Forest Ecology and Management 269 (2012) 214–221

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Invasion of alien *Acacia dealbata* on Spanish *Quercus robur* forests: Impact on soils and vegetation

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ARTICLE INFO

Article history:
Received 3 August 2011
Received in revised form 12 December 2011
Accepted 19 December 2011
Available online 2 February 2012

Keywords:
Alien species
Acacia dealbata
Quercus robur
Soil seed bank
Established vegetation
Floristic composition

ABSTRACT

Invasive tree *Acacia dealbata* was introduced in the Iberian Peninsula in the 19th century. Nowadays, it is spreading in wide areas in which native vegetation has been altered or removed by human-activities, as in the case of *Quercus robur* forests in the northwest of Spain. In this article we assess the impact of *A. dealbata* invasion on soil properties (pH, organic matter, total N, NH_4^+-N and NO_3^--N), light characteristics (direct and diffuse photon flux density and leaf area index) and soil seed bank and established vegetation. We selected three sites where native *Q. robur* forests and *A. dealbata* invaded patches grow nearby. Before 2008 autumn rains, we took soil samples under five trees per species (*A. dealbata* and *Q. robur*) and site to determine soil seed bank floristic composition and soil properties. In spring 2009 we monitored the floristic composition of the vegetation growing under the same trees. Our results show that *A. dealbata* presence increases total N, NH_4^+-N and NO_3^--N and decreases pH in soils but does not affect light characteristics. *Acacia dealbata* modifies soil seed bank composition by decreasing species richness, seed density and the percentage of bryophyte and fern spores, and by increasing the percentage of *Asteraceae* and exotic species. Understorey of invaded *A. dealbata* forests shows a decrease in species richness and plant cover. Finally, *A. dealbata* reduces the similarity between the soil seed bank and the established vegetation. These results suggest that *A. dealbata* invasion produces a deep impact on *Q. robur* forests that hampers their regeneration, even after *A. dealbata* removal.

1. Introduction

Invasive plant species constitute a major environmental problem, as they have profound consequences on biodiversity conservation and on ecosystem processes and functioning (Parker et al., 1999; Levine et al., 2003).

The impacts of invasive plant species on the abiotic characteristics of the ecosystems have been widely studied in the literature of biological invasions (e.g., Vanderhoeven et al., 2005; Ehrenfeld et al., 2001; Evans et al., 2001; Ehrenfeld, 2003; Griffiths et al., 2005). Those impacts can be aggravated if the exotic species introduces a new functional type in the invaded community, such as the ability of N-fixation (Vitousek and Walker, 1989; Mack, 2003) or the production of allelopathic compounds, according to "The novel weapon hypothesis" (Callaway and Aschehoug, 2000). However, the introduction of an exotic species in a territory not only has consequences on the abiotic characteristics of the environment, but also on the floristic composition of the plant communities of the invaded areas. These changes in the invaded community can be due to a reduction of native species richness or diversity and to an increase in the exotic vegetation (see the review of Levine et al., 2003).

One of the elements that can be affected by changes in the native community, and can severely compromise the regeneration of the local flora, is the soil seed bank. A well-preserved soil seed bank is determinant to ensure the persistence of a community in a territory (Bakker et al., 1996). The introduction of a new species can affect the soil seed bank composition by altering the propagule supply or by altering the seeds viability. These changes in the composition of the soil seed bank can have serious consequences for the regeneration of the native community and must be taken into account in prospective plans of ecosystem conservation and restoration. Previous studies show that the presence of invasive species generally diminishes species richness in the soil seed bank (Holmes and Cowling, 1997; Mason et al., 2007; Giantomasi et al., 2008; Marchante et al., 2011). For instance, Gioria and Osborne (2010) compared the effect of three invasive grass species (*Fallopia japonica*, *Gunnera tinctoria* and *Heracleum mantegazzianum*) on soil seed bank and established vegetation sampled in different habitats of Ireland, and found a common tendency to the depletion and homogenization of the soil seed bank through species with long-lived and persistent seeds. On the contrary, Vilà and Gimeno (2007) did not find differences in the richness of soil

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doi:10.1016/j.foreco.2011.12.026

seed bank between non-invaded and invaded sites by the exotic grass *Oxalis pes-caprae* in Menorca (Balearic Islands). Finally, previous studies agree in a persistent low similarity in floristic composition between the soil seed bank and the established vegetation between invaded and non-invaded sites (Holmes and Cowling, 1997; Mason et al., 2007; Vilà and Gimeno, 2007; Giantomasi et al., 2008).

Australian species of the genus *Acacia* are very common invaders in many parts of the world where they provoke deep impacts in the structure and function of ecosystems and, hence, in the services that those ecosystems provide to societies (Le Maitre et al., 2011). *Acacia dealbata* Link, which has been reported to have an "extremely high invasive potential" (Wilson et al., 2011) is widely spread in America (Chile and California), Africa (South Africa and Madagascar) and Europe, especially in France, Spain and Portugal (Richardson and Rejmánek, 2011). In Chile, Fuentes-Ramírez et al. (2010) found that *A. dealbata* changed the floristic composition and reduced species richness in the invaded native forests of *Nothofagus oblique* and, in South Africa, Coetzee et al. (2007) described the negative impact that *A. dealbata* invasion provoked on Coleoptera species diversity. In Europe, despite the large areas currently invaded by *A. dealbata* (Lorenzo et al., 2010a), little is known about the effect of this species on the invaded plant communities.

