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Silvopastoral systems established with *Pinus radiata* D. Don and *Betula pubescens* Ehrh.: tree growth, understorey biomass and vascular plant biodiversity

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In the European Union, the majority of afforestation is carried out on former agricultural land. This afforestation causes fundamental changes in ecosystem structure and functioning, with the trees intercepting light and precipitation, producing litterfall and competing for soil nutrients. All of these effects could potentially have a negative impact on understorey biomass and vascular plant biodiversity in a relatively short time span. This study aims to evaluate the effects of afforestation with Pinus radiata D. Don (Monterey pine: pine) and Betula pubescens Ehrh. (Downy birch: birch), established at two different densities (2500 and 833 trees ha^{-1}) and sown with two different pasture mixtures (Dactylis glomerata L. + Trifolium repens L. + Trifolium pratense L. and Lolium perenne L. + T. repens L. + T. pratense L.), on understorey biomass, alpha plant biodiversity, life cycle type (annuals vs. perennials) and beta biodiversity over a period of 11 years. Pine showed better development than birch throughout the study, although both species were very sensitive to tree density. While increasing density increased pine height and decreased pine diameter, both aspects of birch development were reduced by higher tree densities. Aboveground biomass increased throughout the study. Alpha plant biodiversity was drastically reduced under pine established at high density, 11 years after afforestation. However, the similarities in species richness, species composition and the low beta growth rates found under pine at low density, and birch at both high and low density suggest that, in these cases, the choice of canopy tree has little consequence for understorey biodiversity at this stage of system development.

Introduction

Agronomic land afforestation has become an important issue within the European Union during the last decade, with agri-environmental legislation establishing direct payments for new plantations to be established on former agricultural land (EC, 1997). The significance of this measure at a European level can be seen in the fact that >1 million hectares were afforested between 1994 and 1999 owing to the Regulation 2080/92 (Picard, 2001). Foresters commonly aim to obtain more rapid economic returns from newly afforested lands through the use of exotic fast-growing species (usually conifers) instead of autochthonous deciduous species (Barbier *et al.*, 2008), tending not to take into account the short-, medium- and long-term effects that this practice may have on local biodiversity.

In Spain, one of the biggest European countries, agri-environmental funding was responsible for \sim 685 000 ha of new afforested land between 1994 and 2006, with \sim 10 per cent taking place in Galicia (MAPA, 2006), where the present study was carried out. *Pinus radiata* D. Don (MAPA, 2006) is one of the most extensively

planted tree species in Galicia, usually at high density, over 1100 trees ha^{-1} , which is the minimum planting density to obtain European subsidies for afforestation of land by the Galicia's administration (Xunta, 1993). However, the private owner usually increases this minimum density to 2500 trees ha^{-1} aiming at increasing volume production and initially guaranteeing to provide sufficient trees for performing thinning and producing trees with high commercial value. In these systems, the absence of thinning often translates into low quality timber (used for woodchip) and an early canopy closure (Ferris et al., 2000) which causes early understorey shading. Tree shade tends to be one of the most significant and limiting factors that determines understorey pasture production (Peri et al., 2002; Riqueiro-Rodríguez et al., 2007) in P. radiata stands. Therefore, it is essential to choose adequate sown pastures in such systems. In this regard, Dactylis glomerata L. is well known as a shade tolerant species and has been successfully used in agroforestry systems in Galicia (Riqueiro, 1985) and New Zealand (Peri et al., 2007), as well as having high productivity and nutritional quality (Lin et al., 1999; Mosquera-Losada et al., 2006). However,

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species with only a slight shade tolerance, such as *Lolium perenne* L., are more recommended for use during tree establishment, in low-density tree plantations, or to accompany tree species with open canopy structures (Lin *et al.*, 1999).

Understorey biodiversity evolution in agroforestry systems depends on tree species and cover. Dense *P. radiata* plantations have been shown to reduce plant biodiversity evolution in silvopastoral systems established on poor soils (Mosquera-Losada *et al.*, 2009), although few studies have been carried out comparing the effect of autochthonous and broadleaved tree species such as *Betula pubescens* with exotic species such as *P. radiata* on understorey biodiversity evolution in newly afforested land (Rigueiro-Rodríguez *et al.*, 2011). These two types of tree could differently affect the evolution of understorey plant species due to the branch structure of the former (modifying light canopy interception) and periodic leaf fall.

The objective of this study was to evaluate the effect of tree species (*P. radiata vs B. pubescens*), canopy density (833 vs 2500 trees ha⁻¹) and sown pasture (*D. glomerata* + *Trifolium repens* L. + *Trifolium pratense* L. vs L. perenne + *T. repens* L. + *T. pratense* L.) on tree growth, understorey production, understorey components and alpha and beta plant biodiversity 11 years after the establishment of a silvopastoral system.

