mill. and *Pseudotsuga menziesii* (Mirb.) Franco. The total stand density is constant in all the treatments but the proportions of the two component species varies. This design is often used when productivity of both species is of interest (Forrester et al. 2006b).

Experimental design

A set of twenty-one permanent plots was established in the winter of 1981 using a complete randomized block design of *C. sativa* and *P. menziesii* (Maia 1988, Luís & Monteiro 1998). Each 512 m^2 plot was planted using a 4 × 2 m spacing for a total of 64 trees. Plots were set up in three blocks (two species per block) with no buffer between the blocks. Each block contains seven treatments in four proportions (Fig. 1). The treatments are as follows (T is treatment, C is *C. sativa* and P is *P. menziesii*):

(1) Mixtures

- Row mixtures with species changing in the planting line:
  - T1: 25% *C. sativa* 75% *P. menziesii* - 1 C and 3 P in the line (25C:75P)
  - T2: 25% *C. sativa* 75% *P. menziesii* - 2 P and 1 C in the line (25C:75P)
  - T3: 50% *C. sativa* 50% *P. menziesii* - 1 C and 1 P in the line (50C:50P)
- Lines mixtures with species changing between planting line:
  - T4: 50% *C. sativa* 50% *P. menziesii* - 1 line of C and 1 line of P (50C:50P)
  - T5: 25% *C. sativa* 75% *P. menziesii* - 2

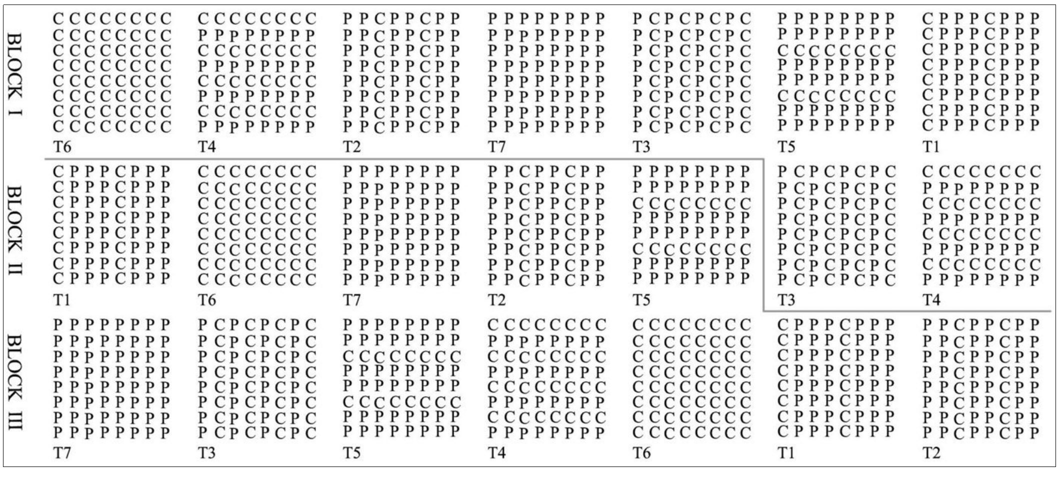

Fig. 1 - Framework of the different planting designs of *C. sativa* (C) and *P. menziesii* (P) plots at the study site. The grey line separates the plots destroyed by a wildfire in 2003 (upper part) from those survived to fire.

lines of P and 1 line of C (25C:75P)

(2) Pure treatments

- T6: 100% *C. sativa* (100C:0P)
- T7: 100% *P. menziesii* (0C:100P)

Details about the plantation establishment are documented in Maia (1988) and Luís & Monteiro (1998).

Field work and laboratory methods

After the establishment of the research site several basic biometric measurements were made to analyze tree growth in the different treatments (Luís & Monteiro 1998). All trees were numbered in each block and the initial height and diameter at breast height (DBH - 1.30 m above the ground) of each tree were measured in 1988. The height and DBH were measured again in 1992, 1996, 1998, 2000 and 2008. The final assessment was made in 2009.

DBH was measured with a steel diameter tape and two measurements were made in each tree to avoid errors. These data were used to calculate the basal area and density. Total height, defined as the maximum vertical distance from the ground level to the tree top, was measured for all the trees using a height pole. Averages of these variables were calculated for all treatments.

Soil depth was measured at four sampling locations in each plot, and the average was calculated to represent the soil depth at the plot. Moreover, soil samples in two horizon layers (horizon A: 0-20 cm; horizon B: 21-60 cm depths) were collected to analyze soil properties (Nunes et al. 2011) and to test if species composition had effect on soil nutrient content.

Data are available for all plots until the year 2000. In 2003 a wildfire destroyed all the seven treatments in block I and two plots of mixtures in block II. Since then, measurements were made only on plots saved from the fire.

Aboveground biomass and net primary production

Total aboveground biomass was calculated for each tree component (stem, branch and foliage) using allometric equations in all the pure and mixed treatments (Tab. 1). Biomass components of both species were estimated using the following model (eqn. 1):

$$B = a \cdot DBH^{b}$$

where *B* is the biomass component (oven-dried weight - Kg), *DBH* is the diameter at breast height (cm) and *a* and *b* are the model parameters. Total biomass was calculated as the sum of the dry biomass of all components: tree leaves/needles, branches and stem. The allometric equations used to estimate biomass for *C. sativa* were taken from Ruiz-Peinado et al. (2012), wherein tree data were collected in the Central Mountain Range and Sierra de Ronda, Spain. Patrício (2006) developed specific equations to predict tree biomass per plant component of *C. sativa* high forest stands located in the northwest of Portugal. However, these equations were not considered in this investigation because of relevant differences between the two datasets as for the range of tree size and age. For *P. menziesii* biomass equations were taken from a work by Gower et al. (1987) carried out in the Cascade Range of central Washington State (USA), given that no specific allometric studies are available for this species in Portugal. For both species, the range of tree structural characteristics corresponds to that observed in our study area.

