



Soil carbon stocks and exchangeable cations in monospecific and mixed pine forests

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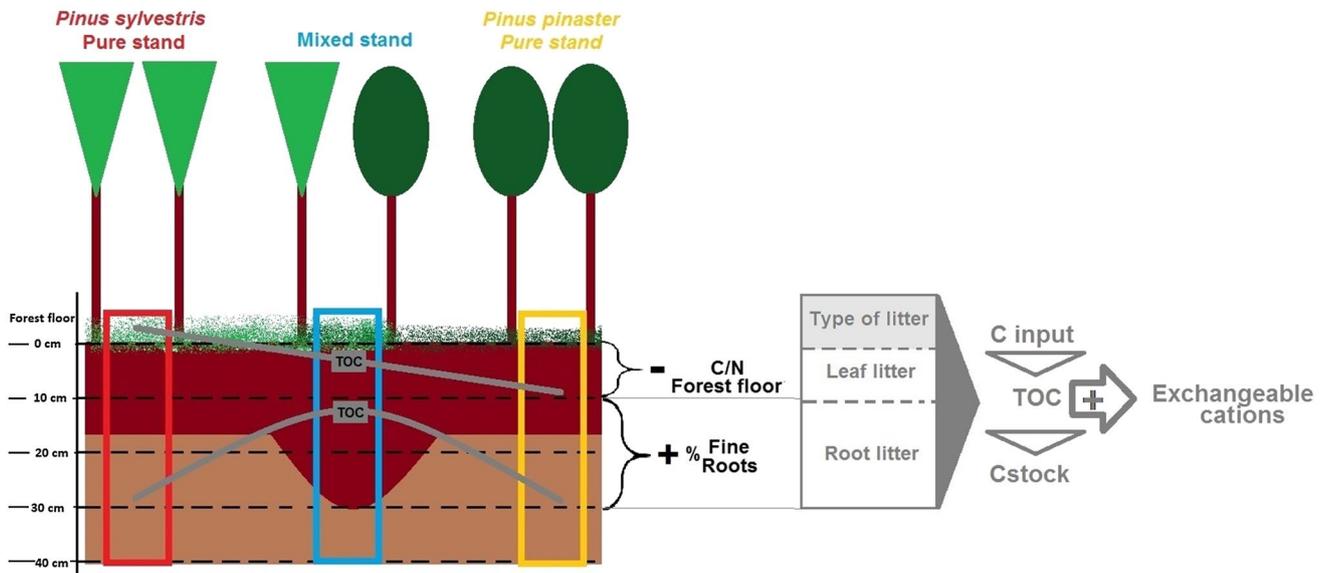
Abstract

Many studies highlight the role of mixed versus monospecific forests to supply numerous ecosystem services. Most reports of positive mixture effects on carbon storage focus on mixtures that combine tree species with contrasting traits, but little is known on the effect of mixing species that are expected to behave quite similarly as they belong to the same genus. In this study, we assessed the effect of mixed versus monospecific stands of *Pinus sylvestris* and *P. pinaster* on carbon storage and exchangeable cations along the soil profile, based on research with six triplets in the northern Iberian Peninsula (Spain). One soil pit of at least 40 cm depth was dug at each plot for organic and mineral horizons characterization. Two trends were found: in the topsoil, higher values of carbon stock and total organic carbon were found in *P. sylvestris* stands, lower in *P. pinaster* stands and intermediate in mixed stands; this pattern was related to the C/N ratio of the forest floor. In the intermediate soil layers, it tends to be higher in mixed stands and is related to percentage of fine roots and to the greater thickness of the first mineral horizon. Differences in soil exchangeable cations among stands were related to the total organic carbon content. These results improve our understanding of the mechanisms underlying soil carbon accumulation in mixed stands and emphasize the use of mixtures as a strategy to combat climate change, due to the advantage in the accumulation of carbon in the subsoil layers.

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Graphical Abstract



Keywords *Pinus sylvestris* L. · *Pinus pinaster* Ait. · Soil profile · C stock · Exchangeable cations

Introduction

Over the last decades, the management of mixed-species forests has taken on greater relevance as a result of the growing evidence that they can supply numerous ecological, economic and socio-cultural goods and services more efficiently than monospecific forests (Gamfeldt et al. 2013). Taking into account that 23% of the land is covered by mixed forests in the pan-European region (FAO 2011), mixed forests management is becoming a new paradigm (Bravo-Oviedo et al. 2014) in order to increase the provision of many high-value goods and ecosystem services (Stenger et al. 2009), including biodiversity conservation or carbon sequestration (European Commission 2010).

Forests play an important role in the global carbon cycle and in the Earth's terrestrial carbon sink (Andivia et al. 2016). Forest ecosystems contain approximately 1725 Pg of carbon and about two-thirds are contained in the forest soil (Pan et al. 2011). However, there is still great uncertainty regarding best management strategies to promote soil organic carbon sequestration (Andivia et al. 2016), including the mixture of different species of trees (Jandl et al. 2007).

Carbon accumulation mechanisms may vary depending on the dominant species (Augusto et al. 2015) and the different layers of the soil (Vesterdal et al. 2013) since the aboveground litter and the root litter are the responsible for soil C input (Rasse et al. 2005). Therefore, the mixture of tree species can affect both the accumulation and the distribution of the carbon along the soil profile (Chapin 2003).

Although a general understanding of the effect of tree species across site types have not yet been reached (Jandl et al. 2007), many authors suggest that the impact on the forest floor or mineral soil depends on the identity of the species, species richness, and kind of mixture (Ruiz-Peinado et al. 2017). In fact, Dawud et al. (2016) revealed that forests with greater diversity had higher soil carbon stocks in deeper layers. However, most reports of positive mixture effects on C storage focus on mixtures that combine species with contrasting traits, such as the mixing of European beech and Norway spruce (Andivia et al. 2016), the mixing of European beech, Douglas fir and Norway spruce (Cremer et al. 2016), or even in plantations of mixed stand vs monocultures in a chronosequence of *Pinus massoniana*–*Cinnamomum camphora* (Liu et al. 2017).

The effect of mixing for species that are expected to behave quite similarly as they belong to the same genus is still unknown, despite being frequent in many environments, such as the admixtures of Scots pine (*Pinus sylvestris* L.) and Maritime pine (*Pinus pinaster* Aiton) in Spain. Both *Pinus* species show similar crown architecture and slight differences in shade tolerance (Riofrío et al. 2017), but clearly differ in leaf traits (e.g. more recalcitrant leaf litter for *P. pinaster*; Herrero et al. 2016; longer *P. pinaster* needles; Amaral Franco 1986), whereas the information on root distribution is not clear, since rooting depth may vary depending on the moisture conditions (Bakker et al. 2006). Maritime pine is an important species of Mediterranean forests and Scots pine is the most widely distributed species of pine in the world

(Bogino and Bravo 2014). They are two of the main forest species in Spain (Scots pine: 1.20 million ha; Maritime pine: 0.68 million ha) and grow in monospecific and mixed stands, either naturally or as a result of species selection for afforestation (Serrada et al. 2008). In addition to their wide distribution and forest area, they hold great ecological and socio-economic value (Riofrío et al. 2016). Mixed stands where these two species coexist are particularly interesting because of their location at the rear-edges for *P. sylvestris* forests, where ecological conditions (high temperatures, frequent droughts) approach the species tolerance limit and the most drastic effects of climate change are predicted (Matías and Jump 2012).

Forest management in general and tree species selection, in particular, have various impacts on soil biological, physical and chemical processes and characteristics (Jandl et al. 2007; Cremer and Prietzel 2017). With regard to the soil chemical properties, soil exchangeable cation concentrations may be affected by tree species composition (Cremer and Prietzel 2017). Different tree species growing under similar

conditions, such as climate, soil type, and land use history differ substantially from each other with respect to foliage nutrient content, root and litter chemistry, all of them having a large impact on soil nutrient input, output, and cycling (Augusto et al. 2015; Cremer and Prietzel 2017). Also, the soil nutrient input could be an indirect consequence of the organic matter contributions to soil (Cremer and Prietzel 2017), since the decomposition of plant tissues in terrestrial ecosystems regulates the transfer of carbon and nutrients to the soil (Wang et al. 2014).