In the northwest of the Iberian Peninsula, *A. dealbata* spreads throughout abandoned agriculture lands, cleared areas after fires, road limits and also throughout the native forests of *Quercus robur* L. affected by human activities (Sanz Elorza et al., 2004). Previous studies have shown that *A. dealbata* increases the amount of potentially available nitrogen, total nitrogen and organic carbon in invaded soils of different ecosystems of northwest of Spain (Lorenzo et al., 2010b). It has been also shown that *A. dealbata* produces allelopathic compounds able to interfere in the germination of native species (Lorenzo et al., 2008). However, there are not previous published studies referring to the consequences of *A. dealbata* invasion on the seed bank and floristic composition of the European native forests.

The aim of this study is to evaluate the effect of the invasion of the exotic tree *A. dealbata* on the abiotic and biotic characteristics of the invaded sites, in comparison with non-invaded adjacent forests of the native tree *Q. robur* in Spain. For this purpose, we evaluated the effect of the invasion of *A. dealbata* on soil properties (pH, organic matter, total N, NH_4^+-N and NO_3^--N) and on the quantity and quality of the light that reaches the soil. We also assessed the effect of *A. dealbata* on the floristic composition of the soil seed bank and the established vegetation. Finally, we evaluated the similarity between the floristic composition of the soil seed bank (potential vegetation) and that expressed in the established vegetation in both native and invaded sites. Our hypothesis is that a higher amount of nitrogen, organic matter and a lower pH will be found in the soils of the invaded forests, as previously reported. We also expect differences in the floristic composition between native and invaded sites, at both the seed bank and the established vegetation levels, with poorer communities in the invaded ones. Finally, we expect a low similarity between the soil seed bank and the established vegetation, especially in the invaded patches.

2. Material and methods

2.1. Study area and species

The study was carried out in the province of Ourense (NW of Spain). We selected three sites where invaded patches of *A. dealbata* grow close to native patches of *Q. robur*: Table 1 shows general characteristics of the three sites: Esposende, Poulo and Merens. All sites share similar macroclimatic conditions and are located in the riverside of the Miño river. The maximum distance between points was 29 km. Sites were selected following three criteria: (1) presence of continuous-homogenous patches of *A. dealbata* or *Q. robur*, (2) majority of adult trees and (3) absence of signs of previous uses (crops, wine plantations, recent fires) or vicinity to roads and tracks that could affect the soils and vegetation. Information about the origin of the invasion in the sites is missing, so we selected only sites in which local population confirmed absence of cultivation for 50 years at least. The three sites presented ustorthent soils, characterized by being immature, lacking the vertical development of horizons and presenting limited moisture (Gómez-Miguel, 2006; Soil Survey Staff, 2010).

Table 1
Geographical coordinates and mean altitude of the three sites.

Site	Longitude	Latitude	Altitude (m)
Esposende	42°20′19.65″N	8°6′42.41″O	205.1
Merens	42°14′5.32″N	8°9′52.85″O	165.1
Poulo	42°12′15.55″N	8°5′47.38″O	465.9

The climate is Atlantic with strong Mediterranean influence, as the area is located in the border of the Eurosiberian and Mediterranean Regions (Rivas-Martínez, 1987). The mean annual maximum temperature is 20.9 °C and the mean annual minimum temperature is 8.4 °C. Mean annual rainfall is 670 mm (data from Orense weather station, Instituto Nacional de Meteorología, 1972–2007).

The native vegetation is dominated by *Q. robur* forests that constitute the climatophilous vegetation type of the Eurosiberian Region. *Quercus robur* is a deciduous tree that grows on slightly acid, deep, fresh soils. It is a frost tolerant species that can resist short periods of drought. It forms mixed forest with other trees as *Castanea sativa* Mill., *Laurus nobilis* L. and, in the warmest areas, *Quercus suber* L. In some places it co-dominates the landscape with *Pinus pinaster* Aiton. *Quercus robur* also appears associated to shrub species as *Ruscus aculeatus* L., *Tamus communis* L., *Rhamnus alaternus* L., *Arbutus unedo* L., *Crataegus monogyna* Jacq. and *Ilex aquifolium* L. among others (Izco, 1987; Blanco Castro et al., 2005). This native vegetation has been profoundly transformed by human activities, especially due to the quality of the soils for the establishment of wine crop fields (Sanz Elorza et al., 2004), to the quality of *Q. robur* wood for the navy industry and also because of the recurrent fires in the area (Izco, 1987; Blanco Castro et al., 2005). At present, *A. dealbata* is widely spreading in road limits, agricultural land borders and abandoned fields and, in general, in all those areas where native vegetation has been totally or partially removed.

A. dealbata is original from the southeast of Australia and was introduced in the Iberian Peninsula in the second half of the 19th century (Sanz Elorza et al., 2004). It is a leguminous, non-deciduous, fast growing species, no frost resistant, with preference for acid soils. The *A. dealbata* resprouting ability and its pyrophyte seeds allow this species to easily establish after fire (Sanz Elorza et al., 2004). *Acacia dealbata* is able to develop symbiotic associations with N-fixing bacteria of the genus *Rhizobium* (Brockwell et al., 2005). It also produces allelopathic leachates (Carballeira and Reigosa, 1999; Lorenzo et al., 2008).