Aboveground net primary production (ANPP) was calculated for all trees on each of the 512 m² plots as the sum of average woody biomass increment (ΔB), of stem and branch, and the annual foliage biomass production. Herbivory was not estimated because it is very difficult to be assessed. However, previous studies suggest it to be less than 10-15% of the net primary production for forests (Gower & Grier 1989). Biomass increments were calculated for each tree component for 2008 and 2009, based on annual diameter increment data and using allometric equations for each species.

Aboveground litterfall was estimated using 40 x 60 cm litter screens randomly placed inside each plot. Litter screens were deployed in July 2008 and litter was collected every 3 months for one year. Litter samples were dried at 70 °C to a constant mass and weighed (± 0.01 g) to determine the dry biomass.

The productivity results in pure and mixed treatments were then compared to provide information on which type of treatment had higher productivity.

Tab. 1 - Allometric coefficients for the species studied using the model reported in eqn. 1. (*B*): biomass component (dry biomass - Kg); (*a*) and (*b*): model parameters. R^2 was calculated using the transformation: ln(*B*) = ln(*a*) *b* ln(*DBH*). Sources: Ruiz-Peinado et al. (2012) for *C. sativa*; Gower et al. (1987) for *P. menziesii*.

Species	Compartment	*a*	*b*	R^2
Castanea sativa	Stem (wood bark)	0.0878	2.1474	0.94
	Branch > 7cm	0.0004	3.491	0.902
	Branch > 2 < 7cm	0.1008	1.9089	0.83
	Branch < 2cm	0.2118	1.6938	0.858
	Foliage	0.15 ($B_{\text{Stem}} + B_{\text{Branches}}$)		
Pseudotsuga menziesii	Stem wood	0.0294	2.798	0.986
	Stem bark	0.017	2.414	0.968
	Live branch	0.0184	2.033	0.895
	Dead branch	0.0184	1.642	0.786
	New twig	0.0003	2.166	0.924
	New foliage	0.0021	1.966	0.886
	Total foliage	0.0419	1.754	0.922

Leaf area index

Leaf area index is defined as the projected area of tree foliage in relation to the total stand area. Leaf area index was calculated as the product of leaf biomass times the specific leaf area. Specific leaf area (fresh area to dry mass, cm² g^{-1}) per species was calculated from 125 leaves/needles randomly chosen from all canopy positions in 5 trees of each species in each treatment. Samples were collected from both species in the mixtures. All leaves were collected in the summer of 2011 after full leaf expansion and before the fall of the deciduous leaves. The projected leaf area of fresh leaf samples was measured in laboratory using a digital image analyzer for each scanned leaf. Reference objects of known area were used for calibration purposes. All samples were oven-dried at 70 °C to a constant dry mass. Specific leaf area was calculated as the sum of the leaf area divided by the sum of their dry mass.

Data analysis

Analysis of variance of a randomized complete block design were performed using the twenty-one plots organized in three blocks with four proportions according to the species composition: pure *C. sativa*, pure *P. menziesii*, mixtures with 1:1 and 1:3 proportions. The equality of means in DBH, height, the height to diameter ratio and aboveground biomass and ANPP among the four proportions were tested. Specific leaf area and leaf area index were also analyzed. Normality and variance homogeneity of residuals were verified. Student-Newman-Keuls's (S-N-K) test was used to determine significant differences within species proportions in balanced and unbalanced design. All statistical analyses were performed using the package IBM SPSS Statistics® (version 21).

The yield of pure and mixed stands is usually compared on a relative basis; thus, the effects of combining the two species were evaluated by comparing the yield of each species in the mixture with its yield in monoculture as per Harper (1977). To analyze the growth outcome of the mixed-species stands in this replacement series, a relative yield (*RY*) was calculated. The yield variable for this analysis was aboveground biomass per hectare, an adequate way to evaluate the productivity whenever the species have different basic densities (Monteiro et al. 1994). The *RY* of each species and the relative yield total (*RYT*) were calculated as follows (eqn. 2 to 4):

$$RY_{C.sativa}=\frac{Yield_{C.sativa}\in mixture}{Yield_{C.sativa}\in monoculture}$$

$$RY_{P.menziesii}=\frac{Yield_{P.menziesii}\in mixture}{Yield_{P.menziesii}\in monoculture}$$

$$RYT=RY_{C.sativa}+RY_{P.menziesii}$$

This index indicates the outcome of all interactions occurring in the stand, including both species interactions and the yield-density functions of either species.

If both species use resources in identical ways, *i.e.*, compete for these resources, *RY* of each species will be equivalent to its proportional contribution in the mixture, with an expected *RYT* = 1. *RY* equal to the proportion of the given species in mixture indicates that, on average, trees were the same size in mixture or monoculture (Forrester et al. 2006b). An *RYT* > 1 indicates either niche separation or the existence of some beneficial relationship between species, leading to a potential productivity gain for the mixture. Contrastingly, *RYT* < 1 indicate an antagonistic or competitive relationship between the species in the mixture. In this study the assumption of the 1:1 mixture proportion grown independently would result in each species having an expected *RY* = 0.5 and *RYT* = 1.0.

Results

Patterns of growth

Tree height for *C. sativa* and for *P. menziesii* was not significantly different among the treatments for either species (*P* > 0.05) for all the studied years (Fig. 2). For *C. sativa*, tree height in different treatments was very similar early in the study, but as the study continued *C. sativa* in pure and 25C:75P treatments become taller until the age 19, when mixtures reached the higher average height (Fig. 2a). *C. sativa* had a smaller growth in pure treatments than in mixtures, on average 0.15 and 0.26 m less in the 1:3 and 1:1 proportions, respectively. Tree height for *P. menziesii* was also very similar among treatments early in the study, but at age 27 and 28, an increase in height growth in mixtures was observed; the 25C:75P and 50C:50P treatments have an average height with 11.9 ± 0.4 and 13.8 ± 0.1 m, respectively (Fig. 2b). Comparing the two species revealed that *P. menziesii* was taller than *C. sativa* (by more than 2 m at age 19 and 4 m at age 28) in all treatments.

