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Lack of superiority of invasive over co-occurring native riparian tree seedling species

N. González-Muñoz · P. Castro-Díez ·
O. Godoy

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Abstract The invasive tree species *Acer negundo*, *Ailanthus altissima*, *Elaeagnus angustifolia* and *Robinia pseudoacacia* are nowadays spreading in inner Spain riparian forests, where they co-occur with the natives *Fraxinus angustifolia*, *Populus alba* and *Ulmus minor*. In these forests, the natural light and soil moisture conditions are being altered by different human activities, as river channelization and regulation. These new environmental conditions may favor invasive species to the detriment of natives. In order to predict potential shifts of species composition in inner Spain riparian forests, we experimentally compared seedling and sapling performance across the four invasive and the three native mentioned species. Seeds 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 plant biomass at the end of the first and second growing seasons, relative growth rates, biomass allocation to roots (RWR), stems (SWR) and leaves (LWR), time to emergence (T_{emerg}) and net assimilation rate per unit of leaf mass (NAR_m) between origins and across species. Biomass accumulation greatly varied across species. However, invaders did not grow on average more than natives. Under high resource conditions, all species tended to grow more and similarly. Only the native *U. minor* and the invader *A. negundo* were not hampered by low moisture and/or low light availabilities. The absence of superiority of invaders over natives suggests that the former will not displace the latter in inner Spain riparian forests. However, human activities promoting shade and drought stress in floodplains may benefit the invasive *A. negundo* in the long term, as the growth of its seedlings is less declined by these conditions than the growth of the rest of the studied species. Thus, management effort should be focused in monitoring and preventing this species spread.

Keywords Invasive species · Biomass · Allocation · Relative growth rate · Seedling niche

Introduction

Invasive species may outcompete natives either due to a higher relative growth rate (Pattison et al. 1998; van

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N. González-Muñoz (✉) · P. Castro-Díez
Departamento de Ecología, Universidad de Alcalá,
Madrid, Spain
e-mail: noelia.gonzalezm@gmail.com

P. Castro-Díez
e-mail: mpilar.castro@uah.es

O. Godoy
Department of Ecology, Evolution and Marine Biology,
University of California, Santa Barbara, CA, USA
e-mail: godoy@msi.ucsb.edu

Kleunen et al. 2010; Lamarque et al. 2011), higher stress tolerance (Glenn and Nagler 2005; Sher and Marshall 2003), 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 invaders over natives or vice versa would depend on the particular environmental conditions where both groups of species coexist (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, 2009). In this habitat, irradiance and/or soil moisture are the main factors limiting plant 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 the gaps 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 erosion of the river bottom, and therefore increases the depth of the water table, raising the chances for the establishment of water-stress tolerant plants (Glenn and Nagler 2005; Sher and Marshall 2003). 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, human disturbance eliminates 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 of whether invasive tree species will be favored by the new environmental conditions over the existing natives.

The performance of tree seedlings 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 low light or soil moisture availabilities (Niinemets and Valladares 2006). If exotic seedlings are able to reach a bigger size at the same time as 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; 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. Besides, small seed sizes have been associated to both high relative growth rates at early stages and long distance dispersion (Marañón and Grubb 1993; Swanborough and Westoby 1996; Reich et al. 1998; Grotkopp et al. 2002), whereas large seed sizes promote more competitive seedlings, with higher survival rates (Howe and Richter 1982; Howe 1990; Moles and Westoby 2004; Quero et al. 2007). In plant invasions, a small seed size has been previously related to invasion success in some fast-grower species, such as pines (Rejmánek and Richardson 1996; Hamilton et al. 2005), but not in others, such as acacias (Castro-Díez et al. 2011). Indeed, the final advantage of having a certain seed size and its consequences on seedling performance will depend on the environmental conditions in which both the seed emergence and the seedling recruitment occurs (Schupp 1995, 1988). Finally, an early emergence may also be a helpful trait as it 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).

Many exotic species occur in the riparian forest of in inner Spain. Among them, *Acer negundo* L. (Sapindaceae), *Ailanthus altissima* (Mill.) Swingle (Simaroubaceae), *Elaeagnus angustifolia* L. (Eleagnaceae) and *Robinia pseudoacacia* L. (Fabaceae) are ranked as "invasive" in the *Atlas of Exotic Invasive Plants in Spain* (Sanz Elorza et al. 2004) and in the *Inventory of Alien Invasive Species in Europe* (DAISIE). These species might be favored by the mentioned environmental changes promoted by human actions to the detriment of the native vegetation, mainly dominated by the tree species *Fraxinus angustifolia* Vahl. (Oleaceae), *Populus alba* L. (Salicaceae) and *Ulmus minor* Mill. (Ulmaceae). However, little information about the environmental preferences of all these species is available so far. To fill in this gap, we assessed native and invasive plant growth under a factorial experiment with four irradiance and two soil moisture treatments, mimicking the wide range of natural and human-mediated environmental conditions existing in Mediterranean riparian forests. We hypothesized that (1) seedlings/saplings of the invasive species would accumulate on average more biomass than those of natives, which in turn would give to the invaders an advantage over co-occurring natives (van Kleunen et al. 2010; Lamarque et al. 2011); (2) both invasive and native species will reach higher biomass under resource-abundant treatments but invaders will perform better than natives, according to the opportunistic strategy attributed to most invasive plant species (Pyšek et al. 1995; Rejmánek and Richardson 1996; Hamilton et al. 2005).