Materials and methods

Characteristics of the study site

The experiment was conducted in Lugo (NW Spain; 43.01 N; 7.40 W; 439 m a.s.l.) in an agricultural area (designated for potato cultivation) on an Umbrisol soil (FAO, 1998) of sandy-silty texture (61 per cent sand, 34 per cent silt and 5 per cent clay). The experiment was initiated in April 1995; the present paper includes data obtained in 1995, 2000 and 2005. The area belongs to the Atlantic bioclimatic region (EEA, 2006) and is characterized by mean total annual precipitation of 1083 mm and mean annual temperature of 12.2°C. During the 3 years of study (1995, 2000 and 2005), average monthly temperatures occasionally (when $T < 6^{\circ}$ C) limited the growth of certain pasture species (Mosquera-Losada et al., 1999); in 2005 this limitation occurred throughout the whole winter period. The highest rainfall values during the experiment were recorded in 2000 (1341 mm), being higher than the mean annual total for the last 30 years (1083 mm). On the contrary, the year with the lowest annual rainfall during the experiment was 2005 (824 mm). Rainfall levels during the summer period, which mainly determines inter-annual variation of pasture production in the area (Mosquera-Losada and González-Rodríguez, 1998), was high in 1995 and low in 2005, at 211 and 84 mm, respectively. In general, moisture deficits limiting vegetation growth were recorded in July and August due to drought.

Experimental design

The experimental design was a randomized complete block with three replicates and eight treatments: two pasture mixtures × two tree densities × two tree species. These treatments represented forest management practices typically used in the studied biogeographic region of Spain. In April 1995 the plots were sown with two different pasture mixtures: (1) mixture Dg: *D. glomerata* L. var. Saborto (25 kg ha⁻¹) + *T. repens* L. var. Ladino (4 kg ha⁻¹) + *T. pratense* L. var. Marino (1 kg ha⁻¹) and (2) mixture Lp: *L. perenne* L. var. Tove (25 kg ha⁻¹) + *T. repens* L. var. Ladino (4 kg ha⁻¹) + *T. pratense* L. var Marino (1 kg ha⁻¹). Two forest species, *P. radiata* D. Don (Monterey pine: pine) (from container plants) and *B. pubescens* Ehrh. (Downy birch: birch) (from bare roots), were planted in May

1995 at two densities: (1) 2500 trees ha⁻¹ with a tree spatial arrangement of $2 \times 2 \text{ m}$ (64 m² per experimental unit) and (2) 833 trees ha⁻¹ with a tree spatial arrangement of $3 \times 4 \text{ m}$ (192 m² per experimental unit). In each experimental unit, 25 trees were planted in an arrangement of 5×5 stems. Fertilization was not applied in order to replicate traditional afforestation practices of agricultural land for this area. With the objective of producing high quality timber, low pruning (at 2 m height) was performed on pine at the end of 2001, while birch was subjected to form pruning in the same year.

Field sampling

Trees

Tree diameter and total height measurements were taken in 1995, 2000 and 2005 from the inner nine trees in each plot, in order to avoid a border effect. In 1995, measurements of diameter (using calipers) were made at the height of the root-collar, while in 2000 and 2005 diameter was measured at breast height (1.30 m). In order to obtain a height measurement, a pole was used in 1995 and 2000, while in the final year (2005) data were collected by a hypsometer.

Aboveground biomass and components

Understorey from each plot was harvested twice (July and December) in 1995. Four harvests were performed per year (May, June, July and December) from 1996 to 2005, excepting those pine plots established at high density (2500 trees ha⁻¹) that were only harvest twice (July and December) due to the lack of understorey growth. Only results from 1995, 2000 and 2005 are shown. During each harvest, the ground surface area delimited by the nine inner trees in each plot was cleared; with the understorey biomass weighed in situ and a representative subsample taken to the laboratory. Understorey samples were hand-separated in the laboratory in order to determine the following individual biomass components: herbaceous alive component (HA) and herbaceous senescent component (HS) under both pine and birch plots, and pine litter fall (PL) in plots established under pine trees. Further subdivision of HA was then undertaken as a determination of biodiversity, with each different species weighed separately on a dry matter basis (48 h at 60°C) in order to determine botanical composition - expressed in terms of annual and perennial species - as well as to estimate alpha and beta plant biodiversity. Annual aboveground biomass (AB), which includes HA and HS under both pine and birch plots, and PL in plots established under pine trees, was obtained by adding up the components of the four harvests.

Plant biodiversity

Diversity index values were estimated based on the data obtained from the botanic separation of dry matter performed in 1995, 2000 and 2005 (Magurran, 2004). Once all the species present in the different samples from each of the established plots had been identified and their relative annual proportions estimated, values of the alpha and beta diversity indices were then determined (Moreno, 2001). To do so, due to the form of the original data (relative proportion in terms of percentage dry weight of each species) the number of individuals was substituted with relative biomass (Magurran, 2004). Alpha diversity – in terms of species richness (SR) (Magurran, 2004) and the Shannon–Weaver index (H') (Shannon and Weaver, 1949) – and beta diversity – in terms of the complementarity index (Colwell and Coddington, 1994) – were calculated for each experimental unit.

Statistical analysis

The variables studied were: tree diameter and height, AB and its components HA, HS and PL), and alpha (SR and H') and beta (complementarity

index) plant biodiversity. For tree measurements and alpha biodiversity, data were analyzed via repeated-measures analysis of variance (ANOVA), using Mauchly's criterion to test sphericity. If the sphericity assumption was met, univariate approach output was used, and if not, multivariate output (Wilks' lambda test used). For all other variables with the exception of beta diversity, data were analyzed via ANOVA following the model:

$$Y_{ijklm} = \mu + S p_i + A_j + B_k + D_l + M_m + \varepsilon_{ijklm},$$

where Y_{ijklm} is the studied variable; μ the variable mean; Sp_i: tree species; A_j : year; B_k : block, D_l : tree density, M_m : pasture mixture and ϵ_{ijklm} the error. The Tukey's HSD test was used to make subsequent pairwise comparisons after a normalization test ($\alpha = 0.05$), but only when factors were significant according to the results of the ANOVA analyses. The statistical software package SAS (2001) was used for all analyses.

