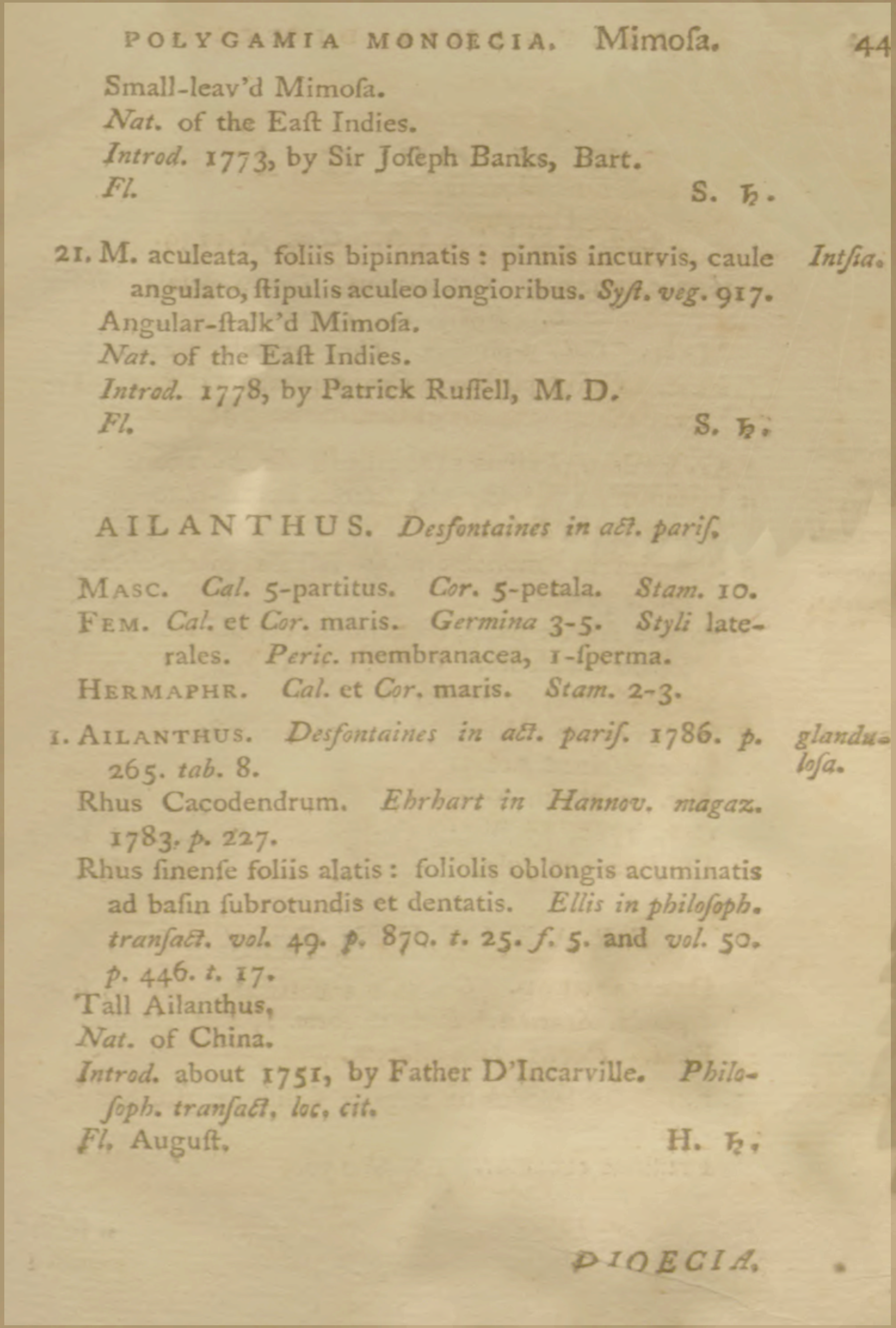

POLYGAMIA MONOECIA. Mimoſa. 44

Small-leav'd Mimoſa.
Nat. of the Eaſt Indies.
Introd. 1773, by Sir Joſeph Banks, Bart.
Fl. S. ♄.

21. M. aculeata, foliis bipinnatis: pinnis incurvis, caule angulato, ſtipulis aculeo longioribus. *Syſt. veg.* 917. *Intſia.*
Angular-ſtalk'd Mimoſa.
Nat. of the Eaſt Indies.
Introd. 1778, by Patrick Ruſſell, M. D.
Fl. S. ♄.

AILANTHUS. *Desfontaines in act. pariſ.*

MASC. *Cal.* 5-partitus. *Cor.* 5-petala. *Stam.* 10.
FEM. *Cal.* et *Cor.* maris. *Germina* 3-5. *Styli* laterales. *Peric.* membranacea, 1-ſperma.
HERMAPHR. *Cal.* et *Cor.* maris. *Stam.* 2-3.

1. AILANTHUS. *Desfontaines in act. pariſ.* 1786. *p.* 265. *tab.* 8. *glanduloſa.*
Rhus Cacodendrum. *Ehrhart in Hannov. magaz.* 1783. *p.* 227.
Rhus ſinenſe foliis alatis: foliolis oblongis acuminatis ad baſin ſubrotundis et dentatis. *Ellis in philoſoph. tranſact. vol.* 49. *p.* 870. *t.* 25. *f.* 5. and *vol.* 50. *p.* 446. *t.* 17.
Tall Ailanthus,
Nat. of China.
Introd. about 1751, by Father D'Incarville. *Philoſoph. tranſact, loc, cit.*
Fl. Auguſt. H. ♄.

DIOECIA.

CAUSES AND CONSEQUENCES OF EXOTIC TREE INVASION IN THE IBERIAN PENINSULA

NOELIA GONZÁLEZ MUÑOZ. TESIS DOCTORAL.

2012

CAUSES AND CONSEQUENCES OF EXOTIC TREE INVASION IN THE IBERIAN PENINSULA

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TESIS DOCTORAL
DEPARTAMENTO DE ECOLOGÍA
UNIVERSIDAD DE ALCALÁ

Universidad
de Alcalá
Departamento de Ecología

Pilar Castro Díez, profesora titular del Departamento de Ecología de la Universidad de Alcalá y directora de esta Tesis Doctoral,

Hace constar:

Que el trabajo descrito en la presente memoria, titulado “Causes and consequences of exotic tree invasion in the Iberian Peninsula”, ha sido realizado bajo su dirección por Noelia González Muñoz en el Departamento de Ecología de la Universidad de Alcalá, dentro del Programa de Doctorado “Ecología, Conservación y Restauración de Ecosistemas”, reuniendo todos los requisitos necesarios para su aprobación como Tesis Doctoral.

Alcalá de Henares, 4 de julio de 2012.

Dra. Pilar Castro Díez

Universidad de Alcalá

Departamento de Ecología

Julio Camargo Benjumeda, director del Departamento de Ecología de la Universidad de Alcalá,

Hace constar:

Que el trabajo descrito en la presente memoria, titulado “Causes and consequences of exotic tree invasion in the Iberian Peninsula”, ha sido realizado dentro del Programa de Doctorado “Ecología, Conservación y Restauración de Ecosistemas”, reuniendo todos los requisitos necesarios para su aprobación como Tesis Doctoral.

Alcalá de Henares, 4 de julio de 2012.

Dr. Julio Camargo Benjumeda

Universidad de Alcalá
Departamento de Ecología

Causes and consequences of exotic tree invasion in the Iberian Peninsula

Memoria presentada para optar al grado de
Doctora por la Universidad de Alcalá

Programa de doctorado:

"Ecología, Conservación y Restauración de Ecosistemas"

Noelia González Muñoz

Directora: Pilar Castro Díez

Alcalá de Henares, Julio de 2012

A los árboles

A las mariposas

A la ciudad de Santa Cruz

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"Y así crecí volando
y volé tan deprisa
que hasta mi propia sombra
de vista me perdió"

Joaquín Sabina
Tan joven, tan viejo

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RESUMEN

Esta Tesis Doctoral se centra en el estudio de especies de árboles exóticos y nativos coexistentes en bosques de ribera del centro de la Península Ibérica y en robledales del Noroeste.

Los objetivos principales son: 1) determinar las condiciones ambientales que favorecen el éxito de establecimiento de árboles nativos y exóticos; 2) evaluar los impactos sobre el ciclo de nitrógeno de las especies exóticas del centro peninsular.

Para el objetivo 1, se realizó un experimento de dos años de duración en el que se comparó el éxito de establecimiento entre árboles nativos y exóticos, bajo distintas combinaciones de tratamientos de luz y de humedad del suelo (**Capítulos 2** y **3**). Para el objetivo 2, se compararon los efectos sobre el suelo de la hojarasca de especies nativas y exóticas (**Capítulo 4**), así como sus estrategias de uso de nitrógeno (**Capítulo 5**).

Las especies estudiadas pueden agruparse en base a sus respuestas a los tratamientos ensayados, con independencia de su origen nativo y exótico, debido a la heterogeneidad en las respuestas de las especies incluidas en cada origen.

Los árboles exóticos pueden provocar cambios en el ciclo de nitrógeno en los bosques de ribera del centro peninsular, debido a diferencias en la calidad de la hojarasca, tasas de descomposición y estrategias de uso del nitrógeno entre árboles nativos y exóticos. Las diferencias en la estrategia de uso de nitrógeno entre las propias especies exóticas muestran un ejemplo claro de la dificultad de predecir los impactos de las invasiones biológicas en los ecosistemas.

Palabras Clave: Árboles exóticos, especies invasoras, bosques de ribera, éxito de establecimiento, luz, humedad del suelo, impactos, ciclo de nitrógeno, descomposición de hojarasca, eficiencia de uso de nutrientes.

ABSTRACT

This Thesis is focused in the study of exotic and native tree species co-occurring in the riparian forests of central Spain and in the mesic forests of the Northwest.

The main aims are: 1) determining the environmental conditions that favour the establishment success of native and exotic tree species; 2) evaluating the impacts on the nitrogen cycling of the exotic species spreading in riparian forests of central Spain.

To achieve aim 1, a two year experiment was conducted to compare differences in the establishment success between native and exotic seedlings under different treatments of light and soil moisture (**Chapters 2** and **3**). To achieve aim 2, we evaluated the effects of exotic and native litter on invaded soils (**Chapter 5**) and compared differences in nitrogen use strategies between native and exotic tree species (**Chapter 4**).

The studied species can be grouped regarding their responses to the light and soil moisture treatments, but independently of their native or exotic origin, due to the heterogeneity found in the responses of the species included in each group.

The exotic species may provoke changes in the nitrogen cycle of the riparian forests of central Spain, due to differences in litter quality, litter decomposition and nitrogen use strategies between native and exotic tree species. The differences found in the nitrogen use strategies among studied exotic species highlight the difficulties of predicting the impacts of exotic species in the invaded ecosystems.

Keywords: Exotic trees, invasive species, riparian forests, establishment success, light, soil moisture, impacts, nitrogen cycling, litter decomposition, nitrogen use efficiency.

Chapter 1

General Introduction

Biological invasions

Biological invasions are defined as the process of introduction, establishment and spread of exotic species (Williamson and Fitter, 1996; Mack et al., 2000; Richardson et al., 2000; Balaguer, 2004; Vilà et al., 2008). Nowadays, biological invasions are considered not only an economic problem (Perrings et al., 2002; Pimentel et al., 2005), but also one of the biggest threats for biodiversity conservation, only after habitat destruction and fragmentation (Vitousek, 1990; Vitousek et al., 1997; Mack et al., 2000).

Not all the exotic species that arrive in a new territory become successful invaders. In 1996, Williamson and Fitter proposed the Tens Rule, which predicts that only 10% of those new species arrived in a new area become causal, 10% of the casuals become naturalized and only 10% of the species naturalized in a territory become invasive (see Box 1 for definitions). However, despite this rule must be considered with caution (Richardson and Pysek, 2006), it is useful to illustrate the contingencies involved in the process of biological invasions, as exotic species must overcome biotic and abiotic filters before becoming successful invaders (Richardson et al., 2000; Richardson and Pysek, 2006; Pysek and Richardson, 2010).

In this context, an invasive plant species is that which has been introduced in a new area, being able to successfully establish and spread during a short period of time (Pysek et al., 2004). The process of plant invasion or, in general, of any biological invasion, can be split in four non-discrete stages: transport, colonization, establishment and spread (Sakai et al., 2001; Teoharides and Dukes, 2007) (Fig. 1).

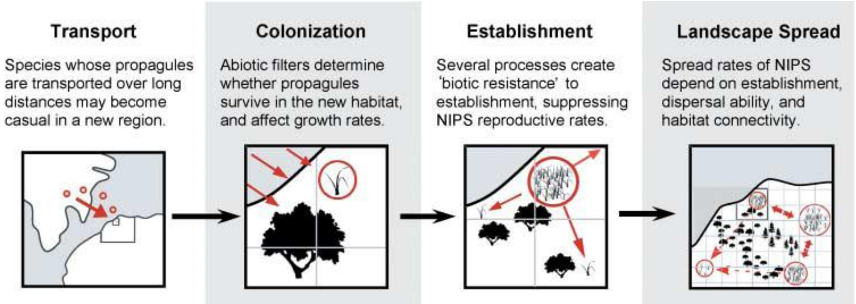


Fig. 1. The four stages in the process of plant invasion and the dominant factors and processes affecting the success in each stage. NIPS (invasive nonindigenous plant species) (taken from Teoharides and Dukes, 2007).

Box 1. Concepts related to invasive species (Vilà et al., 2008).
Exotic: Species original to a foreign area.
Casual/subspontaneous: Species that may reproduce occasionally but whose persistence rely on repeated introductions.
Naturalized: Species that form self-replacing populations.
Invasive: Naturalized species able to spread a far distance in a short period of time.

The invasion starts with the **transport** of a species from its home range to a new territory (Fig. 1). This transport is normally related to human activities. Despite long distance transport has a long history, the pressure of introduction of exotic species has increased during the last 200 hundred years and, especially, since the beginning of the 20th century, due to the intensification of transport and business routes (Mack et al., 2000; Vilà, and Pujadas, 2001; Reichard and White, 2001; McNeely et al., 2001). The most relevant traits to pass this filter are those related to survival to transport and to human selection before transport (disease resistance, showy flowers, high amount of seed production, drought tolerance, fast growth, etc.) (Theoharides and Dukes, 2007). The **colonization** stage starts when the exotic species arrives in the new territory (Fig. 1). At this stage, species success depends on the propagule pressure, the abiotic filters present in the new area (e.g. climate, soil type, resources availability,...) and the biotic filters at neighborhood scale (i.e. interspecific competition, diseases, predators, etc.) (Theoharides and Dukes, 2007). The propagule pressure results from multiplying the number of individuals introduced in a certain event by the frequency of this event (Eppstein and Molofsky, 2007). A high propagule pressure increases the genetic diversity and, therefore decreases the bottle neck effect; it also increases the chances of finding a favorable environment and helps to dominate the seed pool (Williamson and Fitter 1996, Lonsdale, 1999, Colautti et al., 2006; Lockwood et al., 2009). The **establishment** stage is normally longer than the colonization stage, and requires the exotic species to be able to develop self-sustainable populations (Fig. 1). Despite abiotic conditions are still important during this stage, biotic filters, as competitive or facilitative relationships with local flora or other trophic levels (mutualism, herbivory, parasitism, etc.) become more relevant (Theoharides and Dukes, 2007). Finally, to overcome the **spread** stage and to guarantee the invasion success, the exotic species depend on their dispersal abilities and on landscape characteristics (e.g. habitat connectivity, metapopulation dynamics, disturbance events, etc.) (Fig. 1).

Invasiveness and invasibility

The success of an exotic species in a non native area depends on the propagule pressure, on the properties of the species (**invasiveness**) and on the properties of the introduced system (**invasibility**).

The term **invasiveness** referes to the characteristics of the species that may help an exotic species to successfully invade an ecosystem (Williamson and Fitter, 1996; Sakai et al., 2001; Erfmeier and Bruelheide, 2010). Some plant properties previously related to invasiveness are: high competitive ability (Vilà and Weiner, 2004), the ability to reproduce vegetatively (Richardson and Pysek, 2006; van Kleunen et al., 2007), high growth rate (Grotkopp et al., 2002; van Kleunen et al., 2010; Lamarque et al., 2011), low seed size (Rejmánek and Richardson, 1996; but see Castro Díez et al., 2011), short length of the juvenile period and short interval between seed mast years (Rejmánek and Richardson, 1996) or high phenotypic plasticity (Davison et al., 2011). Besides, different hypotheses have been postulated to explain exotic species invasiveness as, for instance, the *novel weapon hypothesis*, which suggests that the invasion success is related to the ability to produce allelopathic compounds (Callaway and Aschehoug, 2000; Hierro and Callaway, 2003).

However, not all these properties appear in all invasive species and not all species showing these traits become invaders (Godoy et al., 2008). Thus, Daehler (2003), in a study comparing 79 pairs of invasive/non-invasive plant species, found that invaders did not show higher growth rates, fecundity or competitive abilities than native species.

Furthermore, Godoy et al. (2011) did not find a higher plasticity in invasive plants over natives. In this sense, Davison et al. (2011), in a meta-analysis performed with 75 invasive/non-invasive pairs of plant species found that, despite invaders showed an overall higher phenotypic plasticity than natives, natives performed as well or even better than invaders when resources were not abundant. This disparity of results is mainly due to the different contexts in which the invasion occurs, as invasion success is very dependent on the environment.

The term **invasibility** involves the properties of the recipient ecosystem (Londsdale, 1999; Sakai et al., 2001, Richardson and Pysek, 2006) which may facilitate or hamper the invasion success. There are several hypotheses intending to explain community invasibility. For instance, the *empty niche hypothesis* (Levine and D´Antonio, 1999) suggests that the absence of certain life forms may favor the establishment of exotic species belonging to that life form, which will be able to exploit a vacant niche. The *invasional meltdown hypothesis* (Simberloff and von Holle, 1999) proposes that the success of exotic species is favored by the presence of other exotic species, due to facilitative relationships. By contrast, the *facilitation hypothesis* (Bruno et al., 2003) suggests that exotic species are facilitated by the natives of the invaded area. The *disturbance hypothesis* (Mack et al., 2000) argues that disturbances may increase resource availability and reset succession, giving native and exotic species the same opportunities to succeed. The *fluctuating resource availability hypothesis* postulates that the exotic species may take advantage of punctual or recurrent resource liberation in space or time, as it happens after a disturbance (Davis et al., 2000). The *enemy release hypothesis* (Keane and Crawley, 2002) proposes that exotic species are favored by the absence of natural enemies in the new territory. Based in this last hypothesis, Blossey and Notzold (1995) postulated the *evolution of increase competitive ability hypothesis*, suggesting that the absence of natural enemies allows invaders to reallocate to reproduction and growth those resources previously allocated to defense. Other properties of the ecosystem that have been described to assist invasive processes are a high habitat connectivity, which facilitates the arrival of exotic propagules (Kowarik, 1983; Vilà and Pujadas, 2001; Hansen and Clevenger, 2005; Gulezian and Nyberg, 2010; Hitchmugh, 2011) and a high landscape heterogeneity (Hobbs and Huenneke, 1992; Maron and Vilà, 2001), which increases the chances for the exotics to find a suitable niche.

In spite of the large amount of previous studies explaining potential causes of invasion success, the literature also shows that no single hypothesis is valid for any invasion case. In this context, several meta-analyses have tested which hypothesis/traits/environmental conditions allow explaining a higher number of invasion events. For instance, van Kleunen et al. (2010) tested whether exotic invasive species differ from native species in physiology, leaf-area allocation, shoot allocation, growth rate, size and fitness. They found that exotic invasive species overcome natives in those traits related to high performance, as growth rate, size and fitness. Besides, Lamarque et al. (2011) conducted a meta-analysis to test which hypotheses about invasibility and invasiveness and which species functional traits better contribute to explain exotic tree invasion success. In this study, they included the enemy release, the evolution of increase competitive ability, the novel weapon, the propagule pressure, the empty niche, the disturbance, the facilitation and the fluctuating resource hypotheses. The species traits evaluated were plant biomass, plant density or cover, germination, growth and survival rates. They found that invasibility and invasiveness equally contributed to exotic tree invasion success. Furthermore, among the hypotheses analyzed, the empty niche contributed the least and the novel weapon the most to explain the invasion success of exotic trees. They also found that the growth rate was the species trait that better explain exotic tree species success, in agreement with van Kleunen et al. (2010) and Grotkopp et al. (2002).

Despite the increasing information available regarding the biology of invasions, predicting invasion events is still difficult, as it requires a profound knowledge of the history of the species introduction, the species attributes, the characteristic of the invaded habitat and the interaction between them (Catford et al., 2009).

The impacts of plant invasions

Catford et al. (2009) suggested a last stage in the process of biological invasions, the **impact** stage, in which the invasive species produces harmful consequences on ecology and/or economy.

In 2005, the classic work of Pimentel et al. estimated that there were around 50000 exotic invasive species in the USA, which caused economic losses of about 120 million dollars per year, due to impacts in forestry, crops and environment. In Spain, Andreu et al. (2009) estimated that the costs of noxious alien species management had been higher than 50 million euros during the previous decade. According to the European Invasive Alien Species Gateway (DAISIE, www.europe-aliens.org), in 2010 there were 10000 exotic species known in Europe. However, there were only ecological impacts documented for 1094 of them and economic impacts for 1347 (Vilà et al., 2010). In 2012, the last update of the same group of experts compiled 11595 exotic species in Europe. In the list of the 100 most harmful exotic invasive species provided by the DAISIE database are included, for instance, the plant species *Ailanthus altissima* (Mill.) Swingle, *Acacia dealbata* Link., *Carpobrotus edulis* (L.), *Cortaderia selloana* (Schult. & Schult. F.) Asch & Graebn, *Opuntia ficus indica* L. and *Robinia pseudoacacia* L., all of them widespread in the Iberian Peninsula.

According to Parker et al. (1999), invasive species can provoke impacts at very different levels: on individuals, genetics (hybridization), population dynamics, community and/or ecosystem processes. The most relevant are probably those that affect the functions, processes and services of the ecosystems. At this level, for instance, previous studies have shown how plant species are able to affect the nutrient cycle (Rice et al., 2004; Castro-Díez et al., 2012; Ehrenfeld, 2010; Mineau et al., 2011), the soil characteristics (May and Attiwill, 2003; Griffiths et al., 2005; Marchante et al., 2008 and 2009; Malcom et al., 2008; DeCant, 2008; Follstad Sha et al., 2010; Qiu et al., 2010; González Muñoz et al., 2012), the soil community composition (Kourtev et al., 2002; Reinhart and VandeVoort, 2006; Lorenzo et al., 2010c), the water cycle (Zavaleta, 2000; Glenn and Nagler, 2005), the species interactions (Morales and Traveset, 2009; Holmes and Cowling, 1997) and the species community composition (Levine et al., 2003; Yelenik et al., 2004; Hellmann et al., 2011; González Muñoz et al., 2012).

All the mentioned previous studies show examples of how invasive species provoke impacts at different levels in the invaded areas. The severity of these impacts will depend on the interaction between the species properties and the characteristics of the invaded ecosystems. Therefore, it is necessary to analyze the invasion events particularly in order to forecast the ecological consequences of biological invasions.

Study cases: Exotic invasive trees in the Iberian Peninsula

This Thesis is focused on the study of native and exotic tree species co-occurring in two botanically, edaphically and climatically contrasted forests: the inner riparian Peninsula floodplains and the mesic forests of the Northwest

Riparian forests of central Iberian Peninsula

The Mediterranean continental climate is characterized by a double stress for plant establishment: the low winter temperatures and the summer drought (Mitrakos, 1980). This double stress prevents the establishment of exotic plants not adapted to this climate. However, in alluvial floodplains, the summer water stress is mitigated by the shallow phreatic table, and by the shade of the dense canopies in non disturbed riparian forest. These circumstances make floodplains more vulnerable to be invaded by exotic species. Indeed, Chytrý et al. (2008, 2009) found that riparian forests, along with coastal areas, are among the most invaded habitats in the Mediterranean regions of Europe. Besides, the natural river dynamic opens gaps after flooding events, favoring the establishment of light demanding pioneer species.

Furthermore, human settlements, which are a source of exotic species, are usually close to rivers, which act as corridors, helping to the propagule dispersion (Richardson et al., 2007).

Our study area in inner Iberian Peninsula were the low stretchs of the alluvial floodplains of the Henares and Manzanares rivers. These forests are dominated by the tree species *Fraxinus angustifolia* Vahl., *Ulmus minor* Mill., *Populus alba* L., *Populus nigra* L. and different species of the genera *Salix* and *Tamarix* (Blanco Castro et al., 2005). This native vegetation has been severely modified by human activities, such as river regulation, river channelization, agriculture, human disturbance, etc. Nowadays, these riparian forests are widely invaded by the exotic tree species *Ailanthus altissima* Mill., *Elaeagnus angustifolia* L., *Acer negundo* L., *Robinia pseudoacacia* L. and *Ulmus pumila* L, which are also profusely spreading in disturbed areas, road and crop borders (Sanz Elorza et al., 2004) (Fig. 2). These species are the object of study of this Thesis in one or more chapters.

Fig. 2. Detail of *Robinia pseudoacacia* presence in a forest gap at the Henares river floodplain (La Canaleja, Alcalá de Henares).

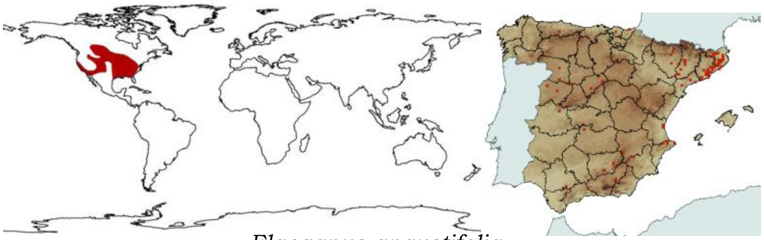
The studied exotic species are native to very different biogeographic regions and were introduced in the Iberian Peninsula between late 18th to early 20th century, mainly because of ornamental purposes. *Robinia pseudoacacia* and *A. negundo* are native to the temperate region of North America and *A. altissima*, *E. angustifolia* and *U. pumila* are native to different parts of Asia (Fig. 3; Sanz Elorza et al., 2004; Weber, 2003; http://www.europe-aliens.org). All of them show species traits related with exotic species success. For instance, *E. angustifolia* and *R. pseudoacacia* are N-fixers, which may confer a certain independence of soil nutrient status, being advantageous in nutrient poor ecosystems

(Boring and Swank, 1984; Katz and Shafroth, 2003). *Ailanthus altissima* bark, roots and leaves have been shown to be strongly allelopathic, able to inhibit other species emergence and growth (Heisey, 1990, 1996; Heisey and Heisey, 2003; de Feo et al., 2005). Besides, all of them produce high amounts of seeds and are able to resprout, favoring their fast spread (Overton, 1990; Katz and Shafroth, 2003; Weber, 2003; Sanz Elorza et al., 2004; Kowarik and Säumel; 2007; Masaka and Yamada, 2009).

Despite the existing previous literature about these species, it is still not well known which environmental factors are favoring their success in Mediterranean areas. Moreover, according to the last IPPC report (2007), climate change models predict a tendency to an increment in mean annual temperature and water summer stress in Mediterranean ecosystems. As we still do not know the niche preferences of these species, it is not possible to predict if they can be favored over natives in a future scenario of climate change.

Ailanthus altissima

Acer negundo



Elaeagnus angustifolia

Robinia pseudoacacia

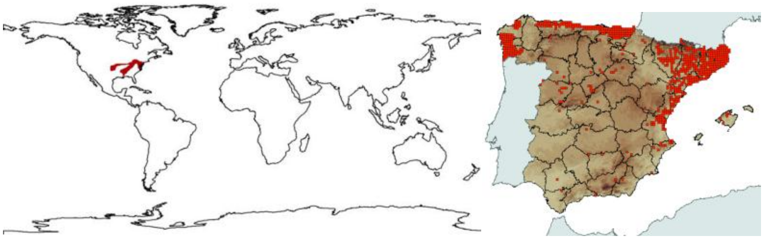


Fig. 3. Native range (left) and distribution in Spain (right) (red) of *Ailanthus altissima*, *Acer negundo*, *Elaeagnus angustifolia* and *Robinia pseudoacacia* (taken from Sanz Elorza et al., 2004). *Ulmus pumila* is native to Center and East Asia (Sanz Elorza et al., 2004) but there are not data published about its distribution in Spain.

Mesic forests of Northwestern Iberian Peninsula

The study area in the Northwest of the Iberian Peninsula was located in the surroundings of the city of Orense (Galicia, Spain), in the border of the Eurosiberian and Mediterranean Regions, where the climate is Atlantic with strong Mediterranean influence (Rivas-Martínez, 1987). In this area, native forests have been severely modified by human activities, as forest destruction for timber purposes, or by recurrent fires (Izco, 1987; Blanco Castro et al., 2005).

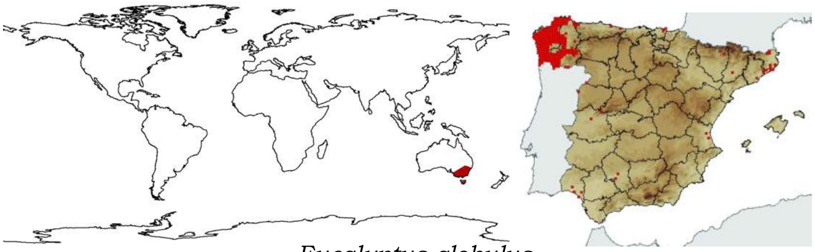
The native tree vegetation is dominated by *Quercus robur* L. and *Quercus pyrenaica* Willd., which form mixed forests with *Castanea sativa* Mill., *Laurus nobilis* L., *Quercus suber* L., *Ruscus aculeatus* L., *Tamus communis* L., *Rhamnus alaternus* L., *Arbutus unedo* L., *Crataegus monogyna* Jaqc. and *Ilex aquifolium* L., among others (Izco, 1987; Blanco et al., 2005). Along with native mature forests, there are also abundant plantations of *Pinus pinaster* Aiton, which has been cultivated since the 19th century for timber purposes (Blanco et al., 2005) and, from there, this species has spread to other areas. Despite *P. pinaster* has sometimes been considered an exotic species in this area, paleobotanical and historical sources confirm its autochthonous character in the area (Valdés et al., 2001). Nowadays, the exotic tree species *Acacia dealbata* Link.

and *Eucalyptus globulus* Labill are spreading throughout Miño river floodplains, forest borders, road limits and native forest gaps (Fig. 4). Besides, it is also easy to find scattered adult trees of *E. globulus* in the native forests.

Fig. 4. Detail of a *Pinus pinaster* forest edge at the province of Orense with an understory colonized by *Acacia dealbata* (Orense province).

Acacia dealbata and *E. globulus* are native to the Southeast of Australia and were introduced in the Iberian Peninsula in the second half of the 19th century, for ornamental and timber production purposes (Fig. 5). Both species produce a high amount of seeds, are able to resprout, are fast-growers and produce allelopathic compounds (Souto et al., 2001, Skolmen and Ledig, 1990, Babu and Kandasamy, 1997; Carballeira and Reigosa, 1999; Sanz Elorza et al., 2004; Lorenzo et al., 2008; Lorenzo et al. 2010a, 2010b and 2010c; Lorenzo et al., 2011; Lorenzo et al., 2012).