Average DBH for all the treatments and species is displayed in Fig. 3. Since the start of the study (1988) DBH was not significantly different among treatments for both species (*P* > 0.05), although significant differences were observed later in the study for *P. menziesii*. *C. sativa* presented the higher DBH growth in mixtures compared with the pure treatment. The treatment 25C:75P had the higher DBH in the first 19 years, with 9.5 ± 2.3 cm in 2000 (Fig. 3a), and at age 28 this tendency was maintained, with an average DBH of 13.2 ± 1.4 cm in the treatment 25C:75P. *P. menziesii* 50C:50P treatments had higher DBH values compared with the pure and the 25C:75P treatments since age 11 with no significant differences (*P* > 0.05), although at age 27 and 28 the DBH in 50C:50P treatment was significantly different (*P* < 0.05) from the pure treatment and 1:3 proportions. These results may indicate that radial growth of *P. menziesii* is higher when mixed with *C. sativa*.

Results show that *P. menziesii* was thicker than *C. sativa* (by more than 4 cm at age 19) in all treatments. Furthermore, these differences appeared early in stand development and were already in the order of 2 cm at age 11.

The height to diameter at breast height ratio (*h/d*) was compared among species growing alone and together at age 11, 19 and 28 (Fig. 4). Changes in the *h/d* patterns may reflect competition between species. Even though some differences in diameter and height growth were evident over the period considered, the *h/d* ratio was very low. *C. sativa* growing in mixtures had a slightly greater *h/d* ratio than in pure treatments, but

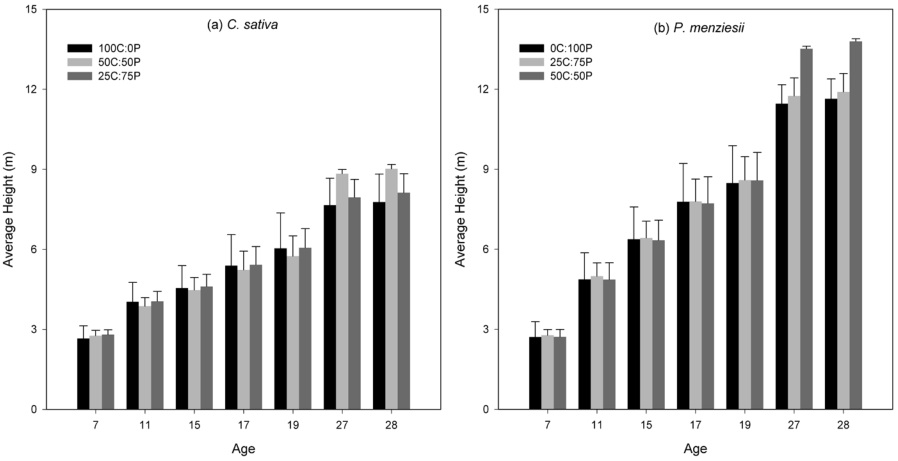

Fig. 2 - Mean total height over time by species for the studied years. Height values were not significantly different (*P* > 0.05) among treatments for both *C. sativa* and *P. menziesii*.

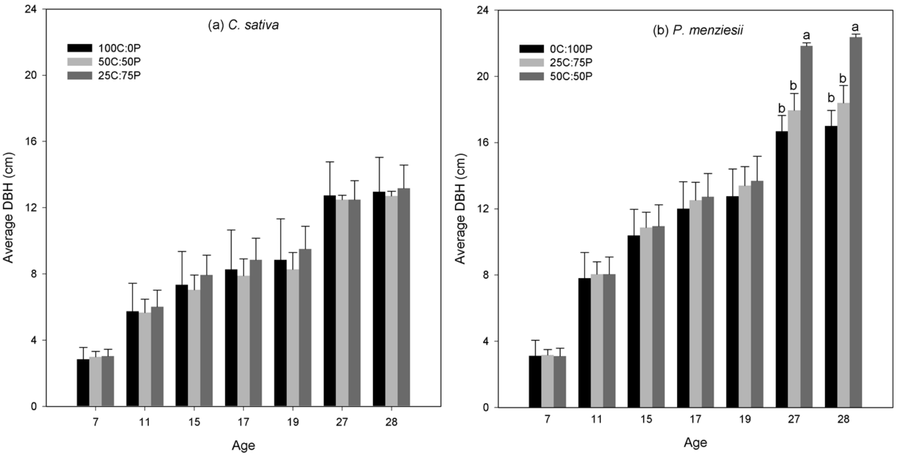

Fig. 3 - Mean diameter at breast height (DBH) over time by species for the studied years. DBH values were not significantly different among treatments for *C. sativa* (*P* > 0.05), but were significantly different for *P. menziesii*. Differences in letters above the bars indicate significant differences in DBH between treatments (*P* < 0.05).

no significant differences were observed among the treatments ($P > 0.05$). *P. menziesii* instead had slightly greater *h/d* ratio when growing in pure treatments. Differences among treatments were statistically significant ($P < 0.05$) only at age 28.

The effects of combining the two species considered in a mixture were analyzed by comparing the yield of each species in mixture with its yield in a pure stand (Harper 1977). Relative yield (*RY*) and relative yield total (*RYT*) were calculated based on the aboveground biomass per hectare for both proportions of mixtures at all the studied ages (Fig. 5).

For the 1:1 mixture (50C:50P), the *RY* index for *C. sativa* was less than 0.5 since age 11 (except for age 7). *P. menziesii* had *RY* values substantially greater than 0.5 since age 11, and at age 27 and 28 the *RY* was greater than 1.0. It is clear that the mixture of the two species benefited the *P. menziesii* since age 11, and this species had the competitive advantage over *C. sativa* on this proportion. Plotting together the RY index obtained for both species, all the values were above 0.5 (above the dashed line reported in Fig. 5a), indicating a higher productivity in mixture. Combined *RYT* was higher than 1.0 for all the studied years (Fig. 5b). Thus, in this proportion, it appears that significant niche separation between these species may exist.

For the 1:3 mixture (25C:75P), the *RY* of *C. sativa* was greater than 0.25 until age 20, and slightly lower afterward. *P. menziesii* instead, had *RY* values smaller than 0.75 until age 11 and greater since age 15. *RYT* for this proportion was higher than 1.0 only after 11 years since planting (Fig. 5b).