Differences in the concentration of cations in the soil may depend on differences between tree species in biomass accumulation rates and/or biomass cation concentrations (Brandtberg et al. 2000). The amount and composition of litter produced also vary between species, and these two factors can, in turn, influence the rate of accumulation of organic matter and properties of the forest floor (Brandtberg et al. 2000). Whether species differ in the depth at which nutrient uptake is concentrated and/or in the rate of

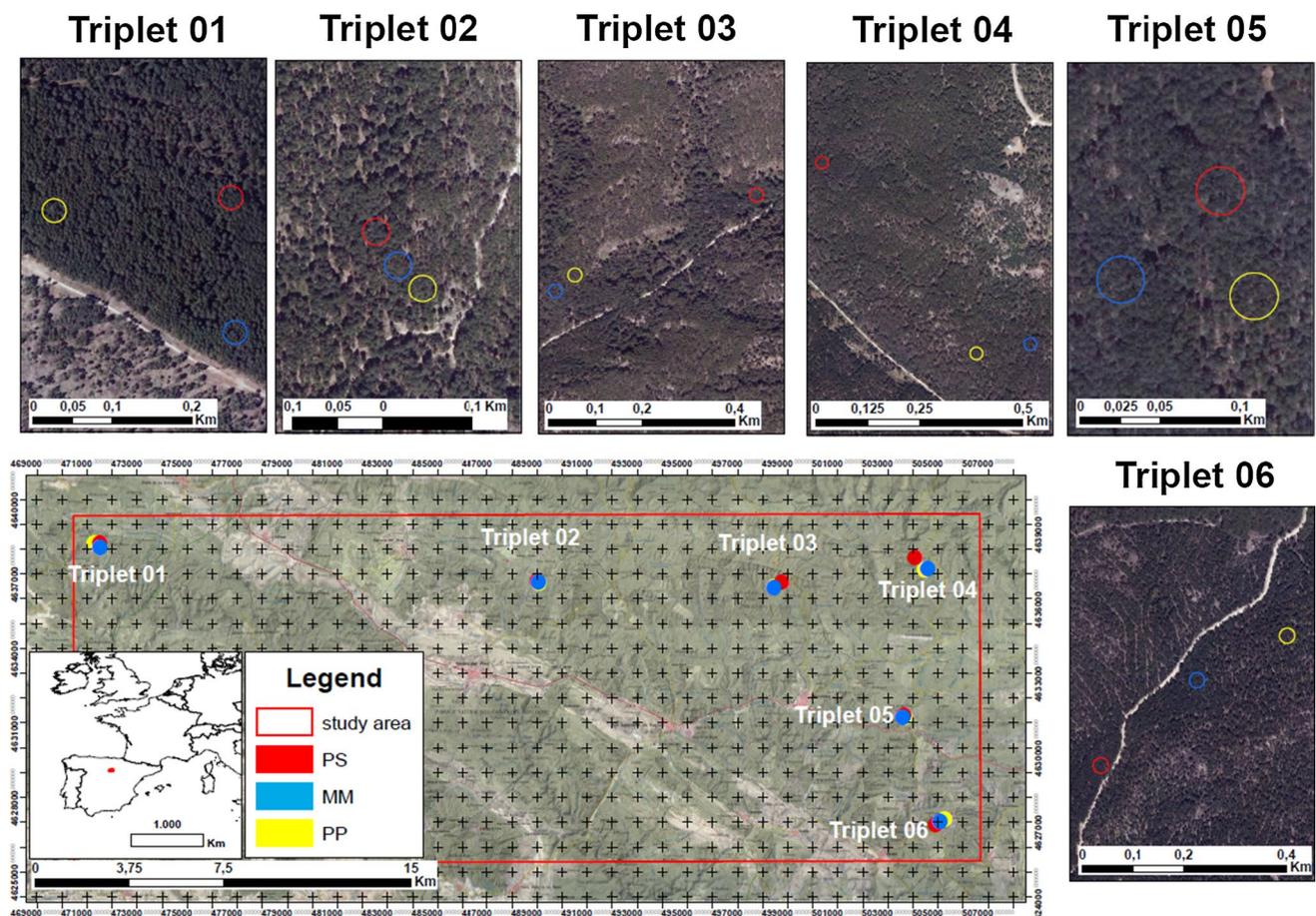


Fig. 1 Location of the triplets in the ‘Sierra de la Demanda’ in the North-Central Spain and location of the plots in each triplet. *P. sylvestris* monospecific stands (PS): red circles; *P. pinaster* monospecific

stand (PP): yellow circles; Mixed stand of *P. sylvestris* and *P. pinaster* (MM): blue circles. (Color figure online)

biocycling, the result may appear in subsoil mineral horizons (Brandtberg et al. 2000).

The forest management practices must be used as a mitigation tool as regards the carbon sequestration because the type of tree species affects forest growth, carbon and nutrient cycling (Augusto et al. 2015). That is why we investigated the impact of the mixture of tree species of the same genus with a wide distribution in Spain (*P. sylvestris* and *P. pinaster*) on C storage along the soil profile in comparison with monospecific stands. We hypothesize that: (1) the stand type influences the C storage and, indirectly, the exchangeable base cations of the mineral soil by the organic matter decomposition effect; (2) differences in the topsoil among stand types are expected to be found; and (3) the admixture of both pine species might have a positive interactive effect on the accumulation of carbon in the soil profile in comparison with monospecific stands. Therefore, the aims of this study were: (1) to quantify the differences among stand types in C storage, including both total accumulation in soil and distribution in the soil profile; (2) to investigate the possible causes of the observed differences; and (3) to explore how the difference in C accumulation might affect the exchangeable cation concentrations.

Materials and methods

Study sites

The research was carried out in eighteen forest plots (6 triplets) located in the ‘Sierra de la Demanda’ between the Burgos and Soria regions, in North-Central Spain (41°47′35″N and 41°53′41″N latitude and 2°56′12″W and 3°20′46″W longitude; Fig. 1). The climate is Temperate Type Cfb and Csb, i.e. temperate with dry or temperate summer and atlantic, respectively, according to the Köppen classification (1936) for the Iberian Peninsula. The mean annual temperature ranges between 8.7 and 9.8 °C and the annual precipitation ranges between 684 and 833 mm (Nafría-García et al. 2013). Altitude varies from 1093 to 1277 m a.s.l., and the slope from 0.9 to 20%. The geological parent materials are sandstones and marl of Mesozoic age (IGME 2015). The soils are Inceptisols with a xeric soil moisture regime and mesic soil temperature regime and they are classified as Typic Dystrochrept or Typic Humixerept (sensu Soil-Survey-Staff 2014). The sandy soil texture was dominant and the pH varies from extremely acid to strongly acid (“Appendix 1”). The natural dominant vegetation in the study area, highly degraded by anthropogenic action, is characterized by Pyrenean oak forests or communities dominated by junipers.

Each triplet consisted of two plots dominated either by *P. sylvestris* (PS) or *P. pinaster* (PP) and one plot with a mixture of both species (MM) located less than 1 km from each

other. Plots were circular of radius 15 m and the tree species composition was the main varying factor. The percentage of the basal area of the dominant species in the monospecific plots was greater than 83% or 95% for *P. sylvestris* or *P. pinaster*, respectively, whereas the basal area percentage of both species in the mixed plots ranged from 33 to 67%. Historically, the area has been occupied by forests and it has been traditionally managed for decades through selective thinning, being *P. sylvestris* benefited. The stands had no silvicultural intervention or damage in the last 10 years. The age of the selected plots ranged between 44 and 151 years, the stand density between 509 and 1429 trees/ha, the basal area between 33.3 and 70.30 m²/ha and the dominant height between 15.60 and 25.04 m (“Appendix 2”). These plots belong to the network of permanent plots of iuFOR-UVa.

Soil sampling

One soil pit of at least 40 cm depth was dug at each plot (eighteen in total) for organic and mineral soil horizons characterization and sampling (“Appendix 3”). A 25 × 25 cm quadrant placed at the top of the pit was used to collect the forest floor or organic horizon. Coarse woody materials, such as large branches, were carefully removed from the forest floor before sampling (Andivia et al. 2016). The forest floor (FF) was separated into three fractions according to van Delft et al. (2006): almost undecomposed litter or fresh fraction (FsL), partially decomposed litter or fragmented fraction (FgL) and mostly decomposed organic matter or humified fraction (HmL).

Two undisturbed soil samples were collected from each mineral horizon of each pit with steel cylinders (98.18 cm³) to keep their original structure (“Appendix 3”). One disturbed sample was also taken from each mineral horizon of each pit (ca. 2.5 kg). The percentages of fine (%FR) and coarse (%CR) roots were estimated visually in each horizon at the time of digging the soil pit, i.e. many, normal, few, very few or no roots coverage in the cross section of the soil profile classified as 80%, 50%, 30%, 10% and 0%, respectively. The roots with a diameter below 5 mm were considered fine roots and those with a diameter above 5 mm as coarse roots.

Laboratory analyses

The three fractions of leaf litter were dried separately at 60 °C during 48 h and weighed (± 0.01 g) to determine the amount of biomass of each litter fraction per hectare (B_{FsL} , B_{FgL} , B_{HmL}). A representative portion of each sample was ground up and analysed with a LECO-CHN 2000 elemental analyser to determine total organic carbon and total nitrogen concentrations (TOC and N, respectively).