Acacia dealbata



Eucalyptus globulus

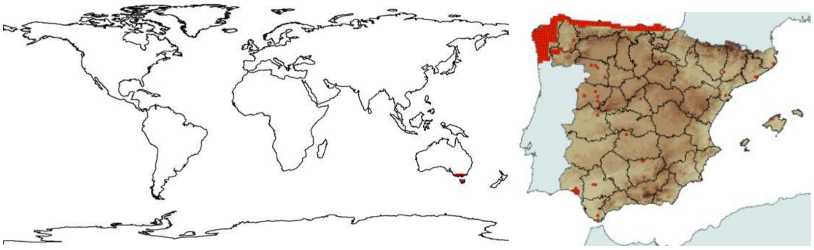


Fig. 5. Native range (left) and distribution in Spain (right) of *Acacia dealbata* and *Eucalyptus globulus* (taken from Sanz Elorza et al., 2004).

Despite the long term presence of these exotic species in the area, there are not so many previous published studies referring to their niche preferences and the impacts that these species provoke in Northwest Spain forests (but see Lorenzo et al., 2010; Lorenzo et al., 2011; Lorenzo et al., 2012; González

Muñoz et al., 2012; Calviño-Cancela et al., 2012; Castro-Díez et al., 2012). In this sense, and as happened with the studied exotic species of central Iberian Peninsula, knowing the environmental conditions that are favouring these species spread is necessary in order to help to make those decisions oriented to their control and management.

General Aims

The general aims of this Thesis are:

1. Identifying the environmental conditions that favor exotic tree species establishment success over natives of both study areas during early life stages.

2. Evaluating the effects of exotic trees on the nitrogen cycling of riparian forests of central Spain, in order to predict the impacts on the invaded ecosystems of shifts in native/exotic tree species dominance.

Thesis Outline

This Thesis is structured in 7 chapters, including this General Introduction (*Chapter 1*). *Chapters 2* to *5* correspond to scientific papers written in English and published or sent to scientific journals. *Chapter 6* includes the General Conclusions of this Thesis. *Chapter 7* shows future research lines.

The Thesis Outline will be explained regarding its main objectives.

Aim 1. Identifying the environmental conditions that favor exotic tree species establishment success over natives of both study areas during early life stages.

Knowing the environmental conditions that favour exotic seedling establishment is necessary to understand exotic species success in the invaded territories. This knowledge can help to make those decisions leading to the control and management of exotic species. *Chapters 2* and *3* are focused in the study of seedling responses to light and soil moisture availabilities, as these conditions are considered the main drivers of plant distribution in ecosystems. We study the seedling stage, as young plants are more vulnerable to stress factors than adults. In each chapter, different species attributes are compared, in order to get an overview of the environmental conditions that favour co-occurring exotic and invasive tree species performance during their first two growing seasons.

Chapter 2. *Establishment success of coexisting native and exotic trees under an experimental gradient of irradiance and soil moisture* (Published in Environmental Management (2011), vol. 48(4), pages 764-773).

In this chapter, we experimentally determine the light and soil moisture scenarios that favor or hamper the establishment of co-occurring exotic and native tree species seedlings, by evaluating seedling emergence, time to emergence and survival. The species included in this chapter are the natives *Fraxinus angustifolia, Ulmus minor*, *Quercus pyrenaica* and *Pinus pinaster* and the exotics *Acer negundo*, *Ailanthus altissima, Elaeagnus angustifolia, Robinia pseudoacacia*, *Eucalyptus globulus* and *Acacia dealbata.*

Chapter 3. *Assessing growth strategies of seedlings of co-occurring native and exotic tree species: an experiment to identify potential regeneration niches in human managed riparian forests* (sent to Journal of Vegetation Science, 2012).

In this chapter, we compare the biomass reached after the first and the second growing seasons and biomass related traits (biomass allocation, relative growth rate, net assimilation rate per unit of leaf mass) between native and exotic species along an experimental gradient of light and soil moisture. The species included in this chapter are the natives *Fraxinus angustifolia, Ulmus minor* and *Populus alba* and the exotics *Acer negundo*, *Ailanthus altissima*, *Elaeagnus angustifolia* and *Robinia pseudoacacia.*

Aim 2. Evaluating the effects of exotic trees on the nitrogen cycling of riparian forests of central Spain, in order to predict the impacts on the invaded ecosystems of shifts in native/exotic tree species dominance.

The introduction of exotic species in a territory may lead to changes in the nitrogen cycling of the ecosystems. These changes can be due to differences in the amount and quality of the litter or in differences in nitrogen economies between the native and the exotic species. In this Thesis, we evaluate the impacts of exotic trees on the nitrogen cycling from two very different approaches. In *Chapter 4*, we assess the effect of leaf litter on soil nitrogen content. In *Chapter 5*, we describe the differences in nitrogen use strategies between native and exotic trees. The results of these chapters help to predict the consequences on the nitrogen cycle of a replace of the studied natives by the exotics. Aim 2 is focused in the study of riparian forests of central Iberian Peninsula.

Chapter 5. *Effects of exotic invasive trees on nitrogen cycling: a case study in Central Spain* (Published in Biological Invasions (2009) vol. 11, pages 1973-1986).

We evaluate the effect of *Ailanthus altissima* and *Robinia pseudoacacia* on the nitrogen cycle by comparing leaf litter quality, litter decomposition rates and nitrogen availability in soils with two co-occurring natives, *Fraxinus angustifolia* and *Ulmus minor*.

Chapter 6. *Differences in nitrogen use strategies between native and exotic tree species: predicting impacts on invaded ecosystems* (Plant and Soil, 2012. *In press*).

We compare differences in nitrogen use efficiency and related traits among three native (*Fraxinus angustifolia, Populus alba* and *Ulmus minor*), and three exotic co-occurring tree species (*Ailanthus altissima*, *Robinia pseudoacacia* and *Ulmus pumila*). Furthermore, we compare differences in leaf phenology, litter production and in the amount of nitrogen returned to the soils.

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Chapter 2

Establishment success of coexisting native and exotic trees under an experimental gradient of irradiance and soil moisture.

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RESUMEN

Los árboles exóticos *Ailanthus altissima, Robinia pseudoacacia*, *Acer negundo* y *Elaeagnus angustifolia* coexisten con los árboles nativos *Fraxinus angustifolia* y *Ulmus minor*, entre otros, en llanuras aluviales del centro de la Península Ibérica. A su vez, los árboles exóticos *Acacia dealbata* y *Eucalyptus globulus* coexisten con los nativos *Quercus pyrenaica* y *Pinus pinaster* en el noroeste peninsular. El objetivo de este capítulo es identificar las condiciones ambientales que favorecen el éxito de establecimiento de estas especies durante la primera estación de crecimiento. Para ello, en primavera de 2008, se sembraron semillas de estas especies bajo cuatro tratamientos de luz (100, 65, 35, 7% respecto de la radiación solar incidente) combinados con tres niveles de riego (Ψ_w= -0.97, -1.52 y -1.77 MPa). Durante la primera estación de crecimiento, se monitorizaron emergencia y supervivencia de plántulas. El efecto de los tratamientos de luz en el éxito de establecimiento fue mayor que el de los tratamientos de riego. Entre las especies del centro peninsular, *A. negundo* fue la especie más tolerante a la sombra, mientras que la falta de riego disminuyó el éxito de *E.*

angustifolia y *A. altissima.* Además, de acuerdo a nuestros resultados, *A. dealbata* y *P. pinaster* pueden ser competidores potenciales para la colonización de escenarios altamente irradiados, mientras que *Q. pyrenaica* y *E. globulus* lo serían en escenarios más sombreados. Por último, una alta humedad del suelo favoreció el establecimiento de *E. globulus*, pero perjudicó el de *A. dealbata.* Nuestros resultados ayudan a definir las condiciones ambientales de luz y humedad del suelo que controlan la segregación espacial de los árboles exóticos y nativos estudiados, pudiendo orientar en la toma de aquellas decisiones dirigidas al control y manejo de estas especies exóticas.

Palabras clave: Emergencia, supervivencia de plántulas, árboles exóticos, tolerancia a la sequía, tolerancia a la sombra.

ABSTRACT

The exotic trees *Ailanthus altissima, Robinia pseudoacacia*, *Acer negundo* and *Elaeagnus angustifolia* coexist with the native trees *Fraxinus angustifolia* and *Ulmus minor* in river banks of central Spain. Similarly, the exotic trees *Acacia dealbata* and *Eucalyptus globulus* co-occur with the natives *Quercus pyrenaica* and *Pinus pinaster* in northwestern Spain. We aim to identify the environmental conditions that favour or hamper the establishment success of these species during their first growing season. In spring 2008, seeds of the studied species were sown under an experimental gradient of light (100, 65, 35, 7% of full sunlight) combined with three levels of soil moisture (Ψ_w= -0.97, -1.52 and -1.77 MPa). During the first growing season, we monitored seed emergence and seedling survival. We found that the effect of light on the establishment success was stronger than the effect of soil moisture. Both exotic and native species of central Spain showed a good performance under high light, *A. negundo* being the most shade tolerant. Water shortage diminished *E. angustifolia* and *A. altissima* success. Among NW Spain species, *A. dealbata* and *P. pinaster* were found to be potential competitors for colonizing high-irradiance scenarios, while *Q. pyrenaica* and *E. globulus* were more successful under moderate shade. High soil moisture favoured *E. globulus* but not *A. dealbata* establishment. These results contribute to understand some of the factors controlling for spatial segregation between coexisting native and exotic tree species, and can help to take decisions orientated to the control and management of these exotic species.

Keywords: Emergence, seedling survival, exotic trees, drought tolerance, shade tolerance.

1. INTRODUCTION

Understanding the differences between coexisting exotic and native species in their seedling responses to resource availability can help us to explain future shifts in species distribution. During the establishment phase, young seedlings are more vulnerable to stress factors, such as low or high irradiance, water shortage, etc., which, in the long term, determine species distribution in the landscape (Niinemets and Valladares, 2006). Therefore, knowing the species requirements during their earlier stage can help us to identify which circumstances can favour exotic species and represent a risk for native ecosystems.

The Mediterranean region is characterised by a double stress for plant establishment and growth: drought summers and cold winters (Mitrakos, 1980; Orshan, 1989). This double stress is highly limiting for plant performance, preventing the establishment of many exotic plants (Chytrý et al., 2008). However, those areas where either one or both of the stresses are alleviated, such as coastal areas or river banks, become especially sensitive to exotic plant invasion (Chytrý et al., 2008).

The tree species *Ailanthus altissima* (Mill.) Swingle, *Acer negundo* L., *Elaeagnus angustifolia* L., *Robinia pseudoacacia* L., *Eucalyptus globulus* Labill and *Acacia dealbata* Link have been recognized as invasive species and are currently spreading worldwide, especially in areas where the natural vegetation has been disturbed by human activities (DAISIE database (http://www.europe-aliens.org); Weber, 2003; Sanz-Elorza et al., 2004). In the Iberian Peninsula, the first four species are spreading through river banks of the continental inner Spain, where they coexist with native riparian trees, such as *Populus* spp., *Fraxinus angustifolia* Vahl and *Ulmus minor* Mill. These habitats are characterised by nutrient-rich soils, due to the deposition of alluvial sediments and by a higher water table, which alleviates the effect of summer drought. *E. globulus* and *A. dealbata* are spreading in more oceanic regions of Northwestern Spain, where they can compete with the natives *Pinus pinaster* Aiton. and *Quercus pyrenaica* Willd., among others. In this region winter cold is mitigated by the oceanic influence. Despite some of these species have been introduced in the Iberian Peninsula since the 18th century (Sanz Elorza et al., 2004), the environmental conditions that favour their establishment are not well-known yet.

The aim of this study was to identify those environmental conditions that favour or hamper the establishment of coexisting exotic and native trees, well-represented in the Iberian Peninsula. This information can help to assess the invasive risk of the selected exotic trees and provide scientific grounds for their management. Particularly we focused on light and soil moisture conditions, as these factors have been considered the main drivers of plant distribution in ecosystems (Niinemets and Valladares, 2006). Besides, the availability of light and soil moisture is being altered by human activities (Valladares, 2004a). We measured establishment success in terms of seed emergence, number of days needed to emerge ($T_{emerg.}$) and survival during the first growing season, as these traits have been previously found to be related with invasion success (Erfmeier and Bruelheide, 2005; Pysek and Richardson, 2007; Perglová et al., 2009; Ferreras and Galetto, 2010).

We hypothesize that the selected exotic species will show higher emergence and survival rates and shorter times to emergence than the co-occurring native species, as these traits contribute to a fast colonization and therefore to an invasion success (hypothesis 1). We also expect that the selected exotic species will be more successful than the native species in resource-rich scenarios, i.e. with high water and light availability (hypothesis 2), as corresponds with the ruderal strategy, claimed by many authors as typical of most invasive plant species (Pattison et al., 1998; Baruch and Bilbao, 1999; Daehler, 2003; Grotkopp and Rejmánek, 2007).

2. MATERIAL AND METHODS

2.1. Experimental design

We conducted a factorial design experiment with three independent factors: irradiance, soil moisture and tree species. The experiment was settled outdoors at the Botanical Garden Juan Carlos I at Alcalá University (Madrid, central Spain 40°30´N, 3°20´W, 596 m a.s.l) from 30th April to 30th September 2008. In this area the climate is continental Mediterranean with hot and dry summers and cold winters. Mean annual maximum and minimum temperatures are 20.5 and 7.8 °C, respectively. Mean annual precipitation is 378 mm (data from Torrejón de Ardoz weather station, Instituto Nacional de Meteorología, 1971-2000).

The exotic tree species were selected among those compiled in the Atlas of the Invasive Alien Species in Spain (Sanz Elorza et al., 2004). The native species were chosen according to a criterion of coexistence in natural areas with the previously selected exotic species. The exotic trees *Ailanthus altissima* (*Simabouracea*), *Acer negundo* (*Sapindaceae*), *Elaeagnus angustifolia* (*Eleagnaceae*) and *Robinia pseudoacacia* (*Fabaceae*) were introduced from between 18th and 20th centuries in the Iberian Peninsula (Sanz Elorza et al., 2004). Nowadays, these species are naturalized in floodplains, crop and road edges in central Spain, where they coexist with native trees, such as *Fraxinus angustifolia* (*Oleaceae*), *Ulmus minor* (*Ulmaceae*) and *Populus alba* (*Salicaceae*) (Sanz Elorza et al., 2004). The exotic trees *Eucalyptus globulus* (*Myrtaceae*) and *Acacia dealbata* (*Fabaceae*) were introduced in the mid early 19th century in the Northwest of the Iberian Peninsula and, currently, they occupy areas where the native forest has been totally or partially removed (Sanz Elorza et al., 2004). In this area, the extensive deforestation produced by recurrent fires or by agriculture activities may have increased the chances for exotic tree establishment.

Seeds of all species above were supplied by the *Dirección General para la Biodiversidad* (Government of Spain) and *Tragsa*, S.A. Throughout April 2008, and based on pre-existent bibliography, we conducted germination treatment essays at the laboratory to optimize emergence. These treatments mimic the processes that seeds undergo in the wild to soften their coats and allow hydration and subsequent emergence (Catalán Bachiller, 1993; García-Fayos, 2001; Piotto and Di Noi, 2001). Germination treatments finally used in this experiment were those producing the highest percentage of emergence in the previous essays. A pool of 30 seeds of each species was weighed after > 72 hours in oven at 60°C (Table 1).

Table 1. Germination pre-treatments used in each species. Average seed dry mass (mg, N=30).

Species	Treatment	Dry mass
A. neg	Soaking in fresh water 1 week.	28
A. alt	None	14
E. ang	None	120
R. pse	Soaking in 80°C water + fresh water 48h	20
F. ang	None	36
U. min	Soaking in distilled water 48 hours.	5
A. deal	Soaking in 80°C water + fresh water 48h	17
E. glob	None	2
P. pin	Soaking in fresh water 48 hours.	54
Q. pyr	None	5000

Four treatments of light (100% -L100-, 65% - L65-, 35% -L35- and 7% -L7- of full sunlight) were combined with three treatments of soil moisture (84% –HW-, 66% –MW-, 55% -LW- of soil gravimetric water content). Light treatments were obtained by covering a soil surface with green nets of different thickness fixed to a metal frame on the top and the four sides (Fig.1). Light treatments mimic, both in quantity and quality, the light gradient existing in a typical Mediterranean forest from the gaps (L100) to the under-canopies of dense forests (L7) (Valladares 2004a; Valladares 2004b) (Fig. 1). Soil moisture levels were selected on the basis of our previous experience (Castro-Díez et al., 2006, 2007), intending to induce changes in species success without causing massive mortality (see Fig. 2 for details of how the soil moisture treatments were placed in each light treatment).

Fig. 1. Experimental plots placed at the Botanical Garden Juan Carlos I, in Alcala University. L100, L65, L35 y L7-100, 65, 35 y 7% of sunlight at midday, respectively.

Before the beginning of the experiment, we conducted a calibration to determine the amount of water needed to keep the target soil moisture in each treatment. Ten experimental trays (the same where the seeds were sown, see below) were filled with experimental soil (1:2 volume mixture of washed river sand and commercial substrate 15-10-20 NPK- Kekkilä Iberia S.L., Valencia, Spain), watered to field capacity and weighed. Trays were left to evaporate outdoors, being weighed at different times. Once the tray weight reached 40% of the initial weight, they were dried in the oven (>72 h at 60°C) to get the soil dry weight. The gravimetric soil water content at each weighing was calculated as the percentage of water weight with respect to the soil dry weight. The gravimetric soil water content was plotted against the tray weight to calculate the weight that experimental trays should keep in each soil moisture treatment. We considered the mass of seeds and seedlings negligible. We also estimated the soil matric potential (Ψ_m) corresponding to each soil water treatment using the filter-paper technique (Deka et al., 1995), which were -0.97, -1.52 and -1.77 MPa in the HW, MW and LW treatments respectively. As the soil is in equilibrium, this matric potential is equal to water potential (Ψ_w).

On 2008 April the 30th, we sowed the seeds of all species. Species with large seeds were sown in multi-pot trays (24 pots of 330 ml per tray, one seed per pot). Species with small seeds or with low percentages of emergence in the germination essays were sown in single trays (28x38x7 cm, 40 seeds per tray). In the case of *Eucalyptus globulus*, given the small seed size and the low emergence obtained in the germination essays (2%), we sow a known weight of seeds (5-9 g), corresponding to 1500-2700 seeds per tray. As seeds emerged they were removed until a maximum of 100 seedlings per tray, in order to avoid competition-induced mortality.

Fig. 2. Detail of how the three soil moisture treatments were placed at the L100 treatment (Botanical Garden Juan Carlos I, Alcala University). 8th July 2008.

Four trays per species were randomly arranged in each one of the twelve treatments (four light x three soil moisture). Trays were randomly re-arranged within each treatment twice a week to guarantee treatment homogenization.

Local air temperature, % of air humidity and available photosynthetic photon flux density (PPFD) were recorded every 5 min throughout the experiment period with climatic sensors connected to data loggers (HOBO model H08-006-04; Onset, Pocasset, MA, USA) (Table 2). The irradiances of May and June (for L65) are missing due to technical problems.

Table 2. Photon flux density (PPFD) mean values ± SE (mol m^{-2} d^{-1}) in every experimental plot from 1st June to 30th September 2008. L100, L65, L35 y L7-100, 65, 35 y 7% of sunlight at midday, respectively. May and June L65 PPFD data are not shown because of technical problems with the data loggers.

Month	L100	L65	L35	L7
June	44.3 ± 2.25	-	9.6 ± 0.72	2.8 ± 0.21
July	44.5 ± 2.27	19.3 ± 1.72	12.1± 0.84	2.5 ± 0.28
August	40.5 ± 2.05	16.7 ± 1.47	8.8 ± 0.60	2.3 ± 0.23
September	28.7 ± 1.83	16.1 ± 1.17	6.0 ± 0.44	1.8 ± 0.13

Differences of mean, maximum and minimum temperature and relative air humidity between light treatments were tested with one-way analysis of variance (ANOVA) followed by *post-hoc* Tukey tests. Light treatments neither differ in mean and minimum temperature nor in relative air humidity, although

L100 and L65 showed a higher maximum temperature than the other treatments (Table 3).

Table 3. Mean daily values ± SE of mean, maximum and minimum temperature (T_{Mean}, T_{Max} y T_{Min}) and relative air humidity (%HR) in each light treatment throughout the experimental period (30th April to 30th September 2008). Different letters across treatments mean significant differences according to *post-hoc* Tukey tests ($p<0.05$). L100, L65, L35 y L7- 100, 65, 35 y 7% of full sunlight at midday, respectively.

Light	T_{Mean} (°C)	T_{Max} (°C)	T_{Min} (°C)	% HR
L100	23.1 ± 0.37a	44.9 ± 0.49a	12.9 ± 0.30a	46.8 ± 1.26a
L65	23.1 ± 0.39a	46.9 ± 0.52a	13.1 ± 0.29a	43.1 ± 1.32a
L35	22.1 ± 0.38a	43.4 ± 0.49b	13.1 ± 0.29a	47.7 ± 1.32a
L7	21.9 ± 0.39a	41.5 ± 0.51c	13.9 ± 0.30a	44.3 ± 1.22a

During the experiment ≥5 trays per treatment were weighed twice a week to estimate their soil gravimetric water content on the basis of the previous calibration. If the weight was lower than that corresponding to the treatment, we added by hand and/or by a watering system the amount of water needed to reach the target soil moisture. One-way ANOVAs, followed by *post-hoc* Tukey tests, revealed significant differences of gravimetric soil water content between watering treatments after watering ($p<0.05$), but not before watering between LW and MW ($p>0.05$, Fig. 3).

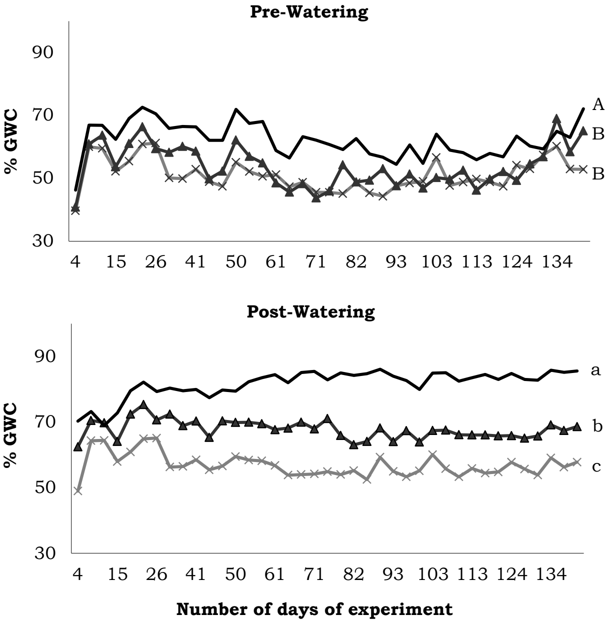

Fig. 3. Average percentage of soil gravimetric water content per treatment (%GWC, HW -flat line-, MW –triangles-, LW –crosses-) throughout the experimental period, before (Pre-Watering) and after watering (Post-Watering). Different capital and small letters mean differences between treatments before and after watering respectively, according to *post-hoc* Tukey tests ($p<0.05$).

2.2. Data collection

Seedling emergence and survival were monitored in every tray during the study period, twice a week in May-June, once a week in July-August and twice a month in September 2008. We considered seedlings to be dead if they did not show green leaves and exhibited easily breakable stems. If apparently dead seedlings resprouted later, we re-categorized them as alive.

The average of days required by a seedling to emerge in a tray (Time to emergence or $T_{emerg.}$) was calculated as:

$$T_{emerg} = \frac{\sum_{i=1}^{n} i \times N.seedlings_i}{N}$$

where i = sampling day, n = total number of days sampled, $N.seedlings_i$ = number of seedlings emerged on day i, N = cumulative number of emerged seedlings until day n.

To get a single index to compare establishment success among treatments within a species, we combined emergence, survival and velocity of emergence ($1/T_{emerg.}$) in the "Establishment Success Index" or ESI as:

$$\text{ESI} = (\text{Emergence} + \text{Survival} + \text{Velocity of emergence})$$

where Emergence=(emergence in a tray/ maximum emergence for that species); Survival=(survival in a tray/ maximum survival for that species); Velocity of emergence=(velocity of emergence in a tray/ maximum velocity of emergence for that species).

2.3. Statistical analyses

The effects of origin (native or exotic), species (nested in origin), light and soil moisture on emergence, $T_{emerg.}$ and survival were assessed with four-way ANOVAs. In order to better interpret interactions of the factor species with any other factor, we also assessed the effect of soil moisture and light treatments on response traits and on ESI in each species with two-way ANOVAs followed by *post-hoc* Tukey tests. Survival of *E. globulus* in the L7-MW treatment was excluded from the analysis because this treatment was affected by a plague that killed all individuals. Variables were checked for homocedasticity (Levene test) and transformed to meet homocedasticity assumptions when necessary (Zar, 1999). Spearman´s correlation coefficient was calculated between seed size and all the studied variables.

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

3. RESULTS

3.1. Establishment Success among Species

We found significant differences on establishment success between species but not between origins (native or exotic) (Table 4 and 5). Among the species of central Spain, the exotic trees *A. altissima* and *R. pseudoacacia* obtained the highest emergence (>80%), followed by the exotics *E. angustifolia* and *A. negundo* and the native *F. angustifolia* (51%, 59% and 57% respectively). The native tree *U. minor* had the lowest emergence (19%). *R. pseudoacacia* was the species that emerged the fastest ($T_{emerg.}$= 14 days), followed by *A. negundo* and *U. minor* (16 days). *A. altissima*, *E. angustifolia* and *F. angustifolia* seeds required longer time to emerge (42, 54 and 55 days respectively). Survival rates were high in all species (≥77%), with the only exception of the exotic *R. pseudoacacia* (35%), whose low survival can be partially explained by the incidence of an aphid plague which affected all treatments during the experimental period. *F. angustifolia* was the species with the highest survival (97%) (Table 4, Fig. 4).

Table 4. Effects of origin (native/exotic), species (nested in origin), light and soil moisture treatments and their interactions on cumulative percentage of emergence (% Emerg.), number of days needed to emerge ($T_{emerg.}$) and cumulative percentage of survival (% Surv.) according to a four-way ANOVA. Statistics F and *p*-values are shown. Levels of significance: ***, p<0.001; **, 0.001≥p<0.01; *, 0.01≥p<0.05; ns, p≥0.05. Results for central Spain species.

	Central Iberian Spain species		
	% Emerg.	$T_{emerg.}$	% Surv.
Origin	3.42 ns	0.05 ns	0.76 ns
Species (Origin)	23.44 ***	40.67 ***	15.29 **
Light	4.35 *	4.06 *	0.25 ns
Soil Moisture	0.99 ns	3.22 ns	3.19 ns
Origin*Light	1.48 ns	0.17 ns	0.57 ns
Origin*Soil Moisture	5.21 *	0.61 ns	2.97 ns
Light*Soil Moisture	2.59 *	3.32 *	1.27 ns
Origin*Light*Soil Moisture	0.17 ns	0.42 ns	0.76 ns
Light*Species(Origin)	5.39 ***	9.68 ***	3.05 *
Soil Moisture*Species(Origin)	0.48 ns	1.00 ns	0.35 ns
Light*Soil Moisture*Species(Origin)	1.99 **	6.16 ***	2.71 ***

Among NW Spain species, the native *P. pinaster* showed the highest emergence (86%) whereas the native *Q. pyrenaica* and the exotic *A. dealbata* showed the same intermediate value (44%) and the exotic *E. globulus* the lowest (24%). Emergence was faster in the exotic trees ($T_{emerg.}$= 25 days in *A. dealbata* and 30 days in *E. globulus)*, whereas $T_{emerg.}$ was 48 days in *P. pinaster* and 73 in *Q. pyrenaica.* In contrast, seedling survival was higher in the native species (98% in *Q. pyrenaica* and *P. pinaster*), closely followed by *E. globulus* (97%, excluding L7-MW) and *A. dealbata* (74%) (Table 5, Fig. 4).

Seed size did not correlate significantly with any of the studied traits ($p > 0.05$).

Table 5. Effects of origin (native/exotic), species (nested in origin), light and soil moisture treatments and their interactions on cumulative percentage of emergence (% Emerg.), number of days needed to emerge ($T_{emerg.}$) and cumulative percentage of survival (% Surv.) according to a four-way ANOVA. Statistics F and *p*-values are shown. Levels of significance: ***, $p<0.001$; **, $0.001 \geq p<0.01$; *, $0.01 \geq p<0.05$; ns, $p \geq 0.05$. Results for NW Spain species.

Northwest Spain species			
	% Emerg.	$T_{emerg.}$	% Surv.
Origin	1.85 ns	7.13 ns	4.23 ns
Species (Origin)	39.27 **	14.19 **	1.52 ns
Light	2.04 ns	1.44 ns	1.21 ns
Soil Moisture	1.30 ns	0.57 ns	0.26 ns
Origin*Light	0.52 ns	0.98 ns	0.92 ns
Origin*Soil Moisture	0.09 ns	0.16 ns	0.51 ns
Light*Soil Moisture	1.01 ns	0.21 ns	1.48 ns
Origin*Light*Soil Moisture	0.38 ns	0.41 ns	1.34 ns
Light*Species(Origin)	2.16 ns	7.88 **	1.73 ns
Soil Moisture*Species(Origin)	4.07 *	1.52 ns	2.43 ns
Light*Soil Moisture*Species(Origin)	1.15 ns	3.31 ***	5.13 ***

3.2. Irradiance and water effects on establishment success

Light, either as main factor or as part of an interaction term, significantly affected the studied traits more often than soil moisture (Table 4 and 5). To better interpret interactions between species and treatments, we present the effects of water and light separately for each species (Table 6). Therefore, Fig. 4 illustrates only the effect of light treatments on each species, although mean values under all combinations of treatments can be consulted in Supplementary Material Appendixes 1 and 2.

High irradiance enhanced emergence of all Central Spain riparian species, except the exotics *E. angustifolia* and *R. pseudoacacia* (Table 6, Fig. 4), and accelerated emergence of all species except *A. negundo* and *U. minor* (Table 6, Fig. 4). High light also increased survival of *A. altissima*, *R. pseudoacacia* and *E. angustifolia* but not *A. negundo*, *F. angustifolia* and *U. minor* (Table 6, Fig. 4). Consequently, the ESI value was maximum at high irradiance (L100 or L65) in all species except in the exotic *A. negundo,* whose ESI was not affected by light (Fig. 5).

Table 6. Effect of light and soil moisture treatments and their interaction (L*M) on cumulative percentage of emergence, number of days needed to emerge ($T_{emerg.}$) and cumulative percentage of survival in every studied species, according to two-way ANOVAs. *p*-values are shown. Levels of significance: ***, p<0.001; **, 0.001≥p<0.01; *, 0.01≥p<0.05; ns, p≥0.05. *Eucalyptus globulus* results were obtained excluding L7 in the statistical analysis, in order to avoid the L7-MW treatment (see Material and Methods).