Fig. 6b combines the results obtained for absolute and relative yield at 3 ages (11, 19 and 28 since planting) for the two proportions of mixtures considered. At the age 11 both the relative and absolute yield (aboveground biomass per hectare) for the mixtures were indistinguishable from those of monocultures. Contrastingly, differences between mixtures and monocoltures in both relative and absolute yield are fairly evident at age 19 and 28.

Plot characteristics

Specific leaf area was not significantly different between treatments in *P. menziesii,* but it was significantly different ($P < 0.05$) in the *C. sativa* 50C:50P treatment when compared with the pure treatments (Tab. 2). Pure treatments of *C. sativa* showed average specific leaf area values nearly doubled compared to pure *P. menziesii*, with values of 122.0 ± 5.7 cm^2 g^{-1} and 63.5 ± 2.3 cm^2 g^{-1}, respectively. Average values of mixtures reached higher values compared to the pure treatments. The 50C:50P treatments had the higher values in both species; the highest value was for *C. sativa*.

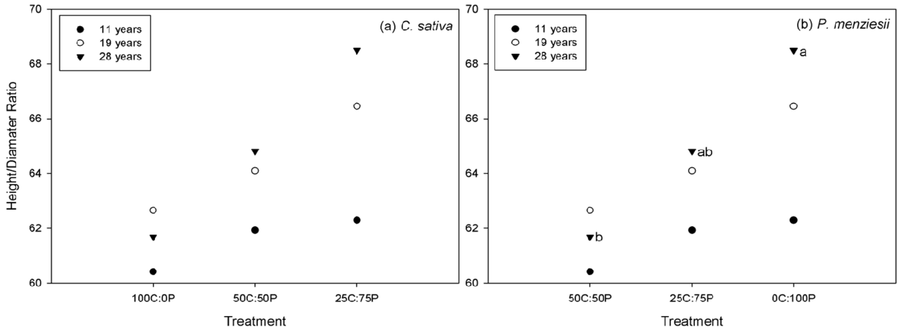

Fig. 4 - Height/diameter ratio (*h/d*) by treatment at age 11, 19 and 28. Significant differences ($P < 0.05$) in *h/d* ratio among treatments are indicated by different letters.

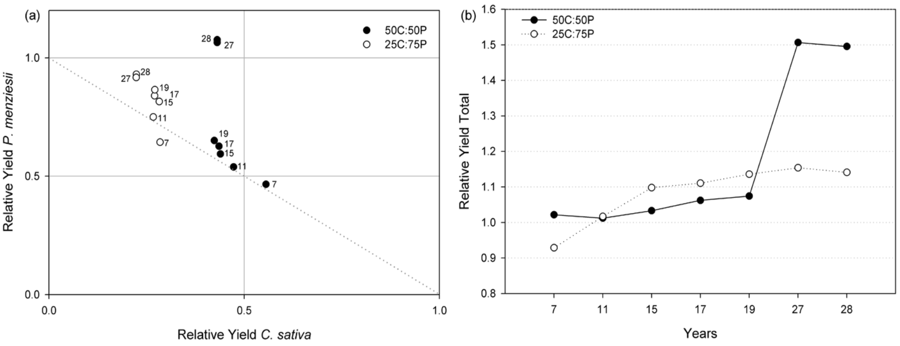

Fig. 5 - Relative yield (a) and relative yield total (b) of aboveground biomass per hectare between age 7 and 28 for *C. sativa* and *P. menziesii* in 1:1 and 1:3 mixtures.

Mean stand characteristics at age 28 for the two pure treatments and mixtures are summarized in Tab. 3. At this stage, the *C. sativa* pure treatment presented a DBH average of 13.0 ± 2.5 cm (range: 4.5-22.4 cm) and a basal area of 14.7 ± 5.9 m^2 ha^{-1}. The average height ranged from 3.3 to 10.8 m. The *P. menziesii* pure treatment presented higher values of DBH, basal area and height compared to pure *C. sativa.* As for density, the pure treatments had similar values, 1064 trees ha^{-1} for *C. sativa* and 1104 trees ha^{-1} for *P. menziesii*, which represented 85% and 88% of the total trees planted, respectively. Mean DBH, height and basal area for *P. menziesii* was 17.0 ± 1.0 m (range: 4.2-26.3 m), 11.6 ± 0.9 m (range: 4.1-16.1 m) and 25.4 ± 5.4 m^2 ha^{-1}, respectively. The mixtures presented some heterogeneity. *P. menziesii* DBH and height were higher in the 50C:50P treatment, but *C. sativa* higher values of DBH were observed in the 25C:75P treatment and higher in height in the 50C:50P treatment. Basal area of *C. sativa* in 50C:50P was less than half of the pure *C. sativa* treatment, and less than expected in the 25C:75P, indicating a negative effect on *C. sativa* growing in mixtures. Total LAI was not significantly different across treatments ($P > 0.05$), ranging from 2.3 m^2 m^{-2} for 0C:100P to 5.9 m^2 m^{-2} for 100C:0P. While the contribution of *P. menziesii* to the total value of LAI in each plot decreased by

Tab. 2 - Specific leaf area (fresh area: dry mass) by species. Different letters indicates significant differences among treatment means ($P < 0.05$).