2.2. Experimental design

2.2.1. Soil seed bank

In each of the three sites we selected five adult and healthy trees of *Q. robur* (in the native forest) and of *A. dealbata* (in the invaded sites). In September 2008, before the autumn rains, we collected five soil samples randomly distributed under each tree canopy by using plastic cylinders (7.5 cm diameter × 10 cm depth) which included the upper layer of soil where the seed bank is mainly concentrated (Godefroid et al., 2006). The soil was air dried in the laboratory where debris and stones were removed. To compare the ability of regeneration by seeds of each dominant species, we calculated their seed production by counting the number of *A. dealbata* seeds and of *Q. robur* acorns contained in each soil sample, expressing this by surface unit. Then, soil seed bank samples were spread into a total of 636 pots (60 × 70 × 73 mm) for germination. Each pot was filled up to 2.5 cm with vermiculite. This layer was covered with a cotton gauze to separate the vermiculite from the soil sample. We removed the *Q. robur* acorns before adding the soil to the pots due to their big size. We also included five control pots with sterile substrate (15-10-20 NPK – Kekkilä Iberia S.L., Valencia, Spain), randomly arranged. From November 2008 to September 2009 the experimental pots were kept under greenhouse conditions at the Botanical Garden Juan Carlos I (Alcalá University, Madrid, central Spain, 40°30′N, 3°20′W, 596 m.a.s.l). Windows at the greenhouse were opened automatically under temperatures higher than 20.5 ± 2 °C. The pots were initially watered to field capacity. Since then, watering was provided when needed. We performed weekly samplings by counting emerged seedlings in each pot until September 2009. Plants were removed after fructification for identification at the laboratory. Non-annual plants that required more time to flower where transplanted to bigger pots until they acquired morphological attributes that allowed us to identify. To compare the differences in the seed bank composition under *A. dealbata* and *Q. robur* we calculated the species richness, seed density (number of emerged seedlings/m^2), percentage of *Asteraceae* species, percentage of exotic species and presence or absence of bryophytes and ferns.

2.2.2. Soil analysis

In September 2008, we also collected three 225 mm deep by 54.5 mm diameter soil cores under the same trees, next to the point where the soil seed bank samples were taken. Soil samples were transported to the laboratory in sealed plastic bags and dried at room temperature, pooled into a single composite sample per tree and passed through a 2 mm sieve to eliminate remaining debris and stones. A fraction of the pooled soil was kept for the analysis of soil pH, percentage of organic matter, mineral nitrogen (NH_4^+-N, NO_3^--N) and total nitrogen content (N_T). Soil pH was measured with a pHmeter (micropH 2001, Crisor Instruments, Barcelona, Spain) following Allen et al. (1986) procedures. Percentage of organic matter in soil was assessed by the Walkley–Black acid digestion method (Porta Casanellas et al., 1982). Total nitrogen content was analyzed at Nutrilab (University of Rey Juan Carlos I, Móstoles, Madrid, Spain) with a segmented flux autoanalyzer (S.F.A.S. Skalar San ++.), after a digestion with H_2SO_4 and $CuKSO_4$. This digestion converts all organic nitrogen into ammonium (NH_4^+-N). Mineral nitrogen content was extracted by shaking for 2 h a solution of 5 g of soil in 100 ml KCl 2 N. The solution was passed through a 0.45 μm Millipore filters and preserved at −20 °C until analysis of NH_4^+-N and NO_3^--N at Nutrilab, also with a segmented flux autoanalyzer (S.F.A.S. Skalar San ++.).

2.2.3. Light analysis

To evaluate the characteristics of the light that passes through *Q. robur* and *A. dealbata* canopies and reaches the soil, we took two hemispherical photographs under each tree (Nikon Coolpix 4500 with a Nikon Fisheye Converter FC-E8 0.21×). Pictures were taken in September 2008 at dusk. The distance between the trunk and the camera was enough to photograph the whole crown of each tree. The camera was attached to a tripod fixed at 1 m above ground. Pictures were analyzed using the Winphot 5 (Hans ter Steege, Utrecht University, 1996) hemispherical photograph analysis computer program. This program was used to calculate the percentage of canopy openness, the direct and diffuse photosynthetic photon flux density (PPFD-dir and PPFD-dif, mol/m^2 and day) and the leaf area index (LAI, m^2/m^2).

2.2.4. Established vegetation

In June 2009, and under the same trees, we sampled the floristic composition of vegetation. The sampling was conducted in June because most of the species flower during this month. We evaluated the species richness and the plant cover in five 50 × 50 cm quadrats randomly distributed under the canopy of each tree. We identified each species and estimated its cover by establishing six categories: 1 (<5%), 2 (5–10%), 3 (10–25%), 4 (25–50%), 5 (50–75%) and 6 (75–100%). Final plant cover under each tree was calculated as the average cover of each species in the five quadrats. Plant samples were harvested to be identified at the laboratory if needed (Tutin et al., 1964–1980; Castroviejo et al., 1986–2006; Valdés et al., 1987; Aizpuru et al., 1999; Romero Buján, 2008).

Finally, we estimated the Jaccard index of similarity (β_j =number of shared species/total number of species, Jaccard, 1912) to evaluate the similarity between the floristic composition of the soil seed bank and the floristic composition expressed in each forest. This index ranges from 0 to 1, being 0 the minimum similarity between the soil seed bank and the established vegetation and 1 the maximum similarity.

2.3. Data analysis

Non-Metric Multidimensional Scaling (NMS) analyses were performed to explore the main variation trends in the floristic composition of the soil seed banks and of the vegetation under the canopies of both species. We used the Sorensen index to locate each tree in the dimensional space in the position that minimizes the fit measure, called stress. NMS were conducted with the program PC-ORD 4.25 (MjM Software, Gleneden Beach, Oregon, USA). To interpret the meaning of the axes of the ordination obtained with the NMS, and to elucidate if our treatments are responsible for the main variation of the data, we performed two-way ANOVAs on the scores obtained by the axis 1 and 2 of both ordinations, being species (*A. dealbata*–*Q. robur*) and site (Poulo, Esposende, Merens) fixed factors.