Both undisturbed and disturbed mineral soil samples were dried at 105 °C during 24 h before analyses. Undisturbed mineral soil samples were weighed (± 0.001 g) and used to calculate the soil bulk density (bD). Disturbed mineral soil samples were sieved (2 mm) before physical and chemical analyses. Physical analyses included percentage by weight of coarse fraction (> 2 mm; stones) and earth fraction (< 2 mm; EF), particle distribution determined by the pipette method (MAPA 1994) and subsequent determination of clay (%clay), sand (%sand) and silt (%silt) contents, and classification according to USDA criteria.

Chemical parameters analysed for each mineral horizon included: exchangeable cations (Ca^{+2} , Mg^{+2} , K^{+} , Na^{+}) were extracted with 1 N ammonium acetate at pH=7 (Schollenberger and Simon 1945) and determined using an atomic absorption/emission spectrometer; TOC was quantified by dry combustion using a Leco CHN 2000 elemental analyser.

Data analyses

The percentage of *P. pinaster* basal area (% PP) was calculated as the ratio between the basal area of *P. pinaster* and the total basal area of each plot. Total FF biomass (B_{FF}) was calculated as the sum of B_{FsL} , B_{FgL} and B_{HmL} . C stocks of FsL, FgL and HmL litter fractions were calculated by multiplying TOC concentration by the biomass of each fraction (Andivia et al. 2016) to obtain C stock_{FsL}, C stock_{FgL}, C stock_{HmL}, respectively. C stock of the FF (C stock_{FF}) was the sum of C stock_{FsL}, C stock_{FgL} and C stock_{HmL}. The C/N ratio was calculated for the fresh (CN_{FgL}), fragmented (CN_{FgL}), and humified litter (CN_{HmL}). C/N of the FF was calculated as the weighted average of C/N of three decomposition fractions.

$$\text{CN}_{\text{FF}} = \left[\left(\frac{B_{\text{FsL}}}{B_{\text{FF}}} \right) \text{CN}_{\text{FsL}} \right] + \left[\left(\frac{B_{\text{FgL}}}{B_{\text{FF}}} \right) \text{CN}_{\text{FgL}} \right] + \left[\left(\frac{B_{\text{HmL}}}{B_{\text{FF}}} \right) \text{CN}_{\text{HmL}} \right]$$

C stock in the mineral soil (C stock_{SOIL}) was calculated as: C stock_{SOIL} = TOCi · bDi · %EFi Ti, being TOCi the total organic

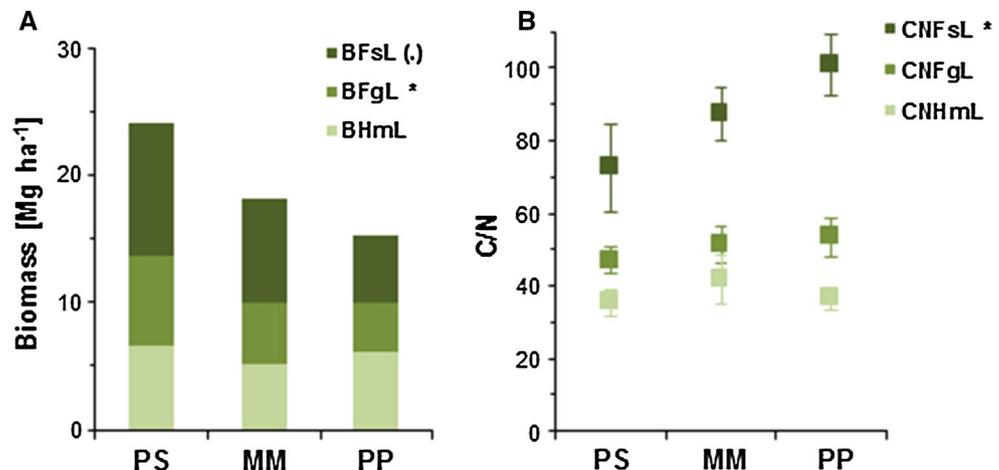
carbon concentration, bDi the measured bulk density, %EFi the percentage of earth fraction and Ti the thickness of the soil horizon. The C stock in the whole mineral soil profile (C stock_{0–40cm}) was calculated as the sum of the C stock of all soil horizons. The sum of bases (SB) was the sum of the Ca^{+2} , Mg^{+2} , K^{+} and Na^{+} concentrations ($\text{cmol}^{+} \text{kg}^{-1}$).

The mineral soil horizon data were converted into four different depths (every 10 cm) calculating weighted averages between the horizons. Some variables were transformed ($\ln x$ or $1/x$) before statistical analysis to achieve residual normality and homoscedasticity.

While soil texture is not expected to be affected by stand species composition, it may have a large impact on C sequestration in the mineral soil (Jandl et al. 2007). In order to remove the effect of the soil texture variability within a triplet, texture variables (sand, silt, clay) were therefore tested as additional fixed effects in the alternative models; based on AIC values, only the sand content was included in the final model.

The possible effects of the type of stand on the C stock_{FF} (C stock_{FF}, C stock_{FsL}, C stock_{FgL} and C stock_{HmL}) as well as on TOC, C stock_{SOIL}, exchangeable cations (Na^{+} , K^{+} , Ca^{+2} , Mg^{+2}), and SB in different mineral soil layers were analysed using Linear Mixed Models (LMM) with the restricted maximum likelihood method (REML; Richards 2005). The type of stand was considered as a categorical variable with three levels: PS, PP and MM. In all cases, a null model considering the random effect of triplet was tested with the alternative model that included the fixed effects of the type of stand plus the soil sand content (%sand). The Akaike information criterion (AIC; Akaike 1973) was used to verify whether the alternative model was more parsimonious, i.e. smaller values of AIC, and the ANOVA was applied to test the significant differences between the null and the alternative models (see “Appendix 4”). One monodominant plot of *P. sylvestris* was considered an outlier and excluded from all analyses because it was the only one that presented aquatic conditions (Soil-Survey-Staff 2014; see triplet 03 in Table 2, “Appendix 1”).

Fig. 2 a Biomass (B, mean value, Mg ha^{-1}) and b C/N ratio (CN, mean \pm SE) of the different fractions of leaf litter (FsL, FgL, HmL: fresh, fragmented and humified, respectively) according to the type of stand. PS ($n=5$): *P. sylvestris* monodominant stands; PP ($n=6$): *P. pinaster* monodominant stand. MM ($n=6$): mixed stands of both species. Signification level: * $p < 0.05$; (•) $p < 0.1$



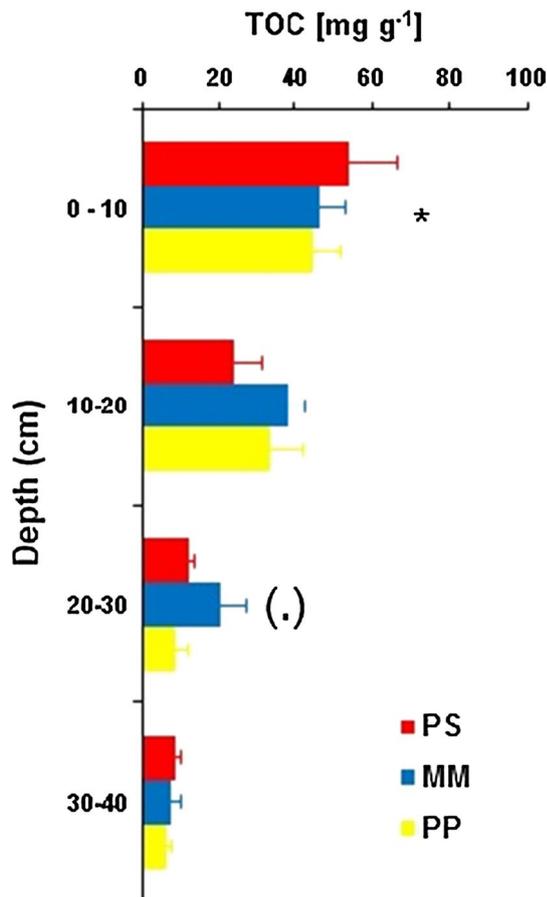


Fig. 3 Mean \pm SE of total organic carbon (TOC mgC g⁻¹) at four different depths of the mineral soil profile according to the type of stand. Other abbreviations as in Fig. 2. Signification level: * $p < 0.05$; (•) $p < 0.1$

Finally, linear correlations between some variables of interest were investigated, using the Pearson's coefficient ($p < 0.05$). In order to test the influence of the type of stand on the nature of the leaf litter and to verify whether the TOC comes from the leaf litter and/or the roots decomposition at different mineral soil layers. Also the relationships between TOC and either the exchangeable cations or SB were tested. All statistical analyses were implemented in the R environment (version 3.3.3, R-Core-Team 2015) using LME4 package for LMM (Bates et al. 2015).