Results

Tree stands

Year (P = 0.0001) and year × tree interaction (P = 0.0001) significantly affected height and diameter, while the interaction between year × mixture (P = 0.013) was also significant for height (Table 1). Pine mean height and diameter were higher than those of birch after 11 years of establishment (Figure 1). The results also revealed that tree mean height and diameter of both tree species was favoured by the Dg pasture mixture, with the exception of those systems planted with pine at low density which had larger diameters when accompanied by the Lp pasture mixture. The positive effect of Dg pasture mixture on tree growth could be explained because, at the beginning of the study, ryegrass was better established than dactylis and therefore

Table 1 Results of repeated-measures multivariate analysis of variance
on tree dimension measurements and alpha biodiversity

	Year	Year × tree	Year × mixture	Mixture	Tree
Tree					
Height					
<i>F</i> -value	1234.33	94.62	4.46	7.67	141.70
df	2	2	2	1	1
Р	0.0001	0.0001	0.013	0.0063	0.0001
Diameter					
F-value	488.11	108.68	2.25	3.40	213.13
df	2	2	2	1	1
Р	0.0001	0.0001	0.120	0.0673	0.0001
Alpha biodive	rsity				
SR					
F-value	8.54	6.02	1.85	4.84	31.48
df	2	2	2	1	1
Р	0.0021	0.0090	0.1834	0.03	0.0001
H'					
F-value	7.23	5.47	2.03	2.95	10.96
df	2	2	2	1	1
P	0.0043	0.0127	0.1580	0.1004	0.0033

SR = species richness; H' = Shannon-Weaver index; P = P-value; df = degrees of freedom.

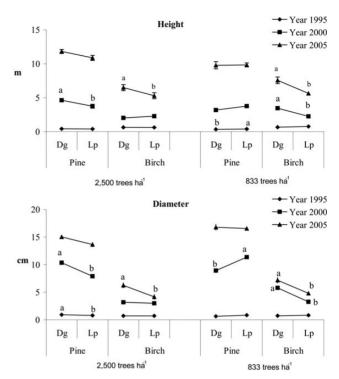


Figure 1 Height (m) and diameter (cm) of *Pinus radiata* D. Don (pine) and *Betula pubescens* Ehrh. (birch) in the years 1995, 2000 and 2005 established at 2500 and 833 trees ha^{-1} . Dg = plots sown with cocksfoot; Lp = plots sown with ryegrass. Different letters indicate significant differences between same-density treatments in the same year. Vertical lines indicate mean standard error.

tree-pasture competition for soil resources was initially higher in those plots sowing with ryegrass. Moreover, the low time persistency of ryegrass compared with cocksfoot has increased the proportion of dicots in the pasture. Dicots usually increase cation uptake reducing soil cation availability for trees and therefore tree growth. Higher competition capacity of the faster growing species (*Pinus*) may overcome this competition by nutrients when it was sown at low density.

The results showed that pine growth was higher than that of birch: 46 and 32 per cent greater in height at 2500 and 833 trees ha⁻¹, respectively, and 64 per cent greater in mean diameter at both densities. On the other hand, pine plots, a high planting density increased mean tree height growth (average of 1.5 m higher at 2500 trees ha⁻¹ compared with 833 trees ha⁻¹) and decreased tree mean diameter growth (2 cm less at high density compared with low density).

Aboveground biomass

Annual aboveground biomass

AB was significantly affected by the interactions year × tree (P = 0.0014) and year × density (P = 0.0045) (Table 2), although these effects were not significant in the first year of the study (Figure 2). Although AB was similar under both tree species during the first 5 years (1995–2000), it increased significantly from 1995 to 2005 in pine plots planted at high density (P = 0.0022; 3.67b,

2.58b and 5.28a in 1995, 2000 and 2005, respectively). Under birch canopy, AB increased by only 2 per cent in high-density plots between 1995 and 2005, while levels were reduced by ~60 per cent in low-density plots during the same period. When comparing the effects of tree development on AB, the results showed AB to have significantly decreased by 50 per cent under birch with respect to pine canopy (P = 0.011; 6.31 and 3.01 Mg DM ha⁻¹ under pine and birch, respectively) in 2005. In contrast, AB significantly increased in 2000 in plots established with pine at low

Table 2 ANOVA of aboveground annual biomass and aboveground
components: herbaceous alive component, herbaceous senescent
component and Monterey pine litterfall

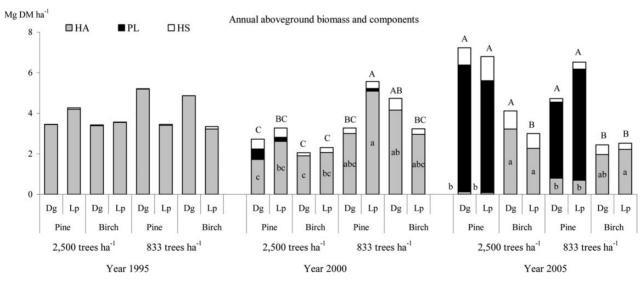
	AB	HA	HS	PL
Year	**	***	***	***
Density	ns	**	*	ns
Tree	***	*	ns	-
Mixture	ns	ns	ns	ns
Year×density	**	**	**	ns
Year × tree	***	***	ns	-
Year × mixture	ns	ns	ns	ns
Density × tree	ns	ns	ns	-
Density × mixture	ns	ns	ns	ns
Tree × mixture	ns	ns	ns	-
Year × density × tree	ns	ns	ns	-
Year × density × mixture	ns	*	ns	ns
Density × tree × mixture	ns	ns	ns	-
Year × density × tree × mixture	ns	ns	ns	-