Sps.		Light		Moisture		L*M	
		F	p	F	p	F	p
A. neg	% Emer.	6.14	**	1.37	ns	1.37	ns
	$T_{emerg.}$	2.61	ns	1.30	ns	1.35	ns
	% Surv.	2.42	ns	3.64	*	0.75	ns
A. alt	% Emer.	5.62	*	2.30	ns	3.97	*
	$T_{emerg.}$	421.63	***	28.65	***	29.78	***
	% Surv.	13.90	***	4.89	*	2.62	*
E. ang	% Emer.	0.97	ns	6.28	*	2.17	ns
	$T_{emerg.}$	36.37	***	2.07	ns	12.78	***
	% Surv.	36.63	***	1.06	ns	1.86	ns
R. pse	% Emer.	2.08	ns	0.69	ns	1.52	ns
	$T_{emerg.}$	6.38	**	1.39	ns	2.19	ns
	% Surv.	6.84	**	1.39	ns	13.36	***
F. ang	% Emer.	35.09	***	1.23	ns	2.51	*
	$T_{emerg.}$	108.14	***	11.48	***	9.36	***
	% Surv.	2.83	ns	0.83	ns	0.29	ns
U. min	% Emer.	31.50	***	1.20	ns	3.35	ns
	$T_{emerg.}$	1.19	ns	2.87	ns	0.28	ns
	% Surv.	1.98	ns	0.18	ns	1.69	ns
A.deal	% Emer.	2.80	ns	7.72	**	1.25	ns
	$T_{emerg.}$	35.83	***	0.83	ns	1.51	ns
	% Surv.	0.36	ns	1.88	ns	0.20	ns
E. glob	% Emer.	0.71	ns	2.86	ns	2.22	ns
	$T_{emerg.}$	50.28	***	23.92	***	3.89	**
	% Surv (no L7)	1.10	ns	1.26	ns	2.34	ns
	% Surv (no MW)	10.78	***	2.15	ns	0.73	ns
P. pin	% Emer.	1.44	ns	1.09	ns	0.83	ns
	$T_{emerg.}$	64.99	***	0.82	ns	1.78	ns
	% Surv.	1.54	ns	0.72	ns	1.71	ns
Q. pyr	% Emer.	4.84	**	3.59	*	0.22	ns
	$T_{emerg.}$	1.30	ns	1.70	ns	2.36	ns
	% Surv.	3.30	*	8.39	**	3.30	*

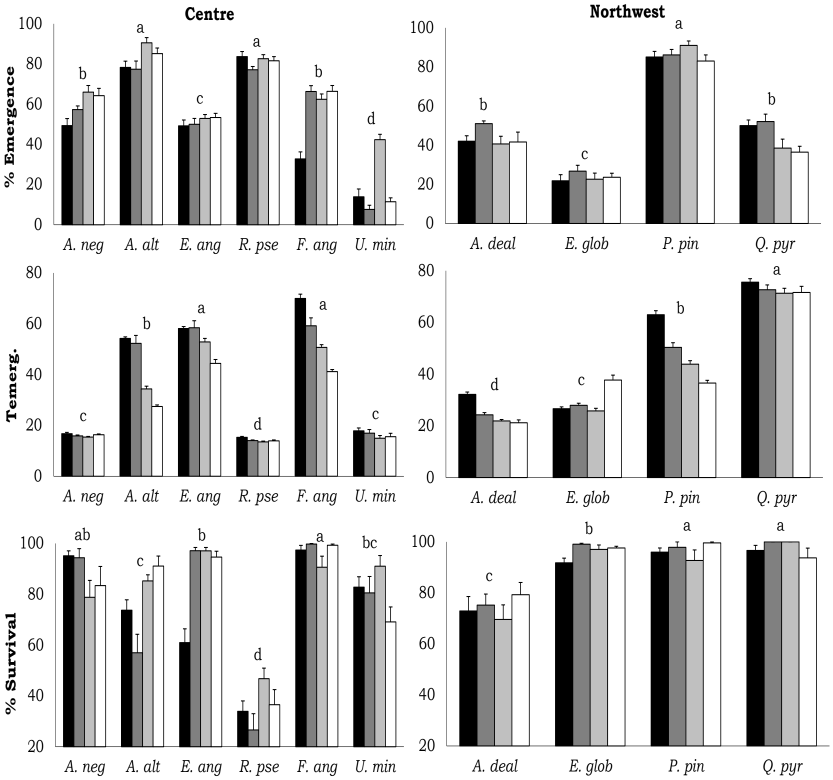

Fig. 4. Average values of cumulative percentage of emergence, number of days needed to emerge ($T_{emerg.}$) and cumulative percentage of survival + SE attained by each species in each light treatment. Results of central (left) and Northwest Spain species (right). In every chart, exotic species are represented in the left side. L100 (white), L65 (light grey), L35 (dark grey) y L7 (black)- 100, 65, 35 y 7% of sunlight at midday. Different letters mean differences between species according to *post-hoc* Tukey tests (p<0.05). *E. globulus* survival was calculated excluding L7-MW.

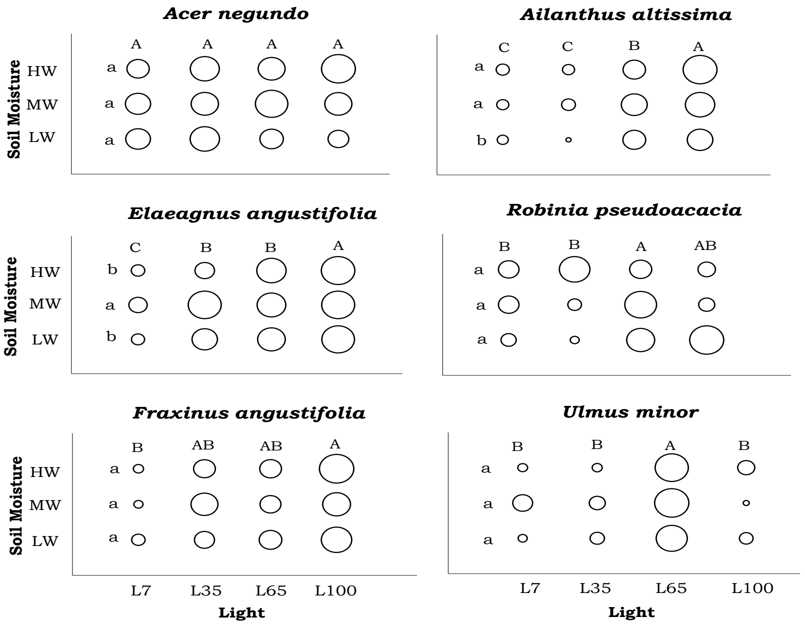

Fig. 5. Bubble chart representing average values of Establishment Success Index (ESI) obtained by each species of central Spain (native species lower charts). Bubble size is proportional to ESI^3 values. We used the third power to represent the ESI values in order to accurate the visualization of the differences between treatments. Different capital letters mean differences between light treatments; different small letters mean differences between soil moisture treatments, according to *post-hoc* Tukey tests ($p<0.05$).

Soil moisture affected emergence of *E. angustifolia* (maximum in MW), $T_{emerg.}$ of *A. altissima* and *F. angustifolia* (maximum in LW and HW respectively) and seedling survival of *A. negundo* and *A. altissima* (higher survival at increasing moisture). Soil moisture also affected seedling survival of *R. pseudoacacia*, with a negative effect under high light and a positive effect under low light (Table 6). Considering all responses combined in the ESI, soil moisture only had an effect in the exotics *A. altissima* (lowest value at LW) and *E. angustifolia* (highest value at MW) (Fig. 5).

Among NW Spain species, high irradiance decreased *Q. pyrenaica* emergence whereas it speeded up *A. dealbata* and *P. pinaster* emergence (Table 6, Fig. 4). In contrast, high light slowed down *E. globulus* emergence (Table 6, Fig. 4). Light only affected survival of *Q. pyrenaica* seedlings, being higher at intermediated light levels (Table 6, Fig. 4). Overall, the ESI showed a higher success of *P. pinaster* and *A. dealbata* at high light while *Q. pyrenaica* and *E. globulus* performed better at moderate shade (Fig. 6).

High soil moisture reduced *A. dealbata* and *Q. pyrenaica* emergence whereas *E. globulus* $T_{emerg.}$ was maximum in MW (Table 6). *Q. pyrenaica* survival increased with soil moisture. Soil moisture treatments only affected ESI in *E. globulus* and *A. dealbata*, but in opposed ways. *E. globulus* showed the highest ESI at HW whereas *A. dealbata* obtained the lowest ESI in that treatment (Fig. 6).

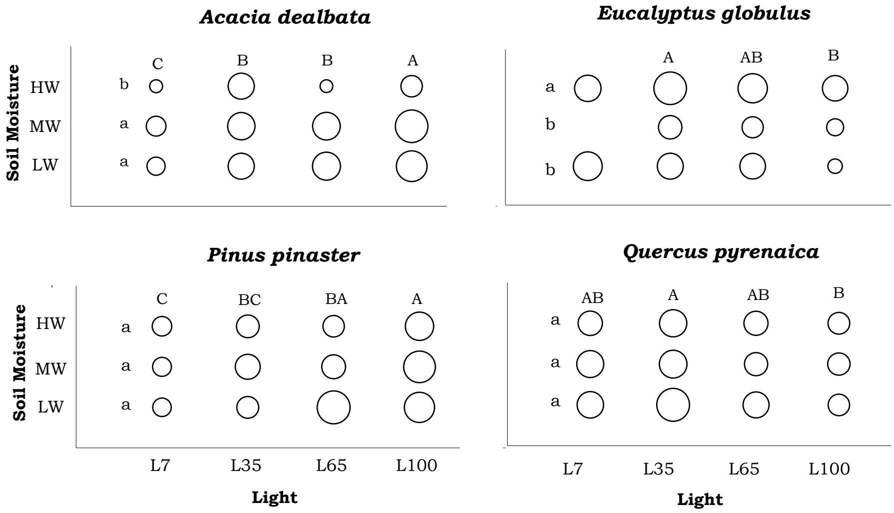

Fig. 6. Bubble chart representing average values of Establishment Success Index (ESI) obtained by each species of NW Spain (native species lower charts). Bubble size is proportional to ESI^3 values. We used the third power to represent the ESI values in order to accurate the visualization of the differences between treatments. Different capital letters mean differences among light treatments; different small letters mean differences among soil moisture treatments, according to *post-hoc* Tukey tests ($p<0.05$). Results of *Eucalyptus globulus* shown here were obtained without including L7 in the statistical analysis, in order to avoid the L7-MW treatment.

4. DISCUSSION

4.1. Comparison between exotic and native trees

Our study showed that the establishment success of the studied species was independent of their native or exotic origin, and varied depending on the analysed trait.

Among central Spain species, *A. altissima* and *R. pseudoacacia* attained the highest emergence, but *R. pseudoacacia*, *A. negundo* and *U. minor* needed less time to emerge and *F. angustifolia* showed the highest seedling survival. These results indicate that, on average, there is no clear superiority of exotic species over coexisting natives against hypothesis 1. Alternatively, the results indicate that species followed different life-history strategies: the exotics *A. altissima* and *R. pseudoacacia* showed small seeds (Table 1), high emergence (>80%) and relatively low seedling survival (Fig. 4); besides, they are vigorous resprouters, produce large seed crops, especially *A. altissima*, and form seed banks (Kowarik and Säumel, 2007; Jung et al., 2009; Masaka and Yamada, 2009). All these traits contribute to efficiently colonize disturbed areas, where intermittent peaks of resources are available for plants (Grime, 1977). In fact, both species have been found to be positively associated with each other in highly disturbed areas (Call and Nilsen, 2003). On the other hand, the native *F. angustifolia* and the exotics *A. negundo* and *E. angustifolia* showed larger seeds (Table 1), lower emergence (<80%) but higher survival (close to 100%) (Fig. 4), which make them more suited to succeed under higher levels of competition (Grime, 1977). Finally, the tiny seeds of *U. minor* (Table 1), its low emergence and intermediate seedling survival (Fig. 4) suggest that this native species is positioned between the two groups defined above.

Among NW Spain species, *P. pinaster* showed the highest emergence, *A. dealbata* and *E. globulus* germinated faster and possess the smallest seeds (Table 1), while *Q. pyrenaica* and *P. pinaster* exhibited the highest survival (Fig. 4). The two exotics (*A. dealbata* and *E. globulus*) have other traits characteristic of efficient colonizers, such as a profuse resprouting ability (Weber, 2003; Sanz Elorza et al., 2004) and strongly allelopathic lecheates (Molina et al., 1991; Babu and Kandasamy, 1997; Carballeira and Reigosa, 1999; Lorenzo et al., 2008; Lorenzo et al., 2011). Moreover, *A. dealbata* possesses N-fixation ability (Lorenzo et al., 2010) which represents an additional advantage to colonize N-poor soils. On the other extreme, *Q. pyrenaica*, with its massive seeds (Table 1), a 100% survival (Fig. 4) and large seedlings (data not shown), would be the most successful to colonize environments with high levels of competition (Grime, 1977). Finally, *P. pinaster* would occupy an intermediate position.

4.2. Environmental conditions favouring native and exotic trees

Our hypothesis 2 postulated that exotic species would be more successful than native species in resource-rich scenarios, in accordance with the ruderal opportunistic strategy attributed to exotic invasive plants by many authors (Pattison et al., 1998; Baruch and Bilbao, 1999; Grotkopp and Rejmánek, 2007). However, we found no support for our hypothesis, as species requirements for light and water were independent of their native or exotic origin.

Irradiance showed a higher effect on the studied traits than soil moisture, most species being favoured by high light or slight shade (L100 or L65) (Figs. 4, 5 and 6). The poor effect of soil moisture can be a consequence of avoiding the use of too restrictive water levels. Therefore, this result should be interpreted with caution, as water stress in the field may be much more restrictive. We discuss below the responses of each group of species to light gradients.

4.3. Central Spain species

The exotic seedlings of central Spain species showed a wide variety of responses to light. In agreement with the colonizer strategy discussed above, the exotics *A. altissima* and *R. pseudoacacia* showed their maximum success under high irradiance (either L100 or L65, see Figs. 4 and 5), according to previous studies (Boring and Swank 1984; Knapp and Canham, 2000; Kowarik and Säumel, 2007). *E. angustifolia* has been previously classified as late-succession species, capable of establishing in shade (Shafroth et al., 1995; Knapp and Canham, 2000). We found that *E. angustifolia* emergence declined with decreasing light, but once emerged, it showed a high survival from 35 to 100% of full sunlight, suggesting a large potential to succeed under a wide range of canopy openness (Figs. 4 and 5). By contrast, *A. negundo* was the only exotic species capable of establishing in the deepest shade, showing >95% of survival at L35 and L7, although it can also cope with full sunlight (Figs. 4 and 5) (Weber, 2003; DeWine and Cooper, 2007 and 2008). These results indicate that the different exotic species are able to establish along a gradient of light availability, from open areas (more vulnerable to *A. altissima* and *R. pseudocacia* establishment) to dense canopies (more vulnerable to *E. angustifolia* and *A. negundo* establishment).

Among the native species, *F. angustifolia* and *U. minor* have been reported to establish and regenerate more effectively in mature old forest, being less dependent on gap-opening disturbances to succeed than other floodplain native trees, such as *Populus* spp. and *Salix* spp. (González et al., 2010). Accordingly, in both natives we found high survival rates at deep or moderate shade (Fig. 4). Although *F. angustifolia* emergence was hampered by deep shade (Fig. 4), once emerged, seedling survival was very high at all light levels. In contrast, considering emergence and survival together, *U. minor* showed a clear preference for a moderate shade (L65) (Fig. 5).

According to our findings, the light conditions that favour the establishment of the exotics *E. angustifolia* and *A. negundo* would overlap with that of the natives *F. angustifolia* and *U. minor*, while *A. altissima* and *R. pseudoacacia* would overlap more with that of the native *Salicaceae* species, such as *Populus* spp. and *Salix* spp., which are more successful at open sites (González et al., 2010). However, the emergence and survival of the natives *Salicaceae* depend on flood events proper of non-regulated rivers (Mahoney and Rood, 1992, 1998; González et al., 2010). This suggests that river regulation, suppressing flood events, can favour the spread of the exotics *A. altissima* and *R. pseudoacacia* over the flood-dependent native *Salicaceae* species.

4.4. Northwest Spain species

NW Spain species can be classified in two groups according to the overall response of their seedlings to our experimental irradiance gradient (summarised in the ESI): *A. dealbata* and *P. pinaster* showed the best performance at full sunlight, while *Q. pyrenaica* and *E. globulus* were more successful under shade (Fig. 6). Therefore, there was no consistency between environmental preferences of the species and their origin, against hypothesis 1. The preference of *A. dealbata* and *P. pinaster* for high light was accounted for by their faster emergence at increasing light (Fig. 4). This response would increase the establishment success of these species in gaps, as an earlier occupation of space by seedlings may confer them competitive success over late-emergence species (Jones and Sharitz, 1989; Miller et al., 1994; Verdú and Traveset, 2005; Castro, 2006). Accordingly, previous reports suggested that these species are more successful in open sites (Sanz Elorza et al., 2004; Sánchez-Gómez et al., 2006a; Sánchez-Gómez et al., 2006b; Lorenzo et al., 2010). *Quercus pyrenaica* preference for shade was accounted for by the higher emergence and higher survival of the seedlings in treatments with certain level of shade (Fig. 4). Therefore, this species can be described as shade-tolerant, according to previous studies (Sánchez-Gómez et al., 2006a; 2006b). The large mass of *Q. pyrenaica* seeds (Table 1) can supply carbon and nutrient demands by developing seedlings, making them quite independent of resource shortages during the first months of growth (Kabeya and Sakai, 2003). The relatively lower establishment success of *E. globulus* at full sunlight was accounted for by the longer time to emerge under this treatment (Fig. 4). However, $T_{\text{emerg.}}$ of *E. globulus* at full sun light was lower than that of coexisting natives: it was much lower than that of *Q. pyrenaica* and similar to that shown by *P. pinaster* in the same treatment. This fact, joined to the absence of light effects on other *E. globulus* fitness-related traits, and to the high survival of this species under all treatments (>90%, Fig. 4), suggest that *E. globulus* is able to establish under a wide range of light intensities. Finally, the two invasive species of the area responded to soil moisture in different ways: while *A. dealbata* emergence was declined by high moisture, *E. globulus* needed more time to emerge at MW and tended to germinate more in HW. These results suggest a low tolerance of *A. dealbata* roots to waterlogging-induced hypoxia in early stages.

5. CONCLUSIONS

Our study demonstrates that the seedlings of the studied exotic species did not share a common response to light and soil moisture availability. On the contrary, these species can be positioned along a successional gradient, indicating that not all of them are opportunistic colonizers. Although information on the preferences of studied exotic tree seedlings for other environmental factors is still needed (e.g. soil type or temperature), our results contribute to identify some of the environmental conditions that favour or hinder their establishment success.

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8. SUPPLEMENTARY MATERIAL

Appendix 1. Average values of cumulative percentage of emergence (%E), T_{emerg}. and cumulative percentage of survival (%S) and SE in each species and treatment. Results of central Spain species. L100, L65, L35 y L7- 100, 65, 35 y 7% of sunlight at midday. **Table A**: LW; **Table B**: MW; **Table C**: HW. LW, MW, HW: 55, 66, 84% of gravimetric water content respectively.

Table A.

		L100		L65		L35		L7	
		LW		LW		LW		LW	
Sps.		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
A.neg	% E	56.3	6.0	69.8	4.3	60.4	1.2	54.2	3.4
	T_{emerg}.	15.9	0.4	15.3	0.5	15.3	0.4	17.5	1.1
	% S	69.2	16.5	61.7	16.0	90.0	10.0	92.0	3.2
A.alt	% E	82.9	7.6	93.8	3.8	61.9	6.2	76.9	4.8
	T_{emerg}.	29.2	0.9	38.7	1.1	49.7	1.9	56.5	0.7
	% S	84.8	12.2	88.0	3.2	31.6	12.8	71.1	2.4
E.ang	% E	50	1.8	53.8	4.6	45.6	2.1	53.1	3.4
	T_{emerg}.	44.0	4.3	56.6	1.5	51.2	1.9	58.9	0.8
	% S	97.2	2.8	98.1	1.9	94.7	3.1	47.8	3.7
R.pse	% E	83.3	4.2	81.3	2.7	72.9	3.6	86.5	4.6
	T_{emerg}.	13.5	0.8	14.7	0.4	14.8	0.6	15.0	0.6
	% S	59.9	4.1	54.9	8.0	7.3	2.8	21.0	7.3
F.ang	% E	62.2	5.8	62.5	6.4	57.7	2.8	43.4	2.1
	T_{emerg}.	39.8	1.6	48.1	0.3	57.5	2.6	67.0	1.8
	% S	100	0.0	89.5	7.5	100	0.0	97.2	2.8
U.min	% E	12.5	2.4	45.7	4.6	12.5	3.8	8.3	1.7
	T_{emerg}.	17.8	3.0	17.0	3.1	18.1	3.0	18.3	1.7
	% S	87.5	12.5	92.0	5.5	75.0	25.0	79.2	12.5

Table B.

		L100		L65		L35		L7	
		MW		MW		MW		MW	
Sps.		$\bar{x}$	SE	$\bar{x}$	E	$\bar{x}$	SE	$\bar{x}$	SE
A.neg	% E	66.7	3.8	68.8	7.7	58.3	3.8	53.1	2.6
	T_{emerg}.	16.5	0.2	15.5	0.5	16.4	0.9	17.4	0.3
	% S	82.2	14.3	89.9	5.8	93.1	4.7	98.1	1.9
A.alt	% E	80.6	2.1	95.6	3.0	84.4	2.6	85	6.7
	T_{emerg}.	27	0.9	31.8	1.0	43.8	1.6	53.0	0.8
	% S	94.6	0.8	82.0	5.7	65.6	7.5	66.3	9.5
E.ang	% E	58.1	3.3	51.9	2.8	61.3	1.3	53.8	3.3
	T_{emerg}.	47.5	1.9	48.6	2.6	53.0	1.6	60.4	0.1
	% S	93.6	4.3	93.1	2.8	98.1	1.9	71.8	6.7
R.pse	% E	78.1	4.3	87.5	1.7	79.2	2.9	86.5	4.6
	T_{emerg}.	14	0.5	12.7	0.3	13.8	0.1	16.1	0.5
	% S	25.1	5.9	49.2	5.9	17.1	2.5	39.7	5.2
F.ang	% E	62.6	4.2	61.6	5.8	67.4	5.5	26.7	7.2
	T_{emerg}.	43.0	1.1	49.8	1.3	48.1	2.2	73.0	3.6
	% S	98.8	1.2	86.2	11.4	99.2	0.8	95.0	5.0
U.min	% E	5.2	2.0	41.7	6.1	2.1	1.2	24.0	10.3
	T_{emerg}.	13.2	1.2	13.6	0.6	14.0	2.0	15.5	1.0
	% S	33.3	16.7	89.7	7.1	100	0.0	88.0	7.0

Table C.

		L100		L65		L35		L7	
		HW		HW		HW		HW	
Sps.		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
A.neg	% E	69.8	7.9	59.4	4.6	53.1	3.1	40.6	9.1
	$T_{emerg.}$	16.6	0.9	15.5	0.5	15.9	0.3	15.2	0.6
	% S	98.8	1.3	84.7	7.3	100	0	95.3	4.7
A.alt	% E	91.8	1.6	82.2	3.9	85.9	4.5	73	3.5
	$T_{emerg.}$	25.8	0.8	32.6	0.9	67.0	1.4	53.1	0.8
	% S	93.9	1.7	85.7	3.9	73.7	4.9	83.8	5.9
E.ang	% E	51.9	4.7	53.1	3.1	43.1	4.5	40.6	6.0
	$T_{emerg.}$	41.6	1.6	53.2	1.2	69.2	1.9	54.9	1.0
	% S	93.1	5.4	100	0.0	98.6	1.4	63.3	12.9
R.pse	% E	83.3	2.4	79.2	4.5	79.2	0	78.1	3.1
	$T_{emerg.}$	14.2	0.8	13.2	0.3	13.2	0.2	14.9	0.7
	% S	24.6	7.7	36.2	5.7	55.3	3.4	41.1	4.4
F.ang	% E	74.2	3.8	63.1	1.9	73.8	3.0	28.1	4.8
	$T_{emerg.}$	40.8	1.4	54.2	2.1	72.0	0.5	70.1	3.2
	% S	99.0	1.0	96.1	1.6	100	0.0	100	0.0
U.min	% E	16.7	2.9	42.7	3.9	8.3	3.4	9.4	2.6
	$T_{emerg.}$	15.2	1.9	14.3	0.4	17.4	0.9	19.9	2.7
	% S	77.5	13.1	91.5	5.5	75.0	14.4	81.3	12.0

Appendix 2. Average values of cumulative percentage of emergence (%E), T_{emerg}. and cumulative percentage of survival (%S) and SE in each species and treatment. Results of Northwest Spain species. L100, L65, L35 y L7- 100, 65, 35 y 7% of sunlight at midday. **Table D**: LW; **Table E**: MW; **Table F**: HW. LW, MW, HW: 55, 66, 84% of gravimetric water content respectively.

Table D.

		L100		L65		L35		L7	
		LW		LW		LW		LW	
Sps.		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
A. deal	% E.	50.0	4.8	51.0	4.3	51.0	2.0	42.7	5.2
	T_{emerg}.	23.1	2.4	22.3	0.4	25.7	0.3	31.0	0.6
	% Sl	81.4	10.9	72.9	10.4	78.9	7.6	78.0	6.1
E.glo	% E.	16.1	3.7	23.0	3.8	24.6	4.2	30.8	1.5
	T_{emerg}.	35.8	1.8	25.8	1.4	27.1	1.5	25.3	0.7
	% S	95.8	1.8	99.5	0.2	98.8	0.7	90.0	2.6
P.pin	% E.	83.3	5.6	97.9	1.2	83.3	5.6	86.5	4.3
	T_{emerg}	36.5	1.6	39.2	1.6	53.4	2.1	64.1	2.8
	% S	100	0.0	100	0	100	0	94.1	0.9
Q.pyr	% E	39.6	6.3	46.9	10.0	58.3	8.7	57.3	5.5
	T_{emerg}.	66.4	1.8	77.5	2.7	70.7	3.4	76.0	0.8
	% S	81.2	8.9	100	0.0	100	0.0	89.9	4.5

Table E.

		100		65		35		7	
		MW		MW		MW		MW	
Sps.		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
A. deal	% E.	43.8	5.5	44.8	5.5	53.1	1.0	45.8	5.1
	T_{emerg}.	18.8	0.5	21.3	1.0	25.0	2.1	31.8	1.3
	% Sl	82.4	5.0	79.1	9.6	76.0	9.2	73.1	16.1
E.glo	% E.	25.3	0.5	21.2	3.0	23.7	6.1	9.5	1.6
	T_{emerg}.	45.7	1.1	27.4	1.6	30.3	1.3	29.3	0.7
	% S	98.3	0.5	92.4	4.8	99.3	0.6		
P.pin	% E.	88.5	5.2	87.5	4.5	90.6	3.1	84.4	6.0
	T_{emerg}	36.4	1.5	46.6	0.8	45.8	2.4	60.8	3.4
	% S	98.8	1.2	94.7	5.3	93.5	6.5	93.8	4.5
Q.pyr	% E	34.4	6.4	37.5	5.9	51.0	7.3	51.0	4.3
	T_{emerg}.	73.7	4.6	72.3	1.0	75.9	3.0	77.2	2.6
	% S	100	0.0	100	0.0	100	0.0	100	0.0

Table F.

Sps.		100		65		35		7	
		HW		HW		HW		HW	
		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
A. deal	% E.	27.8	14.7	26.0	3.1	49.0	3.6	37.5	4.8
	T_{emerg}.	22.2	1.0	22.1	1.4	22.1	1.0	33.7	2.4
	% Sl	68.8	6.3	56.8	8.5	70.7	7.4	67.5	6.3
E.glo	% E.	29.3	2.1	23.6	9.3	32.0	5.3	25.0	4.8
	T_{emerg}.	31.6	1.3	24.0	2.3	26.3	0.9	25.2	0.5
	% S	98.5	0.6	99.2	0.4	99.1	0.4	93.5	2.6
P.pin	% E.	77.1	5.5	87.5	3.4	84.4	6.0	84.4	5.7
	T_{emerg}	36.7	2.7	45.7	2.2	51.8	4.0	64.0	2.2
	% S	100	0.0	83.3	10.6	100	0	100	0.0
Q.pyr	% E	35.4	3.6	31.3	7.1	46.9	3.1	41.7	0.0
	T_{emerg}.	74.6	4.7	64.0	1.1	71.3	3.4	73.6	3.2
	% S	100	0.0	100	0.0	100	0.0	100	0.0

Chapter 3

Assessing seedling growth strategies of co-occurring native and exotic tree species: an experiment to identify potential regeneration niches for exotic trees in human managed riparian forests.

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RESUMEN

El manejo de ríos y la perturbación humana en bosques de ribera están creando nuevos nichos de regeneración que pueden favorecer el establecimiento de especies exóticas. Para predecir la composición de especies en estos nuevos nichos, en este capítulo se comparan la biomasa alcanzada tras las dos primeras estaciones de crecimiento, la tasa de crecimiento relativo, el tiempo necesario para emerger, la tasa de asimilación por unidad de masa de hoja (NAR_m), así como patrones de distribución de biomasa entre cuatro especies de árboles exóticos y tres de árboles nativos. Para ello, se sembraron semillas de las exóticas *Ailanthus altissima*, *Acer negundo*, *Robinia pseudoacacia* y *Elaeagnus angustifolia* y de las nativas *Populus alba*, *Fraxinus angustifolia* y *Ulmus minor* bajo cuatro tratamientos de luz (100, 65, 35, 7% respecto de la radiación incidente) y dos de humedad del suelo (61 y 40% de contenido gravimétrico de agua en suelo) y se practicaron tres cosechas: al final de la primera estación de crecimiento, mitad de la segunda y final de la segunda, respectivamente. Nuestros resultados muestran que no existe una clara superioridad de nativas o exóticas en términos de acumulación de biomasa, así como una respuesta heterogénea entre las especies dentro cada origen. Todas las especies tendieron a crecer más bajo condiciones ricas en recursos, siendo. *U. minor* y *A. negundo* las especies menos afectadas por los tratamientos. En la mayoría de las especies, una mayor biomasa estuvo positivamente asociada con una emergencia temprana, un alto NAR_m y/o una alta inversión en biomasa radical. Nuestros resultados sugieren que los nuevos nichos de regeneración promovidos por las actividades humanas no favorecerán el establecimiento de las especies exóticas sobre las nativas, pero pueden promover cambios en la composición de especies de los bosques de ribera.

Palabras clave: Especies exóticas, bosques de ribera, biomasa, distribución de biomasa, luz, humedad del suelo.