Results

Forest floor quantity and quality

The biomass of the fresh (B_{FsL}) and fragmented (B_{FgL}) leaf litter showed the same trend ($p < 0.05$ for B_{FgL} ; $p < 0.10$ for B_{FsL}) when comparing among stand types (Fig. 2a), being higher in PS, lower in PP and intermediate in MM;

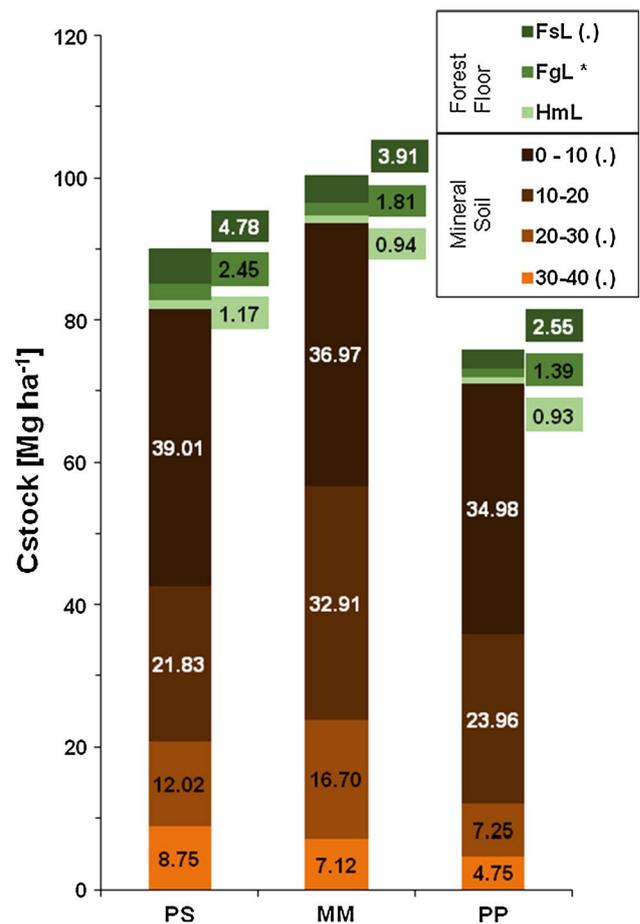


Fig. 4 Carbon stock (C stock, mean value, Mg ha⁻¹) in the forest floor (green tones) for the organic layers (FsL, FgL, HmL: fresh, fragmented and humidified litter, respectively), and in the mineral soil profile (brown tones) at four different depths according to the type of stand. Signification level: * $p < 0.05$; (•) $p < 0.1$

no significant trend was found for B_{HmL} . An opposite significant trend ($p < 0.05$) was found for the C/N ratio of the fresh litter (CN_{FsL}), being higher in PP, lower in PS and intermediate in MM; no clear trend was observed for CN_{FgL} and CN_{HmL} (Fig. 2b). In addition, %PP was positively correlated with CN_{FsL} ($r = 0.64$, $p < 0.005$) and negatively with B_{FsL} ($r = -0.45$; $p < 0.05$), B_{FgL} ($r = -0.54$; $p < 0.025$) and B_{FF} ($r = -0.46$; $p < 0.05$).

TOC in the mineral soil

The total organic carbon concentration (TOC) decreased according to the depth in the three types of stand, as expected (Fig. 3). It differed significantly ($p < 0.05$) among stands in the topsoil (0–10 cm), and almost significantly at the third depth (20–30 cm, $p < 0.10$). In the same way as for the C stockSOIL, two different trends were found for TOC: TOC_{0–10cm} was higher in PS, lower in PP and intermediate

Table 1 Mean \pm SE of exchangeable cations concentration and sum of bases (cmolc kg⁻¹) at four different depths of the mineral soil profile according to the type of stand

	Depth (cm)	PS	MM	PP	<i>p</i>
Na ⁺	0–10	0.86 \pm 0.04	0.87 \pm 0.03	0.80 \pm 0.03	*
	10–20	0.84 \pm 0.03	0.87 \pm 0.02	0.80 \pm 0.02	*
	20–30	0.82 \pm 0.04	0.85 \pm 0.03	0.81 \pm 0.04	
	30–40	0.80 \pm 0.05	0.87 \pm 0.04	0.85 \pm 0.06	*
K ⁺	0–10	0.24 \pm 0.05	0.21 \pm 0.02	0.16 \pm 0.03	*
	10–20	0.18 \pm 0.06	0.20 \pm 0.02	0.14 \pm 0.02	*
	20–30	0.19 \pm 0.07	0.15 \pm 0.04	0.13 \pm 0.04	(•)
	30–40	0.19 \pm 0.07	0.12 \pm 0.03	0.14 \pm 0.04	*
Ca ⁺²	0–10	4.03 \pm 0.63	3.35 \pm 0.48	3.06 \pm 0.49	*
	10–20	2.29 \pm 0.12	2.95 \pm 0.51	2.62 \pm 0.53	
	20–30	1.70 \pm 0.28	2.25 \pm 0.65	1.45 \pm 0.46	(•)
	30–40	1.47 \pm 0.22	1.50 \pm 0.38	1.65 \pm 0.68	*
Mg ⁺²	0–10	0.83 \pm 0.16	0.80 \pm 0.12	0.79 \pm 0.13	*
	10–20	0.56 \pm 0.04	0.74 \pm 0.13	0.70 \pm 0.13	*
	20–30	0.49 \pm 0.07	0.62 \pm 0.15	0.47 \pm 0.12	*
	30–40	0.53 \pm 0.10	0.52 \pm 0.13	0.55 \pm 0.21	*
SB	0–10	6.00 \pm 0.84	5.22 \pm 0.62	4.81 \pm 0.66	*
	10–20	3.87 \pm 0.17	4.76 \pm 0.66	4.29 \pm 0.69	
	20–30	3.20 \pm 0.34	3.87 \pm 0.84	2.86 \pm 0.59	(•)
	30–40	2.99 \pm 0.30	3.00 \pm 0.56	3.18 \pm 0.96	*

Other abbreviations as in Fig. 2

Signification level: * $p < 0.05$; (•) $p < 0.1$

in MM, while TOC_{20–30cm} was higher in MM. This latter tendency, yet not significant, was also found at the second depth (10–20 cm). In addition, TOC_{0–10cm} was negatively correlated with CN_{FF} ($r = -0.46$; $p < 0.05$), and TOC at intermediate depths (10–20 cm and 20–30 cm) was positively correlated with %FR (TOC_{10–20cm}: $r = 0.66$, $p < 0.005$; TOC_{20–30cm}: $r = 0.76$, $p < 0.005$).

C stock in the soil profile

The carbon stock in the forest floor (C stock_{FF}) differed almost significantly among stands ($p < 0.1$), being higher in PS (8.41 \pm 1.43 Mg TOC ha⁻¹), lower in PP (4.87 \pm 0.89 Mg TOC ha⁻¹) and intermediate in MM (6.67 \pm 1.09 Mg TOC ha⁻¹). The same pattern was observed for the three fractions of the litter (Fig. 4), being statistically significant only for the fragmented litter (C stock_{FGL}, $p < 0.05$) and almost significant for the fresh one (C stock_{FSL}, $p < 0.10$).

The carbon stock in the mineral soil (C stock_{SOIL}) decreased with depth in the three types of stand, as expected (Fig. 4), but the differences among stands were only almost significant ($p < 0.10$) at 0–10 cm, 20–30 cm, and 30–40 cm. Two different trends were found: C stock_{0–10cm} and C stock_{30–40cm} were higher in PS, lower in PP and intermediate

in MM; by contrast, C stock_{10–30cm} was the highest in MM. C stock_{0–40cm} was also higher in MM (93.70 \pm 13.63 Mg TOC ha⁻¹), lower in PP (70.94 \pm 10.20 Mg TOC ha⁻¹) and intermediate in PS (81.62 \pm 11.37 Mg TOC ha⁻¹), but these differences were not statistically significant ($p = 0.18$).

