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REGULAR ARTICLE

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

N. González-Muñoz · P. Castro-Díez · I. M. Parker

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Abstract
Background and aim 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.
Methods 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.
Results 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.
Conclusions 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

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; Vilà et al. 2011). The consequences of plant invasions for nutrient cycling have been explored extensively. Changes can be induced by differences

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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.

Previous literature suggests that exotic invasive plants are usually closer to the opportunistic strategy described above (Leishman et al. 2007; Ehrenfeld 2003; 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; 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 Daheler 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 rates 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.

Methods

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 ma.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). 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). 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).

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. 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 1,438 and 1,115 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.

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

Table 1 Average values of perimeter at breast height (PBH), specific leaf mass (SLM), mean residence time (MRT) and N returned to the soil (Nrs) ± SE per species. Values of N content in green (N_{green}) and senescent leaves (N_{sen}) and nitrogen resorption efficiency in summer (NRE_{sum}) and autumn (NRE_{aut}) per species. No SE is shown in these last variables as we pooled the leaf samples previously to the analysis. NRE_{sum} was calculated only for those species that showed a secondary peak of litterfall in summer. The native (N) or exotic (E) origin of each species is also indicated. *N*=8 per species

Species	Origin	PBH (cm)	SLM (mg/cm^2)	MRT (days)	Nrs (Kg/ha)	N_{green} (g N/g cel)	N_{sen} (g N/g cel)	NRE_{sum}	NRE_{aut}
Ailanthus altissima	E	50.7±10.2	7.66±0.02b	467±15b	20.25±7.72ab	0.56	0.12	–	78
Robinia pseudoacacia	E	86.1±11.8	5.47±0.02c	311±7c	6.95±1.50c	0.58	0.36	56	37
Ulmus pumila	E	111.6±7.7	10.01±0.29a	599±23a	13.20±3.88ab	0.38	0.11	–	71
Fraxinus angustifolia	N	55.7±3.3	8.58±0.38ab	525±11ab	11.85±4.04b	0.36	0.11	–	69
Populus alba	N	57.1±6.5	10.11±0.62a	470±33b	12.54±2.45ab	0.22	0.08	69	65
Ulmus minor	N	77.4±11.0	9.06±0.47ab	460±21b	36.11±6.03a	0.27	0.09	65	67

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 h at 60 °C. 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 m above the ground. Litter traps were meshed-bottom cylinders of 16 cm diameter × 19 cm high. 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 (60 °C, 48 h) 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:

$$\mathrm{NRE} = \left(\mathrm{N_{green}} - \mathrm{N_{sen}}/\mathrm{N_{green}}\right)*100 \tag{1}$$

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 h, 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:

$$\mathrm{MRT} = \mathrm{LLS}^{*}(100/100 - \mathrm{NRE}) \qquad (2)$$

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

$$\begin{aligned}\mathrm{MRT} = {} & \%_{\mathrm{sum}}(\mathrm{LLS}_{\mathrm{sum}}{}^{*}(100/100 - \mathrm{NRE}_{\mathrm{sum}})) \\ & + \%_{\mathrm{aut}}(\mathrm{LLS}_{\mathrm{aut}}{}^{*}(100/100 - \mathrm{NRE}_{\mathrm{aut}})) \qquad (3)\end{aligned}$$

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:

$$\mathrm{N\ returned\ to\ soil} = (\mathrm{annual\ leaf\ litter}^{*}\mathrm{N}_{\mathrm{sen}}) \qquad (4)$$

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.

Statistical analysis

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).

Results

We did not find significant differences between exotic and native trees as a group for any of the measured variables (Figs. 1, 2 and 3, 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 ($F_{5,\,95}=21.11$, $p=0.001$). 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).

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. 1), 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. 1). *R. pseudoacacia* also lost its leaves the earliest, followed by *U. minor* (Fig. 1). The longest and shortest LLS in 2008 were found in *F. angustifolia and R. pseudoacacia* respectively (Fig. 1). 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. 1). All species produced their leaves earlier in 2009, probably because of the earlier rise of temperatures (mean March temperature=6.7 and 10.9 °C in 2008 and 2009, respectively) and all species, with the exception of *R. pseudoacacia*, also lost their leaves earlier in 2009 (Fig. 1). 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. 1).