ABSTRACT

River management and human disturbance are creating new tree regeneration niches in riparian forests that can favor exotic species over natives. In order to predict potential outcomes in species composition in this new tree regeneration niches, we compared seedling performance among four exotic *(Ailanthus altissima*, *Robinia pseudoacacia*, *Acer negundo* and *Elaeagnus angustifolia*) and three native tree species (*Fraxinus angustifolia*, *Ulmus minor* and *Populus alba*) co-occurring in inner Iberian Peninsula river banks. Seeds of the selected species were sown along an experimental gradient with four levels of light (100, 65, 35, 7% of full irradiance) factorially combined with two levels of soil moisture (61 and 40% of soil gravimetric water content). We compared seedling biomass after the first two growing seasons, relative growth rate, biomass allocation to roots, stems and leaves, time to emergence and net assimilation rate per unit of leaf mass (NAR_m). Our results show no clear superiority of natives or exotics in terms of biomass accumulation and heterogeneous responses of species in each origin. Under high resource conditions, all species tended to grow more and similarly. However, only *U. minor* and *A. negundo* seemed to be well-adapted to low light and low moisture. Besides, in most species, a higher biomass was positively associated to early emergence, high NAR_m and/ or high investment in roots. Our results suggest that the new tree regeneration niches created by human-activities would not favor the overall establishment of invasive species over natives, but may promote shifts in the species composition of river bank forests.

Keywords: Exotic species, riparian forests, biomass, biomass allocation, light, soil moisture.

1. INTRODUCTION

The establishment and spread of exotic plants may be favored by plant attributes. Previous studies have shown that some invasive species outcompete native seedlings either due to a higher relative growth rate (Pattison et al., 1998; van Kleunen et al., 2010; Lamarque et al., 2011), higher stress tolerance (Sher and Marshall, 2003; Glenn and Nagler, 2005), higher capacity to acclimate to a wider range of conditions (Richards et al., 2006; Davidson et al., 2011), or higher resource use efficiency (Funk and Vitousek, 2007). However, the final relative advantage of exotics over natives (or vice versa) would depend on the particular environmental conditions where both groups of species co-occur (Daehler, 2003).

In the Mediterranean region of Europe, riparian floodplains are among the most vulnerable habitats to plant invasions, because of the mildness of microclimatic conditions and the abundance of resource availability (Chytrý et al., 2008 and 2009). In this habitat, irradiance and/or soil moisture are the main factors limiting seedling performance, as nutrient availability is usually high in floodplains (González et al., 2010). Many riparian trees of the Mediterranean region are light-demanding species and find their regeneration niche in those gaps frequently opened after flooding episodes (González et al., 2010; González-Muñoz et al., 2011). However, human management of rivers has altered these natural disturbance regimens. River channelization increases the erosive power of the river bottom, and therefore increases the depth of the water table, raising the chances for the establishment of water-stress tolerant plants (Sher and Marshall, 2003; Glenn and Nagler, 2005). Furthermore, river regulation declines the natural rate of gap formation in riparian forests, potentially increasing the chances for the establishment of shade-tolerant species. Contrastingly, other human activities eliminate riparian forests, creating open habitats that may favor the establishment of new light demanding species. These non-naturally created tree regeneration niches in Mediterranean riparian forests (increased light-decreased water and decreased light-decreased water availabilities) pose the question whether exotic tree species will be favored by the new environmental conditions over the existing natives.

The performance of tree seedlings under current environmental conditions may determine the future composition of forest communities (Pacala et al., 1996; Kobe and Coates, 1997; Baraloto et al., 2005). Seedlings are more vulnerable than adults to adverse factors, such as extreme light or soil moisture conditions (Niinemets and Valladares, 2006). If exotic seedlings are able to reach a bigger size in the same time than seedlings of co-occurring natives, they would be able to monopolize below and above ground resources, which may lead to a future domination of forest communities (Blumenthal and Hufbauer, 2007; Closset-kopp et al., 2011). Different plant attributes may promote high growth rates in invasive plants such as large specific leaf area (Baruch and Goldstein, 1999; Daehler, 2003; Richardson and Pysek, 2006; Porté et al., 2011), or high foliar nutrient concentrations (Ehrenfeld, 2003, Leishman et al., 2007, Peñuelas et al., 2010), both being associated to a high photosynthetic rate. Large seed size results in large seedling size shortly after germination (Quero et al., 2007), but small seed mass is associated with a high relative growth rate (Marañón and Grubb, 1993; Swanborough and Westoby, 1996, Reich et al., 1998; Grotkopp et al., 2002). An early emergence contributes to an early space occupation and a consequent competitive advantage over late-emerged seedlings (Jones and Sharitz, 1989; Verdú and Traveset, 2005; Castro, 2006).

In this study, we compare seedling growth and potentially associated traits among four exotic and three native tree species which co-occur in the riparian forests of inner Spain. The exotic trees *Ailanthus altissima* (Mill.) Swingle, *Acer negundo* L., *Elaeagnus angustifolia* L. and *Robinia pseudoacacia* L. were introduced between 18th and early 20th centuries in the Iberian Peninsula, where these species are considered as aggressive invaders (Sanz Elorza et al., 2004). Although they are mostly found in disturbed sites, such as road sides or crop borders, they are also invading riparian forests, where they co-occur with the dominant natives *Fraxinus angustifolia* Vahl., *Ulmus minor* Mill. and *Populus alba* L. (Sanz Elorza et al., 2004; Blanco Castro et al., 2005). *A. altissima*, *R. pseudoacacia*, and *P. alba* have been previously described as light demanding species whereas *U. minor*, *F. angustifolia*, *E. angustifolia* and *A. negundo* may establish under shade (González-Muñoz et al., 2011).

We aimed to compare seedling growth between the above native and exotic species under different environmental conditions, in order to predict potential tree regeneration shifts in those scenarios favored by human activities. We conducted a factorial experiment with four irradiance and two soil moisture treatments, mimicking the wide range of natural and new human-mediated environmental conditions existing in Mediterranean riparian forest. Our specific aims were: 1) comparing biomass accumulation and related traits during the first two growing seasons between native and exotic seedlings; 2) assessing the range of light and soil moisture that favor or hamper seedling growth and identifying the attributes that better explain growth differences across treatments. We hypothesize that 1) exotic seedlings would accumulate on average more biomass than natives; 2) both exotic and native species will reach higher biomass under resource-abundant treatments but exotics will perform relatively better than natives, according to the opportunistic strategy attributed to most exotic invasive plants (Pysek et al., 1995; Rejmánek and Richardson, 1996; Hamilton et al., 2005).

2. MATERIAL AND METHODS

2.1. Experimental design

The experiment was set up outdoors at the Botanical Garden of Alcalá University (Madrid, central Spain 40°30´N, 3°20´W, 596 m a.s.l). Climate is continental Mediterranean with hot and dry summers and cold winters. Mean annual maximum and minimum temperatures are 20.5 and 7.8 °C, respectively. Mean annual precipitation is 378 mm (data from Torrejón de Ardoz weather station, *Instituto Nacional de Meteorología*, 1971-2008).

Four light treatments (L100, L65, L35 and L7, corresponding to 100%, 65%, 35% and 7% of full sun irradiance) were established, aiming to mimic the light gradient existing in a typical Mediterranean forest, from the gaps (L100) to the under-canopies of dense forests (L7) (Valladares, 2004a; Valladares, 2004b). Shade treatments were obtained by covering four 6x6 m soil surfaces with green nets on the tops and sides.

These light treatments were crossed with two soil moisture levels, namely 61% (high moisture, HM) and 40% (low moisture, LM) of soil gravimetric water content. These levels corresponded to soil matric potential of -1.63 and -1.99 MPa, respectively, as estimated by the filter-paper technique (Deka et al., 1995). Soil moisture levels were aimed to induce changes in species success without causing massive mortality, based on previous experience (Castro-Díez et al., 2006, 2007). To determine the amount of water needed to keep the target soil moisture in each treatment during the experimental period, we conducted a pot weight-soil moisture calibration before the beginning of the experiment (see details in González-Muñoz et al. (2011), which allowed us to calculate the amount of water needed on the basis of the pot weight. Soil moisture treatments were applied during 2008 and 2009 growing seasons, while in the rest of the period plants just received rainwater. Kurskall-Wallis tests revealed significant differences of soil moisture before (H=112.65, p<0.001) and after watering (H=206.48, p<0.001).

Local air temperature, % of air humidity and available photosynthetic photon flux density (PPFD) were recorded every 5 min throughout the experiment period with climatic sensors connected to data loggers (HOBO model H08-006-04; Onset, Pocasset, MA, USA). We tested the differences in mean, maximum and minimum temperature and relative air humidity between light treatments throughout the growing seasons (May to September 2008 and 2009) with one-way ANOVAs followed by *post hoc* Tukey tests. Light treatments neither differ in mean, minimum or maximum temperature nor in relative air humidity (p> 0.05) (Table 1).

Table 1. Mean values ± SE of mean, maximum and minimum temperature (T_{Mean}, T_{Max} and T_{Min}, °C) and relative air humidity (%HR) in each light treatment throughout the experimental period growing seasons (May to September 2008 and 2009). L100, L65, L35 y L7- 100, 65, 35 y 7% of full sunlight at midday, respectively.

	T_{Mean}	T_{Max}	T_{Min}	%HR
L100	23.36 ± 0.62	36.92 ± 0.85	12.85 ± 1.57	46.07 ± 2.43
L65	23.18 ± 0.57	37.22 ± 0.80	12.87 ± 1.54	48.06 ± 2.30
L35	22.07 ± 0.59	33.83 ± 0.85	13.25 ± 0.56	42.64 ± 2.42
L7	21.74 ± 0.55	29.42 ± 0.70	13.95 ± 0.55	43.30 ± 1.92

2.2. Sowing procedure

Seeds of all species above were supplied by oficial seed banks of the Spanish Ministry of Environment. Before the onset of the experiment, we conducted germination essays at the laboratory to maximize seed emergence (see González-Muñoz et al., 2011 for further details). Average seed mass was assessed for each species by weighting 30 seeds after > 72 hours in the oven at 60°C.

On 2008 April the 30th, we sowed seeds of all species under the eight treatments resulting from crossing the light and soil moisture levels. Species with small seeds or with low percentages of emergence in the germination essays were sown in single trays (28x38x7 cm, 40 seeds per tray) whereas species with big seeds or with high percentages of emergence were sown in multipot trays (24 pots of 330 ml per tray, one seed per pot). The experimental soil was 1:2 volume mixture of washed river sand and commercial substrate 15-10-20 NPK-Kekkilä Iberia S.L., Valencia, Spain.

During the spring and early summer of the first growing season, we sampled the number of seedlings emerged in each tray every three days. The average of days required by a seedling to emerge in a tray (Time to emerge or $T_{emerg.}$) was calculated as:

$$T_{emerg} = \frac{\sum_{i=1}^{n} i \times No.seedlings_i}{N}$$

where i = sampling day, n = total number of days sampled, $No.seedlings_i$= number of seedlings emerged on day i, N = cumulative number of emerged seedlings until day n.

Plants were left in trays until April 2009 with no additional fertilization. Then, 10-20 plants per species and treatment were transplanted to individual 1.5 L pots (Fig. 1). During the second growing season, pots were monthly fertilized with a 100 mg/l solution of NPK 15-10-20 (Peters Professional, The Scott Company, Brantford, Ontario). Trays / pots of all species were randomly arranged in each of the eight treatments and randomly re-arranged within each treatment twice a week to guarantee treatment homogenization.

Fig. 1. Experimental pots at the L65 treatment on the 30th of July 2009.

2.3 Data collection

Seedlings were harvested at the end of the first growing season (November 2008), in the middle of the second growing season (July 2009) and at the end of the second growing season (November 2009) (Fig. 2). *Ulmus minor* under L35 and L100 and *A. altissima* and *R. pseudoacacia* under L35 were not harvested in July 2009 due to the low number of available seedlings. In the rest of cases, 3-9 seedlings were collected per species, treatment and harvest. Once collected, plants were separated into roots, stems and leaves and oven-dried after 48 hours at 60°C. Relative root, stem and leaf weight ratios (RWR, SWR and LWR respectively) were estimated in July 2009 harvest, which was the only one where seedlings presented the full foliage (Fig. 2).

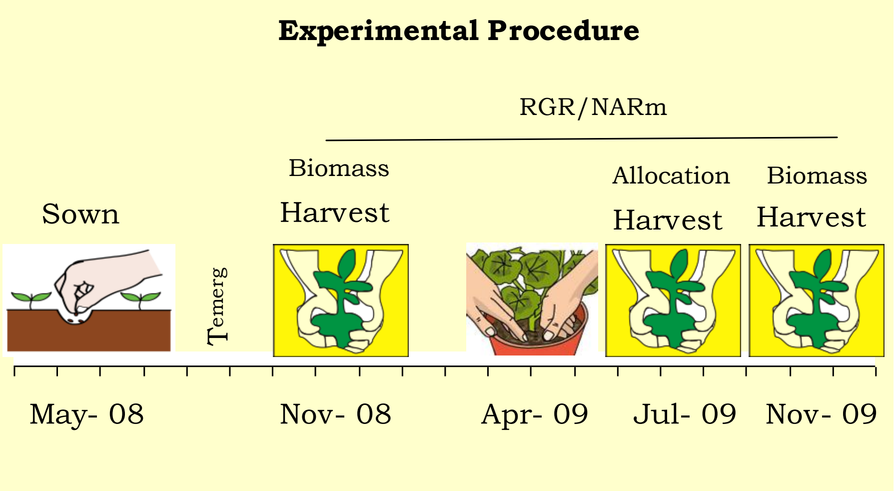

Fig. 2. Experimental procedure. The figure indicates dates, actions and variables calculated or measured.

Seedling biomass of both November were analyzed excluding leaf mass as in this month harvested plants were at different stages of leaf abscission. The average relative growth rate (RGR) of seedlings between the November 2008 and November 2009 harvests was calculated for each species and treatment as:

$$RGR = (\ln(\text{Biomass}_{Nov2009})-\ln(\text{Biomass}_{Nov2008}))/\text{days between harvests}$$

This RGR was used to estimate the net assimilation ratio per unit of leaf mass (NAR_m) as:

$$NAR_m = RGR/LWR_{Jul2009}$$ (Lambers et al., 2008)

2.4 Statistical analyses

We conducted four-way nested ANOVAs to test the effect of origin (native or exotic), species (nested in origin), light and soil moisture on the biomass reached in November 2008 and 2009 and on the RWR, SWR and LWR of July 2009. Differences in RGR, NAR_m, biomass allocation traits and $T_{emerg.}$ between origins and species (nested in origin) were tested with two–way nested ANOVAs. In both analysis, *post hoc* Bonferroni tests were used to assess differences between species. We also tested in each species the effect of light and soil moisture on seedling mass of November 2009 and on the biomass allocation traits by means of two-way ANOVAs. *Post hoc* Bonferroni tests were used to check differences among light treatments. In all cases, data were checked for homoscedasticity (Bartlett test) and normality assumptions (Shapiro Wilk test).

Pearson product-moment correlation coefficients were calculated to assess the linear association between November 2009 seedling mass and RWR, SWR, LWR, NAR_m and $T_{emerg.}$ in each species.

Statistical analyses were conducted using R 2.13 package (library “stats”; R Development Core Team 2011).

3. RESULTS

In November 2008, exotic seedlings were slightly larger than native seedlings, due to the high biomass of *A. negundo* and *E. angustifolia*, but this difference was not significant (Table 2, Fig. 3). By contrast, in November 2009, natives were significantly larger than exotics, due to the low biomass of *A. altissima* (Table 2, Fig. 3). As there was not a consistent effect of origin on seedling mass, we will focus on species responses and traits from now on.

In November 2008, *A. negundo*, *E. angustifolia*, *F. angustifolia* and *U. minor* showed similar biomass and higher than that of *A. altissima*, *R. pseudoacacia* and *P. alba* (Fig. 3). In November 2009, *R. pseudoacacia* and *P. alba* caught up the group of the larger species and only *A. altissima* remained smaller (Fig. 3).

Table 2. Effect of Origin (O), species (nested in Origin) (Sps(O)), light (L), soil moisture (M) and their interactions on the biomass reached by seedlings at the end of the first (Nov 2008, N= 212) and second growing seasons (Nov 2009, N= 360), according to four-way ANOVAs. F, degrees of freedom (df) and significances (p) are shown

		Biomass Nov 2008		Biomass Nov 2009	
	df	F	p	F	p
O	1	1.206	0.274	6.152	0.014
Sps(O)	5	50.731	0.001	28.270	0.001
L	3	28.690	0.001	349.200	0.001
M	1	53.463	0.001	18.639	0.001
L*M	3	2.079	0.105	9.320	0.001
O*L	3	9.451	0.001	2.393	0.068
O*M	1	0.020	0.888	1.058	0.304
L*M*O	3	7.804	0.001	7.209	0.001
L*Sps(O)	15	7.773	0.001	17.457	0.001
M*Sps(O)	5	7.290	0.001	5.386	0.001
L*M*Sps(O)	14	3.473	0.001	1.878	0.028

Robinia pseudocacia and *P. alba* showed the highest RGR and, together with *A. altissima*, the highest LWR (Table 3 and 4). *F. angustifolia* and *E. angustifolia* required longer time to emerge and exhibited the highest investment in roots and stems respectively (Table 3 and 4). There were not significant differences among species in NAR_m (Table 3).

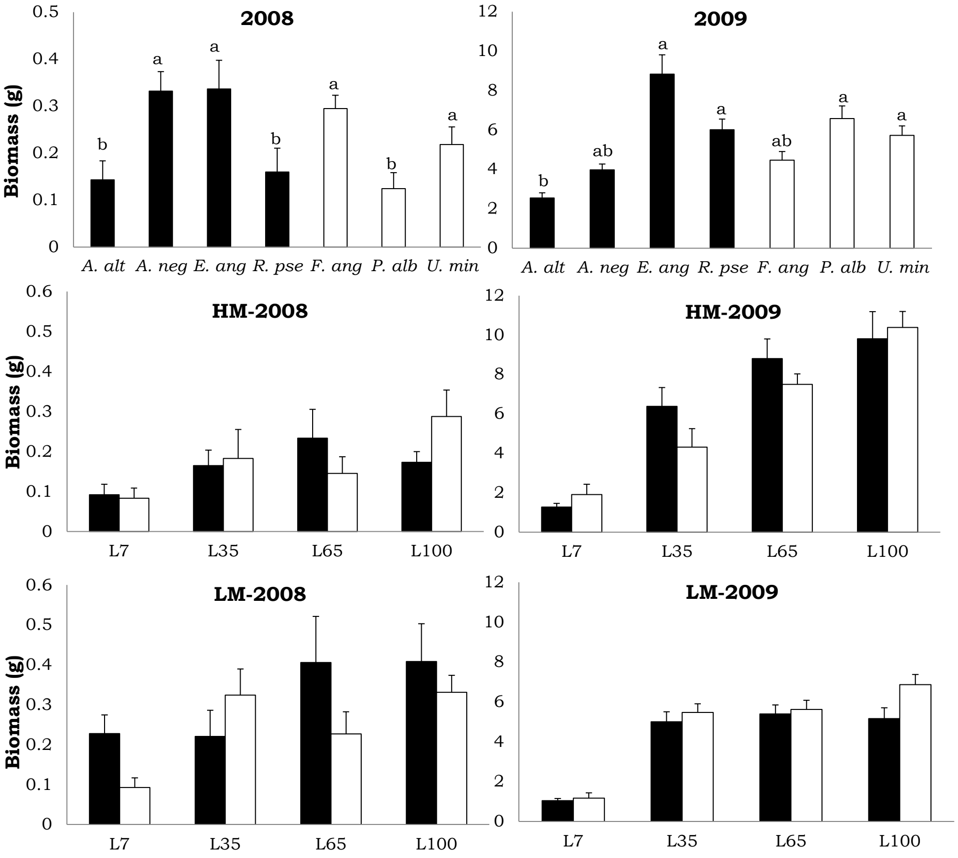

Fig. 3. Upper charts: Average biomass (g) without leaves reached by each species at the end of the first (2008) and second (2009) growing seasons. Different letters mean significant differences among species according to *post-hoc* Bonferroni tests. Lower charts: Average biomass reached by the exotic (black) and native (white) species in every combination of soil moisture (LM- low moisture; HM- high moisture) and light treatments (L7- 7%, L35- 35%, L65- 65% and L100- 100% respect to full irradiance) at the end of the first and second growing seasons (2008 and 2009).

Table 3. Average values ± SE of the relative growth rate calculated from the end of the first to the end of the second growing seasons (RGR), net assimilation ratio per unit of leaf mass (NAR_m), time needed to emerge ($T_{emerg.}$) and seed mass in each origin (exotic or native) and species. Different letters mean significant differences between origins (capital letters) or species (lower case letters), according to *post-hoc* Bonferroni tests.

	RGR (mg/day)	NAR_m (mg/mg leaf)	$T_{emerg.}$ (days)	Seed mass (mg)
Exotic	8.77±0.59A	19.72±1.25B	31.14±3.37A	45.50±24.99
Native	9.48±0.61A	26.67±1.76A	29.88±4.67A	13.77±11.20
A. alt	8.55±0.95ab	16.78±2.29a	39.35±5.14b	14
A. neg	6.84±0.67b	18.92±1.80a	16.20±0.31c	28
E. ang	8.17±0.90ab	21.37±2.71a	52.54±2.05a	120
R. pse	11.50±1.48a	21.52±3.35a	14.33±0.49c	20
F. ang	6.84±0.56b	24.97±2.75a	53.25±4.10a	36
P. alb	12.02±1.05a	28.43±3.31a	13.41±0.57c	0.3
U. min	9.57±0.54ab	26.55±2.67a	16.06±0.10c	5

Table 4. Average values ± SE of the root, stem and leaf weight ratios (RWR, SWR and LWR respectively) in July 2009 (middle second growing season). Different letters mean significant differences between origins (capital letters) or species (lower case letters), according to *post-hoc* Bonferroni tests.

	RWR	SWR	LWR
Exotic	0.29±0.01B	0.29±0.01A	0.42±0.01A
Native	0.40±0.01A	0.25±0.01B	0.35±0.01B
A. alt	0.34±0.02bc	0.16±0.01d	0.49±0.01a
A. neg	0.32±0.01bcd	0.32±0.01b	0.36±0.01c
E. ang	0.23±0.01d	0.37±0.01a	0.39±0.01bc
R. pse	0.26±0.01d	0.24±0.02bc	0.49±0.01a
F. ang	0.49±0.01a	0.23±0.01c	0.28±0.01d
P. alb	0.29±0.01cd	0.28±0.01bc	0.43±0.01ab
U. min	0.38±0.02b	0.26±0.02bc	0.36±0.01bc

Different traits explained the biomass reached by each species in November 2009. $T_{emerg.}$ correlated negatively with biomass in all species but *P. alba* and *U. minor* (Table 5). NAR_m showed positive correlations with the biomass of all species but *A. altissima*, *R. pseudoacacia* and *U. minor* (Table 5). SWR showed negative correlations with the biomass of *A. altissima, R. pseudoacacia* and *F. angustifolia* whereas LWR correlated negatively only with *P. alba* biomass (Table 5). Finally, RWR correlated positively with biomass in *A. altissima*, *E. angustifolia*, *F. angustifolia* and *P. alba* (Table 5).

Table 5. Pearson product-moment correlation coefficients (r) between the logarithm of the biomass reached by each species in November 2009 and the biomass allocation traits in July 2009 (RWR, SWR and LWR), the net assimilation rate per unit of leaf mass weight (NAR_m) and the time needed to emerge ($T_{emerg.}$) For each species, we used each treatment as a replicate (N=8 for all species but *R. pseudoacacia*, *A. altissima* (N= 6) and *U.minor* (N=4). Significant correlations (p<0.05) are shown in bold characters.

	A. neg	*A. alt*	*E. ang*	*R. pse*	*F. ang*	*P. alb*	*U. min*
RWR	.304	**.932**	**.714**	.289	**.749**	**.835**	.743
SWR	.049	**-.958**	.125	**-.865**	**-.721**	.572	-.402
LWR	-.215	-.775	-.591	.686	-.442	**-.841**	-.670
NAR_m	**.829**	.708	**.940**	.342	**.820**	**.713**	.750
$T_{emerg.}$	**-.805**	**-.939**	**-.758**	**-.817**	**-.845**	.495	-.598

All species tended to grow more with higher light, this response being steeper in *P. alba*, *F. angustifolia*, *R. pseudoacacia* and *E. angustifolia* (Fig. 4 and 5). Soil moisture positively affected the biomass of most species under most light treatments (Fig. 4 and 5). Biomass allocation patterns were also affected by light and soil moisture treatments (Table 6, Fig. 4 and 5).

Table 6. Effect of Origin (O), species (nested in Origin) (Sps(O)), Light (L), Soil moisture (M) and their interactions on the RWR, SWR and LWR in July 2009 (N=210), according to four-way ANOVAs. F, degrees of freedom (df) and significances (p) are shown.

		RWR		SWR		LWR	
	df	F	p	F	p	F	p
O	1	219.507	0.001	35.405	0.001	68.263	0.001
Sps(O)	5	71.098	0.001	65.173	0.001	41.906	0.001
L	3	36.935	0.001	16.074	0.001	21.043	0.001
M	1	0.071	0.789	1.335	0.250	0.339	0.561
L*M	3	4.014	0.009	3.206	0.025	6.855	0.001
O*L	3	6.638	0.001	3.341	0.021	9.949	0.001
O*M	1	13.439	0.001	0.174	0.677	6.007	0.015
L*M*O	3	0.670	0.572	0.817	0.486	2.523	0.059
L*Sps(O)	11	4.694	0.001	7.371	0.001	5.178	0.001
M*Sps(O)	5	1.491	0.196	3.992	0.002	3.740	0.003
L*M*Sps(O)	11	1.580	0.109	3.881	0.001	5.298	0.001

Among the exotics, *A. negundo* exhibited a quite balanced allocation between roots, stems and leaves across the light gradient, but increasing moisture enhanced the investment to leaves to the detriment of roots (Fig. 4). *E. angustifolia* invested more biomass in leaves under the extreme light treatments (L100-L7) but increased RWR under the intermediates (L35-L65) (Fig. 4). *Ailanthus altissima* and *R. pseudoacacia* increased SWR with decreasing light (Fig. 4). Besides, *R. pseudoacacia* increased RWR with decreasing soil moisture (Fig. 4). The three natives increased aboveground biomass under L7 (LWR or SWR, Fig. 5). Furthermore, *F. angustifolia* decreased LWR and *P. alba* decreased LWR and increased RWR with increasing soil moisture (Fig. 5) (see Appendix 1 and 2 for statistical results regarding the effect of the light and soil moisture treatments on the biomass allocation traits of each species).

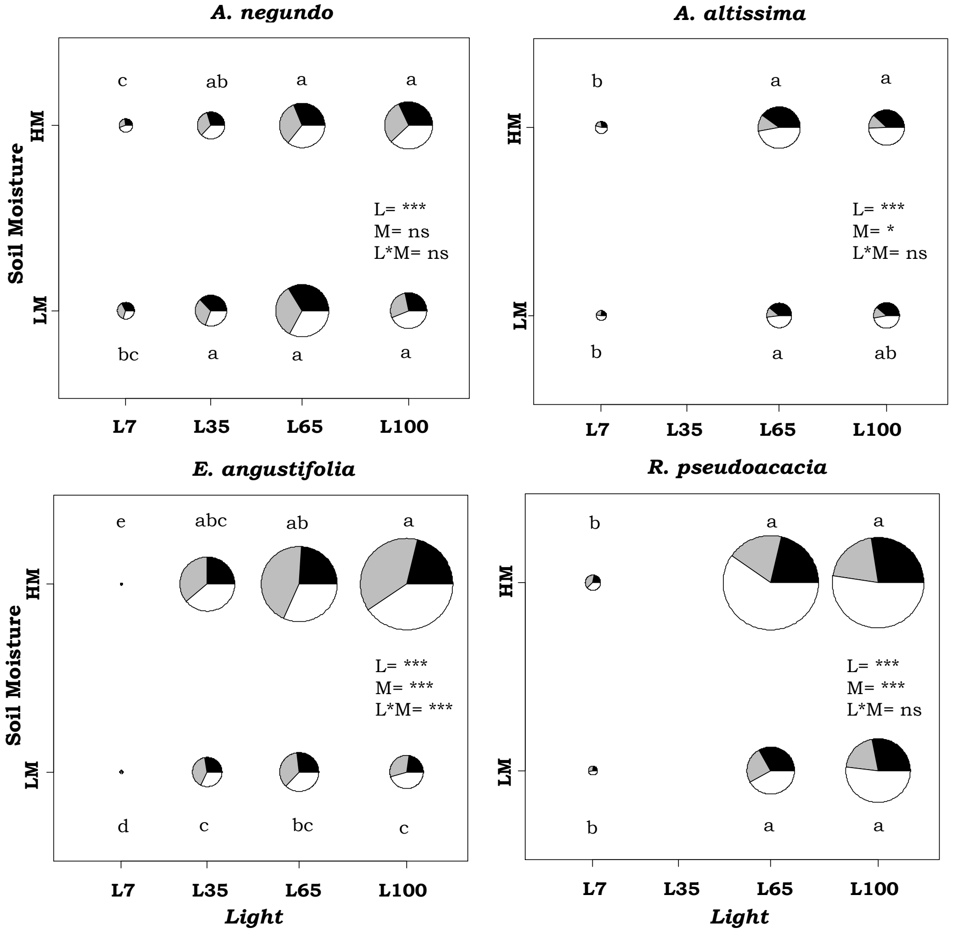

Fig. 4. Pie chart representing RWR (black), SWR (grey) and LWR (white) of exotic species under each combination of light (L7, L35, L65 and L100) and soil moisture treatments (LM and HM) in July 2009. Pie chart area is proportional to the seedling biomass without leaves in November 2009 (x3 in all species but *E. angustifolia* x1.5). Significances resulting from two-way ANOVAs performed on the biomass reached by each species in November 2009 are also shown. Light (L), M (Soil moisture) and their interaction (L*M) were fixed factors. Levels of significance: ***, $p<0.001$; **, $0.001 \geq p < 0.01$; *, $0.01 \geq p < 0.05$; ns, $p \geq 0.05$. *Robinia pseudoacacia* and *A. altissima* graphs appear uncompleted because we did not harvest individuals under those treatments (see Material and Methods).