Materials and methods

Study species

We studied native and invasive tree species co-occurring in riparian forests of inner Spain. In these forests, the native vegetation is structured along a double gradient of soil moisture and flooding frequency, stretching from the river edge to outwards. According to the water requirements and flood tolerance of the species, the inner band of woody vegetation (closer to the river) is dominated by several shrub species of *Salix*, followed by the trees *Salix alba* L. and *Populus nigra* L. The middle part of the gradient is dominated by *P. alba* while the outer part is dominated by *F. angustifolia* and *U. minor* (Blanco Castro et al. 2005). This typical structure of central Spain riparian forests has been severely altered by river regulation and channelization, which particularly threaten the inner band. The group of invaders here studied, *A. negundo*, *A. altissima,* *E. angustifolia* and *R. pseudoacacia,* are spreading along the middle and external bands of the riparian vegetation. These species were introduced between eighteenth and early twentieth centuries in Spain with ornamental purposes (Sanz Elorza et al. 2004). The presence of *A. negundo* and *E. angustifolia* is normally associated to river courses, whereas *R. pseudoacacia* and *A. altissima* can be also found in disturbed sites, such as road sides or crop borders (Sanz Elorza et al. 2004). Nowadays, these tree species are catalogued as invasive by different authors in Spain and Europe (Sanz Elorza et al. 2004; DAISIE), and their demographic trends are defined as "expansive" in Spain (Sanz Elorza et al. 2004). Moreover, *A. altissima* and *R. pseudoacacia* are listed among the 100 worst invasive species in Europe (DAISIE). The invasive group was compared with the natives *P. alba*, *F. angustifolia* and *U. minor* because they are the dominant species in the invaded areas (Sanz Elorza et al. 2004; Lara et al. 1996).

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, b). Light treatments (except L100) were obtained with green nets of different thickness fixed to metal frames on the top and the four sides.

These light treatments were crossed with two soil moisture levels, corresponding to 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 aimed to induce changes in species success without causing massive mortality, based on our 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 from May to October of 2008 and 2009, while in the rest of the experimental period plants just received rainwater. Five trays or 15 pots 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. Kurskall–Wallis tests revealed significant differences of soil moisture before ($H = 112.65$, $p < 0.001$) and after watering ($H = 206.48$, $p < 0.001$) between the two treatments.

Local air temperature, % of air humidity and available photosynthetic photon flux density 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 did not differ either in mean and minimum temperature or relative air humidity ($p > 0.05$). However, the shaded treatments showed a lower maximum temperature, due to the effect of hot alleviation produced by shade ($F_{3,40} = 5.99$; $p = 0.002$) (Appendix 1 of supplementary material). On January 2009, during all species dormant period, there was a strong snowfall that equally affected all the light treatments. The potential effects of this snowfall are considered in the discussion.

Sowing procedure

The seed bank of the Spanish Ministry of Environment supplied seeds of the targeted species (MAGRAMA). 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 h in the oven at 60 °C.

On April 2008, we sowed seeds of all species under the eight treatments resulting from crossing the light and soil moisture levels. *A. altissima*, *E. angustifolia*, *F. angustifolia* and *P. alba* were sown in single trays (38 length × 28 width × 7 depth cm, 40 seeds per tray), as they had small seeds and/or showed low percentages of emergence in the previous germination essays. *U. minor*, *A. negundo* and *R. pseudoacacia* were sown in multipot trays (24 pots of 330 ml per tray, one seed per pot), as they had large seeds and/or high percentages of emergence in the germination essays. 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.

We calculated the average of days required by a seedling to emerge in a tray (time to emerge or T_{emerg}) 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, 15–20 plants per species and treatment were transplanted to individual 1.5 L pots. The number of transplanted plants depended on the amount of individuals available in each species and treatment, which differed among species and treatments due to differences in emergence and survival (see González-Muñoz et al. 2011). 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.

Data collection

Individuals 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). We collected an average of 4 (3–5) and 7 (4–9) individuals per species and treatment in the two first and in the third harvest, respectively. In July 2009, we did not collect plants of *U. minor* under L35 and L100 and of *A. altissima* and *R. pseudoacacia* under L35 due to the low number of available plants.

Later, plants were separated into roots, stems and leaves and oven-dried at 60 °C for 48 h. Relative root, stem and leaf weight ratios (RWR, SWR and LWR respectively) were estimated in July 2009 harvest, when the seedlings presented full foliage.

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

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

This RGR was used to estimate the net assimilation ratio per unit of leaf mass ($\mathrm{NAR_m}$) (Lambers et al. 2008) as:

$$\mathrm{NAR_m} = \mathrm{RGR}/\mathrm{LWR_{Jul2009}}$$

Statistical analyses

We conducted four-way nested ANOVAs to test the effect of origin (native or invasive), species (nested in origin), and treatment (light and soil moisture) on the biomass reached in November 2008 and 2009 and on the RWR, SWR and LWR of July 2009. *Post hoc* Bonferroni tests were conducted to assess differences between species.

Two-way nested ANOVAs were performed to test differences in average RGR, $\mathrm{NAR_m}$ and $\mathrm{T_{emerg}}$ between origins and among species (nested in origin). For these variables, we only had the average value for each species and treatment (see above), so we could not assess the effects of treatment. *Post hoc* Bonferroni tests were also used to assess differences between species.

Finally, in each species, we tested the effect of light and soil moisture on the sapling mass of November 2009 and on the biomass allocation traits by means of two-way ANOVAs. Again, post hoc Bonferroni tests were used to check differences among light treatments. Prior to any analysis, data were checked for homoscedasticity (Bartlett test) and normality assumptions (Shapiro–Wilk test) in any case.

We also conducted Pearson correlations to test the effect of seed size on the biomass reached in November 2008 and 2009, biomass allocation traits, RGR, $\mathrm{T_{emerg}}$ and $\mathrm{NAR_m}$.

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

Results

Differences in biomass between origins

In November 2008, invasive seedlings were slightly larger than native seedlings, due to the high biomass of *A. negundo* and *E. angustifolia*, but this difference was

Table 1 Effect of origin (native or invasive, O), species (nested in origin, Sps(O)), light (L), soil moisture (M) and their interactions on the biomass reached at the end of the first (Nov 2008, N = 210) and second growing seasons (Nov 2009, N = 357) and on the root, stem and leaf weight ratios (RWR, SWR and LWR respectively) shown in July 2009 (N = 207), according to four-way ANOVAs. F, degrees of freedom (*df*) and significances (*p*) are shown