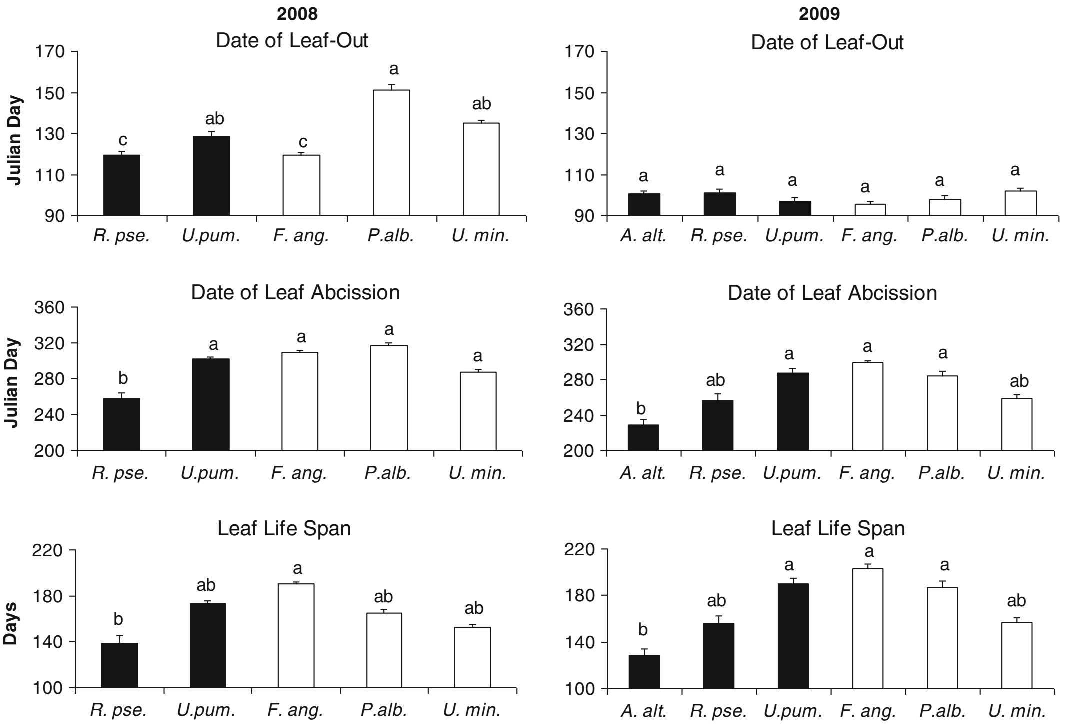


Fig. 1 Average Julian date (number of days since January 1st) of leaf–out and leaf abscission and average leaf life span ± SE per species in 2008 (*left*) and 2009 (*right*). *Solid* and *open bars* represent exotic and native species, respectively. Different letters mean significant differences between 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. 2a). 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. 2a). In 2009 we found the same trends (Fig. 2b) 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 1, Fig. 2c).

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. 3). *R. pseudoacacia* showed two peaks in 2008 (July and November) and only one in 2009 (November) (Fig. 3).

We observed suggestive patterns among species in nitrogen resorption (NRE) (Table 1). 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 1). In *P. alba* and *U. minor* the NRE in summer (69 and 65 % respectively) and autumn (65 and 67 % respectively) were similar (Table 1). However, in *R. pseudoacacia* the NRE in summer was higher than in autumn (56 % and 37 % respectively) (Table 1).

Finally, there was a strong, significant variation among species in the mean residence time (MRT, $F_{5,48}=20.11$, $p=0.001$) (Table 1). 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 1).