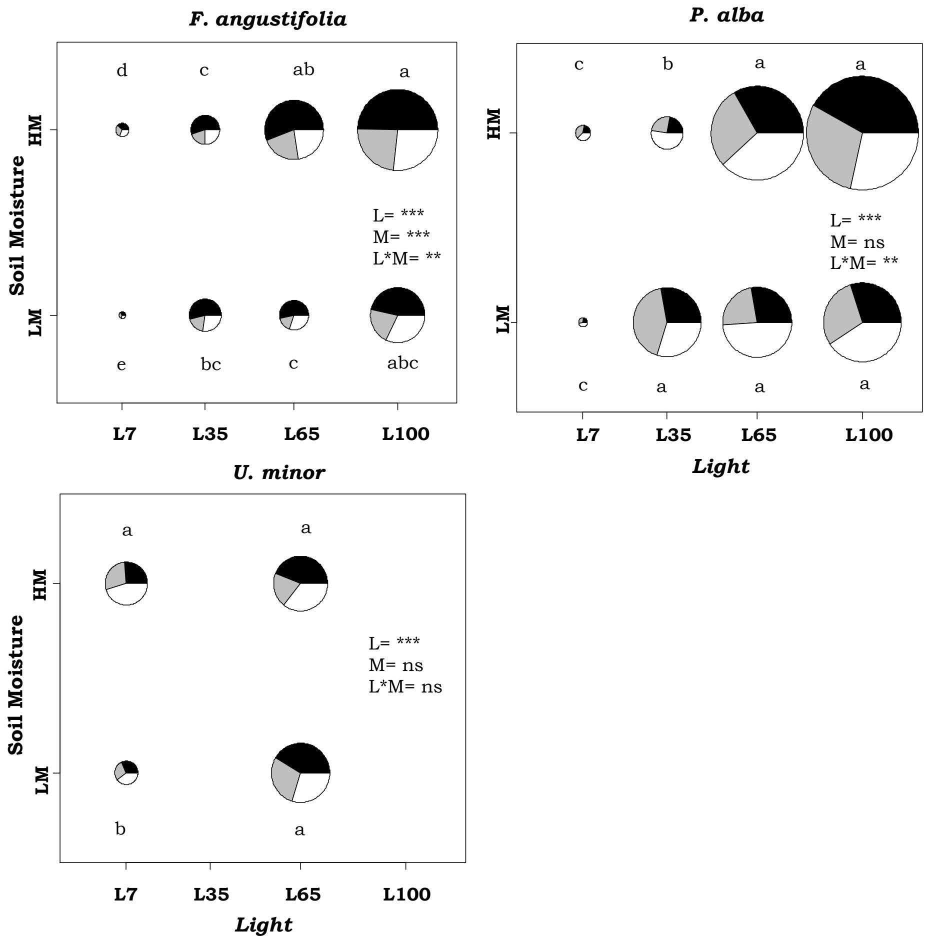

Fig. 5. Pie chart representing RWR (black), SWR (grey) and LWR (white) of native species under each combination of light (L7, L35, L65 and L100) and soil moisture treatments (LM and HM) in July 2009. Pie chart area is proportional to the seedling biomass without leaves in November 2009 (x3 in all species). Significances resulting from two-way ANOVAs performed on the biomass reached by each species in November 2009 are also shown. Light (L), M (Soil moisture) and their interaction (L*M) were fixed factors. Levels of significance: ***, p<0.001; **, 0.001≥p<0.01; *, 0.01≥p<0.05; ns, p≥0.05. *Ulmus minor* graph appears uncompleted because we did not harvest individuals under those treatments (see Material and Methods).

4. DISCUSSION

We aimed to assess native and exotic seedling performance to identify potential shifts in community composition in riparian forests of inner Iberian Peninsula. We expected a superior performance of exotic seedlings over natives in terms of biomass accumulation (hypothesis 1), as a mechanism to explain the success of exotic species in river floodplains of central Spain. However, we did not find support for this hypothesis, as exotic seedlings as a group attained the same biomass as natives in the first growing season, or even less in the second one (Fig. 3). This result agrees with Daehler (2003), who compared pairs of native and exotic species and found that native performance was equal or even superior in most of those cases involving more than one growing condition. Besides, we found a wide variety of growth responses, both within the exotic and within the native species, highlighting that the strategy of each species is independent of its native or exotic origin, as also found before (Bellingham et al., 2004; Feng et al., 2007; Feng and Fu, 2008; Gurevitch et al., 2008).

The exotic *E. angustifolia* was the species that reached the highest biomass after the first two growing seasons, although this difference was not significant (Fig. 3). This larger size may be the consequence of the much larger seed size than that of the next species in the seed mass ranking (see Table 3). It is well known that large seeds produce large seedlings (Marañón and Grubb, 1993), which may confer and advantage to outcompete other plants in the initial stages of their development and also to tolerate shade (Hewitt, 1998; Bond et al., 1999; Sánchez-Gómez et al., 2006). Besides, *E. angustifolia* showed the highest SWR among the studied species, a helpful trait to overtop the seedling layer to reach the light in scenarios promoting competition for light (Fig. 4, Table 4) (Beets and Pollock, 1987; King, 2003). Indeed, *E. angustifolia*'s biomass was only notably decreased by the most intense shade (6% of full sunlight, see Fig. 4). In contrast, *R. pseudoacacia* and *P. alba* showed low biomass after the first growing season, but thanks to a high RGR they were among the largest species after the second (Fig. 3, Table 3). *Robinia pseudoacacia* and *P. alba*, together with *A. altissima*, also showed the highest investment in leaves among studied species (Fig. 4 and 5, Table 4). A high LWR may explain a fast growth, as it contributes to a better light interception (Pearcy et al., 2004) and to high CO_2 uptake at the whole plant level (Chmura et al., 2007). However, *A. altissima* was the species that attained the lowest biomass, showing intermediate RGR, despite having been previously described as fast grower (Fig. 4, Table 3) (Knapp and Canham, 2000; Sanz Elorza et al., 2004; Kowarik and Säumel, 2007). The strong snowfall of January 2009, an uncommon event in the study region, may explain this result, as *A. altissima* seedlings have been described as not frost resistant (San Elorza et al., 2004; Kowarik and Säumel, 2007). This highlights that other environmental factors, such as extremely seasonal frosts, affect species performance and call for further studies exploring its importance on forest composition. Contrary to *R. pseudacacia* and *P. alba*, *A. negundo* and *F. angustifolia* were among the largest species in the first season but turned to be among the smallest after the second, due to their low RGR (Fig. 3, table 3). In the case of *F. angustifolia*, the low RGR may be attributed to a large investment of biomass in roots (the highest among studied species), as this may adversely affect carbon gains, through decreasing leaf mass allocation and increasing root respiratory loss (Weiner, 2004) (Fig. 5, Table 4). In the case of *A. negundo*, the low RGR may be due to its low net assimilation rate per unit of leaf mass (Table 3).

The absence of a clear superiority of most exotic seedlings over natives in terms of biomass suggests that other abilities must explain their success in the study region. For instance, *R. pseudoacacia* and *E. angustifolia* are N-fixers (Weber, 2003; Katz and Shafroth, 2003; Rice et al., 2004; Sanz Elorza et al., 2004), which confers a certain independence of soil nutrient availability; adult trees of *A. altissima* produce allelopathic compounds that may inhibit other species seed germination and seedling growth (Heisey, 1990, 1996; Heisey and Heisey, 2003; de Feo et al., 2005); and all studied exotic species are able to profusely resprout and to produce high amounts of seeds (Weber, 2003; Katz and Shafroth, 2003; Sanz Elorza et al., 2004; Kowarik and Säumel, 2007; Masaka and Yamada, 2009). Alternatively, exotic species may have established in floodplains of central Spain in spatial or temporal empty niches, where they would not need a superior performance over natives to succeed (Godoy et al., 2008).

As expected (hypothesis 2), all species achieved their highest biomass under high irradiance (L65 or L100) and, in most cases, high soil moisture. In most species, this higher performance was accompanied by an earlier emergence (except *P. alba*), a higher NAR_m and a higher investment in roots in detriment of stems and/or leaves (see Table 5). However, against our hypothesis, exotics did not perform better than natives under rich scenarios, as the responses to the treatments were independent of the origin.

Among studied species, *E. angustifolia*, *F. angustifolia*, *P. alba* and *R. pseudoacacia* showed a strong response to resource availability (Fig. 4 and 5). In contrast, *U. minor* and *A. negundo* showed a relative good performance in low resource treatments, in agreement with previous studies that described them as shade tolerant species (Fig. 4 and 5) (DeWine and Cooper, 2007, 2008; González et al., 2010; González-Muñoz et al., 2011; Porté et al., 2011). All species but *A. negundo* increased aboveground biomass (LWR and/or SWR) with decreasing light, in agreement with the optimal allocation theory, which suggests that species tend to allocate more biomass to those organs that favour the capture of the most limiting resource (Weiner, 2004) (Fig. 4 and 5). Furthermore, the three natives and *A. altissima* increased RWR with increasing light, meaning that they would be able improve light acquisition when it is scarce but also to favor water and nutrients acquisition when light is not limiting. *Robinia pseudoacacia* and *A. negundo* responded to decreasing moisture with higher investment in roots, in accordance with the optimal allocation theory (Weiner, 2004) (Fig. 4 and 5).

Which species would find a potential regeneration niche in the two scenarios promoted by human activities? Or results suggest that a scenario with decreased light and soil moisture, as that of regulated river floodplains, would be a suited regeneration niche for the native *U. minor* and the exotic *A. negundo* (Fig. 4 and 5). Indeed, *U. minor* naturally occurs in the most external vegetation band of riparian forests, where water availability and gap-opening disturbances are less frequent (Blanco Castro et al., 2005). However, as its natural populations show a hampered seed production due to the Dutch elm disease (Brasier et al., 2004; Martin et al., 2006), the seedling layer would be potentially dominated by *A. negundo.* However, we should note that, as all studied species are able to resprout, they may keep a vegetative recruitment in closed canopies if parent plants occupy a well-lit position in the canopy (see for instance Sanz Elorza et al., 2004; Blanco Castro et al., 2005; Kowarick and Säumel, 2007). In contrast, the increase of light availability caused by human-mediated forest removal would favor seedling growth of all studied species, but especially *F. angustifolia*, *P. alba*, *A. altissima*, *E. angustifolia* and *R. pseudoacacia*. However, when this increase in light is combined with a decrease in soil moisture, as happens in deforested floodplains of regulated rivers, all species establishment but *U. minor* and *A. negundo* would be hampered.

5. CONCLUSIONS

Our results show that responses of riparian tree seedlings to environmental factors are species-specific, and independent of their native or exotic origin. Seedlings of all species attained larger size under well-lit conditions, and most of them also under higher moisture. However, under low resource conditions only *A. negundo* and *U. minor* were able to keep seedling growth homeostasis. Given that natural populations of *U. minor* have a hampered seed production due to the Dutch elm disease, the shadier-drier scenario would be a potential vacant niche for *A. negundo* seedlings. Shifts in community composition are expected at species level if the new tree regeneration niches promoted by human activities continue being favored.

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8. SUPPLEMENTARY MATERIAL

Appendix 1. Effect of light (L), soil moisture (M) and their interaction (L*M) on the RWR, SWR and LWR shown by exotic species on the harvest performed on July 2009, according to two-way ANOVAs. F and p values are shown. Degrees or freedom were L=3, M=1 and L*M=3 in *Acer negundo* (N=39) and *Elaeagnus angustifolia* (N=37). Degrees or freedom were L=2, M=1 and L*M= 2 in *Ailanthus altissima* (N=25) and *Robinia pseudoacacia* (N=22), as we did not harvest any individual under L35. Levels of significance: ***, p<0.001; **, 0.001≥p<0.01; *, 0.01≥p<0.05; ns, p≥0.05.

		A. neg		*A. alt*		*E. ang*		*R. pse*	
		F	p	F	P	F	P	F	P
RWR	L	2.361	ns	11.927	***	5.310	**	1.103	ns
	M	9.876	**	0.045	ns	1.905	ns	5.202	*
	L*M	6.032	**	0.204	ns	0.074	ns	2.815	ns
SWR	L	1.396	ns	14.321	***	1.112	ns	16.139	***
	M	2.786	ns	1.958	ns	3.573	ns	0.001	ns
	L*M	2.673	ns	0.502	ns	2.026	ns	4.803	*
LWR	L	2.873	ns	1.802	ns	7.622	***	2.235	ns
	M	4.462	*	0.370	ns	0.477	ns	1.911	ns
	L*M	5.469	**	0.119	ns	2.379	ns	4.181	*

Appendix 2. Effect of light (L), soil moisture (M) and their interaction (L*M) on the RWR, SWR and LWR shown by native species on the harvest performed on July 2009, according to two-way ANOVAs. F and p values are shown. Degrees or freedom were L=3, M=1 and L*M=3 in *Populus alba* (N=30). Degrees or freedom were L=1, M=1 and L*M= 1 in *Ulmus minor* (N=16) as we only harvested individuals under L7 and L65. Levels of significance: ***, $p<0.001$; **, $0.001 \geq p<0.01$; *, $0.01 \geq p<0.05$; ns, $p \geq 0.05$.

		F. ang		*P. alb*		*U. min*	
		F	P	F	P	F	p
RWR	L	24.462	***	20.870	***	14.432	**
	M	1.706	ns	9.632	**	0.033	ns
	L*M	0.060	ns	5.759	**	1.301	ns
SWR	L	30.612	***	7.175	***	6.994	***
	M	1.280	ns	0.229	ns	0.416	ns
	L*M	3.707	*	7.721	***	0.902	ns
LWR	L	4.180	*	29.289	***	8.176	*
	M	8.523	**	4.057	ns	3.098	ns
	L*M	3.078	*	19.090	***	0.001	ns

Chapter 4

Effects of exotic invasive trees on nitrogen cycling: a case study in Central Spain.

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RESUMEN

Las tasas de transformación de nitrógeno en suelo pueden verse alteradas como consecuencia del remplazo de árboles nativos por exóticos que difieran en la calidad de su hojarasca. En Noviembre de 2006, se recogieron hojas senescentes de dos especies de árboles nativos *(Ulmus minor* y *Fraxinus angustifolia)* y exóticos (*Ailanthus altissima* y *Robinia pseudoacacia*) presentes en la Península Ibérica. En las hojas senescentes, se compararon C:N ratios y contenido de lignina y nitrógeno entre los pares *U. minor* vs *A. altissima y F. angustifolia* vs *R. pseudoacacia.* Con las hojas senescentes, se prepararon 64 bolsitas que se dejaron descomponer bajo el dosel de la propia especie y bajo el dosel de su par asignado, comparándose cambios en cantidad de materia seca, concentración y pool de nitrógeno tras 5 y 7 meses de descomposición. Además, para valorar el efecto de la hojarasca sobre los suelos, se compararon humedad del suelo, materia orgánica, pH, tasas de mineralización potencial, nitrógeno mineral y disponibilidad de nitrógeno (mediante resinas de intercambio iónico) en tres muestreos distintos. De acuerdo a nuestros resultados, *A. altissima* se descompuso más rápido que *U. minor*, probablemente debido al mayor grosor de las hojas de la nativa. A pesar de su alta concentración de nitrógeno, *R. pseudoacacia* se descompuso más lentamente que *F. angustifolia*, probablemente debido a su alta concentración de lignina. En ambos casos, la hojarasca se descompuso más rápido bajo la copa de las exóticas que de las nativas. La liberación de nitrógeno por unidad de masa de hoja senescente inicial fue mayor bajo los doseles de las invasoras que bajo las nativas. Sin embargo, los suelos bajo los doseles nativo y exótico no difirieron en la tasa de mineralización potencial ni en el contenido en nitrógeno mineral. Esto puede ser debido a un rápido consumo de los nutrientes liberados y/o a un alto acúmulo de materia orgánica en suelos previo la invasión, que puede estar ejerciendo un control mayor sobre la transformación de nitrógeno en suelos que la hojarasca exótica.

Palabras clave: Árboles exóticos, descomposición de hojarasca, tasas de mineralización, disponibilidad de nitrógeno, ciclo de nitrógeno.

ABSTRACT

We assess the hypothesis that rates of nitrogen transformations in the soil are altered upon replacement of native by exotic trees, differing in litter properties. *Ailanthus altissima* and *Robinia pseudoacacia*, two common exotic trees naturalized in the Iberian Peninsula, were compared with the native trees *Ulmus minor* and *Fraxinus angustifolia*, respectively. Naturally senesced leaves of each species were collected and C:N ratio, N and lignin content assessed. We prepared 64 litter bags per species and left them to decompose, below the canopy of the same species and below the canopy of the paired species. Dry mass, N concentration and N pool of the remaining litter were assessed after five and seven months. Soil samples were collected three times during the experiment to assess soil moisture, organic matter, pH, potential mineralization rates and mineral N pools. Mineral N availability was assessed three times in the field by using ion-exchange resin-impregnated membranes. *A. altissima* litter decomposed faster than *U. minor* litter, probably due to the higher toughness of the latter. In spite of its high N content, *R. pseudoacacia* litter decomposed slower than *F. angustifolia* one, probably due to its high lignin content. In both cases, litter decomposition was faster below the exotic than the native canopies. The release of N per unit of initial litter mass was higher under both invaded situations (*A. altissima* below *A. altissima* and *R. pseudoacacia* below *R. pseudoacacia*) than under the native ones. However, soils collected below native and exotic trees neither differed in potential N mineralization rate nor in mineral N. This may be attributed to a quick plant uptake of released N and/or to a high organic matter accumulation in the soil previous to invasion, which can exert a tighter control on soil N transformations than the current exotic litter.

Keywords: Exotic trees, litter decomposition, mineralization rate, nitrogen availability, nitrogen cycle.

1. INTRODUCTION

Human-driven plant introductions, either accidental or on purpose, are occurring at increasing rates in the last decades (Kolar and Lodge, 2001; Mack, 2003). Changes in species composition or abundance may affect the functioning of the ecosystems, especially when they imply changes in functional traits (Vitousek and Walker, 1989; Chapin et al., 1997).

Nutrient cycling is one of the ecosystem processes controlled by species or functional type composition (Hooper and Vitousek, 1998; Hattenschwiler and Vitousek, 2000; Quested et al,. 2005). In terrestrial ecosystems, primary production is often nutrient-limited (Schlesinger, 1991; Bowman et al., 1993; Soudzilovskaia and Onipchenko, 2005). By contrast, in many disturbed ecosystems nutrient availability is above the community uptake capacity, leading to eutrophication of soils and waters (Correll, 1997; Carpenter et al., 1998; Baron et al., 2002). Therefore, the understanding of how exotic plant invasions alter nutrient dynamics is relevant for assessing the impact of the invasion on the host ecosystem. However, the existing literature is biased towards the invasion of oligotrophic soils by N_2-fixing species (Levine et al., 2003; Haubensak et al., 2004; Tateno et al., 2007; Yelenik et al., 2007).

The introduction of exotic plants may alter the nutrient cycle of the system by triggering a chain of effects that finally may lead to additional changes in plant species composition. Firstly, invading plants may alter the physical-chemical site properties (e.g., temperature, soil moisture, pH) below their canopy. In addition, the litter quantity and quality may change, as when N-fixing plants invade oligotrophic soils, increasing the amount of litter (Yelenik et al., 2007) and its N concentration (Vitousek and Walker, 1989; Tateno et al., 2007; Yelenik et al., 2007). Secondly, litter quality controls the litter decomposition rate, either directly, by means of litter physical-chemical features (Gallardo and Merino, 1993; Cornelissen and Thompson, 1997), or indirectly by altering the physical-chemical conditions for decomposition (i.e. soil moisture, temperature, pH, C/N ratio, N pools) (Gallardo and Merino, 1992; Xiong et al., 2008). Thirdly, these physical-chemical soil properties also affect the structure and activity of microbial communities (Gallardo and Merino, 1992; Mack et al., 2001; Hawkes et al., 2005), altering the rate of soil organic matter mineralization, and finally affecting nutrient availability for plants. Nutrient availability, together with the soil properties, can finally exert feedback effects on the species composition of the community (Mack, 2003).

Across Mediterranean-type ecosystems there is limited information on the effects of invasive species on ecosystem processes (Levine et al., 2003). Most studies have been carried out in South Africa (Stock et al., 1995; Le Maitre et al., 1996; Yelenik et al., 2007) and California (Haubensak et al., 2004; Hawkes et al., 2005), whereas few studies have been conducted in the Mediterranean Basin (but see (Vilà et al., 2006)). In this region most exotic plants have colonized coastal areas, while continental ones, such as the inner Iberian Peninsula, are less prone to invasions (Chytrý et al., 2008). This is probably due to the relatively cold winters and drought summers characteristic of these areas (Mitrakos, 1980).

The inner Iberian Peninsula have experienced extensive deforestation during centuries, either for agriculture or grazing use (Bauer Manderscheid, 1980). In such a deforested matrix, mesic forest fragments still remain in river floodplains and in margins of roads, trails or crop fields. In these micro-habitats summer drought is mitigated either by a shallow water table, by runoff accumulation and by shade. The milder conditions, together with frequent disturbance, make these habitats more prone to invasion by exotic plants than the surrounding matrix (Chytrý et al., 2008). The forest fragments play a major role in the regulation of the nutrient cycle at the landscape level, because they uptake large amounts of nutrients that otherwise would be leached from the soil into the rivers, contributing to their eutrophication (Correll, 1997; Carpenter et al., 1998). The extent to which exotic trees, spreading through these microhabitats, transfer nutrients at different rates than native trees is not well known so far.

The aim of this study is to assess the effects of *Ailanthus altissima* and *Robinia pseudoacacia*, two common exotic trees naturalized in the inner Iberian Peninsula, on the nitrogen cycling. We compare litter quality, litter decomposition rate, soil properties, mineralization rates, and N availability below the canopy of each species and native trees naturally growing in the same habitat. A widespread strategy of exotic plants to outcompete native ones is the possession of highly productive leaves (Pattison et al., 1998; Baruch and Bilbao, 1999; Grotkopp and Rejmánek, 2007) and these leaves possess traits typically associated with high decomposition rate (Cornelissen and Thompson, 1997; Lake and Leishman, 2004). We expect therefore 1) a better litter quality of exotic compared to native trees and 2) faster decomposition of exotic litter. As rates of microbial activity have been positively related to total N content of the soil organic matter (Gallardo and Merino, 1992; Prescott et al., 1992), we further expect 3) faster litter decomposition and mineralization rates below the canopy of the exotic trees, and therefore, 4) higher nitrogen availability and larger nitrogen pool sizes in soils below the exotic trees.

2. MATERIAL AND METHODS

2.1. Study species

Two exotic tree species were selected that naturally occur in Central Spain, and are included in the Catalogue of invasive species in Spain (Sanz Elorza et al., 2004). For each exotic species we selected a native tree living in the same or similar habitat, so that we could compare the exotic species with its potential native competitor.

Ailanthus altissima (Mill.) Swingle is a *Simabouracea*, native to China, and introduced in Europe during the 18th century (Kowarik and Saumel, 2007). This species has a high potential for vegetative and generative reproduction, and contains allelopathic compounds in its tissues. It colonizes urban habitats, transportation corridors, borders of agricultural fields, riparian forests and, less frequently, mesic and xeric woodlands (Kowarik and Saumel, 2007). Many of these habitats were formerly dominated by *Ulmus minor* Mill., whose populations have been severely reduced throughout Europe due to the vascular wilt disease of elms (Solla et al., 2005). Today both species are easily found growing side by side.

Robinia pseudoacacia L. is a nitrogen-fixing legume tree, native to North America and common in early-successional stages (Boring and Swank, 1984). It shows a remarkable growth in semi-arid environments, where it has been widely used for reforestation, either for timber or to improve the quality of the soil (Tateno et al., 2007). In Central Spain this tree has been extensively planted in gardens and recreation areas and can also be found in the outermost vegetation strip of disturbed riparian forest, a habitat naturally occupied by *Fraxinus angustifolia* Vahl. However, both species are not easily found together, as *R. pseudoacacia* dominates human-disturbed areas, while *F. angustifolia* dominates well-preserved ones.

2.2. Study sites

For each species pair we selected four sites where the species grew close to each other. All sites were in the provinces of Madrid and Guadalajara (Central Spain) and share similar macroclimatic conditions and similar soils (Appendix 1-3). *A. altissima-U. minor* sites were mostly placed on the Henares River floodplains, within a radius of 17 km (latitudinal range

40° 31-38’N, longitudinal range 3° 12-14’W, altitudinal range 554-824 m). *R. pseudoacacia-F. angustifolia* sites were placed either near the Henares or the Torote River, within a radius of 5.5 km (latitudinal range 40° 30-35’N, longitudinal range 3° 20-24’, altitudinal range 595-651 m). All sites were found in riparian vegetation or vegetation strips alongside roads or agricultural fields, with the exception of the *JB-UAH* site, which is situated in the Botanical Garden of the Alcalá University, where all trees were planted 17 years ago (Appendix 1-3).

2.3. Litter collection and traits

In November 2006 senescent leaves from 12-21 individuals per species were collected in the study area. Leaves were either collected from the soil (recently fallen leaves, with no sign of fungus infection) or from the trees (those which detached with a gentle touch). All leaves from each species were pooled and dried at laboratory temperature. For each species 64 litter bags were prepared (1-mm mesh nylon litter bags with ca. 1g of air-dried leaf litter) (Fig. 1). Five additional litter air-dried samples of ca. 2 g per species were used to correct the air-dry weight to oven-dry weight. These samples were subsequently ground with a Culatti mill (<1mm particle size) for C/N ratio (Elementar varioMAX N/CN, Hanau, Germany), lignin (Van Soest method, Febertec, Ankom Fiber analyzer), organic N content (see below) analysis.

In September 2007, eight trees per species were selected in the study area and 10 green leaves were collected per tree in the south side of the canopy. Leaf or leaflet area was measured for fresh leaves (Delta-T leaf area meter device, Cambridge), and leaves were oven-dried (>48 h 60°C) and weighted. The ratio of leaf or leaflet dry mass to its area (LMA) was determined for each tree as a proxy for leaf toughness (Choong et al., 1992).

Fig. 1. *Ailanthus altissima* litterbags placed under the canopy of an *Ulmus minor* tree (December 2006).

2.4. Experimental design

In each of the study sites two 1m^2-plots were selected, one below the canopy of an adult tree of each species. In all sites plots were 20-100 m far from each other, except for two *R. pseudoacacia-F. angustifolia* sites (*Campus-Canaleja* and *Torote*, Appendix 2), where the distance between *R. pseudoacacia* and *F. angustifolia* plots was 2.5 and 7 km, respectively, due to the difficulty of finding both species growing closer together. The breast height diameter (DBH) of the tree or trees below whose canopy plots were established was measured as a proxy for tree age. However in many cases the trees showed signs of having been coppiced (reported by an asterisk in Appendix 1-2), so the stand age is higher than suggested by DBH. Canopy openness above each study plot was assessed at the beginning of the experiment (December 2006, when trees were leafless) by means of fish-eye digital picture (Nikon Coolpix 4500 with a Nikon Fisheye Converter FC-E8 0.21x) analyzed with WinPhot 5.00 software (Hans ter Steege, Utrecht University, 1996) (Fig. 2).

Fig. 2. Hemispherical photograph taken under *Robinia pseudoacacia* canopy.

2.5. Soil properties

In January, April, May and June two soil cores of 225 mm depth by 54.5 mm diameter were collected next to each plot, pooled and transported to the lab in sealed plastic bags. Samples of April, May and June were used for assessing gravimetric soil water content (soil water mass over soil dry mass). Samples of January, April and June were oven-dried (>72 h at 60°C), sieved (<2mm) and stored for later analysis of pH, organic matter, mineral N pool and mineralization rate. By drying soil samples in the oven at a moderate temperature we minimized the drying period, during which labile organic carbon may substantially decline (Sparling et al., 1985).

For soil pH assessment, 10 ml of deionised water was added to 5 mg of soil, shaken and left for 30-60 minutes before pH was measured with a pH meter (Hendershot et al., 1993). Organic matter was assessed by the Walkley-Black acid digestion method (Porta Casanellas et al., 1982). Mineral N pools in the soil were the amount of NH_4-N, NO_3-N and total mineral N found at the initial date of the mineralization rate experiment (see below)

2.6. Decomposition experiment

Between 4 and 12 December 2006, a two-factor experiment was set up for each species pair by placing litterbags of each species in plots below its own canopy and below the canopy of the paired species. Of the eight litterbags per species-canopy-site combination, four were collected in 20-21 April 2007 and four in 26-27 June 2007. The date of the second harvest was decided after checking that the remaining litter mass was approaching to zero in some litterbags. Litter was extracted from each bag, carefully brushed to remove rests of soil, oven dried, weighted and ground in a Culatti mill to a particle size of 1 mm. Organic N concentration of litter at the starting point and at both harvests was analysed at Nutrilab (University of

Rey Juan Carlos I, Móstoles, Madrid, Spain) with segmented flux autoanalizer (S.F.A.S. Skalar San ++.), after a digestion with H_2SO_4 and Cu-KSO_4, which converts all organic nitrogen into ammonium (NH_4-N). The N pool of each sample was calculated as the product of its dry mass and N concentration.

2.7. Mineralization rates

Five grams of each soil sample were taken and mixed up with 15 g of washed sand (SiO_2, Panreac). Mineral N was extracted with 100 ml KCl 2N during two hours in a shaker. The solution was then filtered through 0.45 µm Millipore filters and preserved in the freezer at 2°C during 14 days. Five additional grams of the soil sample was mixed up with 15 g of sand and 6 ml of distilled water, covered with polyethylene film and incubated for 14 days at 30°C. At the end of this period the same extraction procedure was repeated. Mineral N content (NH_4-N, NO_3-N) was determined by colorimetry with a microplate reader (Sims et al., 1995).

2.8. Mineral nitrogen availability

In 27 January, 8 May and 26 June two 2.5 x 2.5 cm anion and two 2.5 x 2.5 cation exchange resin membranes (types I-100 and I-200, Electropure excellion-inc., Laguna Hills, California) fixed to a plastic label were introduced in the soil of each study plot at ca 5 cm depth, and left for 15 days (Abrams and Jarrell, 1992; Subler et al., 1995). Resin membranes were previously conditioned in the lab by immersing them in demineralized water at 82-90°C for 48 hours. Ions were extracted from the resins using 20-25 ml KCl and ammonia and nitrate content were assessed as before.

2.9. Statistical analysis

Leaf LMA (number of replicates = 8), and litter N and lignin concentration and C:N ratio (number of replicates = 5) were compared between the exotic and the native trees using a Student-t test. The effects of time and canopy on soil water content, pH, organic matter, inorganic N (NH_4-N, NO_3-N and total mineral N) pool and availability, and mineralization, nitrification and ammonification rates of organic matter were assessed by means of repeated-measured ANOVA, with time as intra-subject and canopy as inter-subject factors. The two N availability values obtained by ion exchange membranes for each plot were averaged before analysis. Litter dry weight, N concentration and pool were averaged among the four litterbags of each plot collected each date, and average values were then used as replicates in a repeated-measures ANOVA analysis. Time (initial, intermediate and final) was the intra-subject factor, and species and canopy were the inter-subject factors. A separated test was conducted for each study pair. Data were checked for sphericity and equal variances assumptions before analysis. All analyses were performed with SPSS 15.0. (SPSS Inc., Chicago, USA).

3. RESULTS

3.1. Litter properties

LMA of green leaves was significantly smaller for *A. altissima* than for *U. minor*, whereas all the litter chemical properties were similar between both species (only litter N was slightly higher in *A. altissima* than *U. minor* (P= 0.07)). Conversely, *R. pseudoacacia* and *F. angustifolia* showed similar LMA, but different chemical properties, as initial litter N, lignin and lignin:N were higher in *R. pseudoacacia* than in *F. angustifolia*, with C:N showing the reverse trend (Table 1).

Table 1. LMA values of green leaves and chemical properties of freshly fallen litter of invasive and native species pairs. Each value is the average of 4-5 replicates ± standard error. The results of Student's t tests are shown. ns: $P>0.05$; **: $P < 0.01$; ***: $P<0.001$.

Species	LMA (mg/cm^2)	N (mg/g)	Lignin (%)	C: N	Lignin:N
A. alt	7.91±0.2	5.30±0.4	5.37±0.2	47.24±1.4	10.02±0.6
U. min	11.75±0.5	4.94±0.5	4.91±0.4	41.99±2.0	10.30±0.6
	***	ns	ns	ns	ns
R. pse	8.65±0.6	6.93±0.4	14.34±0.44	29.41±0.4	21.07±1.3
F. ang	7.28±0.5	4.98±0.3	6.03±0.24	52.64±1.0	12.24±1.0
	ns	**	***	***	**

3.2. Site properties

The average canopy openness at the beginning of the experiment was 40 and 45% for *A. altissima* and *U. minor* plots respectively, and 58 and 52% for *R. pseudoacacia* and *F. angustifolia* plots respectively (Appendix 1-2). The paired species plots did not differ significantly in canopy openness (paired t-test, $P \gg 0.05$ in both cases).