We performed two-way ANOVAs to evaluate the effect of species and site on the soil properties (pH, percentage of organic matter, N_T, NO_3^--N and NH_4^+-N), on the soil seed bank characteristics (species richness, plant density and percentage of *Asteraceae* species), on the species richness of the understorey, on the seed production of both dominant species and on the measured light variables (percentage of canopy openness, PPFD-dir and PPFD-dif and LAI). We used *post hoc* Tukey tests to evaluate the differences between groups. Levene tests were performed to check for homoscedasticity assumptions.

Kruskal–Wallis tests were performed to assess the effect of species and site on the percentage of exotic species emerged in the soil seed bank, on the plant cover under *A. dealbata* and *Q. robur* canopies and on the Jaccard index of similarity, as the data did not follow a parametric distribution. We used Bonferroni *post hoc* tests to evaluate differences between groups. Finally, a Chi-square test was used to evaluate differences between *A. dealbata* and *Q. robur* species and between sites in the presence of bryophyte and fern spores in the soils.

All statistics tests were performed using SPSS 17.0 (SPSS, Inc.).

3. Results

3.1. Soil properties and light availability

There were significant differences among native and invaded forests in all the soil characteristics under study (Fig. 1, Table 2). Soils were more acidic under *A. dealbata* (Fig. 1). On average, the percentage of organic matter, as well as N_T, NO_3^--N and NH_4^+-N

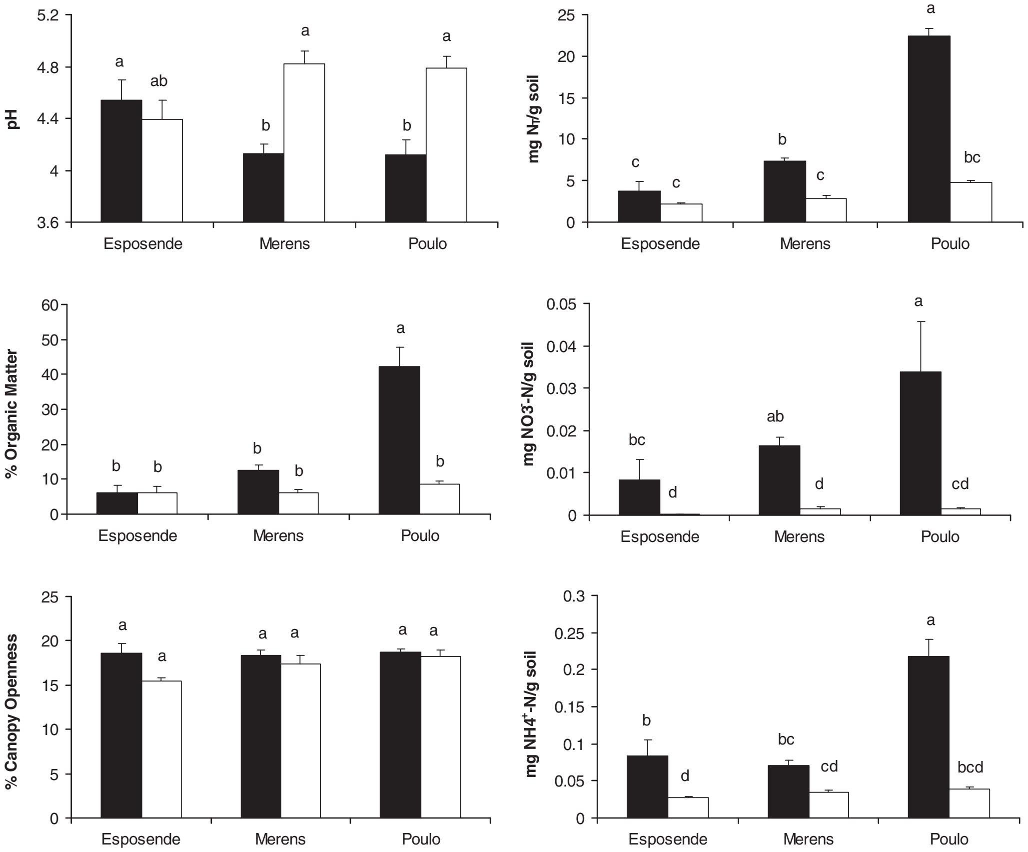

Fig. 1. Mean values + SE of pH, percentage of organic matter, percentage of canopy openness and mg of N_T, NO_3^+-N and NH_4^--N/*g* soil under the canopies of *Acacia dealbata* (black bars) and *Quercus robur* (white bars) in each site. Different letters represent differences between groups, according to *post hoc* Tukey tests ($p < 0.05$).

Table 2
Results of two-way ANOVAs assessing the effect of species (*Acacia dealbata–Quercus robur*) and site (Esposende–Merens–Poulo) on soil properties: pH, percentage of organic matter (% OM), soil mineral nitrogen (NH_4^+-N, NO_3^--N) and total nitrogen (N_T) ($N = 30$).

	pH		% OM		NH_4^+-N		NO_3^--N		N_T	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Species	17.35	0.001	50.73	0.001	80.55	0.001	103.88	0.001	213.06	0.001
Site	0.02	0.978	38.87	0.001	14.46	0.001	14.02	0.001	129.98	0.001
Species ∗ Site	8.05	0.002	28.27	0.001	7.80	0.002	0.60	0.557	75.56	0.001

were higher under *A. dealbata* canopies, this effect being more intense in Poulo except for NO_3^--N (see the significant interaction between species and site, Table 2). The differences between species in the soil characteristics were weaker in Esposende than in the other sites (Fig. 1, Table 2). Finally, there was no effect of species or site on any of the studied light variables ($p > 0.05$; see Fig. 1 for percentage of canopy openness and Appendix 1 for average values of light variables).