	Biomass Nov 2008			Biomass Nov 2009			RWR		SWR		LWR	
	df	F	*p*	F	*p*	*df*	F	*p*	F	*p*	F	*p*
O	1	1.206	0.274	6.152	0.014	1	219.507	0.001	35.405	0.001	68.263	0.001
Sps(O)	5	50.731	0.001	28.270	0.001	5	71.098	0.001	65.173	0.001	41.906	0.001
L	3	28.690	0.001	349.200	0.001	3	36.935	0.001	16.074	0.001	21.043	0.001
M	1	53.463	0.001	18.639	0.001	1	0.071	0.789	1.335	0.250	0.339	0.561
L*M	3	2.079	0.105	9.320	0.001	3	4.014	0.009	3.206	0.025	6.855	0.001
O*L	3	9.451	0.001	2.393	0.068	3	6.638	0.001	3.341	0.021	9.949	0.001
O*M	1	0.020	0.888	1.058	0.304	1	13.439	0.001	0.174	0.677	6.007	0.015
L*M*O	3	7.804	0.001	7.209	0.001	3	0.670	0.572	0.817	0.486	2.523	0.059
L*Sps(O)	15	7.773	0.001	17.457	0.001	11	4.694	0.001	7.371	0.001	5.178	0.001
M*Sps(O)	5	7.290	0.001	5.386	0.001	5	1.491	0.196	3.992	0.002	3.740	0.003
L*M*Sps(O)	14	3.473	0.001	1.878	0.028	11	1.580	0.109	3.881	0.001	5.298	0.001

not significant (Table 1; Fig. 1a). By contrast, in November 2009, native saplings were significantly larger than invaders, due to the low biomass of *A. altissima* (Table 1; Fig. 1b). There was a lower effect of the light and soil moisture treatments on the biomass averaged by origins than on the biomass reached by the species (see the significant interactions in Table 1; Figs. 2a–d, 3).

Differences in biomass and related traits among species

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. 1a). In November 2009, *R. pseudoacacia* and *P. alba* caught up the group of the larger species and only *A. altissima* remained smaller (Fig. 1b). *R. pseudoacacia* and *P. alba* showed the highest RGR and, together with *A. altissima*, the highest LWR (Table 2). *F. angustifolia* and *E. angustifolia* required longer time to emerge and exhibited the highest investment in roots and stems respectively (Table 2). There were no significant differences among species in NAR_m (Table 2). Seed size did not significantly account for the differences found in the final biomass, biomass allocation traits, RGR, NAR_m and T_{emerg} (Appendix 3 of supplementary material).

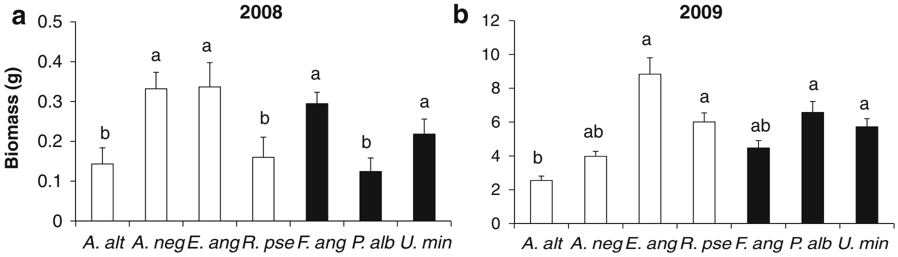

Fig. 1 Biomass (mean + SE, in g) without leaves reached by each species at the end of the first (2008) and second (2009) growing seasons (all treatments averaged). *Different letters* among columns mean significant differences among species according to post hoc Bonferroni tests. Invasive species (*white bars*): *A. altissima* (*A. alt*, $N_{2008} = 33$; $N_{2009} = 47$); *A. negundo* (*A. neg*, $N_{2008} = 32$; $N_{2009} = 57$), *E. angustifolia* (*E. ang*, $N_{2008} = 30$; $N_{2009} = 54$) and *R. pseudoacacia* (*R. pse*, $N_{2008} = 30$; $N_{2009} = 51$). Native species (*black bars*): *F. angustifolia* (*F. ang*, $N_{2008} = 30$; $N_{2009} = 57$), *P. alba* (*P. alb*, $N_{2008} = 28$; $N_{2009} = 48$) and *U. minor* (*U. minor*, $N_{2008} = 27$; $N_{2009} = 43$)

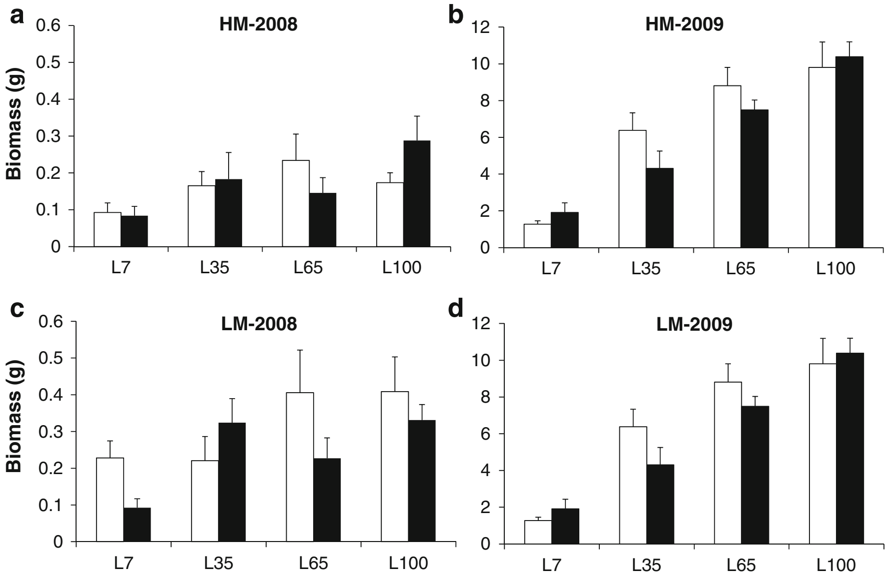

Fig. 2 Biomass (mean ± SE, in g) reached by the invasive (*white*) and native (*black*) species in every combination of soil moisture (*LM* low moisture, *HM* high moisture) and light treatment (L7—7 %, L35—35 %, L65—65 % and L100—100 % respect to full irradiance) at the end of the first and second growing seasons (2008 and 2009, respectively)

Effects of light and soil moisture on the species biomass

After two growing seasons, all species tended to grow more with an increase in light availability, this response being steeper in *P. alba*, *F. angustifolia*, *R. pseudoacacia* and *E. angustifolia* (Fig. 3). Soil moisture positively affected the biomass of all species but *A. negundo* and *U. minor* under most light treatments (Fig. 3).