Species	Plot	Specific leaf area (cm^2 g^{-1})		
		Mean	Range	Standard error
C. sativa	100C:0P	122 ^{b}	95.2-144.9	5.7
	50C:50P	172.8 ^{a}	138.3-189.9	6.4
	25C:75P	143.1 ^{ab}	112.2-204.5	9.6
P. menziesii	0C:100P	63.5 ^{a}	53.8-75.6	2.3
	25C:75P	57.2 ^{a}	44.9-78.1	3.2
	50C:50P	67.2 ^{a}	55.2-89.6	4.3

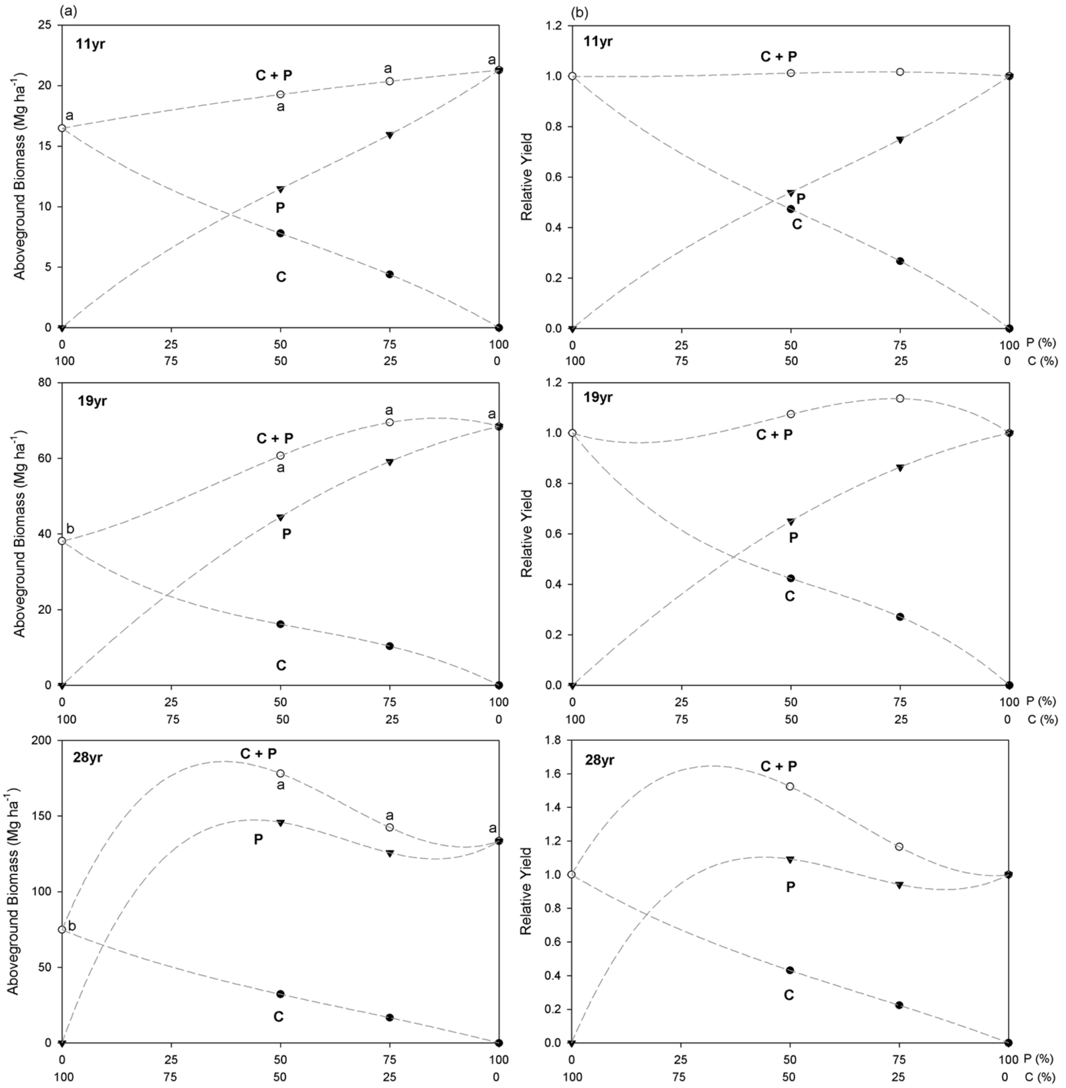

Fig. 6 - Aboveground biomass (a) and absolute and relative yield of aboveground biomass per hectare (b) for the *C. sativa* (C) and *P. menziesii* (P) species at age 11, 19 and 28, with the total number of individuals constant. The proportion of each species in mixture, per treatment, changes from no individuals (0%) up to the total number of individuals (100%). Significant differences (P < 0.05) for aboveground biomass among treatments are indicated by different letters.

0.5 $m^2\ m^{-2}$ from the pure to the mixed treatments, the contribution of *C. sativa* LAI decreased by 4.0 $m^2\ m^{-2}$.

Total biomass and aboveground net primary production

In order to analyze the growth dynamics of the species, the aboveground biomass was estimated at the age 11, 19 and 28, *i.e.*, in the beginning, the middle and the last year of available field data. *P. menziesii* pure treatments had higher aboveground biomass compared to *C. sativa* pure treatments at the 3 ages analyzed, with 133.4 ± 30.8 Mg ha^{-1} for *P. menziesii* and 74.8 ± 30.6 Mg ha^{-1} for *C. sativa* at age 28. At age 11 (Fig. 6a, 11yr) results reveal a low interaction between species (intra- and interspecific competition are the same), since the aboveground biomass in mixtures is similar to pure treatments with no significant differences ($P > 0.05$) between treatments. The growth of the two species in mixture is the result of the contribution of each species to the total aboveground biomass in direct ratio to its original proportion. However, after only eight years, biomass dynamics were greatly influenced by the planting design for the two species, and *P. menziesii* contributed positively to the overall positive mixing effect in both 50C:50P and 25C:75P treatments. The interspecific competition was higher than the intraspecific competition. *P. menziesii* had a greater share

Tab. 3 - Structural characteristics at age 28 by species composition. Mean values are reported (standard error in parentheses). (DBH): average diameter at breast height; (H): average tree height; (N): number of trees per hectare; (BA): average basal area; (SD): average soil depth; (LAI): average leaf area index; (*): Mean values with different letter within LAI differ significantly among the treatments (P < 0.05).