Sum of bases and exchangeable cations in the mineral soil

The same two trends found for TOC and C stock in the mineral soil were observed for the exchangeable cations and the sum of bases (Table 1). In the topsoil (0–10 cm), exchangeable cations (K⁺, Ca⁺², Mg⁺²) and the sum of bases (SB) differ significantly ($p < 0.05$) among stands, being higher in PS, lower in PP and intermediate in MM (Table 1). In addition, K⁺ ($r = 0.61$, $p < 0.005$), Ca⁺² ($r = 0.74$, $p < 0.005$), Mg⁺² ($r = 0.57$, $p < 0.01$) and SB ($r = 0.71$, $p < 0.005$) correlated positively with TOC at this depth. However, in the 10–20 cm soil layer, K⁺ and Mg⁺² reached significantly higher values in MM ($p < 0.05$), and a similar trend but not significant ($p > 0.10$) was found for Ca⁺² and SB. Again, K⁺ ($r = 0.53$, $p < 0.025$), Ca⁺² ($r = 0.73$, $p < 0.005$), Mg⁺² ($r = 0.56$, $p < 0.01$) and SB ($r = 0.70$, $p < 0.005$) correlated positively with TOC at this depth. The same pattern was observed at the third soil depth (20–30 cm), where MM showed significantly higher values for Mg⁺² ($p < 0.05$) and almost significantly ($p < 0.1$) for Ca⁺² and SB. At this depth, only Ca⁺² ($r = 0.91$, $p < 0.005$), Mg⁺² ($r = 0.81$, $p < 0.005$) and SB ($r = 0.90$, $p < 0.005$) correlated positively with TOC.

In the deepest soil layer (30–40 cm), a different pattern was observed: Ca⁺², Mg⁺² and SB were significantly ($p < 0.05$) higher in PP, whereas K⁺ was significantly higher ($p < 0.10$) in PS. Only K⁺ correlated positively with TOC at this depth ($r = 0.53$; $p < 0.025$). Na⁺ showed significantly higher values in MM ($p < 0.05$) at 0–10 cm, 10–20 cm and 30–40 cm, and did not correlate with TOC at any depth.

Discussion

Our results show, that when comparing monospecific and mixed pine forests in central Spain, the carbon stocks and exchangeable cations in the first 30 cm of the mineral soil profile respond in a similar way to the influence of the type of stand within the same soil layer, although patterns differ considerably when comparing between layers. At the topsoil (0–10 cm), C stock and cations reach higher values in PS, lower in PP and intermediate in MM, whereas at the subsoil layers (10–30 cm), it reaches higher values in MM than in monospecific stands.

These different trends could be a consequence of the different mechanisms of soil carbon accumulation caused by the type of litter deposited in each soil layer. In our study,

the % PP was positively correlated with CN_{FL} while CN_{FF} and the topsoil TOC were negatively correlated, while subsoil layers TOC are positively correlated to %FR. In the same way, TOC and exchangeable cations were positively correlated in all soil layer, so it seems the organic matter could be the responsible of the exchangeable cations values. The higher exchangeable cations at the MM subsoil layers could be related to the higher productivity described by other authors in the same study area. In addition, the higher C stock soil confers to the mixed stands a competitive advantage if the forestry goal encourages the climate change mitigation potential of the forests.

Carbon accumulation as a function of stand type

Our results showed that the response of TOC and C stock to tree species composition in the 0–30-cm layer depends on the soil layer, with higher C stocks under PS in the 0–10 cm and greater C accumulation under MM in the 10–30 cm. Below 30 cm, there was only limited evidence of any tree species effect.

We postulate that the different trends between the 0–10- and 10–30-cm layers are mainly related to the type of litter input since the decomposition of plant tissues in terrestrial ecosystems regulates the transfer of carbon and nutrients to the soil (Wang et al. 2014). C inputs to forest soils are related to leaf litter type (Berg 2000; Andivia et al. 2016) and roots (Rasse et al. 2005; Andivia et al. 2016). Possibly, the decomposition of the organic matter of the leaf litter brings the greater content of carbon to the topsoil (0–10 cm), whereas in deeper layers the greatest contribution comes from the roots (Andivia et al. 2016).

Regarding the upper mineral soil layer, we found a significant negative correlation between CN_{FF} and TOC_{0-10cm} . Our results indicate that the monospecific stands of *Pinus pinaster* accumulate less leaf litter (%PP and B_{FF} correlate negatively) than those of *P. sylvestris*. In addition, the *P. pinaster* leaf litter appears to be more recalcitrant than that of *P. sylvestris* since it has a significantly higher C/N ratio in the fresh fraction as also found by Herrero et al. (2016). In fact, CN_{FSL} and %PP correlate positively. Augusto et al. (2015) found that the species with more sclerophyllous foliage have higher lignin content and higher C/N ratio. The presence of more chemically recalcitrant compounds such as lignin could explain the lower decomposition rate of litter (Wang et al. 2016), and in turn the lower C input into the soil as humic substances. As a result, at the topsoil (0–10 cm) the TOC and C stock were higher in PS, lower in PP and intermediate in MM. Gallardo et al. (1991) also found lower carbon content in the first soil horizon in *P. pinaster* stands in relation to *P. sylvestris* stands.

At intermediate depths (10–30 cm), we found a significant positive correlation between TOC and %FR, suggesting

that at deeper soil layers the greatest C input to the soil mainly comes from the decomposition of the organic matter from the fine roots, as found by other authors (Andivia et al. 2016). According to this, the higher TOC and $Cstock_{SOIL}$ values in MM at intermediate depths (10–30 cm) could be related to a higher %FR that, in turn, correlates positively with the richness of the understory vegetation (unpublished data). The higher richness of the understory vegetation due to plant community composition in mixtures may also influence storage of soil carbon through species-specific differences in plant detritus chemical composition and input rates (Ahmed et al. 2016). In plant communities where root litter is composed of inputs of many species, more complex organic forms are formed compared to the root litter of monospecific forests (Ahmed et al. 2016). It has been demonstrated that the highly complex and heterogeneous organic residues found in the soil organic matter of mixed communities alter the residence times of these compounds in the soil due to differences in biodegradability (Ahmed et al. 2016), even it was reported that high diversity of leaf litter promoted the rate of decomposition (King et al. 2002). On the other hand, a positive correlation between the tree species diversity, fine root biomass and C stock in deeper layers of the soil (30–40 cm) has been previously described by Dawud et al. (2016). They comment that the greater inputs of root litter cause higher accumulation of soil carbon stocks and relate the belowground niche complementarity with the mixed forests higher carbon accumulation in deeper layers, i.e. the stratification of roots of different tree species to top and subsoil in different stands (Dawud et al. 2016). In mixed forests also species interactions may increase productivity through the resource use complementarity (Ahmed et al. 2016). Tree species may behave differently in a mixture compared with their behaviour in monospecific stands (Brandtberg et al. 2000). In some cases, it has been shown to change towards a deeper rooting in admixtures (Brandtberg et al. 2000). In addition, different rooting depths and root turnover rates among species impact soil organic carbon distribution (Cremer and Prietzel 2017).

Next to a higher contribution of C inputs from roots in the 10–30-cm layer, higher values of TOC and C stock at intermediate depths could also be related to a greater thickness of the first mineral horizon in mixed stands in relation to monospecific stands (MM = 22.8 ± 3.5 cm, PS = 14.7 ± 3.5 cm, PP = 15.3 ± 1.9 cm; see “Appendix 1”). Schleuß et al. (2014) have already reported the higher thickness of the A horizon in mixed stands in relation to monospecific stands, studying a tree diversity gradient with European beech being increasingly diluted by other species (dominance of 1, 3 or 5 species). Under 30 cm depth, the trends are confusing because TOC was less than 1% and the observed effects of stand type are limited. In the same way, Ahmed et al. (2016) confirmed the lack of differences between treatments

for 40–100 cm depth when comparing admixtures versus monospecific stands of *Betula pendula*, *Alnus glutinosa* and *Fagus sylvatica*.

Some authors have reported that the mixture of tree species significantly affect soil organic carbon stocks (Andivia et al. 2016; Cremer et al. 2016). This effect was reported not only for the topsoil (Andivia et al. 2016) but also for deeper layers of the mineral soil (Jandl et al. 2007), even in plantations (Liu et al. 2017). These authors highlight the positive effect of mixed stands in carbon accumulation (Jandl et al. 2007; Andivia et al. 2016; Cremer et al. 2016), more pronounced along time (Liu et al. 2017), but always when the mixtures combined species with contrasting traits, such as broadleaf–conifer. Despite the effect of admixture on soil C stock and TOC was limited in our study, probably because both tree species belong to the same genus, a relatively strong tree species identity effect was observed in the FF and 0–10 cm layer.