3.2. Soil seed bank

A total of 1990 seedlings emerged in the soil seed bank samples. We identified 1172 of them up to the species level (59 species), 497 up to the genus level (10 genera) and 150 up to the family level (*Asteraceae* and *Poaceae*) (see Appendix 2). Only 8.5% of the seedlings remained unidentified due to early deaths. Soil seed banks of *Q. robur* included 62 taxa, being the most abundant *Digitalis purpurea* L., *Anagallis arvensis* L. and species of the genus *Veronica* and *Conyza* as well as species of the family *Poaceae*. We identified 43 taxa in *A. dealbata* soil seed banks. The most abundant species belonged to genus *Conyza*, followed by *A. dealbata* itself.

The NMS performed on the floristic composition of soil seed banks data showed an effect of both species and site (Fig. 2a), with axis 1 reflecting the principal variability trend. The effects of species and site were confirmed by the ANOVA performed on the coordinates of axis 1 (Species: $F_{1,30} = 49.59$, $p = 0.001$; Site: $F_{2,30} = 6.99$, $p = 0.004$; Species ∗ Site: $F_{2,30} = 20.33$, $p = 0.001$). Site had a bigger effect on *Q. robur* than on *A. dealbata* seed bank floristic composition, as all trees of the exotic species appear close in the ordination, independently of the site.

Species richness and seed density of soil seed banks were higher under *Q. robur* canopies (Fig. 3, Table 3) in two of the sites, this effect being more intense in Merens (see significant interaction between species and site, Table 3). The percentages of *Asteraceae* and exotic species were higher under *A. dealbata* canopies, with a significant interaction between species and site in the latter, as the effect was more intense in Merens (Fig. 3, Table 3). We also found more *A. dealbata* seeds in the invaded sites than *Q. robur* acorns in the native forests (the means were 28669.48 *Acacia*

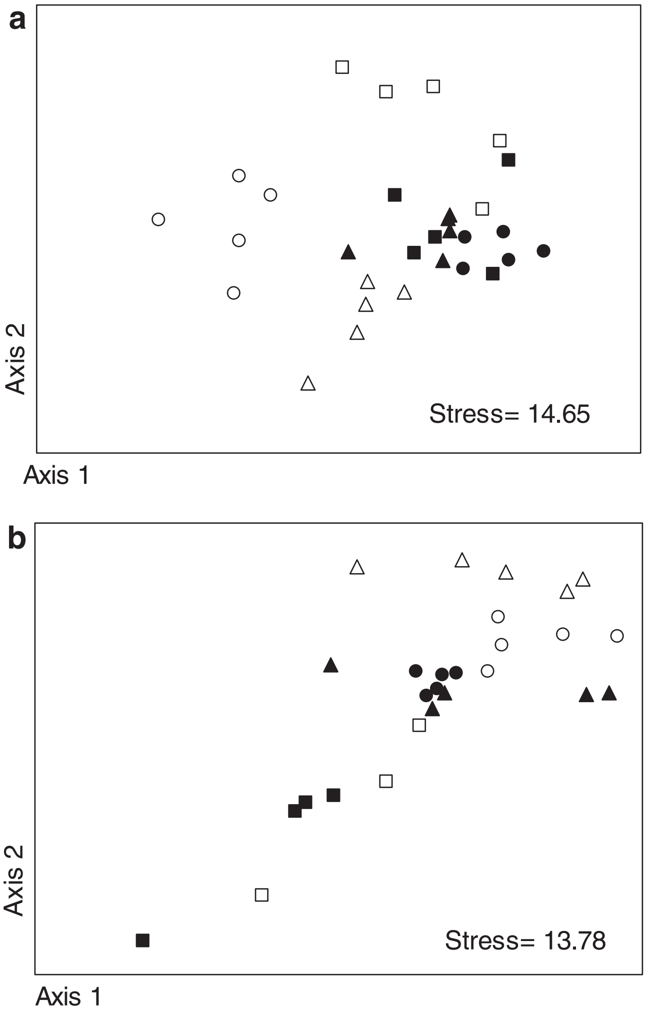

Fig. 2. (a) Results of the NMS ordination of the floristic composition of the soil seed banks. (b) Results of the NMS ordination of the floristic composition of the under-canopy vegetation. Each color represents a species (black: *Acacia dealbata* and white: *Quercus robur*). Each symbol represents a site (Triangles: Poulo; dots: Merens and squares: Esposende).

seeds/m^2 and 1022.05 acorns/m^2, Table 3). Finally, a higher percentage of bryophytes and ferns emerged from spores in the soils of native *Q. robur* forests. Bryophytes and ferns appeared in 74.68% of soil samples of native forests whereas they appeared only in 40% of the samples of the invaded soils (Chi-square test, $\chi^2_{2,2} = 70.33$, $p = 0.001$). There were not differences between sites in the percentage of soil samples with presence of bryophytes and ferns (Chi-square test, $\chi^2_{2,3} = 1.69$, $p > 0.05$).

3.3. Established vegetation

We identified 31 different species and two genera (*Rosa* sp. and *Ulex* sp.) in the established vegetation of native and invaded forests, being 25 species and the two genera represented under *Q. robur* canopies and only 12 species under *A. dealbata* (see Appendix 2). The most abundant species grown under both canopies were *Hedera helix* L., *Rubus ulmifolius* Schott, *Lonicera periclimenum* L. and *Pseudarrhenatherum longifolium* (Thore) Rouy. The NMS performed with data of floristic composition of the established vegetation showed, as in the case of soil seed banks, an effect of species and site (Fig. 2b). We tested this effect with a two-way ANOVA on axis 2 coordinates (Species: $F_{1,27} = 14.09$, $p = 0.001$; Site: $F_{2,27} = 44.33$, $p = 0.001$; Species $*$ Site: $F_{2,27} = 2.25$, $p = 0.130$).