Treatment	Species	DBH (cm)	Range DBH (cm)	H (m)	Range H (m)	N	BA ($m^2\ ha^{-1}$)	SD (cm)	LAI ($m^2\ m^{-2}$)
100C:0P	*C. sativa*	13.0 (2.5)	4.5 (2.1) - 22.4 (3.4)	7.8 (1.3)	3.3 (0.9) - 10.8 (1.3)	1064 (29)	14.7 (5.9)	77 (3.9)	5.9 (2.4) ^{a}
50C:50P	*C. sativa*	12.7 (0.5)	5.6 (0.2) - 19.2 (0.2)	9.0 (0.3)	4.7 (1.3) - 12.4 (0.3)	508 (39)	6.4 (0.0)	74 (2.2)	5.7 (0.2) ^{a}
	P. menziesii	22.4 (0.3)	6.4 (1.8) - 34.4 (1.5)	13.8 (0.2)	4.7 (1.4) - 18.6 (0.1)	596 (29)	23.4 (1.9)		
25C:75P	*C. sativa*	13.2 (1.7)	6.0 (0.9) - 20.3 (1.6)	8.1 (0.9)	4.5 (0.7) - 11.1 (0.9)	244 (19)	3.3 (0.6)	70 (2.9)	3.3 (0.4) ^{a}
	P. menziesii	18.4 (1.3)	6.8 (1.3) - 28.9 (2.0)	11.9 (0.9)	6.0 (0.7) - 16.5 (0.6)	827 (27)	22.3 (2.9)		
0C:100P	*P. menziesii*	17.0 (1.0)	4.2 (0.1) - 26.3 (0.9)	11.6 (0.9)	4.1 (0.5) - 16.1 (0.6)	1104 (88)	25.4 (5.4)	75 (2.4)	2.3 (0.5) ^{a}

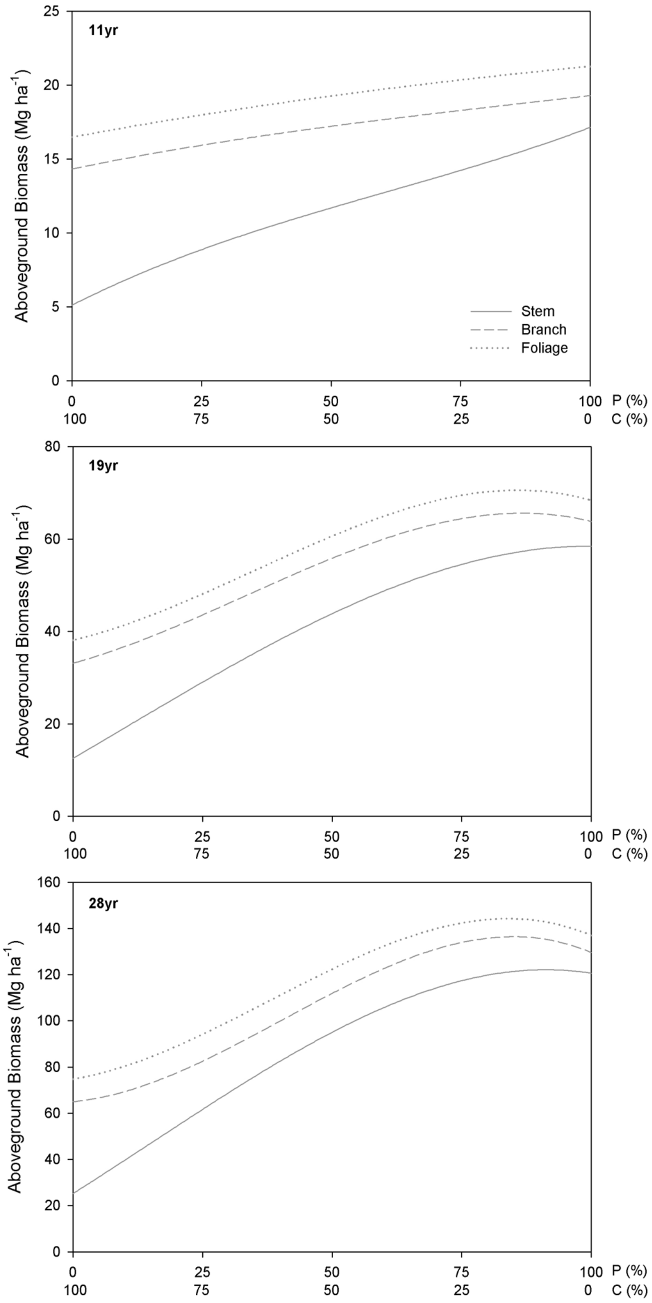

Fig. 7 - Aboveground biomass per hectare and tree component (values of branches and foliage are cumulated to the stem values) for the *C. sativa* (C) and *P. menziesii* (P) species at age 11, 19 and 28, with the total number of individuals constant. The proportion of each species in mixture, per treatment, changes from no individuals (0%) up to the total number of individuals (100%).

of resources in mixture than in pure treatments. Aboveground biomass of *C. sativa* in 50C:50P was less than half of the pure *C. sativa* treatment, and a similar pattern was found for the 25C:75P treatment. The *C. sativa* pure treatment had lower biomass with significant differences ($P < 0.05$) from the other treatments (Fig. 6a, 19yr). The differences in aboveground biomass continued to increase until 2009, at age 28. After this age, the experimental design was unbalanced because of the wildfire occurred in 2003. Nonetheless, the *post-hoc* tests carried out on data collected in 2009 (and 2008) confirmed the results obtained for previous years (1998 and 2000), when the design was complete and fully balanced. The aboveground biomass in mixtures was significantly different from pure *C. sativa* treatments (P < 0.05), but no significant differences from pure *P. menziesii* treatments were found. The 100C:0P treatment still had the lowest aboveground biomass. These results indicated greater aboveground biomass in pure *P. menziesii* and in mixtures than in pure *C. sativa* treatments. Looking only at mixed treatments, the higher value of aboveground biomass was observed in treatments with a higher proportion of deciduous species (Fig. 6a, 28yr).

Analysis of the aboveground biomass per tree component among treatments at age 11 indicated larger stem biomass for *P. menziesii* (17.1 ± 9.4 Mg ha^{-1}) and greater branch and foliage biomass for *C. sativa* pure treatments (9.2 ± 4.6 and 2.2 ± 1.1 Mg ha^{-1}, respectively - Fig. 7, 11yr). Similar results were found for biomass components at age 19 (Fig. 7, 19yr). However at age 28, stem biomass was higher in the 50C:50P treatment (142.3 ± 11.3 Mg ha^{-1}, 80% of the total biomass) in respect to other treatments, and the foliage biomass with 10.5 ± 0.5 Mg ha^{-1} was also higher (Fig. 7, 28yr). Branch biomass was greater in the 100C:0P treatment (39.8 ± 15.9 Mg ha^{-1}, 53% of the total biomass; stem biomass comprised 32% of the total biomass).