Soil moisture decreased in all sites as the summer advanced, but it did not differ between the paired species canopies. Soil pH was over 7.5 in all sites, showing a low dispersion across sites and months. Mean soil organic matter per canopy type ranged between 3.5 and 6.1%, although these values varied widely across sites for *A. altissima* and *U. minor* canopies (see high SE values in Table 2). Neither soil pH nor organic matter was affected by time or canopy type in *A. altissima-U. minor* comparison, whereas in the *R. pseudoacacia-F. angustifolia* sites only organic matter change with time, slightly declining in April (Table 2). pH values ranged from 7.83 ± 0.08 under *F. angustifolia* canopy and 8.14 ± 0.06 under *A. altissima*.

Table 2. Properties of soils collected below the canopy of exotic and native tree species. Values are the mean of four replicate sites (average ± SE). Moisture and organic matter values are shown for the three sampling dates. Significant factors (*P*<0.05), resulting from repeated-measures ANOVA (date as a within-subject factor and canopy as between-subject factor), are shown below each species pair.

Canopy	Moisture (%)			Organic matter (%)		
	Apr	May	Jun	Jan	Apr	Jun
A. alt	27.0±5.9	23.7±3.9	14.7±3.7	4.9±2.2	5.0±2.6	4.6±1.8
U. min	29.7±5.9	28.4±4.8	16.1±4.9	4.9±2.5	6.1±3.3	4.6±1.3
Sign. factor		Date			-	
R. pse	20.1±2.9	22.7±2.4	13.3±2.7	4.3±1.0	3.5±0.4	5.1±1.2
F. ang	26.1±2.5	27.9±1.9	15.0±1.8	4.5±0.7	4.1±0.5	4.4±0.6
Sign. factor		Date			Date	

3.3. Litter decomposition

Litter mass significantly decreased through the time in all species x canopy type combinations, but the rate of change varied across species and canopy types (i.e., there is a significant interaction between time and species, and time and canopy type, Table 3).

Table 3. *P*-values of a repeated measures two-way ANOVA assessing the effects of time (T, January, May and June) as within-subject factor, and species (Sp) and canopy (Can) as inter-subject factors, on litter dry mass (DM), nitrogen concentration ([N]) and litter nitrogen pool (Npool) of litterbags. Significant effects are shown in bold.

	A. alt/U. min			*R. pse/F. ang*		
Within-Subjects Effects	DM	[N]	Npool	DM	[N]	Npool
T	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.002**
T * Sp	**0.001**	0.859	**0.001**	**0.000**	**0.000**	0.088
T* Can	**0.010**	0.724	0.169	0.068	0.681	**0.004**
T* Sp *Can	0.379	0.446	0.975	0.828	0.400	0.285
Between-Subjects Effects	DM	[N]	Npool	DM	[N]	Npool
Sp	**0.011**	0.069	0.555	**0.000**	**0.005**	**0.000**
Can	0.390	0.897	0.578	0.072	0.819	**0.000**
Sp * Can	0.758	0.787	0.797	0.708	0.818	0.073

In the first species pair, the exotic litter of *A. altissima* decomposed faster than the native litter of *U. minor*, but in the second pair, the exotic litter of *R. pseudoacacia* decomposed slower than the native litter of *F. angustifolia* (Fig. 3). In both species pairs decomposition tended to be faster below the canopy of the exotic tree (i.e., there is a steeper negative slope of dry mass versus time in Fig. 3 and a significant time x canopy type interaction on leaf dry mass in Table 3), although this effect was marginally significant in the *R. pseudoacacia-F.*

angustifolia comparison (Table 3). Litter N concentration significantly increased over time. The rate of increase was similar between litter and canopy types in the *A. altissima-U. minor* comparison, but faster in *F. angustifolia* than in *R. pseudoacacia* litter (Fig. 3, Table 3). Litter N pool significantly changed over time, decreasing faster in *A. altissima* than in *U. minor* litter, and below *R. pseudoacacia* than below *F. angustifolia* canopy (see slopes of Fig. 3, and interactions of time with species or canopy in Table 3). The final N pool was similar to the initial one for native litter incubated below native canopies and for *R. pseudoacacia* litter below *F. angustifolia* (Fig. 3).

3.4. Potential mineralization rate

Soil potential net rates of nitrification, ammonification and total N mineralization exhibited negative values in all cases, denoting that microbes immobilized mineral N from the soil when the soil was transferred to the optimal temperature and moisture conditions of the incubation chamber (Fig. 4). These rates varied widely between sites (large error bars in Fig. 4), did not show a consistent trend over time, and did not differ between canopy types (Tables 4 and 5).

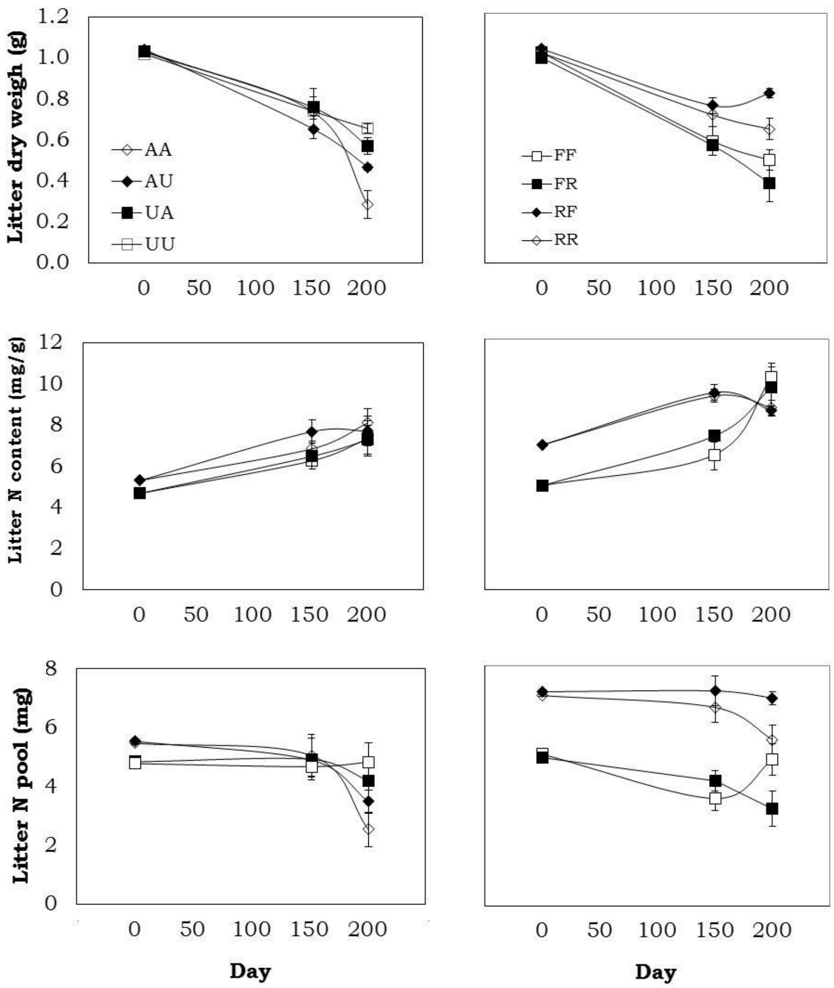

Fig. 3. Changes in leaf dry weight, leaf N concentration and leaf N pool through the time in litter bags in the two pairs of compared species. Each point is the average of four replicated sites ± SE. Legend codes: A-*A. altissima*, U-*U. minor*, R-*R. pseudoacacia*, F-*F. angustifolia*. The first letter refers to the species from which the litter was, and the second letter to the canopy below which litter bags were incubated

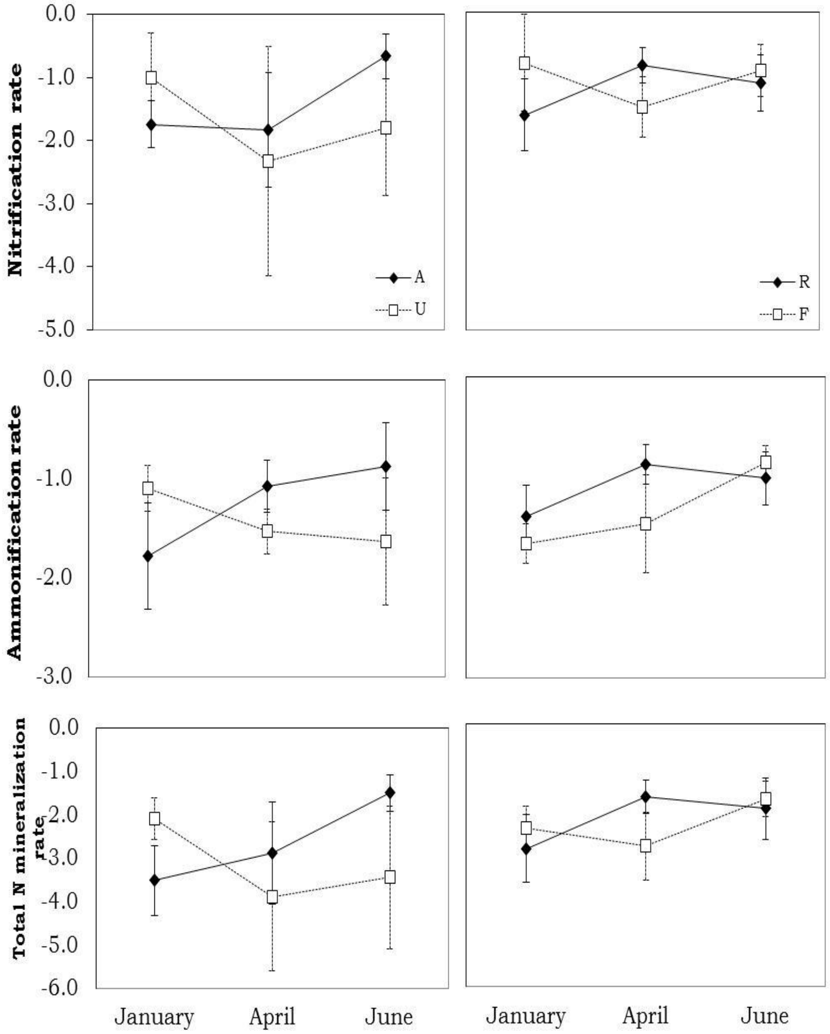

Fig. 4. Potential net nitrification, ammonification and total N mineralization rates (µmol NO_3, NH_4 or total mineral N per soil gram and day) of soils collected below the canopy of *Ailanthus* (A), *Ulmus* (U), *Robinia* (R) and *Fraxinus* (F) in different seasons. Each point represents the average of four sites. Bars represent the standard error and the mean

3.5. Mineral nitrogen in the soil

Soil nitrate, ammonium and total mineral N pools (nitrate plus ammonium) varied widely between sites below the same canopy type (Figure 5). Such variability obscured possible effects of time or canopy type, which were non significant in the repeated-measures ANOVA (Table 4 and 5). By contrast, the availability of the same N compounds, assessed by means of adsorption resin membranes, tended to decline with time, except for NH_4-N which peaked in spring (Fig. 6). The most abundant form of available mineral nitrogen was NO_3-N. The repeated-measures ANOVA revealed no significant effect of canopy type on N availability (Table 4 and 5)

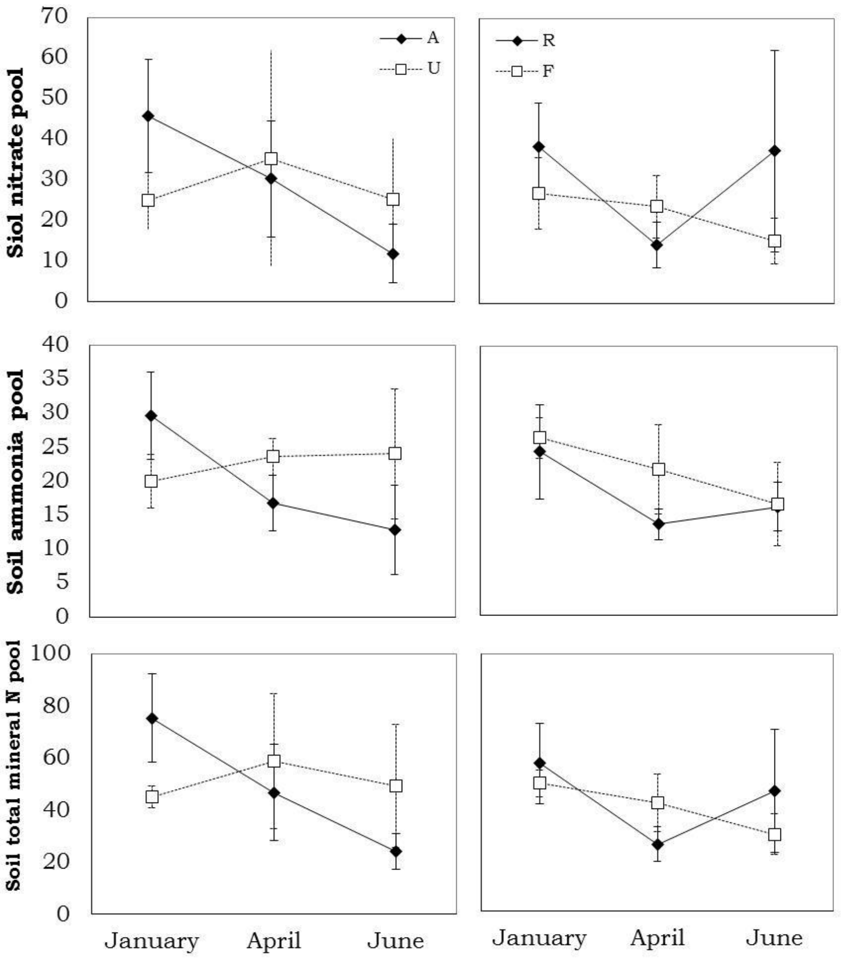

Fig. 5. Ammonium (NH$_4$-N), nitrate (NO$_3$-N) and total mineral N pools (μg/g soil) over time in soils collected below the canopy of exotic (A-*A. altissima* and R-*R. pseudoacacia*) and native (U-*U. minor* and F- *F. angustifolia*) species

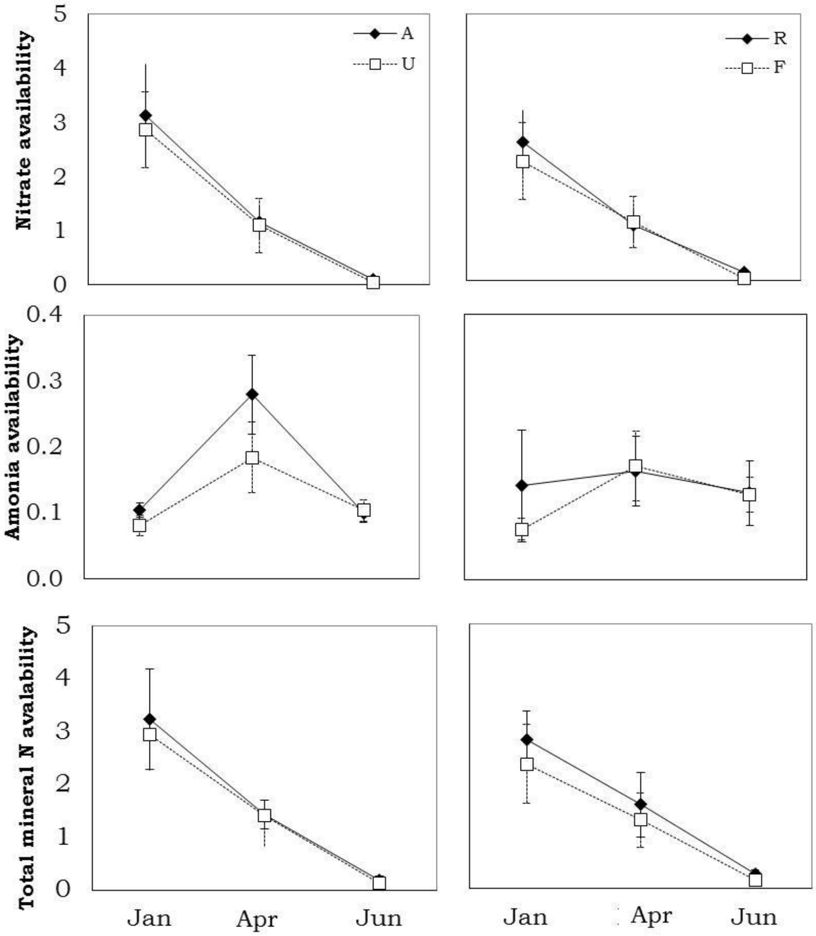

Fig. 6. Ammonium, nitrate and total mineral N pools (microg/cm^2 soil) assessed by means of adsoption resin membranes below the canopy of each study species (A-*A. altissima*, R-*R. pseudoacacia*, U-*U. minor* and F- *F. angustifolia*).

Table 4. Results of a repeated-measure ANOVA assessing the effect of time (T, intra-subject factor) and canopy (Can, inter-subject effect) on soil mineral nitrogen (NH_4 and NO_3 and the summ of both, N_{min}) pools, mineralization rates and mineral N availability. Significant effects are given in bold. Results for *A. altissima* and *U. minor*.

		A. altissima/U. minor		
			Source	
		NH_4-N	NO_3-N	Nmin
Time	Mineralization rates	0.912	0.586	0.593
Time * Can		0.255	0.563	0.188
Can		0.601	0.778	0.707
T	N Pools	0.513	0.421	0.196
T * Can		0.185	0.436	0.107
Can		0.629	0.963	0.915
T	N Availability	**0.001**	**0.000**	**0.000**
T * Can		0.305	0.964	0.945
Can		0.284	0.827	0.843

Table 5. Results of a repeated-measure ANOVA assessing the effect of time (T, intra-subject factor) and canopy (Can, inter-subject effect) on soil mineral nitrogen (NH_4 and NO_3 and the summ of both, N_{min}) pools, mineralization rates and mineral N availability. Significant effects are given in bold. Results for *R. pseudoacacia* and *F. angustifolia.*

		R. pseudoacacia/F. angustifolia		
			Source	
		NH_4-N	NO_3-N	Nmin
T		0.082	0.753	0.103
T * Can	Mineralization rates	0.327	**0.051**	0.070
Can		0.480	0.856	0.859
T		0.101	0.257	**0.011**
T * Can	N Pools	0.626	0.166	0.257
Can		0.546	0.615	0.377
T		0.183	**0.000**	**0.000**
T * Can	N Availability	0.441	0.860	0.915
Can		0.765	0.781	0.615

4. DISCUSSION

4.1. Effects of litter type on decomposition rates

Litter properties notably differed between the exotic trees and their native pairs. The exotic litter exhibited a better quality for decomposition in terms of either lower LMA or higher N concentration than the native litters, which is in line with our first hypothesis. Accordingly, the exotic *A. altissima* decomposed faster than the native *U. minor*, as predicted by our second hypothesis. The greater LMA of *U. minor* leaves may account for this result, as this trait is associated with a greater leaf toughness (Choong et al., 1992), and leaf toughness has been found to be negatively associated to decomposition rate in cross-species studies (Gallardo and Merino, 1993; Cornelissen et al., 1999). Although the studied chemical properties did not differ between both species, *A. altissima* leaves are known to possess allelopathic compounds, such as ailanthone, that are toxic to numerous plant species in the laboratory (Heisey and Heisey, 2003; Kowarik and Saumel, 2007). However ailanthone does not seem to hinder leaf decomposition of *A. altissima* as much as the high LMA of *U. minor* did, supporting the suggestion that ailanthone is quickly degraded by microbes (Heisey and Heisey, 2003). In the case of *R. pseudoacacia-F. angustifolia*, *R. pseudoacacia* litter possessed higher N content and lower C:N ratio, as could be expected because of the N-fixing ability of *R. pseudoacacia*, but a slower decomposition rate than *F. angustifolia*. The latter result was unexpected, given the numerous studies showing that low C:N ratios lead to high decomposition rates (Berg, 1984; Taylor et al., 1989; Cornelissen et al., 1999; Evans et al., 2001) and that litter decomposition rates of N-fixing species are higher than those of non-N-fixing species (Aerts and Chapin III, 2000). The high lignin concentration found in *R. pseudoacacia* litter (more than twice than the rest of species) may explain its slow decomposition, given that lignin and other polyphenols may form complexes with proteins that are resistant to most decomposing organisms (Taylor et al., 1989; Gallardo and Merino, 1993; Hattenschwiler and Vitousek, 2000). The consequence of this particular chemical composition is that *R. pseudoacacia* provides the soil with high amounts of N trapped in a litter which is more resistant to decomposition than the litter of the native species, therefore contributing to the retention of organic N in the soil. A similar result was reported by (Yelenik et al., 2007) who found that the N-rich litter of the exotic *Acacia saligna* invading the South African fynbos did not decompose faster than the N-poor native litter.

4.2. Effects of canopy type on litter decomposition

Litter decomposition was accelerated underneath the canopy of both exotic tree species (Fig. 1, Table 3), which is in line with the third hypothesis. However, this effect cannot be attributed to any of the site properties studied here, as canopy openness, soil pH, soil moisture and soil organic matter were similar underneath the compared exotic and native canopies (Table 2). In the case of *R. pseudoacacia-F. angustifolia*, N pools of both litter types remained constant or even increased below the native *F. angustifolia* canopy, while below *R. pseudoacacia* N pool declined over the time (Fig. 3). (Gallardo and Merino, 1992) also found differences in N immobilization of the same litter type between sites and attributed them to site-specific variations in the amount and activity of the microbial biomass. In our case, the higher N immobilization below *F. angustifolia* canopy suggests that the litter-decomposer community is N-limited (microbes retain all N from the litter in their biomass, or even uptake additional N from the surroundings), which is in line with the high C:N ratio of the *F. angustifolia* litter forming the topsoil. By contrast, the topsoil below the *R. pseudoacacia* canopy must be richer in organic N, derived either from the lignin-rich *R. pseudoacacia* litter and/or from root exudation of organic N compounds (Uselman et al., 1999). These N-rich organic compounds may represent a slow-release, but steady, source of N for microbes. This is in accordance with Vitousek and Walker (1989) who found faster litter decomposition below the N-fixing exotic *Myrica* than below native *Metrosideros* canopies in Hawai'i. Faster decomposition rates below the *A. altissima* canopy may be attributed to the faster release of N from *A. altissima* litter and its positive feedback effect on microbial biomass and activity.

4.3. Potential net mineralization rates

Potential rates of nitrification, ammonification and total N mineralization of soils were negative in all sites and dates, which indicates a high potential of the microbial biomass for immobilizing N. Given that carbon input into the rhizosphere has been suggested to limit N release from the soil organic matter (Berendse et al., 1989), the high potential for N immobilization may be attributed to a great input of carbon-rich woody plant material in these soils. None of these rates differed between canopy types, which contrast with our expectations (hypothesis 4). Similarly, Stock et al. (1995) found that in an unfertile fynbos ecosystem, field-measured N mineralization rates did not increase upon invasion by *Acacia* spp., in spite of the increase of N, and decline of C:N of the top soil. Changes in litter quality might take a long time to translate to altered rates of organic matter N mineralization when soils have a high capacity to sequester C (Mack et al., 2001). Similarly, Berendse et al. 1989 suggested that invading grasses in a heathland ecosystem had a smaller effect on mineralization rates than expected, because the soil organic matter was still dominated by the remains of low-quality heather litter.

4.4. Mineral nitrogen pool and availability in the soil

The notable soil moisture decline in June (almost half that of the previous months, Table 2) may help explain the significant summer decline of adsorption resin-assessed N mineral availability, as resin membranes are dependent on water for transferring ions from the soil to the resin (Yelenik et al., 2004). Soil inorganic N pool and availability were not affected by replacement of native by exotic trees (Figures 5-6), in contrast to our fourth prediction. This result contrasts sharply with the observed patterns of litter N loss, mainly when only native (native litter and canopy) and invaded (exotic litter and canopy) situations are compared. In both study cases, the exotic litter had higher N pool at the beginning of the experiment ($F=96.5$, $P<0.001$ and $F=1777.9$, $P<0.001$ for *A.*

altissima-U. minor and *R. pseudoacacia-F. angustifolia*, respectively). Seven months later, the N pool of *A. altissima* litter below *A. altissima* canopy was lower than the N pool of *U. minor* litter below *U. minor* canopy (F=6.74, P=0.04). By contrast, N pools of *R. pseudoacacia* and *F. angustifolia* litters below their own canopies converged to similar values (F=0.825, P=0.399) due to the N immobilization that occurred under *F. angustifolia* canopy. Therefore, in both cases a higher amount of N was released from the litter in the invaded situations, but this N was not found in the mineral N of the soil, which was similar between the two situations (Table 4-5). Instead, it was likely to be trapped in the soil organic matter (as argued before for *R. pseudoacacia*) and/or quickly absorbed by plants or microbes. Similarly, (Yelenik et al., 2007) found that an exotic N-fixing lupine invading South African velds, returned high amounts of N to the soil, but total N in the soil did not increase because of the fast rate at which it was absorbed by plants.

5. CONCLUSIONS

This study shows that an eventual displacement of native trees by exotic trees alter the dynamics of litter decomposition in different ways, due to physical and chemical differences between native and exotic litter, and to different decomposer activity below native and exotic canopies. In both study cases, a higher amount of N was released from the litter in the invaded than in the native situations. However, these differences neither translated to altered rates of potential N mineralization rate, nor to shifts in the amount of soil mineral N. This may be attributed to the excess of N being trapped in recalcitrant organic compounds, to a quick plant/microbe uptake of released N, and/or to high soil inertia provided by large accumulation of organic matter previous to invasion.

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8. SUPPLEMENTARY MATERIAL

Appendix 1. Characteristics of the study sites. In each site two plots were selected below the canopy of an exotic (A-*Ailanthus altissima*) and a native tree (U-*Ulmus minor*). Habitat type, altitude, distance to the river, mean annual precipitation and temperature of the closest weather station[1] (from October 2006 to September 2007) for each site, while canopy openness and mean trunk diameter at breast height (DHB) are given for each plot. (Asterisks denote that trunks correspond to resprouts after coppicing).

Site name	Canopy	Habitat type	Altitude (m)	Distance to a river (m)	Pm (Lm^{-2})	Tm (ºC)	Canopy openness (%)	Mean DBH (cm)
El Encín	A	Riparian forest	599	430	545	13.1	50.9	13
	U						33.7	14
Chiloeches	A	Road/crop side	824	6000	450	13.5	39.6	6*
	U						50.9	21*
Mejorada	A	Riparian forest	554	50	569	14.8	57.1	9*
	U						57.8	13*
Cabanillas	A	Road/crop side	640	1000	450	13.5	49.1	21
	U						38.6	9*

[1]Climatic data for Cabanillas and Chiloeches sites derive from Guadalajara weather station, data for El Encín came from Alcalá-El Encín weather station and Mejorada data were taken from Torrejón de Ardoz weather station.

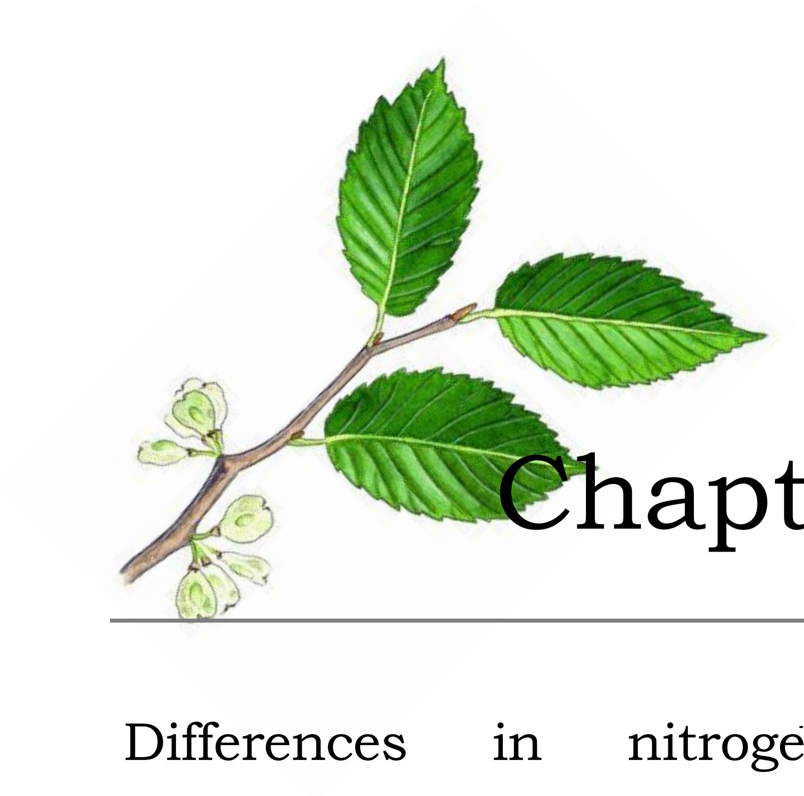
Appendix 2. Characteristics of the study sites. In each site two plots were selected below the canopy of an exotic (R-*Robinia pseudoacacia*) and a native tree (F-*Fraxinus angustifolia*). Habitat type, altitude, distance to the river, mean annual precipitation and temperature of the closest weather station[2] (from October 2006 to September 2007) for each site, while canopy openness and mean trunk diameter at breast height (DHB) are given for each plot. (Asterisks denote that trunks correspond to resprouts after coppicing).

Site name	Canopy	Habitat type	Altitude (m)	Distance to a river (m)	Pm (Lm^{-2})	Tm (°C)	Canopy openness (%)	Mean DBH (cm)
El Encín	R	Riparian forest	599	150	545	13.1	41.2	10
	F						35.2	86
JB-UAH	R	Botanical garden	602	910	545	13.1	68.6	11
	F						75.8	8
Campus-Canaleja	R	Forest plantation	595	890	545	13.1	70.1	28
	F	Riparian forest	595	50			46.8	6*
Torote	R	Road/crop side	635	263	569	14.8	51.1	7
	F	Riparian forest	651	144			50.8	32

[2]Climatic data for JB-UAH, El Encín and Campus-Canaleja sites came from Alcalá-El Encín weather station. Torote data were taken from Torrejón de Ardoz weather station.

Appendix 3. Soil association in each site below the canopy of an exotic (A-*Ailanthus altissima*, R- *Robina pseudoacacia*) and a native tree (U-*Ulmus minor*, F- *Fraxinus angustifolia*) (Guerra and Monturiol, 1970; Monturiol and Alcalá, 1990),

Site name	Canopy	Soil association
El Encín	A	Calcaric Fluvisols+Eutric Fluvisols
	U	
Chiloeches	A	Eutric Leptosols
	U	
Mejorada	A	Calcaric Fluvisols+Eutric Fluvisols
	U	
Cabanillas	A	Calcic Luvisols
	U	
El Encín	R	Calcaric Fluvisols+Eutric Fluvisols
	F	
JB-UAH	R	Haplic Calcisols+Calcic Luvisols
	F	
Campus-Canaleja	R	Haplic Calcisols+Calcic Luvisols
	F	Calcaric Fluvisols+Eutric Fluvisols
Torote	R	Calcaric Fluvisols+Calcaric Regosols+Calcic Gypsisols
	F	



Chapter 5

Differences in nitrogen use strategies between native and exotic tree species: predicting impacts on invaded ecosystems.