Effects of light and soil moisture on the species biomass allocation

Biomass allocation patterns were affected by light and soil moisture treatments (Table 1; Fig. 4). Among the

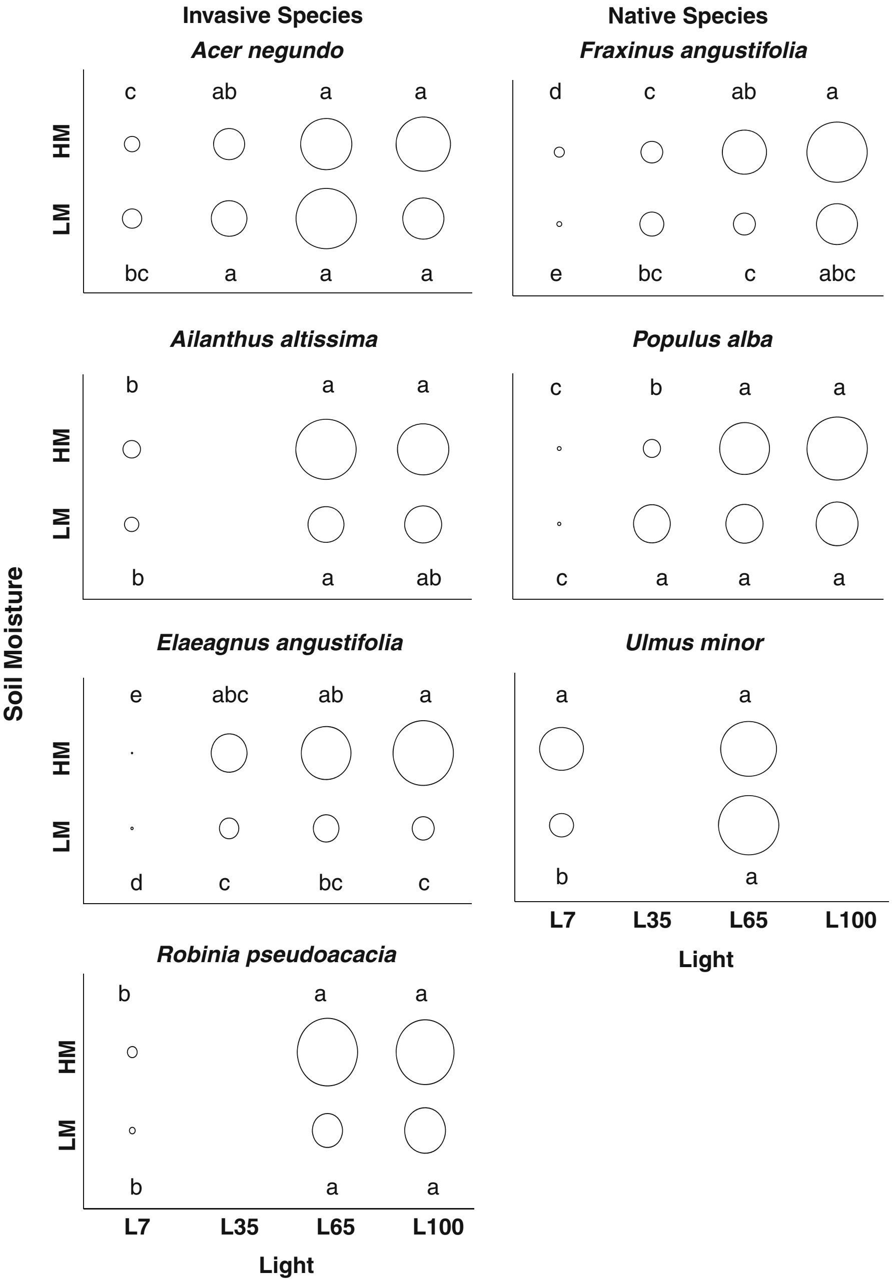

Fig. 3 Biomass responses to the light and soil moisture treatments showed by each species after two growing seasons. The bubble size is proportional to the mean seedling biomass without leaves achieved in November 2009. *Different letters* mean significant differences between treatments, according to post hoc Bonferroni tests. L7, L35, L65 and L100 correspond to 7, 35, 65 and 100 % respect to full irradiance, respectively. *LM* and *HM* correspond to low moisture and high moisture respectively. Missing values are due to insufficient number of individuals in some species and treatments. See Appendix 2 of supplementary material for further information about the statistical results

invaders, *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, Appendix 2 of supplementary material). *E. angustifolia* invested more biomass in leaves under the extreme light treatments (L100-L7) but increased RWR under the intermediates (L35–L65) (Fig. 4, Appendix 2 of supplementary material). *A. altissima* and *R. pseudoacacia* increased SWR with decreasing light (Fig. 4, Appendix 2 of supplementary material). Moreover, *R. pseudoacacia* increased RWR with decreasing soil moisture (Fig. 4, Appendix 2 of supplementary material). The three natives increased aboveground biomass under L7 (LWR or SWR, Fig. 4, Appendix 2 of supplementary material). *F. angustifolia* decreased LWR and *P. alba* decreased LWR and increased RWR with increasing soil moisture (Fig. 4, Appendix 2 of supplementary material).