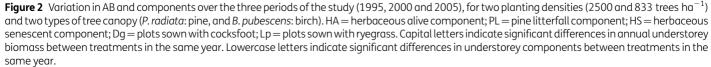
The symbols *, ** and *** indicate significant differences at a P < 0.05, P < 0.01 and P < 0.001 level, respectively.

density and the Lp pasture mixture with respect to those under high planting density. The same pattern was observed in plots under birch sown with the Dg pasture mixture. By the second period of data collection (2000), AB had significantly increased in plots under pine planted at low density when sown with the Lp pasture mixture compared with the Dg mixture. While after the first 5 years of the study, AB tended to be higher in plots established under low-planting density birch when sown with the Dg mixture, by the final year (2005) AB was similar under the two pasture mixtures (Dg and Lp).

Aboveground biomass components

Variation in aboveground biomass components (HA, HS and PL) of the different treatments over the 3 years of data collection is shown in Figure 2. Depending on the year, HA was significantly affected by tree species ($P_{year \times tree} = 0.0003$) (Table 2), with similar values observed during the first 5 years for both tree species (4.05 and 3.75 Mg DM ha^{-1} in 1995 under pine and birch, respectively, and 3.10 and 2.80 Mg DM ha^{-1} in 2000 under pine and birch, respectively) but significantly reduced levels in the last year of the experiment under pine (0.42 Mg DM ha^{-1}) compared with birch (2.41 Mg DM ha^{-1}). Although no effect of treatment type on HA was observed in 1995, 5 years after establishment the results showed HA to be significantly increased (P = 0.0025) in plots established with pine at low density and Lp compared with those under a high density. The same response was observed in plots under birch canopy and the Dg pasture mixture. A pasture mixture effect was only significant in plots established under pine planted at low density, with HA increasing in Lp compared with Dg mixture plots. With respect to the effect of tree species on HA, in plots planted at low density and with the Lp pasture mixture, HA was significantly reduced under birch compared with pine in 2000. However, HA had significantly increased under birch





canopy (independent of pasture mixture in high tree density plots, and only under the Lp mixture in low tree density plots) compared with pine by the final year of the study (2005). In the last year of the study, the average HA levels were 2.7 and 2.1 Mg DM ha^{-1} at high and low density under birch canopy, respectively, and 0.7 Mg DM ha^{-1} under pine at low planting density.

The results showed that treatment type largely had no significant effect on HS and PL throughout the study. However, HS was significantly influenced by tree density depending on the year of data collection ($P_{\text{year} \times \text{density}} = 0.0064$) (Table 2), increasing from lower levels in 1995 (0.035b) and 2000 (0.33b) to a higher level in 2005 (0.92a) in high tree density plots. In low tree density plots, a significant increase was observed after the fifth year (0.05b, 0.37a and 0.32a for the years 1995, 2000 and 2005, respectively) only under pine. PL also significantly increased between the first year of data collection and 2005, with the average contribution made by PL to total aboveground biomass five times higher in the later with respect to the previous year of collection (2000) (P = 0.0003: 0b, 0.21b and 5.25a in 1995, 2000 and 2005, respectively). In the last year of the study, the average PL production was 6 and 5 Mg DM ha⁻¹ in high and low planting density systems, respectively.

Alpha plant biodiversity

During the three studied years, a total of 62 species were found, belonging to 19 different families. The families with the greatest representation were *Compositae* (13 sp.), *Poaceae* (10 sp.), *Leguminosae* (9 sp.), *Brassicaceae* (6 sp.) and *Polygonaceae* (5 sp.). 25 species were annuals, 31 perennials and six were annual – biennial. In the first year of the study (1995), annual species were clearly dominant in all systems (Figure 3) with the exception of plots under pine established at low density. Five years later (2000), all treatments were characterized by the dominance of perennial over annual species. However, the most significant difference was observed in the final year of the experiment (2005), with zero annual species found in plots under pine established at a density of 2500 trees ha⁻¹, and in the other systems comprising only 12–26 per cent of total species.

In 1995, some annual species were found in all systems, whatever the tree density, tree species or pasture mixture (*Cerastium*

alomeratum Thuill, Silene gallica L., Spergula arvensis L., Crepis capillaris (L.) Wallr and Polygonum hydropiper L.). Some annual species were only found 5 years later (2000) after the establishment like Cirsium arvense L., and Lolium multiflorum, both species under pine and Lp mixture, while others such as Conyza canadensis L. and Mentha suaveolens Ehrh. were found only in the final year of data collection in plots established at 833 trees ha^{-1} . In addition, a number of annual species were seen solely in systems established under pine (Illecebrum verticillatum L., Coleostephus myconis (L.) Rchb.f), whereas others were associated only with birch systems (Lupinus angustifolius L., Scleranthus annuus L., Stellaria media L. (Vill) and Bromus diandrus Roth). Some species (all perennial) were found only in plots established at high tree planting density (2500 trees ha⁻¹), namely Montia fontana L., Poa trivialis L., Polygonum aviculare L., Rhinanthus minor L. and Lupinus luteus L., while other perennial species such as Lepidium heterophyllum Bentham and Juncus effusus L. were associated solely with systems established at low tree density.