González-Muñoz, N., Castro-Díez, P., Parker, I.M.
2012. Plant and Soil. *In press*.

RESUMEN

Las plantas exóticas invasoras pueden alterar el ciclo de nutrientes en los ecosistemas invadidos. En este capítulo, analizamos las diferencias en las estrategias de uso de nitrógeno y dinámicas de producción de hojarasca entre tres especies de árboles nativos (*Fraxinus angustifolia, Populus alba* y *Ulmus minor*) y tres de árboles exóticos (*Ailanthus altissima*, *Robinia pseudoacacia* y *Ulmus pumila*) coexistentes en bosques de ribera del centro de la Península Ibérica. Nuestro objetivo es predecir las consecuencias ecológicas de un reemplazo de las especies nativas por las exóticas. Para ello, comparamos, entre dichas nativas y exóticas, el lifespan de las hojas, la eficiencia en la retranslocación así como el tiempo medio de residencia del nitrógeno en hojas, las dinámicas de producción de hojarasca y la cantidad de nitrógeno aportado al suelo. De acuerdo a nuestros resultados, las especies pueden ser ordenadas según sus estrategias en el uso del nitrógeno. *U. pumila* fue la especie más conservadora, seguida por las tres nativas (con una estrategia intermedia), después por *A. altissima* y, finalmente, por *R. pseudoacacia.* Las especies exóticas estudiadas producirán efectos contrastados en el ciclo de nitrógeno de los ecosistemas invadidos. Así, predecimos poco impacto en caso de un dominio de *U. pumila*. A pesar de ser fijadora de nitrógeno, *R. pseudocacia* no aumentaría la disponibilidad de nitrógeno en el área de estudio, debido a su baja producción y tasas de descomposición de hojarasca. Sin embargo, predecimos un incremento en la disponibilidad de nitrógeno en suelos en caso de un dominio de *A. altissima*, ya que esta especie produce una alta cantidad de hojarasca rica en nitrógeno y fácil de descomponer. Este estudio ofrece un ejemplo de la dificultad de predecir los impactos de las invasiones de plantas exóticas en los ecosistemas.

Palabras clave: Estrategia de uso de nitrógeno, retranslocación, tiempo medio de residencia, producción de hojarasca, árboles exóticos, bosques de ribera.

ABSTRACT

Exotic plant species can alter the nitrogen cycle in invaded ecosystems. We assess the differences in nitrogen use strategies and litter production and dynamics among three native riparian trees (*Fraxinus angustifolia*, *Populus alba* and *Ulmus minor*) and three co-occurring exotics (*Ailanthus altissima*, *Robinia pseudoacacia* and *Ulmus pumila*), currently spreading throughout river banks in inner Spain. We aim to predict the ecological consequences of a replacement of the natives by the exotics. We compared the leaf lifespan, nitrogen resorption efficiency in leaves, nitrogen mean residence time, amount and timing of litter production and amount of nitrogen returned to soils between these native and exotic species. We found differences among species in all the variables measured, but not between native or exotic origins. Species were ranked from the most to the least conservative nitrogen use strategy as follows: *U. pumila* was the most conservative species, followed by the three natives (with an intermediate strategy), *A. altissima* and finally by the nitrogen-fixer *R. pseudoacacia*. The studied exotic species would produce contrasting impacts on the nitrogen cycle upon invasion. On the basis of our results, we predict little impacts on the nitrogen cycle if *U. pumila* dominates the landscape. Despite being nitrogen-fixer *R. pseudocacia* would not increase soil nitrogen availability in the study area due to its low litter production and litter decomposition rates. In contrast, we predict an increase in nitrogen availability of soils upon *A. altissima* invasion, as this species produces a high amount of nitrogen rich and labile litter. This study offers a striking example of the contingencies involved in predicting the ecosystem impacts of exotic plant invasion.

Keywords: Nitrogen use strategy, nitrogen resorption, mean residence time, litter production, exotic trees, riparian forests.

1. INTRODUCTION

Exotic invasive plant species can alter the nutrient cycling of a community especially if they differ from the dominant native species in their nutrient use strategy (Ehrenfeld 2003; Liao et al. 2008; Ehrenfeld 2010; Vilá et al. 2011). The consequences of plant invasions for nutrient cycling have been explored extensively. Changes can be induced by differences between native and exotic species in the amount and chemical properties of the litter, which has consequences for litter decomposition processes (Tateno et al. 2007; Liao et al. 2008; Castro-Díez et al. 2009; Belote and Jones 2009; Alonso et al. 2010; Godoy et al. 2010), for the structure and activity of soil microbial and invertebrate communities (Kourtev et al. 2002; Tuttle et al. 2009) and for the structure of plant communities growing under their canopies (Mack et al. 2001; Evans et al. 2001; Levine et al. 2003). However, few studies have compared other components of the nutrient use strategies between native and exotic species, such as resorption efficiency or mean residence time (but see Urgenson et al. 2009). These traits are related with the nutrient economy of the plant and they can help explain the success of exotic species as well as their impact on invaded ecosystems.

Nitrogen availability may be particularly likely to facilitate or hinder plant invasions, as it limits primary production in most temperate ecosystems (Bowman et al. 1993; Soudzilovskaia et al. 2005; LeBauer and Treseder 2008). Species largely differ in their use and conservation of nitrogen in plant tissues, which also implies differences in nutrient cycles. Plants adapted to nitrogen-poor ecosystems have been usually selected for a more conservative nitrogen use strategy, i.e. long leaf life spans, high nitrogen resorption efficiency, low leaf nitrogen content, leaf tissues physically or chemically protected against herbivores, which result in low litter decomposition rates (Cornelissen et al. 1999, Aerts and Chapin 2000). Consequently, in ecosystems dominated by nitrogen-conservative plants, a high proportion of the ecosystem nitrogen is locked in plant tissues. In contrast, plants adapted to nitrogen-rich ecosystems tend to adopt opportunistic nitrogen use strategies. This implies short leaf life spans, poorly defended leaves and litter with high nutrient concentration and high decomposition rates. All these traits lead to a higher proportion of the ecosystem nitrogen being in the soil, readily available for organisms.

revious literature suggests that exotic invasive plants are usually closer to the opportunistic strategy described above (Leishman et al. 2007; Ehrenfeld 2003 and 2010, Liao et al. 2008, but see Godoy et al. 2010). Thus, if an exotic species that produces large quantities of easy to decompose nitrogen-rich litter invades ecosystems dominated by nitrogen conservative species, we can expect an increase in nitrogen availability in soils (Scott et al. 2001; Vanderhoeven et al. 2005; Dassonville et al. 2008). This change may influence species composition by favouring other opportunistic exotic species to the detriment of more conservative natives (eg: Maron and Connors 1996; Kalmbacher and Martin 1996; Paschke et al. 2000; Seabloom et al. 2003; Suding et al. 2005). The impact of exotic species can be aggravated if they introduce a novel function in the invaded area, such as N-fixation. Exotic N-fixing species have been shown to increase the amount of nitrogen in soils (Haubensak and Parker 2004; Ehrenfeld 2003; Hughes and Denslow 2005; Marchante et al. 2008 and 2009 among others). This increase in nitrogen availability may favour the growth, establishment and spread of other non-native species, particularly in previously nitrogen poor ecosystems (Adler et al. 1998; Simberloff and Von Holle 1999; Carino and Daehler 2002; Hughes and Denslow 2005; Simberloff 2006).

In central areas of the Iberian Peninsula, the exotic trees *Ailanthus altissima* Mill. (*Simabouracea*), *Robinia pseudoacacia* L. (*Fabaceae*) and *Ulmus pumila* L. (*Ulmaceae*) are expanding their distribution along crop and road borders, but also in floodplains, where they co-occur with the native trees *Fraxinus angustifolia* Vahl. (*Oleaceae*), *Populus alba* L. (*Salicaceae*) and *Ulmus minor* Mill. (*Ulmaceae*), among others (Sanz-Elorza et al. 2004). In a previous study (Castro-Díez et al. 2009) we compared soil N content and N mineralization rates below the crowns of two exotic (*A. altissima* and *R. pseudoacacia*) and two native riparian trees (*F. angustifolia*, *U. minor*), but found no differences, in spite of the large differences in litter quality and decomposition rate among species. This result was partly attributed to the soil inertia provided by the high accumulation of organic matter previous to invasion, and suggests that longer time since invasion is needed to find clear impacts on soil properties (Castro-Díez et al. 2009). Therefore, in the present paper we aim to predict the ecological consequences of potential shifts in community composition from a different approach, i.e, by comparing the nitrogen use strategy of native (*F. angustifolia*, *U. minor* and *P. alba*) and invasive trees (*A. altissima, R. pseudoacacia* and *U. pumila*). We first evaluated differences in leaf traits related to the nitrogen use strategy of these trees, such as leaf lifespan, leaf nitrogen resorption efficiency and nitrogen mean residence time. Second, we compared the timing and amount of leaf litter production, by placing litter traps below the crown of adult trees of each species. We finally estimated the impact of the different species in the nitrogen cycle by calculating the total annual amount of nitrogen returned to soils from the leaf litter. We assessed differences in traits, litter dynamics and nitrogen returned to soil regarding leaves over other plant components (fruits, branches, flowers, inflorescences) as falling leaves accomplish around 70% of total litter (O'Neill and DeAngelis 1981). All these issues are addressed in the study case of a medium-low stretch of the Henares River in central Spain.

If invasive plants tend to show opportunistic strategies, we expect the exotic species to show shorter leaf lifespans, higher leaf nitrogen content, lower nitrogen resorption efficiency, lower mean residence time and higher production of nitrogen-rich litter than natives. As a consequence, we also expect exotic species to return a higher amount of nitrogen to the soil than natives. Among all the studied species, we hypothesize that the exotic *Robinia pseudoacacia*, the only N-fixing species, will show the least conservative strategy, with the lowest nitrogen resorption, the lowest mean residence time and the highest amount of nitrogen returned to soils.

2. MATERIAL AND METHODS

2.1. Study area and species

We selected the floodplains of a medium-low stretch of the Henares River in central Spain (Province of Madrid) to conduct this study. The study area spans 22 km, from the location of Alcalá de Henares to Mejorada del Campo. Along this stretch environmental conditions and vegetation structure was considered to be homogeneous (Lara et al. 1996). Altitude ranged from 554 to 602 m a.s.l. Climate is continental Mediterranean with hot and dry summers and cold winters. Mean annual temperature and mean annual precipitation in the study area are 13.5 °C and 358.4 mm (data from "El Encín" weather station, National Institute of Meteorology, 1970-2009) (Fig. 1). The study years, 2008 and 2009, were colder and warmer than the mean (mean annual temperatures = 12.0 and 14.4 °C, respectively), and slightly moister and drier than the mean (annual precipitation= 392.6 and 309.4 mm in 2008 and 2009 respectively) (Fig. 1). Soils are luvisols and fluvisols (Guerra and Monturiol 1970; Monturiol and Alcalá, 1990). The soil pH is around 8 and the percentage of organic matter ranges from 4.6 to 9 (see Castro-Díez et al. 2009, 2012).

The dominant native tree species of the study area are *Fraxinus angustifolia* Vahl., *Ulmus minor* Mill. and *Populus alba* L. Other native co-occurring trees are *Populus nigra* L. and different species of the genera *Salix* and *Tamarix.* The most abundant exotic trees in the area are *Ailanthus altissima* Mill.*, Robinia pseudoacacia* L. and *Ulmus pumila* L. These species were introduced in the Iberian Peninsula primarily for ornamental purposes and now they are spreading in mesic woodlands, borders of agricultural fields and roads, and riparian forests of central Spain (Sanz Elorza et al. 2004). *Ailanthus altissima* is native to China and was introduced in the Iberian Peninsula in the end of the 18th century, whereas the exotics *Robinia pseudoacacia* and *Ulmus pumila* are native to North America and were introduced at the end of the 19th or the early 20th century (Sanz Elorza et al. 2004).

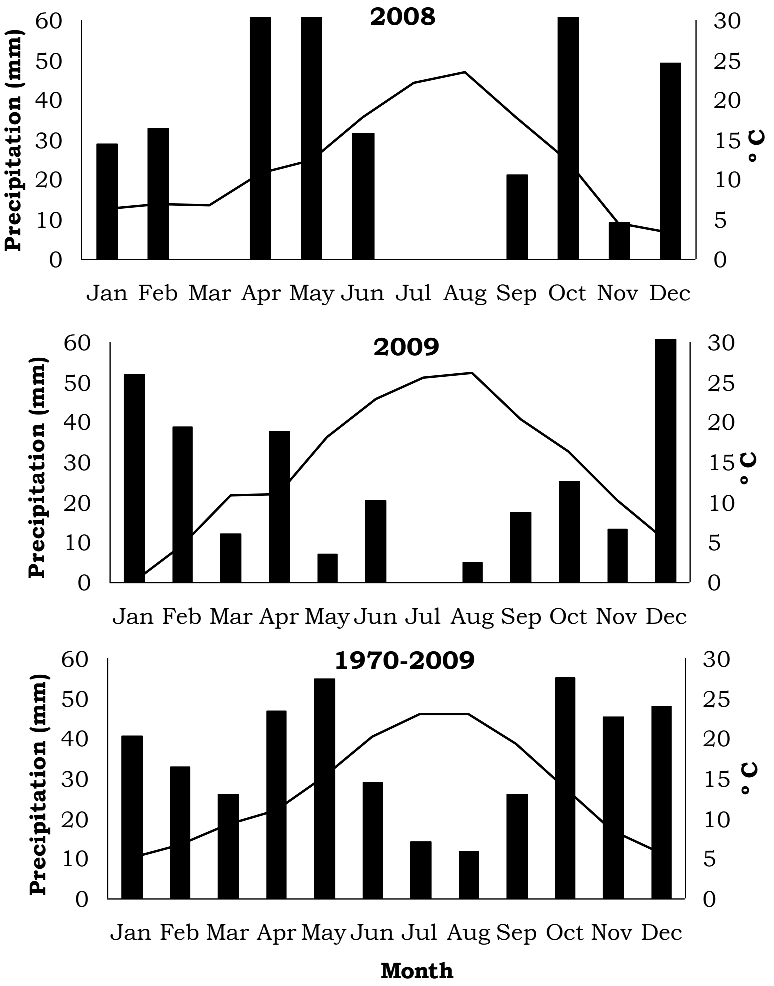


Fig. 1. Average monthly temperature (ºC) and rainfall (mm) during 2008 and 2009 (study period) and average monthly temperature and rainfall from 1970 to 2009. Data from El Encín weather station, National Institute of Meteorology, Government of Spain.

2.2. Field sampling and calculations

For each species, we selected eight adult trees whose size was typical for mature adult trees in the natural populations of our study area. In most species, average trunk perimeter at breast height ranged between 50 and 86 cm, except *U. pumila* which was on average thicker (Table 1). In March 2008 and 2009 we marked three apical, south oriented, mid-crown buds in each tree (Fig. 2). Weekly for each tree, we counted and numbered every leaf arising from each bud, which allowed us to follow the fate of each individual leaf until its abscission. This made a total of 1438 and 1115 leaves followed in 2008 and 2009, respectively. This allowed us a very accurate estimation of each species leaf life span (LLS). LLS in each year was calculated for every single leaf as the difference between the first date of presence and the first date of absence. In each tree, the dates of leaf out, leaf abscission and LLS were averaged across all sampled leaves. Leaf phenology in *Ailanthus altissima* was monitored only during 2009, due to failure of most tagged buds in 2008.

Fig. 2. Details of apical buds of two different trees of *Fraxinus angustifolia* on the 3rd of April of 2009.

In June, July and August 2008 we harvested two green leaves or leaflets (in the case of compound-leaves) per marked branch in five of the selected trees per species (6 leaves per tree) to determine the maximum specific leaf mass (leaf dry mass per unit area) and the maximum leaf nitrogen content of fully expanded leaves (N_{green}, see below) of each species. In *A. altissima*, which produced its leaves later, we also collected leaves in September. Green leaf/leaflet area was measured

with a Delta-T leaf area meter (Delta-T devices, Cambrige, UK). The leaf/leaflet dry mass was estimated after at least 48 hours at 60ºC. Specific leaf mass was calculated as the leaf dry mass (mg)/leaf area (cm^2). We did not find differences in the specific leaf mass among months in any species (results not shown).

We monitored leaf shedding following the methodology of Milla et al. (2005). In June 2008, before leaf senescence started, we tied one litter trap to the stem of each sampled tree, at 2 meters above the ground. Litter traps were meshed-bottom cylinders of 16 cm diameter x 19 cm high (Fig. 3). Litter trap content in each tree was monthly sampled until December 2009. We separated the litter trap contents into flowers, fruits and leaves. Leaf litter was oven-dried (60ºC, 48 hours) and weighed. The quantity of leaf litter produced per year by each tree was expressed as litter dry weight per square meter.

To characterize the strategy of nitrogen use in each species, we estimated the nitrogen resorption efficiency (NRE) and the nitrogen mean residence time (MRT) with those samples collected in 2008 (see below). The nitrogen resorption efficiency (NRE) was calculated as the ratio of the difference in nitrogen content between green (N_{green}) and senescent leaves (N_{sen}), following the formula:

$$NRE= (N_{green} -N_{sen}/ N_{green}) *100$$

Fig. 3. Detail of one of the litter traps placed on a *Ulmus minor* tree.

Leaves of all species were fully expanded by May-June and started to senesce in August-October. The maximum amount of nitrogen in fully expanded leaves (N_{green}) was obtained by pooling those leaves collected in June or July 2008, depending on the species. The nitrogen content remaining in leaves after senescence (N_{sen}) was estimated from the senescent leaves collected in the traps during the month of 2008 with the maximum peak of litter fall (which varied between species). Although all species shed their leaves in fall, some of them also showed a secondary peak in summer (see Results). In these cases we also estimated the nitrogen content in leaves collected in the litter traps during the summer litter fall peak and calculated NRE for both peaks (NRE_{aut} and NRE_{sum}).

Before nitrogen analysis, we pooled all senescent leaves collected in each litter fall peak within species, as the amount of leaves collected in some of the litter traps was too low to use each tree as a replicate. To avoid an overrepresentation of some individuals, the pooled sample contained the same amount of leaves from each tree. Pooled leaf samples were oven-dried (48 hours, 60°C) and then ground to a particle size <1 mm (PM100, Retsch Haan, Germany). Organic nitrogen was analyzed at Nutrilab (Universidad Rey Juan Carlos, Móstoles, Madrid, Spain) with a segmented flux autoanalyzer (S:F:A:S Skalar San ++) after a digestion with H_2SO_4 and Cu-KSO_4. We expressed the nitrogen content of both green and senescent leaves with respect to cellulose content, to avoid biases produced by area shrinkage or weight loss during senescence (van Heerwaarden et al. 2003). Cellulose was estimated using the Van Soest procedure (Febertec, Ankom Fiber analyzer).

The mean residence time (MRT) assesses how long a unit of a nutrient remains in the plant, and it is defined by both the leaf lifespan (LLS) and the nitrogen resorption (NRE) (Eckstein et al. 1999) as:

$$MRT = LLS*(100/100-NRE)$$

In those species with two peaks of litterfall (summer and autumn), we calculated MRT as follows:

$$MRT=\%_{sum}(LLS_{sum}*(100/100-NRE_{sum}))+\%_{aut}(LLS_{aut}*(100/100-NRE_{aut}))$$

where $\%_{sum}$ and $\%_{aut}$ refer to the percentage of the collected leaves fallen in summer and autumn respectively. LLS_{sum} and LLS_{aut} are the average leaf life span of leaves fallen in summer and autumn, respectively. In *Ailanthus altissima* we calculated the MRT by combining the NRE value of 2008 with the LLS found in 2009.

The total amount of nitrogen returned to the soil by each species (Kg/ha) was calculated for 2008 as:

$$\text{N returned to soil} = (\text{annual leaf litter} * N_{sen})$$

where N_{sen} was expressed on mass basis.

Finally, as the size or age of the tree can affect any of the studied variables mentioned above, we measured the perimeter at breast height (PBH) as an estimate of tree size and included it as a covariate in all the statistical analyses.

2.3. Statistical analyses

We tested the effect of origin (native/exotic) and species (nested within origin) on specific leaf mass, dates of leaf out and leaf abscission, leaf life span (LLS), mean retention time (MRT), annual leaf litterfall per unit of area (g/m^2) and N returned to soils (kg/ha) with nested analysis of variance. The perimeter at breast height (PBH) was included as a covariate in all analyses except that of specific leaf mass, to control for the effect of plant size on the variables. As origin was not a significant factor in any measured trait, we reduced the model to the factor species and the cofactor PBH. We performed *post-hoc* Tukey tests for multiple comparisons among species. Variables were checked for homoscedasticity (Levene test) and transformed to meet homoscedasticity assumptions when necessary (Zar, 1999). The differences in the percentage of nitrogen resorption (NRE) were not statistically analyzed because samples were pooled for chemical analyses and we lacked true replicates.

All statistical analyses were carried out using SPSS 17.0 (SPSS, Inc., Chicago, USA).

3. RESULTS

We did not find significant differences between exotic and native trees as a group for any of the measured variables (Figures 4-6, all $p > 0.05$). However, we found significant differences among the individual species for most of the analyzed traits (see results below). Therefore, we focus the rest of this section on inter-specific differences.

There were significant differences among species in specific leaf mass ($F_{5,\ 95}=21.11$, $p=0.001$) (Table 1). The native *P. alba* and the exotic *U. pumila* showed the highest specific leaf mass, almost twice as high as the exotic N-fixing *R. pseudoacacia*, which showed the lowest (Table 1).

Table 1. Average values of perimeter at breast height (PBH) and specific leaf mass (SLM) in each studied species. The native or exotic origin is indicated. Different letters mean significant differences between species according to a Tukey test ($p<0.05$). N= 8 per species.

Species	Origin	PBH (cm)	SLM (mg/cm^2)
Ailanthus altissima	Exotic	50.7±10.2	7.66±0.02b
Robinia pseudoacacia	Exotic	86.1±11.8	5.47±0.02c
Ulmus pumila	Exotic	111.6±7.7	10.01±0.29a
Fraxinus angustifolia	Native	55.7±3.3	8.58±0.38ab
Populus alba	Native	57.1±6.5	10.11±0.62a
Ulmus minor	Native	77.4±11.0	9.06±0.47ab

In 2008, there were significant differences among species in the date of leaf out ($F_{4,40}$=3.33, p= 0.022), date of leaf abscission ($F_{4,40}$=7.08, p=0.001) and in the leaf lifespan (LLS, $F_{4,40}$=6.62, p=0.001) (Fig. 4), once the effect of tree size was controlled for (PBH had a positive effect on the date of leaf abscission ($F_{1,40}$=6.07, p=0.190) and on LLS ($F_{1,40}$=9.85, p=0.004). *R. pseudoacacia* and *F. angustifolia* were the earliest producing leaves, followed by *U.minor* and *U. pumila*, *P. alba* being the latest (Fig. 4). *R. pseudoacacia* also lost its leaves the earliest, followed by *U. minor* (Fig. 4). The longest and shortest LLS in 2008 were found in *F. angustifolia and R. pseudoacacia* respectively (Fig. 4). In 2009 trends were similar to 2008, but across species differences were smaller, only differences in the date of leaf abscission and in LLS being significant ($F_{5,48}$=4.33, p=0.003 and $F_{5,48}$=6.35, p=0.001, respectively) (Fig. 4). All species produced their leaves earlier in 2009, probably because of the earlier rise of temperatures (mean March temperature = 6.7 and 10.9 ºC in 2008 and 2009, respectively) (Fig. 1) and all species, with the exception of *R. pseudoacacia*, also lost their leaves earlier in 2009 (Fig. 4). Differences in the date of leaf out between years ranged from 18 (*R. pseudoacacia*) to 54 days (*P. alba*) whereas differences in the date of leaf abscission between years ranged from 11 days (*F. angustifolia*) to 32 (*P. alba*) (Fig. 4).

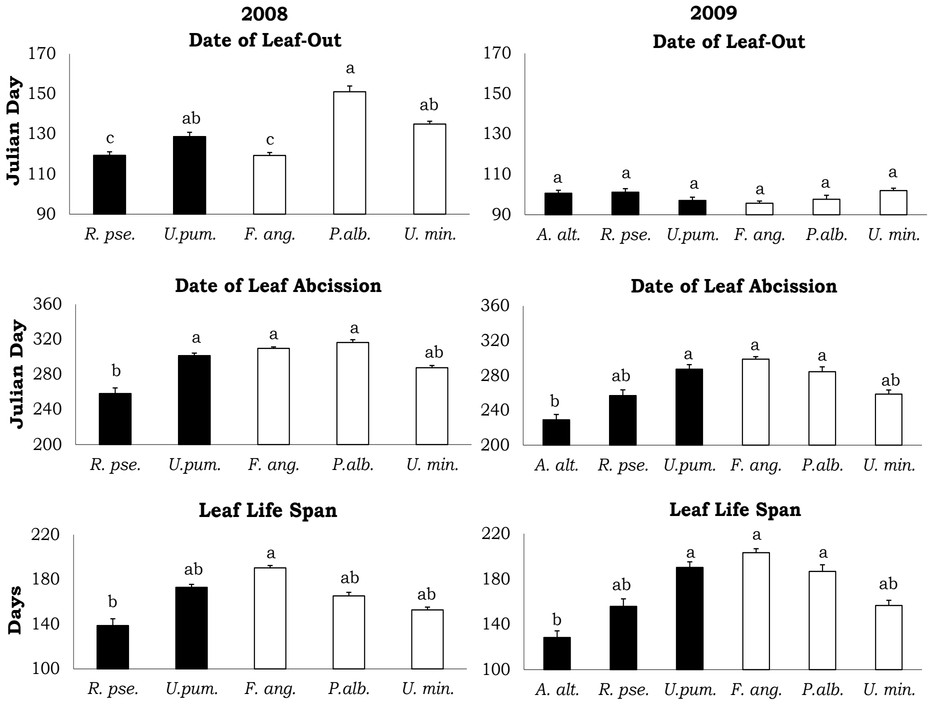


Fig. 4. Average Julian date (number of days since January 1st) of leaf–out and leaf abscission and average leaf life span + SE per species in 2008 (left) and 2009 (right). Solid and open bars represent exotic and native species, respectively. Different letters mean significant differences between species according to Tukey tests ($p<0.05$)

Species also differed in the amount of leaf litter produced in 2008 ($F_{5,48}=3.72$, $p=0.007$), being the highest in *U. minor,* followed by *A. altissima,* and being the lowest in *R. pseudoacacia* (Fig. 5a). Although larger trees obviously produced more litter than smaller trees (PBH $F_{1,48}=6.15$, $p=0.017$), this did not explain cross-species differences in litter production, as species was significant once accounted for PBH effect. Indeed, the species with largest average size (*U. pumila*) produced a similar amount of litter as the species with smaller size (*P. alba* and *F. angustifolia*, see Fig. 5a). In 2009 we found the same trends (Fig. 5b) but differences across species were not significant ($F_{5,48}$=0.779, p>0.05).

After accounting for tree size, we still found significant differences among species in the total amount of N returned to the soil in 2008 ($F_{5,48}$=3.39, p=0.017), *U. minor* being the species that returned the most, followed by *A. altissima*, *U. pumila* and *P. alba,* then by *F. angustifolia* and finally by *R. pseudoacacia* (Table 2, Fig. 5c).

Regarding the timing of leaf litter production, both in 2008 and 2009, we observed two pulses of leaf abscission in *U. minor* and *P. alba* (August and December), whereas *F. angustifolia*, *A. altissima* and *U. pumila* showed only one pulse in November (Fig. 6). *R. pseudoacacia* showed two peaks in 2008 (July and November) and only one in 2009 (November) (Fig. 6).

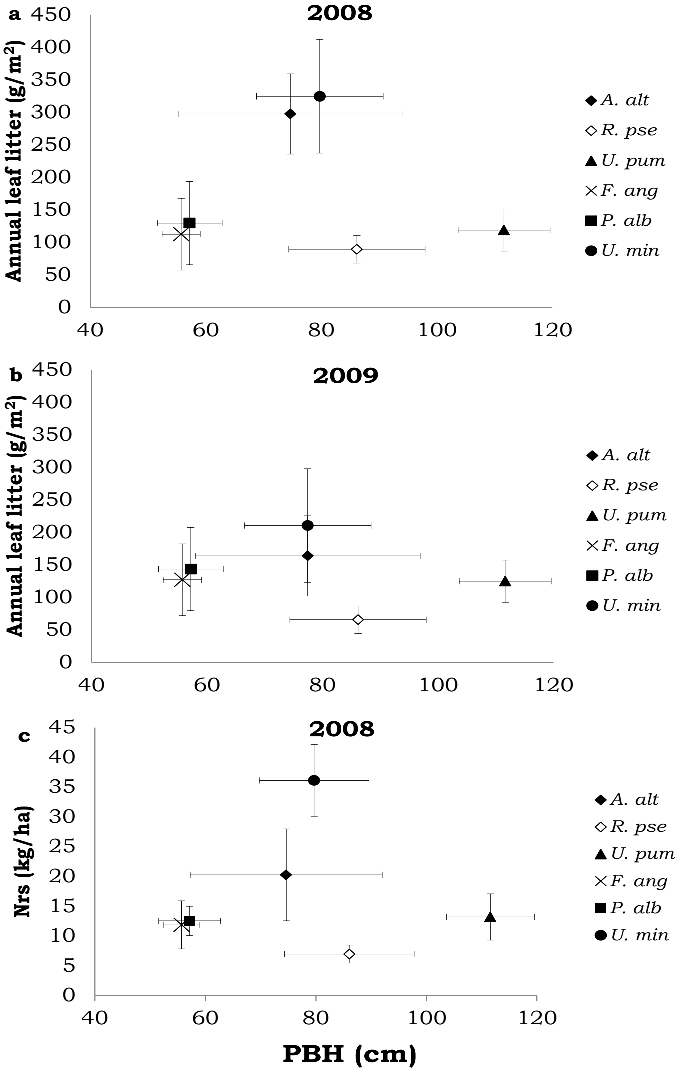


Fig. 5a and b. Relationship between the average annual leaf litter (g/m^2) collected in the litter traps in 2008 (a) and 2009 (b) and the average perimeter at breast height (PBH, cm) ± SE in each species. **Fig. 5c.** Relationship between the amount of nitrogen returned to soil (Nrs, kg/ha) in 2008 and the average perimeter at breast height ± SE. Each point represents a different species.