ANPP (total and by tree component) was calculated for each treatment for 2008 and 2009 (Tab. 4). Results from the total ANPP analysis indicated higher productivity in mixtures compared with pure treatments, although no significant differences ($P > 0.05$) were found. In respect to pure treatments, *C. sativa* had a higher productivity (7.9 ± 0.0 Mg ha^{-1} yr^{-1}, 18% and 70% of the total ANPP due to the branch and foliage components, respectively) than *P. menziesii*, the latter being the treatment with the lowest ANPP value (7.0 ± 0.8 Mg ha^{-1} yr^{-1}, with 84% of the total ANPP due to the stem component). Finally, significant differences among treatments ($P < 0.05$) were found in branch, stem and foliage components.

Tab. 4 - Aboveground net primary production (Mg ha^{-1} yr^{-1}), total and per tree component at age 28 (percentage of total ANPP in each component in parentheses). Values ± standard error in the same column followed by the same letter are not significantly different ($P > 0.05$).

Treatment	Stem	Branch	Foliage	Total
100C:0P	0.93 ± 0.5 ^{b} (12%)	1.39 ± 0.7 ^{a} (18%)	5.55 ± 1.2 ^{a} (70%)	7.86 ± 0.0 ^{a}
50C:50P	8.93 ± 0.7 ^{a} (61%)	0.95 ± 0.1 ^{ab} (6%)	4.87 ± 0.7 ^{ab} (33%)	14.76 ± 1.6 ^{a}
25C:75P	7.14 ± 1.5 ^{a} (66%)	0.63 ± 0.1 ^{ab} (6%)	3.02 ± 0.4 ^{ab} (28%)	10.78 ± 1.9 ^{a}
0C:100P	5.83 ± 0.7 ^{ab} (84%)	0.31 ± 0.0 ^{b} (4%)	0.84 ± 0.2 ^{b} (12%)	6.98 ± 0.8 ^{a}

Discussion

Growth patterns

Stratified canopies in mixed stands tend to develop naturally because of differences in the auto-ecology of the species involved.

Shade-intolerant species generally have higher rates of juvenile height growth than shade-tolerant species, while shade-tolerant species are able to survive in reduced light environments (Kelty 1992, Oliver & Larson 1996, Smith et al. 1997). Kelty (2006) also stated that the overall growth rate of mixed-species plantations with stratified canopies would be affected by their shade tolerance as well as the density of the upper canopy.

In this study the influence of mixtures on the height of both species was evident all along the analyzed timespan. *P. menziesii* and *C. sativa* differ in their tolerance to shade, and different height growth patterns (along with stratification) were observed for the two species after 11 years of planting. Interspecific competition on mixtures also leads to stratified canopies (Laclau et al. 2008). In this study, *C. sativa* formed the lower canopy stratum in the mixture as a consequence of its lowered height growth. Amoroso & Turnblom (2006) found greater height, diameter and individual tree volume for *P. menziesii* than for *Tsuga heterophylla* (Rag.) Sarg. in 50/50 mixture plantations. Analogously, *P. menziesii* showed a higher total height in this study, making up the upper part of the canopy in the mixtures. Other studies also found greater yield in mixed than in pure stands for most tree components (Kelty 1989, Brown 1992, DeBell et al. 1997, Khanna 1997, Man & Lieffers 1999, Bauhus et al. 2000, Garber & Maguire 2004). This study shows that by age 19 *P. menziesii* has outgrown *C. sativa* by 4 m (on average). Differences in growth between the two species had been increasing over the period of time measured, and are expected to continue in the near future.

The observed difference between *C. sativa* DBH growing in pure and 50C:50P treatments was at most 0.7 cm. Such small difference indicates that *C. sativa* growth was not significantly influenced by the presence of *P. menziesii*. Nevertheless, a higher mean value was observed in the 25C:75P treatment compared with the pure plots, though no significant differences among treatments were observed. Mean DBH of *P. menziesii* amounted to 22.4 cm in the 1:1 proportion, compared to 17.0 cm in the pure treatments (+31%, $P < 0.05$). In contrast, *C. sativa* achieved an average DBH of 12.7 cm in the 1:1 proportion and 13.0 cm in the pure treatments. Pretzsch et al. (2010) observed similar behavior in pure and mixed stands of Norway spruce (*Picea abies* (L.) H. Karst.) and European beech (*Fagus sylvatica* L.) throughout central Europe.

Dominant trees within a stand tend to capture more light and to use it more efficiently for their growth. According to Binkley et al. (2013) faster growth of large trees typically results from a combination of increased light absorption (accounting for about three-fourths of the effect) and increased efficiency of light use (about one-fourth of the effect). Light use and light use efficiency were not analyzed in the present study, although results from Campoe et al. (2013), Gspaltl et al. (2013) and Le Maire at al. (2013) provide new information and understanding about growth rates. Campoe et al. (2013) found in a study with *Eucalyptus grandis* that the faster growth of dominant trees was driven exclusively by a more efficient light use. Contrastingly, Gspaltl et al. (2013) observed that larger trees used more light and use the intercepted light more efficiently for growth in a study on *Picea abies*, while Le Maire et al. (2013) observed a more efficient light use of taller trees in *Acacia mangium* and *Eucalyptus grandis*. Hints of a higher light use efficiency for dominant trees are also strong in these studies. Future works on how light use efficiency accounts for differences in growth among *C. sativa* and *P. menziesii* will contribute for a better understanding of the mechanisms involved in overyielding in mixtures.

Interspecific and intraspecific competition

The more efficient utilization of site resources by different species in mixed stands may result in a greater total productivity in comparison to pure stands, as a consequence of the less intense interspecific than intraspecific competition in mixed stands (Kelty 1992).