Sown species including *Lithodora prostata* Loisel, *S. annuus* L., *Coleostephus myconis, Leontodon saxatilis* Lam and *Mentha suaveolens* were found only in Dg plots, while *Cirsium arvense*, *B. diandrus, J. effusus* and *Lupinus angustifolius* were present only in Lp plots.

D. glomerata was the sole species to be found in all systems throughout the study. Other monocot species such as *A. capillaris* L. and *Holcus lanatus* L. were observed in all years of data collection with the exception of 2005, in plots under pine planted at a density of 2500 trees ha⁻¹ and sown with Dg. System development over time favoured the presence of some dicot species such as *Senecio jacobea* L., *Taraxacum officinale* Weber and *Daucus carota* L., which were found only in 2000 and 2005.

Year ($P_{SR} = 0.0021$ and $P_{H'} = 0.0043$) and year × tree interaction ($P_{SR} = 0.0090$ and $P_{H'} = 0.0127$) significantly affected SR and H', while the initial pasture mixture sown also significantly affected SR ($P_{SR} = 0.030$) (Table 1). SR rose significantly when accompanied by the Lp mixture in the first year of the study in systems established under birch at low density, as well as in plots under pine, independent of density, in 2000. On the other hand, SR was significantly reduced in plots under pine planted at 833 trees ha⁻¹ and sown with Dg in 1995 compared with those established at high tree density (Figure 4). The same negative response to lower tree

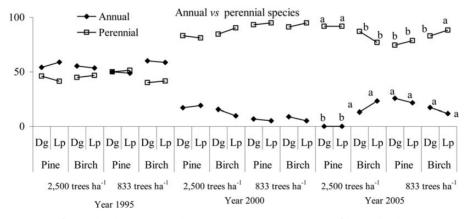


Figure 3 Variation in the percentage of annual and perennial understorey species over the 3 years of data collection (1995, 2000 and 2005) in the systems established under pine and birch trees, for each planting density (2500 and 833 trees ha^{-1}) and pasture mixture. Dg = plots sown with cocksfoot; Lp = plots sown with ryegrass.

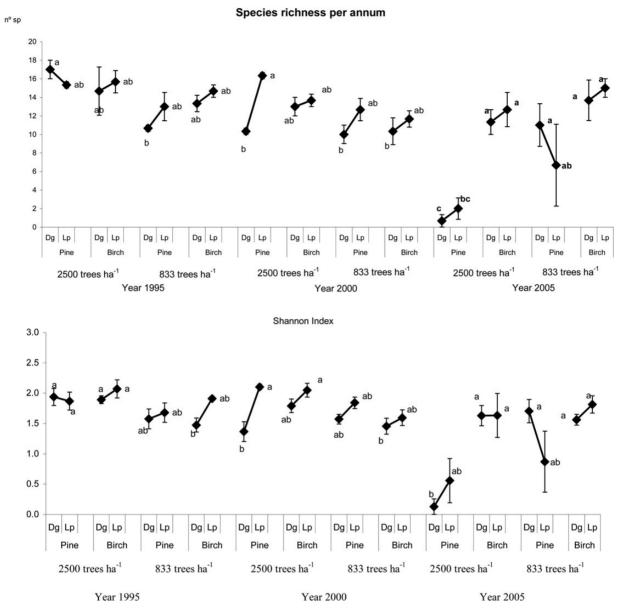


Figure 4 Variation in understorey Species Richness per annum and H' values over the 3 years of data collection in the systems established under pine and downy birch trees, for each planting density and pasture mixture. Dg = plots sown with cocksfoot; Lp = plots sown with ryegrass. Different letters indicate significant differences between treatments in the same year. Vertical lines indicate mean standard error.

density was observed in birch plots sown with Dg, in 2000. In the last year of data collection (2005), SR was drastically reduced in systems established at 2500 pine trees ha^{-1} (three species compared with 7–15 species in the rest of the treatments), independent of pasture mixture (Dg or Lp).

In the last year of the study, 36 species were identified under pine at low density and 40 species under birch, independent of planting density. On the other hand, the results showed that the percentage of species that disappeared, appeared and coincided during the study were average of 40, 27 and 33 per cent, respectively. The fact that 40 per cent of the species cited in the first year of the study were not present in the last year of the study indicates that tree development had an important effect on alpha vascular plant biodiversity. Moreover, \sim 27 per cent of species were only present in the last year of the study confirming the presence of understorey species adapted to tree shade. The percentage of monocot species under pine at low planting density and birch, independently of planting density remained the same (20 per cent) throughout the study.

H' varied between 1.9-2.1, 1.4-2.1 and 0.1-1.6 in plots established at 2500 trees ha⁻¹ in 1995, 2000 and 2005, respectively (Figure 4). In plots planted at 833 trees ha⁻¹, these values were 1.5-1.9, 1.5-1.8 and 0.9-1.8 for the same years. *H'* was significantly increased in plots under birch canopy planted at low density containing the Lp pasture mixture with respect to the Dg mixture in the first year of the study (1995), and under pine

canopy at high planting density in 2000. In contrast, H' was significantly higher in 1995 in systems established under birch at high density and sown with the Dg mixture compared with those established at low planting density. The same response to planting density was found 5 years later, but in this case in downy birch systems sown with the Lp pasture mixture. Furthermore, H' values were significantly greater in the final year of the study in plots established with pine at low density and sown with Dq, compared with those established at high density. With respect to the effect of tree species, H' was negatively influenced by system establishment with pine, both in plots planted at high density (independent of pasture mixture) and those at low density when sown with Lp, compared with birch in the final year of the study.