Discussion

Differences in biomass between origins

Invasive species as a group attained the same biomass as natives in the first growing season, or even less in the second one, in contrast to our initial hypothesis (Fig. 1a, b). This suggests that other species traits, different to those evaluated in this work, must explain their establishment success in inner Spain riparian forests. A high interspecific competitive ability together with a high tolerance to intraspecific competition have been suggested to promote both dense stands of invasive species and the competitive exclusion of native species (Baker 1965; Roy 1990). This was corroborated by the extensive meta-analysis of Vilà and Weiner (2004), which showed that the competitive effect of invasive species on natives is usually stronger than vice versa. Other features have been suggested to confer high competitive ability to invasive plants, such as high fecundity, high propagule pressure, the ability of profusely resprout, the production of allelopathic compounds, and a reduced herbivory damage (Rejmánek and Richardson 1996; Callaway and Aschehoug 2000; Keane and Crawley 2002; Richardson and Pyšek 2006). For instance, adults of *A. altissima* produce allelopathic compounds that may inhibit the seed germination and seedling growth of other species (Heisey 1990, 1996; Heisey and Heisey 2003; de Feo et al. 2005). Besides, all our studied invasive species are able to profusely resprout and to produce a high amount of seeds (Weber 2003; Katz and Shafroth 2003; Sanz Elorza et al. 2004; Kowarik and Säumel 2007; Masaka and Yamada 2009). Finally, the studied invaders may have benefited from the spatial or temporal empty niches that floods generates in river sides, where they would not need a superior performance over natives to succeed (Godoy et al. 2009).

Table 2 Mean values (±SE) of the relative growth rate calculated from the end of the first to the end of the second growing seasons (RGR), root, stem and leaf weight ratios in middle second growing season (RWR, SWR and LWR respectively), net assimilation ratio per unit of leaf mass (NAR$_m$), time needed to emerge (T$_{emerg}$) and seed mass in each origin (invasive or native) and species

	RGR (mg/day)	RWR	SWR	LWR	NAR$_m$ (mg/mg leaf)	T$_{emerg}$ (days)	Seed mass (mg)
Invasive	8.77 ± 0.59A	0.29 ± 0.01B	0.29 ± 0.01A	0.42 ± 0.01A	19.72 ± 1.25B	31.14 ± 3.37A	45.50 ± 24.99
Native	9.48 ± 0.61A	0.40 ± 0.01A	0.25 ± 0.01B	0.35 ± 0.01B	26.67 ± 1.76A	29.88 ± 4.67A	13.77 ± 11.20
Ailanthus altíssima (I)	8.55 ± 0.95ab	0.34 ± 0.02bc	0.16 ± 0.01d	0.49 ± 0.01a	16.78 ± 2.29a	39.35 ± 5.14b	14
A. negundo (I)	6.84 ± 0.67b	0.32 ± 0.01bcd	0.32 ± 0.01b	0.36 ± 0.01c	18.92 ± 1.80a	16.20 ± 0.31c	28
E. angustifolia (I)	8.17 ± 0.90ab	0.23 ± 0.01d	0.37 ± 0.01a	0.39 ± 0.01bc	21.37 ± 2.71a	52.54 ± 2.05a	120
R. pseudoacacia (I)	11.50 ± 1.48a	0.26 ± 0.01d	0.24 ± 0.02bc	0.49 ± 0.01a	21.52 ± 3.35a	14.33 ± 0.49c	20
F. angustifolia (N)	6.84 ± 0.56b	0.49 ± 0.01a	0.23 ± 0.01c	0.28 ± 0.01d	24.97 ± 2.75a	53.25 ± 4.10a	36
P. alba (N)	12.02 ± 1.05a	0.29 ± 0.01cd	0.28 ± 0.01bc	0.43 ± 0.01ab	28.43 ± 3.31a	13.41 ± 0.57c	0.3
U. minor (N)	9.57 ± 0.54ab	0.38 ± 0.02b	0.26 ± 0.02bc	0.36 ± 0.01bc	26.55 ± 2.67a	16.06 ± 0.10c	5

The invasive (I) or native (N) origin is shown beside the specific name. Different letters mean significant differences between origins (capital letters) or species (lower case letters), according to post hoc Bonferroni tests

Differences in biomass and related traits among species

We found strong differences among species in all studied variables. Thus, the invader *E. angustifolia* reached the highest biomass after two growing seasons (although this difference was not significant) whereas *A. altissima* attained the lowest (Fig. 1b, Table 2). This result disagrees with previous studies that describe *A. altissima* as fast grower (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 low growth, as *A. altissima* seedlings have been described as not frost resistant (Sanz Elorza et al. 2004; Kowarik and Säumel 2007). The large biomass reached by *E. angustifolia* may be consequence of its large seed size, nearly four times larger than that of the next species in the seed mass ranking (see Table 2).

The invader *R. pseudoacacia* and the native *P. alba* attained the highest RGR among studied species whereas the invader *A. negundo* and the native *F. angustifolia* attained the lowest (Table 2). The high investment in leaves of the former two species may explain their high RGR, as this trait contributes both to a better light interception (Pearcy et al. 2004)