Exchangeable cations

An indirect effect of exchangeable cations and sum of bases was also reported due to the different carbon amounts. It is likely that the effect of tree species composition on exchangeable cations and SB is mediated by their effect on the carbon (Cremer and Prietzel 2017). Soil organic matter improves the soil capacity to retain nutrients including exchangeable cations (Beldin et al. 2007), but also litter decomposition returns nutrients bound in organic material to mineral form in the soil (Gartner and Cardon 2004). In fact, we found a positive correlation between TOC and exchangeable cations from 0 to 30 cm depth, because soil organic matter plays an essential role in retaining soil base cations especially in sandy soils (Wang et al. 2017). As a result, exchangeable cations and SB describe the same two tendencies found for the carbon storage: higher values in PS, lower in PP and intermediate in MM, at the topsoil, but higher values in MM at intermediate soil layers.

Also it should be mentioned that in mixed forests composed by species with different rooting depth, deep system species absorbed nutrients from deeper soil horizons and redistributed the basic cations to the upper layers of the soil (Brandtberg et al. 2000). This fact could not be contrasted since there is no agreement in the literature on the rooting depth of the two species under study. According to Bravo-Oviedo and Montero (2008), *P. sylvestris* has a xeric-mesophilic character with a powerful root system: long main root and oblique secondary radical system, and *P. pinaster* has a xerophytic character with a potent radical system: very deep main root and horizontal secondary radical system. Other authors describe the highest density of roots for *P. sylvestris* (Finér et al. 2007), and for *P. pinaster* (Sudmeyer et al. 2004) at the first 50 cm, and Montero et al. (2005) mention that the

21.4% of the total biomass in *P. sylvestris* is root biomass and the 22.1% for *P. pinaster*.

Implications for forest management

We would like to point out that our results have important implications for forest management in the context of adaptation and mitigation to climate change through carbon sequestration or at least soil carbon preservation (Schleuß et al. 2014).

Even though the differences in TOC and C stock between stands at the intermediate layers of mineral soil were not statistically significant, the significant higher values of some exchangeable cations at intermediate soil layers in MM should make us reflect on the management strategies of Scots and Maritime pine stands in Spain. First, because Scots and Maritime pine forests occupy an important area in Spain, growing in monospecific and mixed stands (Serrada et al. 2008). Second, because the subsoil carbon is known to be more effectively stabilized as compared to topsoil or litter layer carbon (Rumpel and Kögel-Knabner 2011); therefore, potential losses of soil carbon from subsoil induced by warming will lag in time and provide a temporal buffer (Schleuß et al. 2014). Third, because exchangeable cations serve as good indicators of soil fertility and are critical nutrients for both plant and microbial metabolism; in fact, the lack of exchangeable cations availability constraints net primary productivity (Wang et al. 2017). And, fourth, because in mixed-species communities, species interactions may either increase productivity through resource use complementarity (Ahmed et al. 2016). Some authors have reported a positive effect of species mixing by light use efficiency, in mixtures of *P. sylvestris* and *P. nigra* (Jucker et al. 2014), by water use efficiency, in Mediterranean areas (Vilà et al. 2007), or by growth efficiency, in admixtures of *P. sylvestris* and *P. pinaster* at the same study area (Riofrío et al. 2016; Ruiz-Peinado et al. 2017), although the effect of mixing on productivity varies with stand development stage, stand density and site conditions (Ruiz-Peinado et al. 2017). In the same study area, Riofrío et al. (2017) have found a canopy vertical stratification by the complementarity of the crown in the mixed stand of Scots and Maritime pines in relation to monocultures that could affect productivity.

Conclusions

Despite the effect of the studied admixture on soil C stock and TOC is limited, probably because both tree species belong to the same genus, a relatively strong tree species identity effect is observed in the FF and 0–10-cm layer. Moreover, the influence of stand type on the first 30 cm of the mineral soil shows different patterns when comparing between layers:

in the topsoil (0–10 cm) C stock is higher in monospecific Scots pine stands whereas in the subsoil C stock is higher in the mixed pine stand. These different patterns could be related to the amount and type of litter deposited in each soil layer (leaf and/or root litter) and to the different thickness of the first mineral soil horizon. Finally, these influences of the stand type on carbon of the mineral soil profile are reflected in differences in the exchangeable cations.

The positive effects on goods and services, such as carbon sequestration, in mixed stands in relation to monospecific stands of the same genus species should make us to reflect on: (1) the use of mixtures as a strategy to combat climate change, due to the advantage in the accumulation of carbon in the subsoil layers where it is protected from external disturbance; and (2) the implementation of the adaptive forest

management that includes a non-monetary good and services (carbon sequestration or biodiversity conservation) as is demanded in a new climate change scenery.

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Appendix 1

See Tables 2, 3 and 4.

Table 2 General soil properties of the soil profiles excavated under the monospecific stands of Scots pine (*P. sylvestris*)

Stand type	<i>Pinus sylvestris</i> —monospecific stands					
Triplet	01	02	03	04	05	06
Soil type	Typic dystroxerept	Typic dystroxerept	Aquic humixerept	Typic dystroxerept	Typic humixerept	Typic dystroxerept
Horizon	Ah	Ah	Ah	Ah	Ah	Ah
Colour						
Dry	10YR 4/2	10YR 4/2	10YR 4/1	10YR 5/2	10YR 4/2	10YR 7/2
Wet	10YR 2/2	10YR 3/2	10YR 2/1	10YR 3/1	10YR 2/1	10YR 6/3
Thickness (cm)	0–10	0–15	0–12	0–8	0–15	0–28
Soil texture	Sandy loam	Loamy fine sand	Loam	Sandy loam	Sandy loam	Sandy loam
Sand/silt/clay	51/36/10	75/15/6	44/30/18	56/21/14	55/21/13	81/9/8
Stones (%)	2.25	7.90	6.11	9.04	2.68	13.03
pH (H ₂ O)	4.22	3.95	4.35	4.63	4.05	4.45
Horizon	AB	AC	AC	AB	AB	C
Colour						
Dry	10YR 6/4	10YR 7/3	10YR 6/1	10YR 6/6	10YR 6/3	10YR 4/1
Wet	7.5YR 4/6	10 YR 5/4	10YR 4/1	10YR 3/2	10YR 5/3	10YR 5/6
Thickness (cm)	10–40	15–35	12–30	08–30	15–40	28–65+
Soil texture	Loam	Loamy fine sand	sandy loam	loam	Sandy loam	Loamy fine sand
Sand/silt/clay	35/39/17	79/10/8	58/26//12	48/41/12	53/23/12	74/12/11
Stones (%)	24.61	11.83	20.24	25.68	11.68	5.53
pH (H ₂ O)	4.79	4.22	4.77	5.37	4.75	4.60
Horizon	Bw	C	Cg	C	C	–
Colour						
Dry	7.5 YR 5/6	10 YR 6/6	10YR 8/1	10 YR 7/4	10 YR 7/4	–
Wet	5 YR 4/6	10 YR 4/6	10YR 6/1	10YR 5/8	10YR 5/8	–
Thickness (cm)	40–60+	35–65+	30–60+	30–60+	40–60+	–
Soil texture	Loam	Sandy loam	Sandy loam	Loam	Sandy loam	–
Sand/silt/clay	34/31/23	77/10/10	60/21/11	35/35/22	49/26/16	–
Stones (%)	33.20	8.39	22.27	25.56	16.09	–
pH (H ₂ O)	4.82	4.76	4.69	4.98	5.31	–

Soil: soil classification according to Soil-Survey-Staff (2014); Colour: dry and wet matrix colour (Hue Value/Chroma); Thickness: thickness of each horizon; Soil texture: textural class according to Soil-Survey-Staff (2014); Sand/Silt/Clay: % of sand, silt and clay determined by the pipette method (MAPA 1994); Stones: coarse soil material (> 2 mm); pH (H₂O): pH according to MAPA (1994)

Table 3 General soil properties of the soil profiles excavated under the monospecific stands of Maritime pine (*P. pinaster*)