Species richness and plant cover of the established vegetation were higher under *Q. robur* than under *A. dealbata* canopies (Fig. 4, Table 4), this effect being stronger in Poulo and Merens (see species and site interaction in Table 4).

3.4. Similarity between the soil seed bank and the vegetation

There was a significant effect of species on the similarity between the floristic composition of the soil seed banks and the established vegetation ($H = 5.37$, $p = 0.02$), this similarity being higher in *Q. robur* forests (Fig. 5). Only 14.5% of the species present in *Q. robur* soil seed banks was expressed in the established vegetation (*Centaurea nigra* L., *H. helix* L., *Lithodora prostrata* (Loisel.) Griseb., *R. ulmifolius* Schott., *Rumex acetosa* L., *Stellaria holostea* L., *Teucrium scorodonia* L., *Ulex minor* Roth. and *Viola riviniana* Reichenb.) whereas this percentage decreased to 7% in the case of *A. dealbata* (*H. helix*, *R. ulmifolius* and *Sonchus oleraceus* L.).

4. Discussion

Our results show that *A. dealbata* invasion of native *Q. robur* forest of NW Spain modifies the biotic and the abiotic component of this ecosystem. Soil properties are affected through an increase in nitrogen availability and a decrease in pH (Table 2, Fig. 1), which agrees with previous studies (Lorenzo et al., 2010b). In general, soils of native oak forests are oligotrophic or mesotrophic (Hardtle et al., 2005), and in Galicia they are considered poor in nutrients (Díaz-Maroto and Vila-Lameiro, 2007; Díaz-Maroto et al., 2009). An increase in soil nitrogen can imply a great impact for these communities, as it favors the spread of fast-growing exotic species to the detriment of the native species adapted to nitrogen poor ecosystems (Vitousek and Walker, 1989). In this sense, we found a higher percentage of exotic species in the soil seed banks under *A. dealbata* canopies than under *Q. robur* (Table 3, Fig. 3). Most of the exotic species that emerged in the *A. dealbata* seed banks (65%) belonged to the genus *Conyza*. The exotic species of this genus currently spreading in the Iberian Peninsula are annual, herbaceous, wind-dispersed and nitrophylous plants, generally favored by open, removed areas (Sanz Elorza et al., 2004). The association between *A. dealbata* canopies and the increase of exotic species agrees with the "invasional meltdown hypothesis" (Simberloff and Von Holle, 1999), which suggests that the presence of exotic species in a certain territory can facilitate the establishment of new exotic species. In any case, soil enrichment by *A. dealbata* forests can result in the facilitation of nitrophilous species, thus changing microbial systems and plant communities (Le Maitre et al., 2011). The increase in the amount of exotic species was also observed by Marchante et al. (2011) in Portuguese dune ecosystems invaded by the congeneric *Acacia longifolia*, with also species of the genus *Conyza* dominating recently invaded sites (<20 years).

Acacia dealbata decreased the species richness of the soil seed bank and the species richness and abundance of the established vegetation, in comparison with the native forests (Tables 3 and 4; Figs. 3 and 4). Similar results were found by Fuentes-Ramírez et al. (2010) in native forests of the south-center of Chile invaded by *A. dealbata*. We believe that this may be determined by the structure of this species forests. *Acacia dealbata* is a heliophilous tree whose stems grow in any direction, not only vertically, being possible to find tree canopies at different heights (*personal observation*). It also produces big leaves, which with the tortuous growth of the trunks, can block the arrival of seeds from adjacent areas. The seeds that can overcome the physical barrier established by *A. dealbata* canopies must be able to reach the soil, which is