In this study, interspecific and intraspecific competition were assessed by comparing tree growth in mixture and in pure treatments for each species (Menalled et al. 1998). After 20 years of planting, *P. menziesii* experienced a substantial increase in DBH, height, and aboveground biomass in mixtures compared to their growth in pure treatments. The analysis of height/diameter ratio (*h/d*) can give an insight on interspecific and intraspecific competition (Kramer 1994). Trees allocate more carbon to height than to diameter growth to participate in the canopy (Bauhus et al. 2000). The slightly lower *h/d* that *P. menziesii* trees exhibited in mixtures compared to monoculture is consistent with the results by Wang et al. (2000), who reported that shade-intolerant species growing in mixed stands allocated more carbon to stem wood. *C. sativa*, instead, presented higher (though not significant) *h/d* ratios in mixtures compared to the pure treatments. This result suggests that interspecific competition is greater than intraspecific competition in the mixed stands studied, in that *C. sativa* needed to allocate relatively more resources to height growth to participate in the canopy, while *P. menziesii* reach the canopy earlier and could therefore allocate more resources to its radial growth. However, our results confirmed that the development of mixed-species plantations is highly influenced by the relative growth rate of each species (Forrester et al. 2005). When *P. menziesii* was surrounded by a larger proportion of *C. sativa, P. menziesii* height and stem diameter was increased. Furthermore, interspecific competition between species influenced mainly the height and less the DBH in *C. sativa*, while for *P. menziesii* both height and DBH growth were affected.

The high productive potential of *P. menziesii* in the mountains areas of northern Portugal has been recognized (Louro & Cabrita 1989, Luís 1989). Indeed, the good performances of this species in the study area may be explained by several environmental factors of the study site (Fontes et al. 2003). However, Maia et al. (1990) demonstrated that *P. menziesii* in Portugal performed better in terms of height growth than several other species, like *Pinus pinaster* Aiton, *C. sativa, P. nigra* var. *maritima* (Ait.) Melv., *Cedrus atlantica* (Endl.) Carr. and *P. sylvestris* L.

The small number of mixed-species plantations worldwide make difficult to identify the general patterns for tree interspecific interactions (Rothe & Binkley 2001, Forrester et al. 2006b), and to predict their effect all along the stand development (Forrester et al. 2004). Nonetheless, evaluation of interaction and competition between neighboring trees in this study is still being done.

Overall productivity: pure vs. mixed stands

The productivity between pure and mixed treatments was compared both on a relative (relative yield, *sensu* Harper 1977) and absolute basis (aboveground biomass per ha). In mixture 1:1, the *RYT* was higher than 1.0 for all the studied years. Since age 11, the relative yield for *P. menziesii* was as expected (0.5) or higher than expected; instead, it was lower than expectations for *C. sativa*. In the mixture 1:3, a combined *RYT* value higher than 1.0 was also found, except at age 7. This could imply a nursing effect by the species in mixtures. Bauhus et al. (2000) observed similar *RY* in a mixed plantation.

Aboveground biomass per ha had similar yield in pure and mixed treatments in the first years after plantation. As the years passed, an increase in aboveground biomass was observed in mixtures (in comparison to pure plots) as a result of the enhanced biomass of *P. menziesii*, probably due to an increase in light interception (Amoroso & Turnblom 2006). In contrast, the yield of *C. sativa* was lower compared with the results in pure treatments. This may indicate a positive interaction and a complementary benefit between *C. sativa* and *P. menziesii* when growing together (Forrester et al. 2004). According to Kelty (2006), the competition intensity depends on the ability of mixtures to better exploit site resources for biomass production compared to pure treatments. Canopy stratification of both species (Forrester et al. 2004) can also partially explain these results, as well as a better use of the site resources (Amoroso & Turnblom 2006). The multilayer structure with light gaps enables subdominant and understory *C. sativa* trees to survive in the plantation. Amoroso & Turnblom (2006) observed similar results with an increase in productivity in mixtures with high densities. Species interactions involve a complex balance of competition and facilitation (Kelty 1992, Callaway & Walker 1997, Pretzsch et al. 2010). Competition and facilitation are frequently coupled, making them difficult to distinguish experimentally (Callaway & Walker 1997).

Higher productivity in mixtures indicates a facilitation of *P. menziesii* by *C. sativa*, since the productivity of the former in mixtures exceeds the productivity in pure treatments. ANPP variations in pure *C. sativa* treatments where consistent with the results from Zianis & Mencuccini (2005), although the stem wood production value was lower than the one observed by the above authors. Stem wood production depends not only on total net production but also on its allocation (Zianis & Mencuccini 2005), and stem has a longer residence time of cumulative biomass than both branches and foliage. On average, in pure *C. sativa* treatment, 88% of ANPP was allocated to crown (branch and foliage), whereas in pure *P. menziesii* and mixed treatments the allocation was about 16% and up to 33%, respectively. Binkley et al. (2013) reported that stands with low basal area typically have less stem wood than stands with moderate or high basal areas, largely owing to smaller canopies and lower absorption of light. In this study, low basal area was found for the *C. sativa* pure treatment, where the stem component represents only 12% of the ANPP. The mixtures had higher (though not significant) average productivity values than the pure treatments. Considering that *P. menziesii* is a fast growing species providing revenues in the short term, and *C. sativa* a more valuable species with slower growth and revenues in the long term, it will be important to monitor species growth and evaluate their productivity to the final rotation.

Conclusion

C. sativa and *P. menziesii* growth and productivity were assessed in mixtures and pure treatments within the same planting site, under shared soil and climatic conditions. Overall, mixtures reached higher yield than pure treatments. Moreover, positive interactions in mixtures have been found between *C. sativa* and *P. menziesii* in terms of aboveground productivity, leading to higher ANPP compared with pure treatments. Canopy stratification seems the major underlying mechanism (*C. sativa* in the lower and *P. menziesii* in the upper canopy stratum), with an increase in the light capture in mixtures. The results of this study improved our knowledge of the growth dynamics of these species in northern Portugal.

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