Stand type	<i>P. pinaster</i> monospecific stands					
	01	02	03	04	05	06
Triplet						
Soil type	Typic dystroxerept	Typic humixerept	Typic humixerept	Typic dystroxerept	Typic humixerept	Typic dystroxerept
Horizon	Ah	Ah	Ah	Ah	Ah	Ah
Colour						
Dry	10YR 5/3	10YR 4/1	10YR 5/2	10YR 6/2	10YR 5/1	10YR 6/2
Wet	10YR 3/2	10YR 2/1	10YR 3/1	10YR 3/1	10YR 2/1	10YR 4/1
Thickness (cm)	0–15	0–20	0–17	0–8	0–20	0–12
Soil texture	Loam	Sandy loam	Sandy loam	Sandy loam	Sandy loam	Loamy fine sand
Sand/silt/clay	52/34/13	64/16/11	66/18/8	80/12/5	65/16/11	85/9/5
Stones (%)	3.14	31.84	59.50	5.62	12.01	6.44
pH (H ₂ O)	4.67	3.98	5.04	4.75	4.45	4.90
Horizon	AB	C	C	AC	AC	C
Colour						
Dry	10YR 6/4	10YR 7/4	10YR 6/6	10YR 6/6	10YR 6/2	10YR 7/3
Wet	10YR 4/4	10YR 5/6	10YR 4/6	10YR 3/2	10YR 4/2	10YR 6/4
Thickness (cm)	15–30	20–60+	17–57+	08–34	20–30	12–50+
Soil texture	Loam	Sandy loam	Sandy loam	Sandy loam	Sandy loam	Loamy fine sand
Sand/silt/clay	48/37/14	72/10/13/	68/15/10	74/13/8	59/24/11	84/8/6
Stones (%)	34.12	21.66	58.56	9.29	52.86	9.07
pH (H ₂ O)	5.23	4.72	4.80	5.15	4.91	5.16
Horizon	Bw	–	–	C	C	–
Colour						
Dry	5YR 5/6	–	–	10YR 7/4	10YR 6/4	–
Wet	5YR 4/6	–	–	10YR 5/8	10YR 4/4	–
Thickness (cm)	30–60+	–	–	34–60+	30–52+	–
Soil texture	Clay	–	–	Loam	Sandy loam	–
Sand/silt/clay	15/31/52	–	–	64/16/14	61/23/8	–
Stones (%)	38.09	–	–	12.75	65.63	–
pH (H ₂ O)	4.78	–	–	5.01	4.41	–

Soil: soil classification according to Soil-Survey-Staff (2014); Colour: dry and wet matrix colour (Value/Chroma); Thickness: thickness of each horizon; Soil texture: textural class according to Soil-Survey-Staff (2014); sand/silt/clay: % of sand, silt and clay determined by the pipette method (MAPA 1994); stones: coarse soil material (> 2 mm); pH (H₂O): pH according to MAPA (1994)

Table 4 General soil properties of the soil profiles excavated under the mixed stands of Scots (*P. sylvestris*) and Maritime (*P. pinaster*) pines

Stand type	Mixed Stands					
	01	02	03	04	05	06
Triplet						
Soil type	Typic humixerept	Typic humixerept	Typic humixerept	Typic dystroxerept	Typic dystroxerept	Typic dystroxerept
Horizon	Ah	Ah	Ah	Ah	Ah	Ah
Colour						
Dry	10YR 5/3	10 YR 5/2	10 YR 4/1	10 YR 6/2	10 YR 4/1	10 YR 6/1
Wet	10 YR 3/2	10 YR 3/1	10 YR 2/2	10 YR 4/1	10 YR 2/1	10 YR 3/1
Thickness (cm)	0–35	0–23	0–17	0–20	0–12	0–30
Soil texture	Loam	Sandy loam	Sandy loam	Loamy fine sand	Sandy loam	Sandy loam
Sand/silt/clay	43/46/11	66/11/13	53/23/15	77/14/5	51/24/18	72/14/9
Stones (%)	15.79	5.21	15.02	15.12	11.70	47.93
pH (H ₂ O)	5.30	3.97	4.42	5.16	4.38	4.56
Horizon	Bw	C	C	C	AC	C
Colour						
Dry	7.5 YR 6/6	10 YR 7/4	10 YR 6/3	10 YR 6/6	10 YR 6/3	10 YR 8/3
Wet	5 YR 5/8	10 YR 6/6	10 YR 5/3	10YR 5/8	10 YR 4/4	10 YR 5/6
Thickness (cm)	35–75+	32–60+	17–54+	20–50	12–24	30–70+
Soil texture	Clay loam	Sandy loam	Sandy loam	Sandy loam	Sandy loam	Loamy Fine Sand
Sand/silt/clay	24/33/31	69/14/15	72/12/11	71/14/11	47/22/17	78/14/5
Stones (%)	34.80	8.33	60.57	35.15	15.27	11.88
pH (H ₂ O)	4.77	5.16	4.72	5.20	4.47	5.02
Horizon	–	–	–	–	C	–
Colour						
Dry	–	–	–	–	10 YR 6/6	–
Wet	–	–	–	–	10 YR 4/6	–
Thickness (cm)	–	–	–	–	24–50+	–
Soil texture	–	–	–	–	Sandy loam	–
Sand/silt/clay	–	–	–	–	45/22/18	–
Stones (%)	–	–	–	–	17.88	–
pH (H ₂ O)	–	–	–	–	4.55	–

Soil: soil classification according to Soil-Survey-Staff (2014); Colour: wet matrix colour (Value/Chroma); Thickness: thickness of each horizon; Soil texture: textural class according to Soil-Survey-Staff (2014); sand/silt/clay: % of sand, silt and clay determined by the pipette method (MAPA 1994); Stones: coarse soil material (> 2 mm); pH (H₂O): pH according to MAPA (1994)

Appendix 2

See Tables 5, 6 and 7.

Table 5 General stand variables for monospecific stands of *P. sylvestris*

Stand type	<i>Pinus sylvestris</i> monospecific stands						Mean ± SE
	1	2	3	4	5	6	
Triplet							
<i>N</i> (trees ha ⁻¹)							
Total	821.0	509.3	665.0	636.6	651.0	821.0	684.0 ± 48.9
Scots	806.0	495.1	651.0	580.0	651.0	778.0	660.2 ± 48.0
Maritime	14.0	14.1	14.0	56.6	0.0	42.0	23.5 ± 8.7
<i>G</i> (m ² ha ⁻¹)							
Total	54.2	49.2	47.7	48.9	54.9	33.3	48.0 ± 3.2
Scots	50.7	47.0	45.5	40.7	54.9	30.8	44.9 ± 3.4
Maritime	3.6	2.2	2.3	8.2	0.0	2.6	3.2 ± 1.1
DBH (cm)							
Total	28.0 ± 1.2	34.4 ± 1.1	27.5 ± 1.8	30.4 ± 1.2	32.4 ± 1.2	22.5 ± 0.5	29.2 ± 1.7
Scots	27.8 ± 1.1	32.3 ± 1.0	27.2 ± 1.8	29.3 ± 1.0	32.4 ± 1.2	22.2 ± 0.4	28.5 ± 1.6
Maritime	56.7 ± 0.0	44.7 ± 0.0	45.3 ± 0.0	45.4 ± 5.8	0.0 ± 0.0	27.7 ± 0.3	36.6 ± 8.2
Ho (m)							
Total	17.0 ± 0.3	19.3 ± 0.3	18.5 ± 0.8	22.1 ± 0.2	21.8 ± 0.3	16.8 ± 0.2	19.3 ± 0.9
Scots	17.1 ± 0.3	19.3 ± 0.3	18.4 ± 0.8	22.1 ± 0.2	21.8 ± 0.3	16.6 ± 0.1	19.2 ± 0.9
Maritime	16.2 ± 0.0	19.9 ± 0.0	24.5 ± 0.0	22.2 ± 1.3	0.0 ± 0.0	19.5 ± 1.0	17.1 ± 3.6
Age (years)							
Scots	100	151	105	78	121	44	99.8 ± 14.9
Maritime	0	0	0	0	0	0	0.0 ± 0.0

N: stems per hectare; *G*: basal area per hectare; Ho: dominant height; DHB: quadratic mean diameter. Age: normal age

Table 6 General stand variables for monospecific stands of *Pinus pinaster*

Stand type	<i>P. pinaster</i> monospecific stands						Mean ± SE
	1	2	3	4	5	6	
Triplet							
<i>N</i> (trees ha ⁻¹)							
Total	566.0	806.4	538.0	1429.0	722.0	594.2	775.9 ± 137.1
Scots	57.0	14.1	0.0	283.0	0.0	0.0	59.0 ± 45.7
Maritime	509.0	792.2	538.0	1146.0	722.0	594.2	716.9 ± 96.6
<i>G</i> (m ² ha ⁻¹)							
Total	59.4	67.9	68.6	69.4	70.3	37.5	62.2 ± 5.2
Scots	1.2	0.1	0.0	3.3	0.0	0.0	0.8 ± 0.5
Maritime	58.2	67.8	68.6	66.0	70.3	37.5	61.4 ± 5.1
DBH (cm)							
Total	36.2 ± 1.7	32.0 ± 1.2	39.6 ± 1.3	22.6 ± 1.1	34.9 ± 0.9	28.2 ± 0.7	32.3 ± 2.5
Scots	15.8 ± 2.2	9.7 ± 0.0	0.0 ± 0.0	9.5 ± 1.8	0.0 ± 0.0	0.0 ± 0.0	5.8 ± 2.8
Maritime	38.6 ± 1.3	32.4 ± 1.1	39.6 ± 1.3	26.0 ± 0.9	34.9 ± 0.9	28.2 ± 0.7	33.3 ± 2.2
Ho (m)							
Total	17.3 ± 0.5	16.3 ± 0.3	20.5 ± 0.2	12.4 ± 0.4	19.5 ± 0.3	15.6 ± 0.2	16.9 ± 1.2
Scots	10.8 ± 1.8	7.0 ± 0.0	0.0 ± 0.0	7.3 ± 0.9	0.0 ± 0.0	0.0 ± 0.0	4.2 ± 1.9
Maritime	18.0 ± 0.3	16.5 ± 0.2	20.5 ± 0.2	13.6 ± 0.3	19.5 ± 0.3	15.6 ± 0.2	17.3 ± 1.0
Age (years)							
Scots	0	0	0	0	0	0	0.0 ± 0.0
Maritime	118	78	105	80	115	49	90.8 ± 10.9