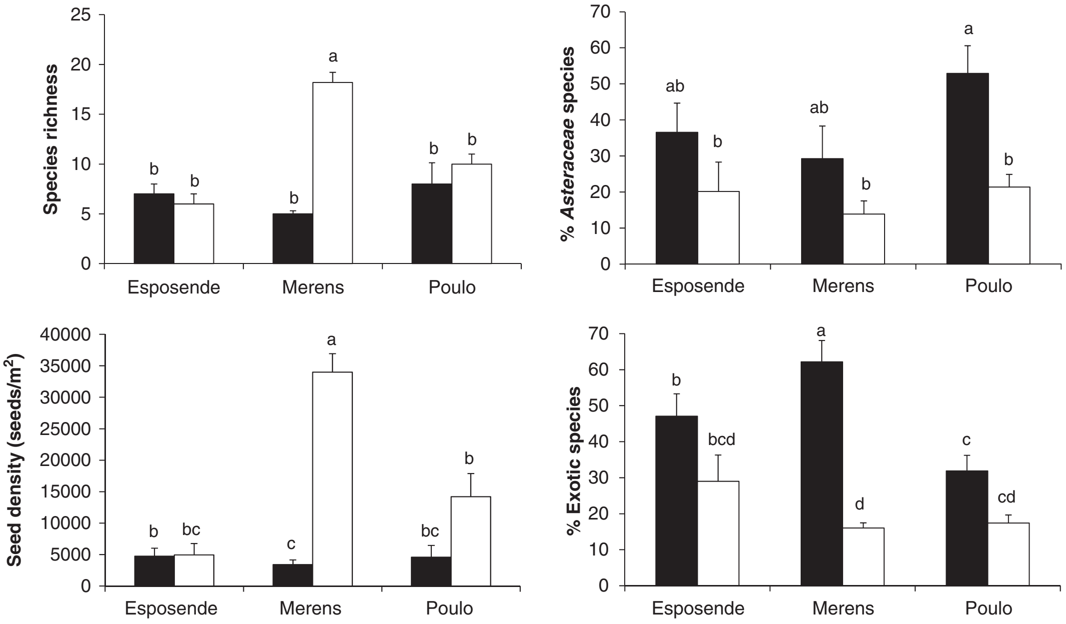

Fig. 3. Mean values + SE of species richness, seed density (number of emerged seedlings/m^2), percentage of *Asteraceae* species and percentage of exotic species in the soil seed bank samples collected under *Acacia dealbata* (black bars) and *Quercus robur* (white bars). Different letters mean significant differences between groups ($p < 0.05$), according to *post hoc* tests (Tukey or Bonferroni, see Section 2).

Table 3

Results of two way ANOVAs assessing the effect of species (*Acacia dealbata–Quercus robur*) and site (Esposende–Merens–Poulo) on the following seed bank characteristics: seed density (number of seedlings/m^2), species richness, percentage of *Asteraceae* species and seed production (number of *Q. robur* acorns or *A. dealbata* seeds/m^2). The percentage of exotic species was analyzed with Kruskal–Wallis tests, as the data were not homoscedastic ($N = 30$).

	Seed density		Species richness		% of *Asteraceae*		% of exotic species		Seed production	
	F	*p*	*F*	*p*	*F*	*p*	*H*	*p*	*F*	*p*
Species	46.40	0.001	21.30	0.001	13.38	0.001	12.14	0.001	95.87	0.001
Site	17.56	0.001	10.51	0.001	2.45	0.108	2.24	0.326	0.79	0.465
Species * Site	23.01	0.001	15.30	0.001	0.82	0.451	16.70	0.005	4.53	0.021

covered by a thick layer of litter and fruits (Le Maitre et al., 2011). If seeds reach the soil and germinate, the seedlings and future saplings must cope also with the vigorous resprouting ability of *A. dealbata* (Sanz Elorza et al., 2004; Weber, 2003; Sheppard et al., 2006; Lorenzo et al., 2010a). Also, this species creates a root net in the upper soil layers, due to its extensive creeping rhizomatous root system (Fuentes-Ramírez et al., 2011) that can prevent the establishment of new plants. Furthermore, it has been previously shown that *A. dealbata* flowers produce leachates that inhibit seed germination and seedling radicle growth (Carballeira and Reigosa, 1999; Lorenzo et al., 2010b). Therefore, we suggest that *A. dealbata* modifies the soil seed bank and the established vegetation floristic composition by means of a positive feedback cycle. Firstly, *A. dealbata* alters the propagule supply because of the forest structure and the thick litter layer. Secondly, it also alters seed germination and seedling emergence because of its allelopathic effects. Finally, as *A. dealbata* hinders the plant establishment under its canopies, the regeneration of the understorey mostly depends on the seed inputs from adjacent areas. However, as previously explained, the structure of the forest compromises the arrival of new propagules. As a consequence, the regeneration of the native community under *A. dealbata* is seriously affected. Some authors as Gioria and Osborne (2010) also suggested that the differences in the vertical structure between native and exotic communities and the thick exotic litter layer may hinder the seed dispersal and may be the cause of the depletion of the seed bank in the invaded areas.

The same rationale could also explain the high percentage of *Asteraceae* species in the understorey of *A. dealbata* (Table 3, Fig. 3). Plants of this family produce a high amount of tiny, wind-dispersed seeds. This may facilitate the arrival of *Asteraceae* seeds from adjacent areas in contrast with other species with different seed dispersal mechanisms. Our results agree with those found by Holmes and Cowling (1997) in South-African fynbos invaded by *A. saligna* and Marchante et al. (2011) in Portuguese dunes invaded by *A. longifolia*. In both studies, *Acacia* invasion impoverished the soil seed bank, increasing the presence of wind dispersed species. Marchante et al. (2011) also suggested that the dense canopy and the thick litter layer in *A. longifolia* long term invaded sites must be the cause of the prevention of zoochorous seed deposition.

We found a lower similarity between the floristic composition of the soil seed banks and the established vegetation under *A. dealbata* than under *Q. robur* canopies (Fig. 5). According to previous studies, a lower diversity in the expressed vegetation than in the soil seed bank is always expected, due to losses from the viable seeds reservoir in the soil or to scarce seed inputs (Whipple, 1978; Godefroid et al., 2006; Vilà and Gimeno, 2007). The lower similarity found in *A. dealbata* forests supports our hypothesis about the structure of this forest as an obstacle for the propagules arrival and seedling emergence.