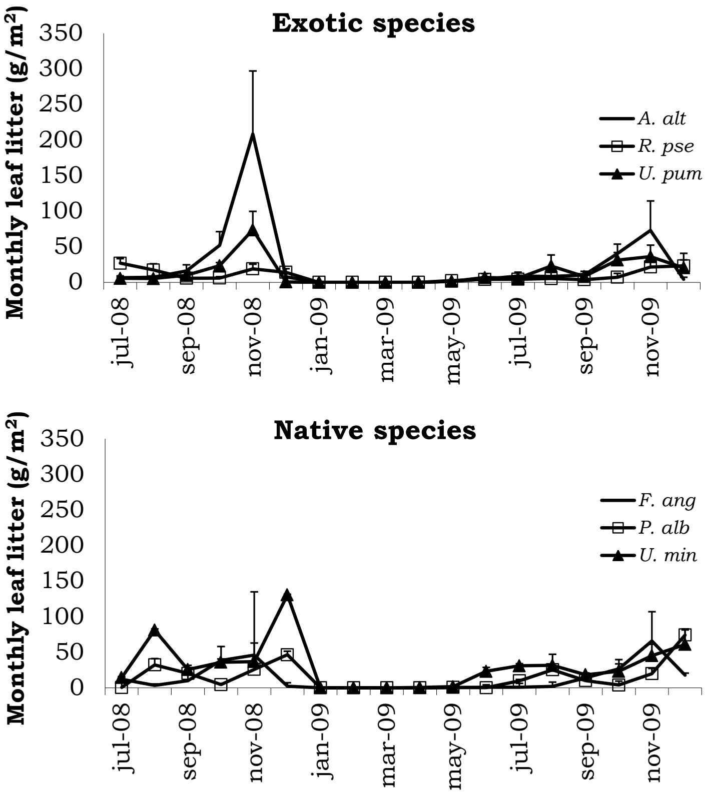


Fig. 6. Monthly amount of leaf litter (g/m^2) + SE collected in litter traps of exotic (above) and native species (below) from July 2008 to December 2009.

We observed suggestive patterns among species in nitrogen resorption (NRE) (Table 2). The legume *R. pseudoacacia* showed the lowest NRE, consistent with our initial hypothesis, while the exotics *A. altissima* and *U. pumila* showed the highest values and the native species shared similar and intermediate values (Table 2). In *P. alba* and *U. minor* the NRE in summer and autumn were similar (Table 2). However, in *R. pseudoacacia* the NRE in summer was higher than in autumn (Table 2).

Finally, there was a strong, significant variation among species in the mean residence time (MRT, $F_{5,48}$=20.11, p=0.001) (Table 2). As with NRE, *R. pseudoacacia* showed the lowest value, the exotic *U. pumila* showed the highest MRT, whereas the exotic *A. altissima* shared similar intermediate values with the natives (Table 2).

Table 2. Average mean residence time (MRT, days) and N returned to the soil (Nrs, Kg/ha) ± SE per species. Values of N content in green (N_{green}, g N/g cel) and senescent leaves (N_{sen}, g N/g cel) and nitrogen resorption efficiency in autumn (NRE_{aut}) and summer (NRE_{sum}) per species. No SE is shown in these last variables as we pooled the leaf samples previously to the analysis. Different letters mean significant differences between species according to Tukey tests (p<0.05). N= 8 per species.

Species	MRT	Nrs	N_{green}	N_{sen}	NRE_{aut}	NRE_{sum}
A. alt	467±15b	20.25±7.72ab	0.56	0.12	78	-
R. pse	311±7c	6.95±1.50c	0.58	0.36	37	56
U. pum	599±23a	13.20±3.88ab	0.38	0.11	71	-
F. ang	525±11ab	11.85±4.04b	0.36	0.11	69	-
P. alb	470±33b	12.54±2.45ab	0.22	0.08	65	69
U. min	460±21b	36.11±6.03a	0.27	0.09	67	65

4. DISCUSSION

We found differences among species in most of the analyzed traits. However, these differences did not differentiate between the groups of native and exotic species, contrary to our initial hypothesis.

The three native species showed a similar nitrogen use strategy that can be positioned in the middle of a conservative-opportunistic gradient, on the basis of the studied traits. They all showed similar, intermediate specific leaf masses, leaf lifespans, nitrogen resorptions and mean residence times. The high amount of nitrogen returned to soils by *U. minor* made this species somewhat less conservative than the other two natives. This strategy followed by the natives may be explained by their occurrence in riparian habitats, which are characterised by relatively nitrogen-rich soils (see González, 2010).

What would be the predicted impact of the replacement of these native riparian species by the exotics in this system? Because the three exotics followed completely different strategies in terms of their nitrogen use strategy, the outcome would entirely depend on the details of which exotic species dominates the invasion, as explained in the following paragraphs.

Ulmus pumila showed a more conservative nitrogen use strategy than native trees. This is because *U. pumila* showed the longest mean residence time, which means that it retains the nitrogen in the plant for longer than the other species, reducing the nitrogen availability in the system. In addition, it showed the second highest resorption efficiency among the studied species, being similar to that shown by the natives. Castro-Díez et al. (2012) found that the decomposition rate of *U. pumila* senescent leaves under controlled conditions was low and similar to that found in *R. pseudoacacia* (see below) and *F. angustifolia,* while lower than that of *A. altissima* and *U. minor.* This relatively slow litter decomposition would extend further the time needed by a unit of inorganic nitrogen to return to the soil. Consequently*,* if *U. pumila* becomes dominant in riparian ecosystems, the impact on the nitrogen cycle would be little in the short term, as its NRE is not so different from that of the natives, but tending to an impoverishment of soils in the long term due to the high mean resident time and low decomposition rates. This finding contrasts with our initial hypothesis predicting that exotics would show opportunistic N-use strategies and would return larger amounts of N to the soil.

Ailanthus altissima showed combined traits of both opportunistic and conservative strategies. On the opportunistic side, *A. altissima* produced the second largest amount of leaf litter among the studied species, and its leaves showed a high nitrogen content, which was similar even to leaves of *R. pseudoacacia*, the only N-fixing of the group. On the conservative side, *A. altissima* showed the highest nitrogen resorption efficiency (78%). Furthermore, previous studies showed that *A. altissima* litter decomposed relatively faster than co-occurring native species in a similar Spanish riparian ecosystem (Castro-Díez et al. 2009; Alonso et al. 2010), and also in a Maryland forest (USA) (Swan and Healey 2008). Consequently, *A. altissima* would increase the availability of mineral nitrogen under its canopy, through a high amount of fast to decompose litter, being readily available for plant uptake while, at the same time, it is able to use the nitrogen for a relatively long time, thanks to its efficient resorption. This means that *A. altissima* is very efficient in taking up nitrogen from soils but also in preserving it. The impacts of *A. altissima* have been previously addressed by Vilà et al. (2006) in several Mediterranean islands. They found that *A. altissima* presence increased nitrogen content, organic carbon and pH in soils and decreased the C/N ratio, accompanied by a 24% decline in species richness. This decline in species richness may reflect a positive feedback for *A. altissima* growth mediated by soil changes, with negative consequences for the co-occurring native species. Thus, we suggest that the efficient but also opportunistic nitrogen use strategy shown by *A. altissima* helps to explain the invasion success of this species in Mediterranean areas.

Finally, the exotic legume *R. pseudoacacia* showed the least conservative nitrogen use strategy among the studied species, consistent with our initial hypothesis. This was expected, as the ability to fix atmospheric nitrogen makes this species more independent of the nitrogen availability in the soil. *R. pseudoacacia* showed the lowest nitrogen resorption, the highest nitrogen content in green and senescent leaves, the shortest mean residence time and the lowest specific leaf mass. However, despite the litter properties pointing to a fast potential decomposition rate, previous studies reported that *R. pseudoacacia* litter decomposed slower than that of *F. angustifolia*, *A. altissima* and *U. minor*, probably due to its extremely high lignin content (Castro-Díez et al. 2009; Alonso et al. 2010). Lignin binds to litter proteins, forming organic complexes that are difficult to metabolize by soil microorganisms, which decreases decomposition rates (Gallardo and Merino, 1993). *R. pseudoacacia* also produced the lowest amount of litter among the studied species, contrary to our expectation for an opportunistic, N-fixing species. Because of that, and despite being the species with the highest nitrogen content in senescent leaves, it was the species that returned least nitrogen to soils (nearly six times less that *U. minor*). Our findings contrast with those reported by other authors, showing that *R. pseudoacacia* increases the soil nitrogen pools in nitrogen-poor soils (Montagnini et al. 1986 and 1991; Rice et al. 2004; Malcom et al. 2008). However, Castro-Díez et al. (2009) found no effect of *R. pseudoacacia* litter on soils of the same riparian forests studied here. We believe that these contrasting results may be explained by two non-exclusive arguments. First, the richer riparian soils in our study may dampen the impacts of N-fixing species relative to that same species in nutrient poor sites. Second, *R. pseudoacacia* trees in our study area show more open crowns, with sparse leaves and dead branches, as compared with the other species, which could explain the small quantity of leaf litter we observed. Finally we should note that these results are area-specific and might be different under different environmental circumstances.

Taken together, our findings suggest that domination by *R. pseudoacacia* would reduce nitrogen availability for plants in our study area, due to the addition of litter that is nitrogen-rich but scarce and difficult to decompose. In this case, the main consequence of the replacement of native trees by *R. pseudoacacia* would be an increase of the atmospheric nitrogen input to the ecosystem; this nitrogen would remain in tree crowns for a shorter time and accumulate in the soil in the form of recalcitrant organic compounds, not being readily available for plants or microorganisms. As a consequence, the soil organic matter would be the ecosystem pool where nitrogen would increase at a higher rate. In other studies, other impacts of *R. pseudoacacia* on plant communities have been reported, such as the alteration of the light environment, a decrease in plant species diversity and the facilitation of other non-native plant species (Boring and Swank 1984; Peloquin and Hiebert 1999; Matus et al. 2003). In our system, *R. pseudoacacia* might have negative impacts on native species, but we would not predict nitrogen enrichment to be a mechanism for these impacts.

5. CONCLUSIONS

Among the studied species, the native trees showed a nitrogen strategy that was intermediate between conservative and opportunistic. However, the three exotics followed very different strategies, with *U. pumila* being the most conservative and *R. pseudoacacia* the most opportunistic. *A. altissima* showed properties of both conservative and opportunistic strategies. In the case of a replacement of the native riparian vegetation by these exotic trees, we predict a weak impact on the nitrogen cycle in the case of *U. pumila* dominance, an impoverishment of soils in the case of *R. pseudoacacia,* and an increase in nitrogen availability in the case of *A. altissima*. This system offers a striking example of the contingencies involved in predicting the ecosystem impacts of exotic plant invasion.

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Chapter 6

General Conclusions

General Conclusions

1. Seedling performance was not related to the exotic or native origin of the species. The species in each group exhibited different responses to the light and soil moisture gradients (**Chapter 2** and **3**).

2. Seedlings of most species, either exotic or native, exhibited better performance under well-lit/moisturized conditions. Seedlings of the exotics *Ailanthus altissima*, *Robinia pseudoacacia*, *Elaeagnus angustifolia* and *Acacia dealbata,* the natives *Populus alba* and *Fraxinus angustifolia* and the naturalized *Pinus pinaster* are shown as clearly shade intolerant (**Chapter 2** and **3**).

3. Shaded environments are a suitable tree regeneration niche for the natives *Ulmus minor* and *Quercus pyrenaica* and the exotics *Acer negundo* and *Eucalyptus globulus*. However, as all the species included in the previous group are able to reproduce vegetatively, the shaded environments can be also colonized by their resprouts, as long as the mother tree receives light enough (**Chapter 2** and **3**).

4. Preserving overstory both in the riparian forests of central Spain and in the mesic forests of the Northwest, seems the best action oriented to the control of the studied exotic species, as shade hamper seed recruitment in most of the exotic studied species.

6. Changes in the nitrogen cycle in riparian forests of central Spain are expected upon invasion by *Ailanthus altissima* and *Robinia pseudoacacia,* due to differences in litter qualities and litter decomposition dynamics between these species and the dominant natives (**Chapter 4**).

7. Exotics species followed very different nitrogen use strategies. *Ulmus pumila* was the most conservative species, *Robinia pseudoacacia* the most opportunistic, whereas *Ailanthus altissima* showed properties of both conservative and opportunistic nitrogen use strategies. The native species showed an intermediate conservative nitrogen use strategy (**Chapter 5**).

8. We predict a weak impact of *Ulmus pumila* on the nitrogen cycle of invaded ecosystems, due to its conservative and similar to the native nitrogen use strategy. Contrastingly, a *Robinia pseudoacacia* dominance may lead to an impoverishment of soils, mainly due to its difficult to decompose litter. Finally, *Ailanthus altissima* may increase nitrogen availability in soils, due to the high amount of nitrogen rich and easy to decompose litter (**Chapters 4** and **5**).

9. The differences in the impacts on the nitrogen cycle showed by studied exotic species offer an example of the difficulties involved in predicting the consequences of exotic plant invasions on the invaded ecosystems (**Chapter 4** and **5**).

Chapter 7

Future Research Lines

Future Research Lines

The results achieved in this Thesis have contributed to the identification of some of the environmental conditions that favour the establishment of seedlings of native and exotic species co-occurring in the Iberian Peninsula. However, there are other factors different to light and soil moisture that may favour or hamper these species success. Furthermore, other life stages different than the seedling stage should be studied, as environmental factors may have different effects along the ontogeny of the individuals.

Nowadays, I continue working on the causes that are leading exotic species to success. Here are shown some of the preliminary results and future research lines.

1.- Which are the main climate factors controlling studied species radial growth?

In Chapters 2 and 3 we identified some of the environmental conditions that favour studied species performance. However, we focus on the seedling stage and further studies are necessary regarding other life stages. In this sense, dendrochronology provides the tools to study long-term growth responses of adult trees to different environmental conditions, as climate, competition or disturbances (Fritts, 1966, 1976; Fritts and Swetnam, 1989). However, despite the potential of dendrochronology, there are only few studies using this tool to describe the climate conditions that help exotic species to succeed in invaded areas (Kilgore and Telewski, 2004; Glawenda and Koprowski, 2012).

We are conducting a study aiming to describe the climate conditions that favour the radial growth of native and exotic co-occurring tree species by means of dendrochronology. We also aim to construct models that may help to predict the consequences of the climate conditions forecasted by the IPCC (2007) for the next century on radial growth.

We have constructed a ring width chronology for three exotic and five native species co-occuring in two edaphically, botanically and climatically contrasted areas (Fig 1a and b). The species selected for this study are the exotics *Ailanthus altissima* and *Robinia pseudoacacia* and the natives *Fraxinus angustifolia* and *Ulmus minor,* which co-occur in riparian forests of central Spain, and the exotic *Acacia dealbata* and the natives *Quercus pyrenaica*, *Quercus robur* and *Pinus pinaster*, which co-occur in mesic forests of the Northwest. We expected that the environmental variables controlling exotic species radial growth be related to the growth-limiting factors in their natural distribution areas. We also expect that the most restrictive conditions predicted by the IPCC will restrict secondary growth in those exotic species native to humid areas.

Our preliminary results show a weak signal of climate on the radial growth of Northwest Iberian Peninsula species, probably due to the mildness of the precipitation of the area (Fig 1a). Among the species of central Spain riparian forests, *F. angustifolia* shows the highest sensivity to climate (Fig 1b), whereas *U. minor* and *R. pseudoacacia* show the lowest. This suggests that other factors different to temperature and rainfall must be controlling these species growth. Finally, *A. altissima* radial growth is positively associated to soft annual temperatures (especially soft winters) and high rainfall, overall in winter and autumn, in agreement with our initial hypothesis.

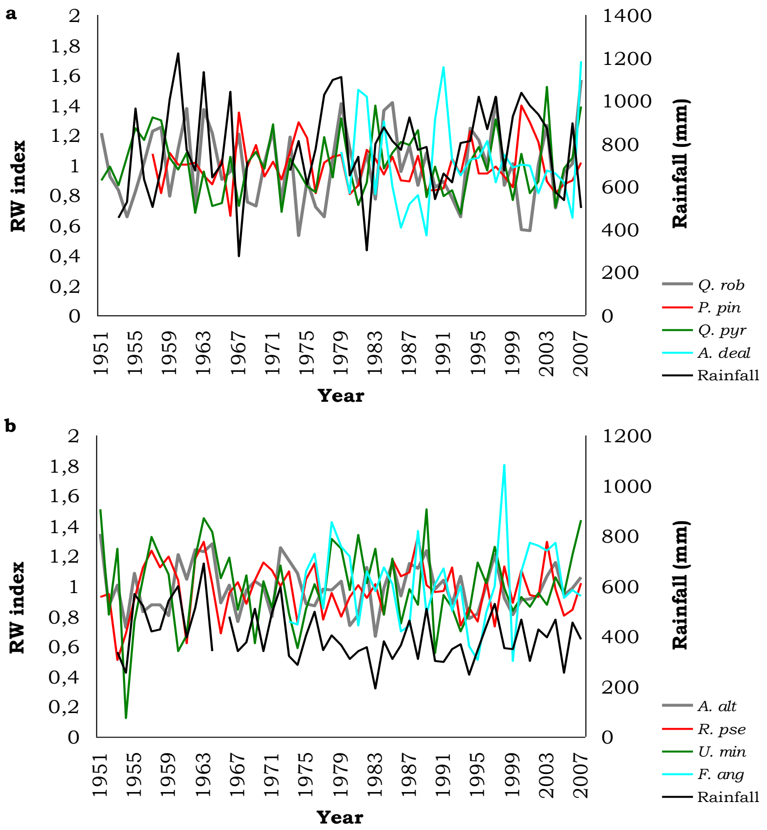

Fig. 1a. Ring width chronologies of *Quercus robur* (*Q. rob*), *Pinus pinaster* (*P. pin*), *Quercus pyrenaica* (*Q. pyr*) and *Acacia dealbata* (*A. deal*) plotted versus annual rainfall. Data from Orense weather station, Government of Spain. **Fig. 1b.** Ring width chronologies of *Ailanthus altissima* (*A. alt*), *Robinia pseudoacacia* (*R. pse*), *Ulmus minor* (*U. min*) and *Fraxinus angustifolia* (*F. ang*) plotted versus annual rainfall. Data from Torrejón de Ardoz weather station, Government of Spain.

We are currently working in building models aiming to help to predict the effects of climate change on these species radial growth

This work is being developed in collaboration with Ute Sass Klaassen (Forest Ecology and Forest Management Group, Wageningen University, The Netherlands).

2.- Do exotic species show a lower water use efficiency than natives?

The IPCC (2007) predicts an increase in mean temperatures and in CO_2 atmospheric, together with more severe droughts for the next century. These changes pose the question whether the forecasted environmental conditions will favour or hamper exotic species over natives.

The analysis of carbon isotope discrimination in tree rings is a helpful method to study how climate affects the water balance during the growth period. The isotope discrimination between the carbon of atmospheric CO_2 and the plant carbon in C_3 plants is the result of the preferential use of the light isotope (^{12}C) during photosynthesis (Farquhar and Richards, 1984).

The water use efficiency (WUE) can be estimated from the values of C stable isotope ratios ($^{13}C/^{12}C$; $\delta^{13}C$) obtained from the tree-ring wood (McCarroll and Loader, 2004).

We aim to compare differences in WUE between the exotics *Robinia pseudoacacia* and *Ailanthus altissima* and the natives *Ulmus minor* and *Fraxinus angustifolia*. We expect a higher WUE in native species than in exotics, as these species are adapted to the stressful conditions of Mediterranean summer. We also expect the lowest WUE in *R. pseudoacacia*, as this species is native to areas with a humid to superhumid temperate climate (Overton, 1990).

This work will be developed in collaboration with Juan Carlos Linares Calderón (Departamento de Biología Animal, Vegetal y Evolutiva, Universidad de Jaén).

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Fritts, H.C., Swetnam, T.W. (1989) Dendroecology: a tool for evaluating variations in past and present forests environments. Advances in Ecological Research 19, 111-188.

Glawenda, M., Koprowski, M. (2012) Dendrochronological analysis of radial growth of western hemlock (*Tsuga heterophylla* Sarg.) from Western Pomerania (Dobrzany Forest District) Sylwam 156 (4), 287-293.

Huntley, J.V. (1990) *Robinia Pseudoacacia*. In: Burns, RM., Honkala., BH. (Eds) Silvics of North America 2: Hardwoods. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington DC.

IPCC (2007) Climate change 2007, the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambrigde.

Kilgore, J.S., Telewski, F.W. (2004) Climate-growth relationships for native and nonnative *Pinaceae* in Northern Michigan´s Pine barrens. Tree-ring Research 60(1), 3-13.

McCarroll, D., Loader, N.J. (2004) Stable isotopes in tree rings. Quaternary Science Reviews 23, 771-801.

Curriculum

1. LIST OF PUBLICATIONS

Noelia González Muñoz, Pilar Castro Díez, Oscar Godoy (2012) Assessing seedling growth strategies of co-occurring native and exotic tree species: an experiment to identify potential regeneration niches for exotic trees in human managed riparian forests. Sent to Journal of Vegetation Science in July 2012.

Noelia González Muñoz, Pilar Castro Díez, Ingrid M. Parker (2012) Differences in nitrogen use strategies between native and exotic tree species: predicting impacts on invaded ecosystems. Plant and Soil. *In press*.

Pilar Castro Díez, Natalia Fierro Brunnenmeister, **Noelia González Muñoz**, Antonio Gallardo (2012) Effects of exotic and native tree leaf litter on soil properties of two contrasting sites in the Iberian Peninsula. Plant and Soil 350, 179-191.

Noelia González Muñoz, Margarita Costa Tenorio, Tíscar Espigares (2012) Invasion of alien *Acacia dealbata* on Spanish *Quercus robur* forests: Impact on soils and vegetation. Forest Ecology and Management 269, 214-221.

Noelia González Muñoz, Pilar Castro Díez, Natalia Fierro Brunnenmeister (2011) Establishment success of coexisting native and exotic trees under an experimental gradient of irradiance and soil moisture. Environmental Management 48, 764-773.

Álvaro Alonso Fernández, **Noelia González Muñoz**, Pilar Castro Díez (2010) Comparison of leaf decomposition and macroinvertebrate colonization between exotic and native trees in a freshwater ecosystem. Ecological Research 25, 647-653.

Pilar Castro Díez, **Noelia González Muñoz**, Álvaro Alonso Fernández, Antonio Gallardo, Lourens Poorter (2009) Effects of exotic invasive trees on nitrogen cycling: a case study in Central Spain. Biological Invasions 11, 1973-1986.

Pilar Castro Díez, **Noelia González Muñoz**, Álvaro Alonso Fernández (2008) Los árboles exóticos invasores alteran la tasa de descomposición de la hojarasca. Cuadernos de la Sociedad Española de Ciencias Forestales 25, 99-104.

Noelia González Muñoz, Pilar Castro Díez, Natalia Fierro-Brunnenmeister, Elena Varas García (2008) Diferencias en emergencia y mortalidad entre plantas exóticas y nativas sometidas a diferentes tratamientos de luz y humedad del suelo durante la primera estación de crecimiento. II Jornadas de jóvenes investigadores de la UAH, 31-39.

2. CONGRESS AND MEETINGS

Oscar Godoy, **Noelia González Muñoz,** Jonathan Levine (2012) The role of phenotypic plasticity for species coexistence. 97th Annual Meeting of the Ecological Society of America. Portland (USA). Oral presentation.

Noelia González Muñoz, Pilar Castro Díez, Ingrid M. Parker (2012) Contrasting impacts on the nitrogen cycle of co-occurring exotic species. 97th Annual Meeting of the Ecological Society of America. Portland (USA). Poster.

Noelia González Muñoz, Oscar Godoy, Pilar Castro Díez (2012) Assessing the invasion risk of human-managed riparian forest by comparing seedling performance of co-occurring native and exotic tree species through an experimental gradient of light and soil moisture. 7th European Conference on Biological Invasions. Pontevedra (Spain). Poster.

Guillermo Valle Torres, Pilar Castro Díez, **Noelia González Muñoz** (2012) Differences in temporal niche among exotic tree species co-occurring in riparian forest of the Iberian Peninsula. 7th European Conference on Biological Invasions. Pontevedra (Spain). Poster.

Silvia Medina Villar, Álvaro Alonso Fernández, Esther Pérez Corona, Susana Rodríguez Echeverría, **Noelia González Muñoz**, Guillermo Valle Torres, Pilar Castro Díez (2012) Effects of invasive trees (*Ailanthus altissima* and *Robinia pseudoacacia*) on nutrients and enzymatic activity of a riparian soil. 7th European Conference on Biological Invasions. Pontevedra (Spain). Poster.

Noelia González Muñoz, Pilar Castro Díez, Natalia Fierro Brunnenmeister, Evelyn Beliën (2012) Diferencias en el éxito de establecimiento entre árboles nativos y exóticos en distintas condiciones experimentales de luz y humedad del suelo. III Jornadas Técnicas de los Jardines Botánicos. Alcalá de Henares (Spain). Poster.

Noelia González Muñoz, Pilar Castro Díez, Natalia Fierro Brunnenmeister, Evelyn Beliën (2012) Diferencias en la fenología foliar y producción de hojarasca entre árboles nativos y exóticos coexistentes en la Península Ibérica. III

Jornadas Técnicas de los Jardines Botánicos. Alcalá de Henares (Spain). Poster.

Noelia González Muñoz, Margarita Costa Tenorio, Tíscar Espigares (2012) La invasión de *Acacia dealbata* en los bosques de *Quercus robur*: impactos en el banco de semillas y comunidad vegetal. III Jornadas Técnicas de los Jardines Botánicos. Alcalá de Henares (Spain). Poster.

Noelia González Muñoz, Pilar Castro Díez, Natalia Fierro Brunnenmeister, Evelyn Beliën (2010) Comparison of leaf phenology between native and invasive trees in the Iberian Peninsula. 6th European Conference on Biological Invasions. Copenhagen (Denmark). Poster.

Ainara Ballesteros, Pilar Castro Díez, **Noelia González Muñoz** (2010) Competition between seedlings of a native (*Pinus pinaster*) and an exotic tree (*Acacia dealbata*) in Spain under different environments. 6th European Conference on Biological Invasions. Copenhagen (Denmark). Poster.

Noelia González Muñoz, Pilar Castro Díez, Natalia Fierro Brunnenmeister, Elena Varas García (2009) Differences in emergence, seedling mortality and morphology between coexisting native and alien plant species under different soil

moisture and irradiance. eMAPI. Stellenbosch (South Africa). Poster.

Natalia Fierro Brunnenmeister, Pilar Castro Díez, **Noelia González Muñoz**, Elena Varas García, Antonio Gallardo (2009) Exotic and native tree litter effects on soil properties in two contrasting sites in the Iberian Peninsula. eMAPI. Stellenbosch (South Africa). Poster.

Álvaro Alonso Fernández, **Noelia González Muñoz**, Pilar Castro Díez (2009) Comparison of leaf decomposition between exotic and native trees in a freshwater ecosystem. eMAPI. Stellenbosch (South Africa). Poster.

Natalia Fierro Brunnenmeister, **Noelia González Muñoz**, Antonio Gallardo, Pilar Castro Díez (2009) Efectos de la descomposición de hojarasca de especies nativas e invasoras en las propiedades del suelo. 5º Congreso Forestal Español. Ávila (Spain). Poster.

Noelia González Muñoz, Elena Varas García, Margarita Costa Tenorio, Tíscar Espigares (2009) Invasion of alien species *Acacia dealbata* on *Quercus robur* forests: Impact on vegetation community under its canopy. Biolief. Oporto (Portugal). Poster.

Noelia González Muñoz, Pilar Castro Díez, Natalia Fierro Brunnenmeister, Evelyn Beliën (2008) Comparison of emergence and survival rates between pairs of coexisting alien and native species under different levels of irradiance and watering. 6th European Conference on Biological Invasions. Prague (Czech Republic). Poster.

Noelia González Muñoz, Pilar Castro Díez, Natalia Fierro Brunnenmeister, Elena Varas García (2008) Diferencias en emergencia y mortalidad entre plantas exóticas y nativas sometidas a diferentes tratamientos de luz y humedad del suelo durante la primera estación de crecimiento. II jornadas de Jóvenes Investigadores de la UAH. Alcalá de Henares (Spain). Oral Presentation.

Pilar Castro Díez, **Noelia González Muñoz**, Álvaro Alonso Fernández (2008) Los árboles exóticos invasores alteran la tasa de descomposición de la hojarasca. II Reunión del grupo de trabajo de Ecología, Ecofisiología y suelos forestales Salamanca (Spain). Oral Presentation.

3. STAYS ABROAD

Wageningen University Forest Ecology and Forest Management Group. The Netherlands, January-April 2009.

Wageningen University Forest Ecology and Forest Management Group. The Netherlands, November-December 2009.

University of California (Santa Cruz) Department of Ecology and Evolutionary Biology. USA, September-December 2010.

University of California (Santa Barbara) Department of Ecology, Evolution and Marine Biology. USA, April-July 2011.

4. PARTICIPATION IN RESEARCH PROJECTS

Evaluación del riesgo invasor de árboles exóticos: patrones de distribución, éxito invasor e impacto en los ecosistemas *Ministerio de Ciencia e Innovación*. January 2010-December 2013.

Evaluación integral de los impactos de los árboles exóticos invasores sobre los ecosistemas fluviales y de ribera de Castilla La Mancha. *Junta de Comunidades de Castilla La Mancha*. April 2010- March 2013.

Causas y consecuencias de las invasiones de plantas exóticas en la Península Ibérica. *Ministerio de Ciencia e Innovación*. October 2007- September 2010.

5. TEACHING

140 hours. Faculties of biology and Environmental Sciences.

6. LANGUAGES

English. Pre-Proficiency. May 2012.

7. FUNDS

2008-2012 FPI Predoctoral fellowship. Government of Spain.

2008 Alcala University Predoctoral fellowship.

2006-2007 Pre Graduate students fellowship.

2007 MsC Biology Conservation. Alcala University.

2005 BsC Biology. Alcala University.

1999 BsC Physiotherapy. Alcala University.

8. OTHERS

2009 Best Student of the year. *Consejo de Estudiantes*. Alcala University.


BORIS GUARDABA DENTRO DE SÍ UN SECRETO.
UN SECRETO QUE LE ROÍA EL ALMA Y ATORMENTABA SU ESPÍRITU.
UN SECRETO QUE NO PODÍA REVELAR A SU ESPOSA PORQUE, HORRORIZADA, DEJARÍA DE SER SU ESPOSA.
NI A SU MEJOR AMIGO, PORQUE ALLÍ TERMINARÍA SU AMISTAD.
NI TAMPOCO AL CIELO, POR TEMOR A UNA ETERNA PUNICIÓN DIVINA.
A PUNTO DE ENLOQUECER, UNA NOCHE BORIS DECIDIÓ PONER FIN A TAN INSOPORTABLE SITUACIÓN.
BUSCÓ EL ÁRBOL MÁS ALTO DEL PUEBLO...
...Y DURANTE HORAS LE CONTÓ EN UN INCESANTE MURMULLO TODO SU SECRETO.
REGRESÓ A CASA Y DURMIÓ MUY LARGA Y DESAHOGADAMENTE CON DESCONOCIDA PLACIDEZ.
DESDE ENTONCES LA BRISA QUE PASA POR AQUEL ARBOL LLEVA A OÍDOS DE TODOS EL SECRETO DE BORIS.
PERO BORIS PASEA TRANQUILO PORQUE SABE QUE, EN SU SOBERBIA, AL GÉNERO HUMANO NO LE INTERESA COMPRENDER NADA DE LO QUE LE CUENTAN LAS DEMÁS ESPECIES.
QUINO