N: stems per hectare; *G*: basal area per hectare; Ho: dominant height; DHB: quadratic mean diameter. Age: normal age

Table 7 General stand variables for mixed stands of scots and maritime pines

Stand type	Mixed stands						Mean ± SE
	1	2	3	4	5	6	
Triplet							
<i>N</i> (trees ha ⁻¹)							
Total	523.0	693.2	693.0	1330.0	552.0	679.0	745.0 ± 120.9
Scots	241.0	325.4	495.0	764.0	354.0	396.0	429.2 ± 75.1
Maritime	283.0	367.8	198.0	566.0	198.0	283.0	316.0 ± 56.3
<i>G</i> (m ² ha ⁻¹)							
Total	53.0	58.2	63.5	55.3	68.2	33.3	55.3 ± 4.9
Scots	19.9	19.2	33.0	23.2	45.9	13.0	25.7 ± 4.8
Maritime	33.1	38.9	30.5	32.1	22.3	20.2	29.5 ± 2.9
DBH (cm)							
Total	32.3 ± 1.6	31.6 ± 1.2	32.0 ± 1.8	20.2 ± 1.2	39.4 ± 0.8	24.2 ± 0.9	30.0 ± 2.8
Scots	32.3 ± 2.0	26.4 ± 1.6	27.3 ± 1.8	16.6 ± 1.5	40.3 ± 1.1	20.2 ± 0.6	27.2 ± 3.5
Maritime	40.3 ± 2.2	36.4 ± 1.3	43.5 ± 2.4	25.0 ± 1.6	37.6 ± 1.1	29.8 ± 1.1	35.4 ± 2.8
Ho (m)							
Total	18.0 ± 0.4	16.4 ± 0.4	20.9 ± 0.7	13.1 ± 0.5	24.6 ± 0.3	14.8 ± 0.2	18.0 ± 1.7
Scots	17.5 ± 0.6	14.5 ± 0.6	19.8 ± 0.8	12.3 ± 0.7	24.3 ± 0.2	14.0 ± 0.3	17.1 ± 1.8
Maritime	18.5 ± 0.3	18.1 ± 0.3	23.7 ± 0.5	14.2 ± 0.6	25.0 ± 0.6	15.9 ± 0.2	19.2 ± 1.7
Age (years)							
Scots	118	117	100	78	109	44	94.3 ± 11.7
Maritime	113	93	95	79	118	49	91.2 ± 10.2

N: stems per hectare; *G*: basal area per hectare; Ho: dominant height; DHB: quadratic mean diameter. Age: normal age

Appendix 3

See Fig. 5.

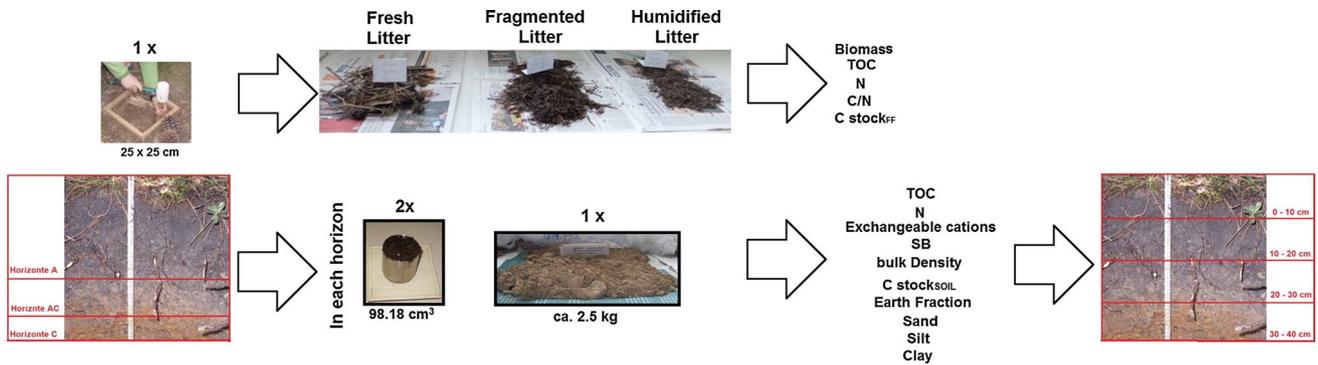


Fig. 5 Soil sampling design

Appendix 4

See Tables 8 and 9.

Table 8 Likelihood ratio test results

	AIC		
	Null	Alternative	<i>p</i> value
C stock _{FF}	89.39	88.38	0.08
C stock _{FsL}	32.26	31.59	0.10
C stock _{FgL}	28.49	25.52	0.03
C stock _{HmL}	28.67	31.77	0.64
C stock _{SOIL 0–40 cm}	166.69	167.84	0.18
C stock _{SOIL 0–10 cm}	– 18.17	– 18.42	0.10
C stock _{SOIL 10–20 cm}	139.24	141.40	0.28
C stock _{SOIL 20–30 cm}	13.64	12.94	0.08
C stock _{SOIL 30–40 cm}	– 34.18	– 35.44	0.06
<i>B</i> _{FF}	120.31	119.21	0.08
<i>B</i> _{FsL}	32.59	30.94	0.06
<i>B</i> _{FgL}	78.76	75.18	0.02
<i>B</i> _{HmL}	86.36	89.37	0.61
CN _{FF}	141.63	147.70	0.14
CN _{FsL}	160.46	154.86	0.01
CN _{FgL}	2.78	4.24	0.28
CN _{HmL}	– 105.94	– 102.33	0.82
TOC _{0–10 cm}	74.39	69.36	0.01
TOC _{10–20 cm}	70.47	73.42	0.38
TOC _{20–30 cm}	41.13	40.27	0.08
TOC _{30–40 cm}	34.09	36.43	0.30

The *p* values of the likelihood ratio tests are provided as well as the Akaike information criterion (AIC) of the null model (triplet as a random effect) and of the alternative model (triplet as a random effect + stand type as a fixed effect + %Sand as a fixed effect for the mineral soil). Other abbreviations as in Figs. 2, 3 and 4

Table 9 Likelihood ratio test results

	AIC		<i>p</i> value
	Null	Alternative	
Na ⁺ _{0–10 cm}	– 35.80	– 38.67	0.03
Na ⁺ _{10–20 cm}	– 43.74	– 52.42	0.00
Na ⁺ _{20–30 cm}	– 40.36	– 40.01	0.13
Na ⁺ _{30–40 cm}	– 33.44	– 39.13	0.01
K ⁺ _{0–10 cm}	– 32.98	– 52.19	0.00
K ⁺ _{10–20 cm}	26.61	23.96	0.03
K ⁺ _{20–30 cm}	34.36	32.79	0.06
K ⁺ _{30–40 cm}	30.01	22.70	0.00
Ca ⁺² _{0–10 cm}	58.54	41.12	0.00
Ca ⁺² _{10–20 cm}	54.49	56.08	0.23
Ca ⁺² _{20–30 cm}	56.11	55.57	0.09
Ca ⁺² _{30–40 cm}	6.12	– 7.99	0.00
Mg ⁺² _{0–10 cm}	5.83	– 14.65	0.00
Mg ⁺² _{10–20 cm}	6.60	4.11	0.04
Mg ⁺² _{20–30 cm}	5.22	3.04	0.04
Mg ⁺² _{30–40 cm}	45.80	24.22	0.00
SB _{0–10 cm}	66.92	48.79	0.00
SB _{10–20 cm}	63.16	63.90	0.15
SB _{20–30 cm}	64.21	63.10	0.07
SB _{30–40 cm}	11.98	– 5.69	0.00

The *p* values of the likelihood ratio tests are provided as well as the Akaike information criterion (AIC) of the null model (triplet as a random effect) and of the alternative model (triplet as a random effect + stand type as a fixed effect + %Sand as a fixed effect). Other abbreviations as in Fig. 2 and Table 1

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