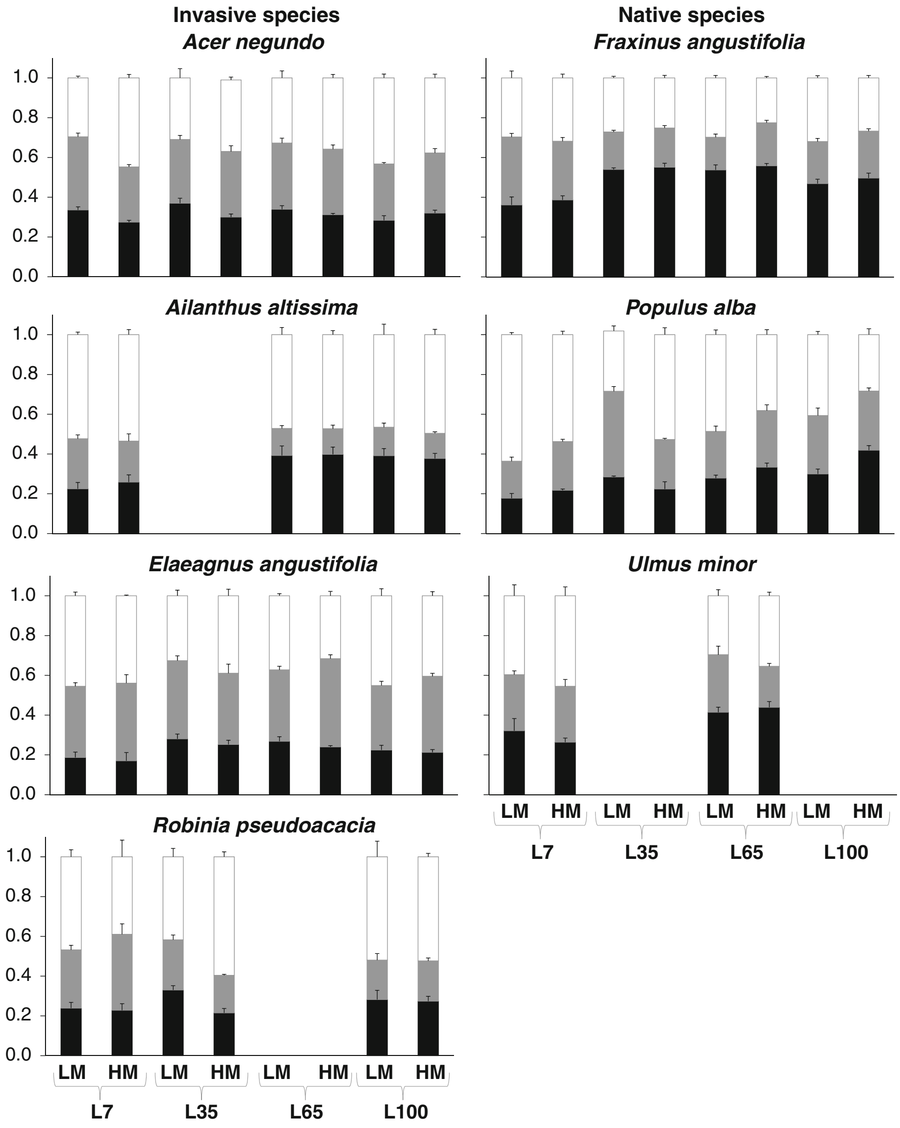

Fig. 4 Root weight ratio (RWR, *black*), stem weight ratio (SRW, *grey*) and leave weight ratio (LWR, *white*) values (mean + SE) showed by each species under each combination of soil moisture (*LM* low moisture, *HM* high moisture) and light (L7—7 %, L35—35 %, L65—65 % and L100—100 % respect to full irradiance) in July 2009. Missing values are due to insufficient number of individuals in some species and treatments

and to high CO_2 uptake at the whole plant level (Chmura et al. 2007) (Fig. 4, Table 2). The low RGR of *F. angustifolia* may be attributed to its large investment in roots (the highest among studied species), what may adversely affect carbon gains, through decreasing leaf mass allocation and increasing root respiratory loss (Weiner 2004); (Fig. 4, Table 2). Finally, the low RGR of *A. negundo* may be due to its low net assimilation rate per unit of leaf mass (Table 2).

Recent frameworks aiming to predict invasiveness have considered the seed size as an important trait (Moles et al. 2008). However, according to our results, the differences in biomass and related traits found here were not explained by the species seed size. This can be due to the existing similarity between the studied species life strategies (all species were deciduous trees), as the role of seed size can be more relevant between contrasted habitats and between life forms with different productivities (Moles et al. 2008).

The high heterogeneity of growth patterns found in both natives and invaders has also been described in other studies and highlights the independence of the species strategies to their native or invasive origin (Bellingham et al. 2004; Feng et al. 2007; Feng and Fu 2008; Gurevitch et al. 2008) and explains why we did not find differences of growth among invasive and native seedlings.

Effect of light and soil moisture on the biomass and biomass allocation of native and invasive species

All species achieved their highest biomass under high irradiance (L65 or L100) and, in most cases, high soil moisture, as we hypothesized. In low resource conditions, only the native *U. minor* and the invader *A. negundo* showed a relative good performance, in accordance to previous studies that described them as shade tolerant species (Fig. 3); (DeWine and Cooper 2007, 2008; González et al. 2010; González-Muñoz et al. 2011; Porté et al. 2011). Indeed, *U. minor* naturally occurs in the most external vegetation band of riparian forests, where water availability is lower and gap-opening by natural disturbances is less frequent (Blanco Castro et al. 2005).

Regarding biomass allocation patterns, most of the studied species responded to the light and soil moisture treatments following the optimal allocation theory (Weiner 2004). This theory suggests that the species tend to allocate more biomass to the tissues that may favour the capture of the most limiting resource. Indeed, all species except *A. negundo* increased aboveground biomass (LWR and/or SWR) with decreasing light and *A. negundo* and *R. pseudoacacia* increased their investment in roots with decreasing moisture (Fig. 4). Interestingly, the three natives and *A. altissima* not only increased aboveground biomass when light was low, but also increased RWR with increasing light, then favoring water and nutrients acquisition when light is not limiting.

Conclusions

The lack of superior performance of invasive seedlings/saplings over natives in terms of biomass gain suggests that other mechanisms, such as reproduction strategies or the production of allelopathic compounds may explain their invasion success. Under low resource conditions, as it happens in the floodplains of regulated rivers, either in gaps (high light/low moisture) or under dense canopies (low light/low moisture), only the establishment of the native *U. minor* and the invader *A. negundo* would not be hampered (Fig. 3). As *U. minor* seed recruitment is reduced by the Dutch elm disease in our study area (Brasier et al. 2004; Martín et al. 2006), *A. negundo* young plants would potentially dominate these scenarios. Therefore, special care should be paid to monitor the presence of *A. negundo* populations in the floodplains of regulated rivers. Due to the difficulties to restore river channelization, an early detection and eradication of emergent populations is probably the best option to avoid the spread of *A. negundo* throughout floodplains.