It must be also highlighted the large amount of seeds produced by *A. dealbata* in comparison with the amount of acorns found under *Q. robur* canopies. In general, *Acacia* species accumulate a very large seed bank in the soil (Dean et al., 1986; Marchante et al., 2011). These seeds are long-term persistent, even more than 50 years, according to Holmes (1989), due to the physical dormancy caused by the impermeability of their seed coats. According

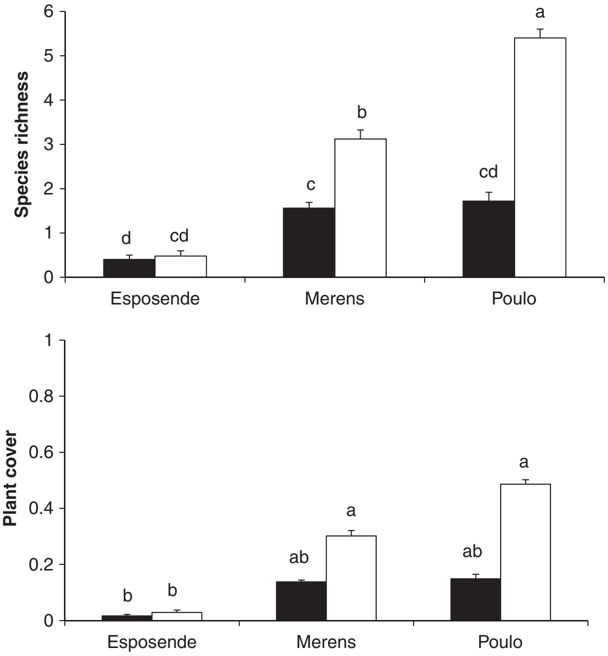

Fig. 4. Mean values + SE of species richness and plant cover of the vegetation established under *Acacia dealbata* (black bars) and *Quercus robur* (white bars). Different letters mean significant differences between groups ($p < 0.05$), according to *post hoc* tests (Tukey or Bonferroni, see Section 2).

Table 4
Results of Kruskal–Wallis tests assessing the effect of species (*Acacia dealbata*–*Quercus robur*) and site (Esposende–Merens–Poulo) on the under-canopy plant cover. Results of a two way ANOVA assessing the effect of species and site on the under-canopy species richness ($N = 30$).

	Plant cover		Species richness	
	H	*p*	*F*	*p*
Species	4.05	0.044	75.82	0.001
Site	19.78	0.001	68.20	0.001
Species ∗ Site	26.28	0.001	26.76	0.001

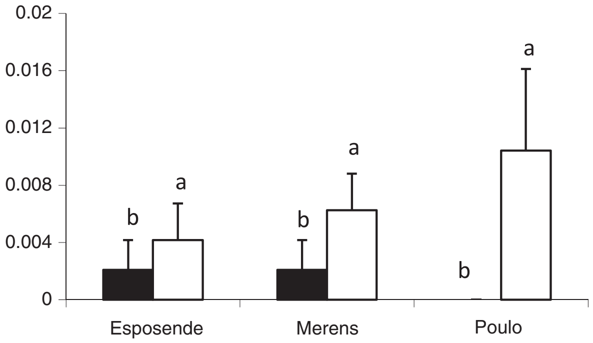

Fig. 5. Average values of the Jaccard's index of similarity + SE between the floristic composition of the soil the seed banks and the floristic composition of the expressed vegetation of the under-canopies of *Acacia dealbata* (black bars) and *Quercus robur* (white bars). Different letters mean significant differences between groups ($p < 0.05$), according to Bonferroni *post hoc* test.

to Richardson and Kluge (2008), *A. dealbata* seeds belong to the Type IV persistent seed bank in the model of Thompson and Grime (1979), which confers potential for regeneration in unpredictable disturbed habitats such as those adapted to fire. These characteristics largely contrast with the generally low density and shortlife of the non-fire adapted *Q. robur* acorns (Sonesson, 1994; Reyes and Casal, 2006). In our study area, summer fires are recurrent. We suggest that the large amount of seeds produced by *A. dealbata*, the physical adaptation of its seeds to fire, its resprouting ability and its precocity to produce seeds (Gibson et al., 2011), together with the progressive destruction of the native forests, must be the causes of this species propagation in this area.

Understanding the driving factors of the invasion and the changes in the biotic and abiotic components in the invaded ecosystems is essential to design effective control and restoration projects (Le Maitre et al., 2011). Recent efforts have been made in order to increase the effectiveness of management plans to control invasive *Acacia* species in South Africa (van Wilgen et al., 2011). In the case of invasive widespread species, as is the case of *A. dealbata* populations in South Africa and also in Spain, van Wilgen et al. (2011) suggest that the best strategy would be to contain the spread and to focus on eradication efforts, prioritizing in accordance to conservation criteria. Our results show that *A. dealbata* severely impacts the soil properties and vegetation of native *Q. robur* forests. The depletion of the soil seed bank, the impoverishment of the established vegetation and the low similarity between the soil seed bank and the understorey vegetation highlight the difficulty of natural restoration of the native community even if the invasive *A. dealbata* were eradicated. As a consequence, active restoration will be needed in order to rehabilitate invaded areas towards the original native forests. The loss of the original soil seed bank will demand the introduction of propagules of the native species to accelerate ecological succession. In any case, management must be adaptive, and much more research is needed in the case of *A. dealbata* invasion of European forests to test the success of different eradication methods as well as to assess the performance of native species reintroduction in cleared post-invasion areas.

Acknowledgments

This study was supported by the projects CGL2007-61873/BOS, CGL2010-16388/BOS of the Ministerio de Ciencia e Innovación and POII10-0179-4700 of the Junta de Comunidades de Castilla-La Mancha. Noelia González-Muñoz was supported by a Grant of the Ministerio de Ciencia e Innovación (FPI fellowship, BES-2008-002457) and by a Grant of the Universidad de Alcalá. We acknowledge Rosendo Elvira and the staff of the Jardín Botánico Juan Carlos I for their support to perform this experiment. We are grateful to the support of the REMEDINAL-2 network (Comunidad de Madrid). We also thank Natalia Fierro-Brunnenmeister and Elena Varas García for their valuable help with the plant measurements, Oscar Godoy for his comments to improve the quality of this manuscript and Jesús Romero-Trillo for the English editing.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2011.12.026.

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