From the abundance diagrams (Figures 5 and 6), it is clear that the establishment of a pine plantation at high density, whatever the initial pasture mixture (Dg or Lp), negatively affected alpha biodiversity after 11 years of plantation development (2005). D. glomerata was clearly dominant from the year of plot establishment until 2005 in all plots in which it was sown, independent of forest species and initial tree density. In contrast, L. perenne reached 50 per cent dominance only during the first year and in those plots in which it was sown (Lp), being later replaced by monocotyledons such as D. glomerata, A. capillaris and H. lanatus, and the dicotyledons Plantago lanceolata and T. officinale, among others.

Beta plant biodiversity

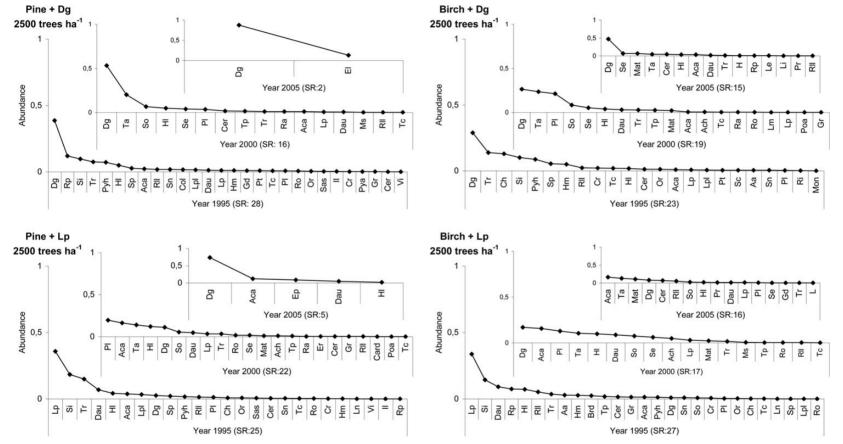
Species turnover (beta biodiversity) between the initial (agricultural land, 1995) and final site situation (silvopastoral system, 2005), as measured by the complementarity index, ranged between 70-97 per cent in plots planted at high density and between 67 and 75 per cent in those at low density (Figure 7). These high percentages are a clear indication that the two systems are sufficiently different. The number of species shared between the initial and final situation was lower under pine canopy at high density (1 and 4 species at Dg and Lp, respectively) compared with the systems established under birch canopy at the same density (6 and 10 species under Dg and Lp, respectively), and compared with the systems established at low density (average of 8.5 species).

In terms of beta biodiversity variation with tree species (pine vs birch), values of the complementarity index were highest in 2005 in plots established at high density (94 and 76 per cent under Dg and Lp, respectively), intermediate in those established at low density (41–54 per cent) and lowest in plots planted at high density and with the Lp pasture mixture in 1995 (27 per cent) (Figure 7). The lowest number of species shared was found between systems established at high density with the Dg pasture mixture in 2005 (1 species), while in the rest of comparisons, species shared ranged from 12 to 18.

Discussion

Although both tree species considered here are regarded as pioneers, from the beginning of the experiment the growth of pine was higher than that of birch. Pine in the present study also exhibited a higher growth rate than that found in the same species in Galicia (Sánchez et al., 2003), likely due the better edaphic conditions of the former site (Mosquera-Losada et al., 2006), but lower than that described in New Zealand (Lavery, 1986) due to the restriction of growth in our area caused by the summer drought period. Downy birch tree growth rate in the present study was similar to both that reported by Diéquez-Aranda et al. (2006) in Galicia and by Karlsson et al. (1998) in Sweden. However, the development of both tree species was very sensitive to planting density. In pine plots, a high planting density increased tree height growth and decreased tree diameter growth. In contrast, birch development (height and diameter) was reduced by a higher planting density because, being a light-demanding tree species, its crown development and stem growth are retarded when growing at high densities (Hynynen et al., 2010), resulting in a very slender stem form.

Because of the change in tree growth rhythms and densities, the quantity and the proportions of the components of the AB varied during the course of the study. With respect to quantity, the results showed an important reduction of AB in systems established under low planting density birch in 2005 compared with 1995, while under pine, AB increased independent of planting density. In the case of birch, the observed reduction in AB may reflect the fact that birch has a dense root system (Ostonen et al., 2007) whose development is favoured by a lower planting density (Aphalo and Rikala, 2003), thus increasing the competition for water and nutrients between tree and aboveground biomass. Canopy closure in P. radiata stands is known to take place early (5 years after planting in this case) when this species is established at high density (Rigueiro-Rodríguez et al., 2011), with subsequent greater needle fall (PL) therefore contributing to increased AB. However, the high proportion of needles within this AB then reduces the possibility for most of the litter to be used for livestock feeding, thus reducing the short- and medium-term revenues that can be obtained in these systems. Recent research carried out in our region (Fernández-Núñez et al., 2007;2009; Pasalodos-Tato et al., 2009) has shown that the minimum amount of HA required to feed one sheep per hectare per year – and therefore the minimum HA production required to generate income for the farmer – is $0.3 \text{ Mg DM ha}^{-1}$. During the first 5 years of the present study (1995-2000), the relative proportion of aboveground biomass components was HA > HS > PL, with the concentration of HA > 0.3 Mg DM ha⁻¹ in all treatments potentially beneficial to farmers if a livestock production system were to be established. In the last year of the study, HA levels remained sufficient for feed production, both in plots under birch canopy independent of tree density and mixture, and in plots under pine at low planting density. However, in the silvopastoral system established with pine at high density, the results showed HA production to be drastically reduced in 2005 to levels insufficient for livestock feed production, reducing the benefits for farmers unless a large area were to be used. Such a system would be difficult in Galicia where the farm units are typically minifundia. It is important to also consider the nutritional quality of this forage for animal feeding. Reductions in quality often take the form of lower protein content, feed digestibility or even reduce intake by the animal. In this sense, our results showed that D. glomerata was the species with the highest abundance in the last year of the study in all systems. Previous research showed that crude protein content and macronutrient concentrations of D. glomerata increase slightly with shade level and digestibility values were not greatly influenced by shade in silvopastoral systems established with P. radiata in New Zealand (Peri et al., 2007). However, the presence of species such as L. perenne, Trifolium sp, were drastically reduced in the last year of the study; and therefore, nutritive qualities were diluted by the increased abundance of shade tolerant species such as A. capillaris, and invasive weeds