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References

Baker HG (1965) Characteristics and modes of origin of weeds. In: Baker HG, Stebbins GL (eds) The genetics of colonizing species. Academic Press, New York

Baraloto C, Goldberg DE, Bonal D (2005) Performance trade-offs among tree seedlings in contrasting microhabitats. Ecology 86(9):2461–2472

Baruch Z, Goldstein G (1999) Leaf construction cost, nutrient concentration, and net CO_2 assimilation of native and invasive species in Hawaii. Oecologia 121(2):183–192

Bellingham PJ, Duncan RP, Lee WG, Buxton RP (2004) Seedling growth rate and survival do not predict invasiveness in naturalized woody plants in New Zealand. Oikos 106:308–316

Blanco Castro E, Casado González MA, Costa Tenorio M, Escribano Bombín R, García Antón M, Génova Fuster M, Gómez Manzaneque MA, Gómez Manzaneque F, Moreno Saiz JC, Morla Juaristi C, Regato Pajares P, Sainz Ollero H (2005) Los bosques ibéricos: una interpretación geobotánica. Editorial Planeta, Barcelona

Blumenthal DM, Hufbauer RA (2007) Increased plant size in exotic populations: a common garden test with 14 invasive species. Ecology 88(11):2758–2765

Brasier CM, Buck K, Paoletti M, Crawford L, Kirk S (2004) Molecular analysis of evolutionary changes in populations of *Ophiostoma novo-ulmi*. Inv Agr: Sist y Rec For 13:93–103

Callaway RM, Aschehoug ET (2000) Invasive plants versus their new and old neighbours: a mechanism for exotic invasion. Science 290:521–523

Castro J (2006) Short delay in timing of emergence determines establishment success in *Pinus sylvestris* across microhabitats. Ann Bot 98:1233–1240

Castro-Díez P, Navarro J, Pintado A, Sancho LG, Maestro M (2006) Interactive effects of shade and watering on the performance of seedlings of three Mediterranean *Quercus* species. Tree Physiol 26:389–400

Castro-Díez P, Navarro J, Maestro M (2007) Effects of moderate shade and irrigation with eutrophicated water on the nitrogen economy of Mediterranean oak seedlings. Flora 203(3):243–253

Castro-Díez P, Godoy O, Saldaña A, Richardson DM (2011) Predicting invasiveness of Australian acacias on the basis of their native climatic affinities, life history traits and human use. Divers Distrib 17:934–945

Chmura DJ, Rahman MS, Tjoelker MG (2007) Crown structure and biomass allocation patterns modulate aboveground productivity in young loblolly pine and slash pine. For Ecol Manag 243(2–3):219–230

Chytrý M, Maskell LC, Pino J, Pyšek P, Vilà M, Font X, Smart SM (2008) Habitat invasions by alien plants: a quantitative comparison among Mediterranean, sub continental and oceanic regions of Europe. J Appl Ecol 45:448–458

Chytrý M, Pyšek P, Wild J, Pino J, Maskell LC, Vilà M (2009) European map of alien plant invasions based on the quantitative assessment across habitats. J Appl Ecol 15(1):98–107

Closset-Kopp D, Saguez R, Decocq G (2011) Differential growth patterns and fitness may explain contrasted performances of the invasive *Prunus serotina* in its exotic range. Biol Invasions 13:1341–1355

Daehler CC (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. Annu Rev Ecol Evol Syst 34: 183–211

Davidson AM, Jennions M, Nicotra AB (2011) Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptative? A meta-analysis. Ecol Lett 14(4):419–431

de Feo V, de Martino L, Santoro A, Leone A, Pizza C, Franceschelli S, Pascale M (2005) Antiproliferative effects of tree-of-heaven (*Ailanthus altissima* Swingle). Phytother Res 19:226–230

Deka RN, Wairiu M, Mtakwa PW, Mullins CE, Veenendaal EM, Townend J (1995) Use and accuracy of the filter paper technique for measurement of soil matric potential. Eur J Soil Sci 46:233–238

DeWine JM, Cooper DJ (2007) Effects of river regulation on riparian box elder (*Acer negundo*) forest in canyons of the upper Colorado River basin, USA. Wetlands 27:278–289

DeWine JM, Cooper DJ (2008) Canopy shade and the successional replacement of tamarisk by native box elder. J Appl Ecol 45:505–514

Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6(6):503–523

Feng YL, Fu GL (2008) Nitrogen allocation, partitioning and use efficiency in three invasive plant species in comparison with their native congeners. Biol Invasions 10:891–902

Feng Y, Wang J, Sang W (2007) Biomass allocation, morphology and photosynthesis of invasive and non invasive exotic species at four irradiance levels. Acta Oecol 31:40–47

Funk JL, Vitousek PM (2007) Resource-use efficiency and plant invasion in low-resource systems. Nature 446:1079–1081

Glenn EW, Nagler PL (2005) Comparative ecophysiology of *Tamarix ramosissima* and native trees in western US riparian zones. J Arid Environ 61:419–446

Godoy O, Castro-Díez P, Valladares F, Costa-Tenorio M (2009) Different flowering phenology of alien invasive species in Spain: evidence for the use of an empty temporal niche? Plant Biol 11(6):803–811

González E, González-Sanchís M, Cabezas A, Comín FA, Muller E (2010) Recent changes in the riparian forest of a large regulated Mediterranean river: implications for management. Environ Manage 45:669–681

González-Muñoz N, Castro-Díez P, Fierro-Brunnenmeister N (2011) Establishment success of coexisting native and exotic trees under an experimental gradient of irradiance and soil moisture. Environ Manage 48:764–773

Grotkopp E, Rejmánek M, Rost TL (2002) Towards a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (*Pinus*) species. Am Nat 159(4):396–419

Gurevitch J, Howard TG, Ashton IW, Leger EA, Howe KM, Woo E, Lerdau M (2008) Effects of experimental manipulation of light and nutrients on establishment of seedlings of native and invasive woody species in Long Island, NY forests. Biol Invasions 10:821–831

Hamilton MA, Murray BR, Cadotte MW, Hose GC, Baker AC, Harris CJ, Licari D (2005) Life-history correlates of plant invasiveness at regional and continental scales. Ecol Lett 8:1066–1074

Heisey RM (1990) Evidence for allelopathy by tree of heaven (*Ailanthus altissima*). J Chem Ecol 16(6):2039–2055

Heisey RM (1996) Identification of an allelopathic compound from *Ailanthus altissima* (Simaroubaceae) and characterization of its herbicidal activity. Am J Bot 83(2):192–200

Heisey RM, Heisey TK (2003) Herbicidal effects under field conditions of *Ailanthus altissima* bark extract which contains ailanthone. Plant Soil 256:85–99

Howe HF (1990) Survival and growth of juvenile *Virola surinamensis* in Panama: effects of herbivory and canopy closure. J Trop Ecol 6:259–280

Howe HF, Richter W (1982) Effects of seed size on seedling size in *Virola surinamensis*: a within and between tree analysis. Oecologia 53:347–351