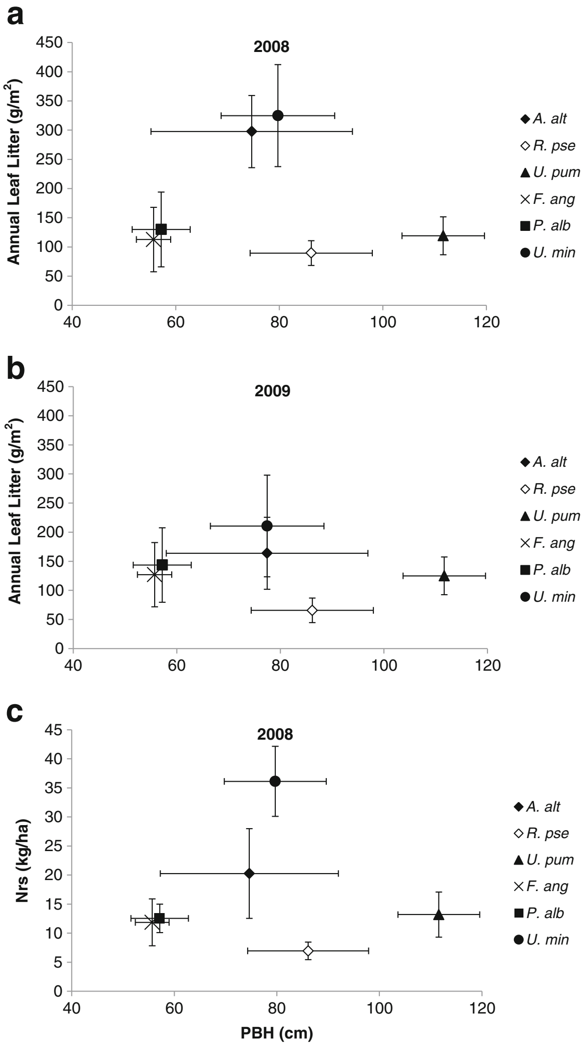


Fig. 2 **a** and **b.** Relationship between the average annual leaf litter (g/m^2) collected in the litter traps in 2008 (**a**) and 2009 (**b**) and the average perimeter at breast height (PBH, cm)±SE in each species. **c.** Relationship between the amount of nitrogen returned to soil (Nrs, kg/ha)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

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.

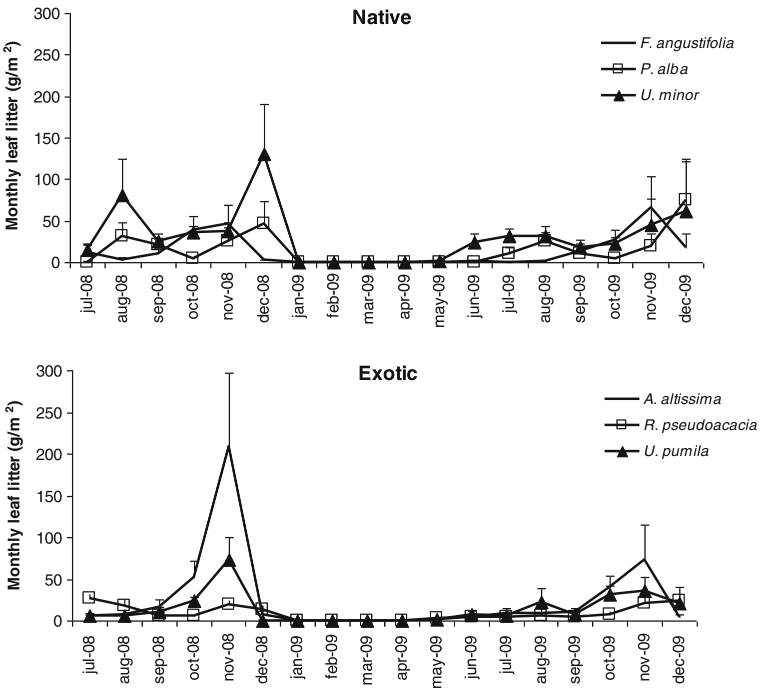
The three native species showed a similar nitrogen use strategy that can be positioned in the middle of a conservative-opportunistic gradient, on the basis of the studied traits. They all showed similar, intermediate specific leaf masses, leaf lifespans, nitrogen resorptions and mean residence times. 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.

U. 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.

A. 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-

Fig. 3 Monthly amount of leaf litter (g/m^2) collected in litter traps of native (above) and exotic species (below) from July 2008 to December 2009



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; 1991; Rice et al. 2004; Malcolm 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 nonexclusive 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.

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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