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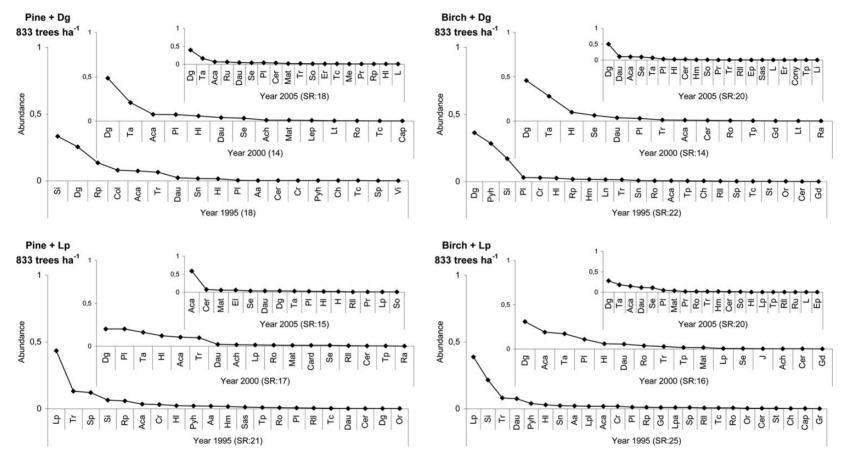


Figure 6 Abundance diagrams corresponding to the 3 years of data collection (1995, 2000 and 2005) in the systems established under pine and birch trees, for a planting density of 833 trees ha^{-1} and each pasture mixture. SR = Species richness; Dg = plots sown with cocksfoot; Lp = plots sown with ryegrass. Species codes are shown in Supplementary data Table S1.

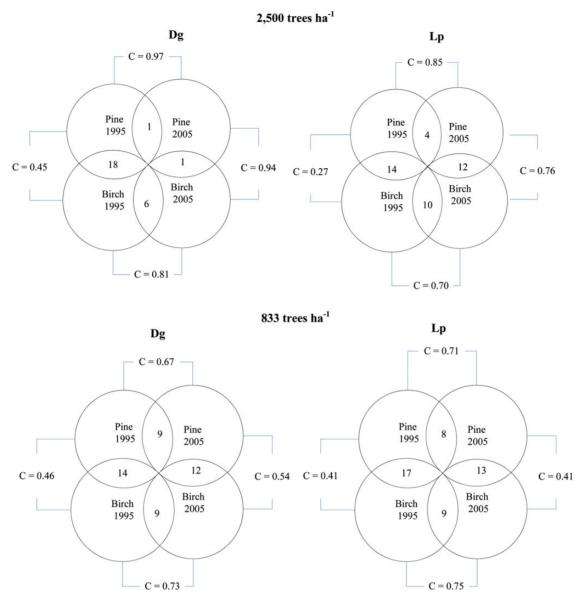


Figure 7 Venn diagram illustrating values of the complementarity index (C) between systems. Overlap indicates shared species. Index values range from 0 (species lists of two vegetation types are identical) to 1 (no species shared).

with low nutritive value such as *S. jacobea* (Suter *et al.*, 2007); *T. officinale* and *Chamomilla recutita* resulting in a reduction of forage quality in the systems.

The initial disturbances experienced in the systems (e.g. ploughing, grading etc.) and the higher initial radiation input to the soil (Diaz-Villa et al., 2003) could explain the increased presence of annual species in the first year of the study (1995) in all treatments. However, 5 years after plot establishment, the development of trees likely reduced light levels (Papanastasis, 2004), intercepted precipitation (Moreno *et al.*, 2005) and increased competition for soil nutrients and water (Maltez-Mouro *et al.*, 2005), as well as creating a shadier environment that inhibited the presence of annual species and favoured that of perennial species since the latter are more shade tolerant. Several authors have concluded that planting coniferous tree species rather than native hardwoods reduces species richness (Amezaga and Onaindia, 1997), since coniferous litterfall (PL) decomposition (higher lignin and lower nitrogen concentrations) may be slower than that of deciduous species (Augusto *et al.*, 2003), while needle accumulation reduces plant development due to drought (Barbier *et al.*, 2008). Given these assertions, we expected to observe clear differences in alpha plant biodiversity between pine and birch treatments due to the high PL production found in 2005 in plots under pine canopy. However, these differences were only observed in high planting density pine plots, which may reflect early canopy closure according to Abella and Covington (2007) and Rigueiro-Rodríguez *et al.* (2011), who found shading to be more important than litter in suppressing aboveground