Jones RH, Sharitz RR (1989) Potential advantages and disadvantages of germinating early for trees in floodplain forests. Oecologia 81:443–449

Katz GL, Shafroth PB (2003) Biology, ecology and management of *Elaeagnus angustifolia* L. (Russian olive) in western North America. Wetlands 23(4):763–777

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170

Knapp LB, Canham CD (2000) Invasion of an old growth forest in New York by *Ailanthus altissima*: sapling growth and recruitment in canopy gaps. J Torrey Bot Soc 127:307–315

Kobe RK, Coates KD (1997) Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species in northwestern British Columbia. Can J For Res 27(2):227–236

Kowarik I, Säumel I (2007) Biological flora of central Europe: *Ailanthus altissima* (Mill) Swingle. Perspect Plant Ecol Evol Syst 8:207–237

Lamarque JL, Delzon S, Lortie CJ (2011) Tree invasions: a comparative test of the dominant hypotheses and functional traits. Biol Invasions 13:1969–1989

Lambers H, Chapin FS, Pons TL (2008) Plant physiological ecology. Springer, New York

Lara F, Garillete R, Ramírez P (1996) Estudio de la vegetación de los ríos carpetanos de la cuenca del Jarama. Centro de Estudios y Experimentación de Obras Públicas. Ministerio de Fomento, Madrid

Leishman MR, Haslehurst T, Ares A (2007) Leaf trait relationships of native and invasive plants: community and global-scale comparisons. New Phytol 176(3):635–643

Marañón T, Grubb PJ (1993) Physiological-basis and ecological significance of the seed size and relative growth rate relationship in Mediterranean annuals. Funct Ecol 7(5):591–599

Martín JA, Solla A, Burón M, López-Almansa JC, Gil L (2006) Caracterización histórica, ecológica, taxonómica y fitosanitaria de una olmeda en Rivas-Vaciamadrid (Madrid). Inv Agr: Sist y Rec For 15(2):208–217

Masaka K, Yamada K (2009) Variation in germination character of *Robinia pseudoacacia* L. (Leguminosae) seeds at individual tree level. J For Res 14:167–177

Moles AT, Westoby M (2004) Seedling survival and seed size: a synthesis of the literature. J Ecol 92:372–383

Moles AT, Gruber MAM, Bonser SP (2008) A new framework for predicting invasive plant species. J Ecol 96:13–17

Niinemets Ü, Valladares F (2006) Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. Ecol Monogr 76:521–547

Pacala SW, Canham CD, Saponara J, Silander JA, Kobe RK, Ribbens E (1996) Forest models defined by field measurements: estimation, error analysis and dynamics. Ecol Monogr 66(1):1–43

Pattison RR, Goldstein G, Ares A (1998) Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. Oecologia 117(4):449–459

Pearcy RW, Valladares F, Wright SJ, de Paulis EL (2004) A functional analysis of the crown architecture of tropical forest *Psychotria* species: do species vary in light capture efficiency and consequently in carbon gain and growth? Oecologia 139:163–177

Peñuelas J, Sardans J, Llusià J, Owen SM, Carnicer J, Giambelluca TW, Rezendes E, Waite M, Niinemets U (2010) Faster returns on "leaf economics" and different biogeochemical niche in invasive compared with native plant species. Global Change Biol 16:2171–2185

Porté AJ, Lamarque LJ, Lortie CJ, Michalet R, Delzon S (2011) Invasive *Acer negundo* outperforms native species in non-limiting resource environments due to its higher phenotypic plasticity. BMC Ecol 11(28):1–12

Pyšek P, Prach D, Smilauer P (1995) Plant invasions: general aspects and special problems. SPB, Amsterdam

Quero JL, Villar R, Marañón T, Zamora R, Poorter L (2007) Seed-mass effects in four Mediterranean *Quercus* species (Fagaceae) growing in contrasting light environments. Am J Bot 94(11):1795–1803

Reich PB, Tjoelker MG, Walters MB, Vander Klein DW, Buschena C (1998) Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. Funct Ecol 12:327–338

Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? Ecology 77:1655–1661

Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecol Lett 9:981–993

Richardson DM, Pyšek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. Prog Phys Geogr 30:409–431

Roy J (1990) In search of the characteristics of plant invaders. In: Di Castri F, Hansen AJ, Debussche M (eds) Biological invasions in Europe and the Mediterranean basin. Kluwer, Dordrecht

Sanz Elorza M, Dana Sánchez ED, Sobrino Vespertinas E (2004) Atlas de plantas alóctonas invasoras en España. Ministerio de Medio Ambiente, Madrid

Schupp EW (1988) Seed and early seedling predation in the forest understory and in treefall gaps. Oikos 51:71–78

Schupp EW (1995) Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. Am J Bot 82:399–409

Sher AA, Marshall DL (2003) Seedling competition between native *Populus deltoides* (Salicaceae) and exotic *Tamarix ramosissima* (Tamaricaceae) across water regimes and substrate types. Am J Bot 90:413–422

Swanborough P, Westoby M (1996) Seedling relative growth rate and its components in relation to seed size: phylogenetically independent contrasts. Funct Ecol 10:176–184

Valladares F (2004a) Ecología del bosque mediterráneo en un mundo cambiante. Ministerio de Medio Ambiente, Organismo Autónomo de Parques Naturales, Madrid, Spain

Valladares F (2004b) Global change and radiation in Mediterranean forest ecosystems: a meeting point for ecology and management. In: Arianoutsou M, Papanastasis V (eds) Ecology, conservation and sustainable managements of Mediterranean type ecosystems of the world. Mill press, Rotterdam

van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. Ecol Lett 13:235–245

Verdú M, Traveset A (2005) Early emergence enhances plant fitness: a phylogenetically controlled meta-analysis. Ecology 86:1385–1394

Vilà M, Weiner J (2004) Are invasive plant species better competitors than native plant species? Evidence from pairwise experiments. Oikos 105:229–238

Weber E (2003) Invasive plant species of the world. A reference guide to environmental weeds. CABI, Zurich

Weiner J (2004) Allocation, plasticity and allometry in plants. Perspect Plant Ecol Evol Syst 6(4):207–215