vegetation. It should also be taken into account that under full canopy closure, PL accumulation is likely higher due to the low incorporation rate caused by the low temperatures and high humidity experienced under these conditions. In the case of the other three systems studied (pine at low density, and birch at low and high density), the effect of tree growth on aboveground composition was very similar 10 years after afforestation (2005), both in terms of the number of species identified and the percentage of species that disappeared, appeared and coincided during the study. Thus, species such as Anthemis arvensis L., Chenopodium album L., Crepis capillaris (L.) Wallr, Ornithopus compressus L., Polygonum hydropiper L. Silene gallica L., Solanum nigrum L. and S. arvensis L. disappeared from all three systems in 2005, while species such as C. recutita L., Prunella vulgaris L., Senecio jacobaea L. and T. officinale Weber appeared in all three only in 2005. Furthermore, the percentage of monocot species coinciding in these three silvopastoral systems remained the same throughout the study; in all the three families with the greatest representation in 1995 were Leguminosae and Poaceae, while in the last year of the study the most commonly represented families were Compositae and Poaceae. The similarities in SR and species composition shared by plots under pine planted at low density and those under birch (at both high and low density) throughout the study therefore suggest that the choice of canopy tree results in similar consequences for understorey biodiversity, at least after 10 years. Similar results were found by Soo et al. (2009) in silver birch (2113 trees ha^{-1} and 7 years old) and hybrid aspen (1110 trees ha^{-1} and 9 years old) plantations established in Estonia; in the latter study the reported average SR was 15, compared with an average of 14 species found in this study.

On the other hand, the reduction in alpha biodiversity observed after the beginning of the experiment was more significant in systems sown with the Dg pasture mixture than in those with Lp. This may be a result not only of greater tree development found in these plots, increasing competition for resources between trees and pasture, but also because of the low persistence of L. perenne when compared with D. glomerata.

Typically, plantations of exotic tree species (in this case, Monterey pine) have been criticized for having little relevance as a habitat for biodiversity, in contrast with that normally associated with native tree species (Downy birch) (Quine and Humphrey, 2009). In our case, this negative effect was obtained in a relatively short period of time (11 years), but only where Monterey pine had been established at high density, thus highlighting the importance of the initial choice of canopy density and/or adequate thinning programs from the point of view of vascular plant biodiversity. Silvopastoral systems established at low planting density showed similar alpha and low beta rates throughout the study. These results could be explained by the greater light availability and lower litterfall accumulation occurring in plots planted at this density, since it is widely known that a reduction in light availability due to tree development is the most important mechanism influencing understorey species composition. As has previously been documented (Riqueiro-Rodríguez et al., 2011), the establishment of coniferous plantations at high density creates harsh understorey conditions, since their dense canopy decreases light transmission while the high rate of litterfall accumulation does not allow vascular plants to develop. In the present study, this process contributed to reduce alpha biodiversity and increase beta biodiversity 11 years after initial afforestation. A higher density of pine trees brings about the need for correct management, e.g. thinning. Research has shown that thinning typically reduces the ground cover of litter and increases the amount of soil exposed to light, thus creating a favourable habitat for colonizing vascular plants (Wolk and Rocca, 2009). Recent studies carried out in Galicia with P. radiata plantations established on agricultural land (Castedo-Dorado et al., 2009) have recommended that the first thinning should be carried out after 8 years when this particular species is planted at high density.

Furthermore, and as noted in our introduction, the Galicia region is characterized by an abundance of forest fires, which spread easily in high-density systems. In this sense, Monterey pine thinning reduces fire risk because it both increases soil water content in the short-term and reduces needle fall (Harrington and Edwards, 1999).

Conclusion

Downy birch development was reduced at high density and thus understorey biomass increased in these plots. High planting densities favoured Monterey pine height and reduced diameter growth, while above around biomass increased in the form of needle fall, independent of tree density. The herbaceous live component, used for livestock feeding and therefore beneficial to farmers, was strongly reduced in plots under Monterey pine planted at high density. The severe conditions created by high-density Monterey pine growth (decreased light transmission, increased litter accumulation) also contributed to reduced alpha biodiversity and increased beta biodiversity when compared with levels at the beginning of the study. However, plots established under downy birch (high or low density) or Monterey pine at low density exhibited similar alpha and low beta index values throughout the study. This study has demonstrated that tree canopy density is a crucial characteristic to be taken into account when establishing a silvopastoral system with a coniferous species such as Monterey pine. At high density this species' development reduced the herbaceous live component, simplified understorey flora and led to a decrease in species richness. However, in a low density Monterey pine plantation these negative impacts were lessened, with disturbances in the community considerably reduced to levels similar to those observed in deciduous plantations. Future research should be designed to test different thinning regimes in these and other plantation systems, providing information regarding the response of variables such as soil pH, aboveground biomass and biodiversity.

Supplementary data

Supplementary Material is available at Forestry online.

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Conflict of interest statement

None declared.

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Appendix A

Pine: Birch: Dg: Lp: AB: HA: HS: PL:	Pinus radiata D. Don (Monterey pine) Betula pubescens Ehrh. (Downy birch) Pasture mixture Dactylis glomerata L. + clovers Pasture mixture Lolium perenne L. + clovers Annual aboveground biomass Herbaceous alive component Herbaceous senescent component Pine litterfall
	•
SR:	Species richness
H':	Shannon – Weaver index