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RESEARCH ARTICLE

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Contrasting secondary growth and water-use efficiency patterns in native and exotic trees co-occurring in inner Spain riparian forests

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Abstract

Aim of study: The invasive trees *Ailanthus altissima* and *Robinia pseudoacacia* are widely spreading in inner Spain riparian forests, where they co-occur with the natives *Fraxinus angustifolia* and *Ulmus minor*. In a climate change context, we aimed to identify some of the species traits that are leading these species to success (Basal Area Increment (BAI) and water-use efficiency ($_i$WUE)). We also aimed to describe the main environmental variables controlling studied species BAI.

Area of study: Riparian forests of central Spain.

Material and Methods: We measured tree-ring width and converted it to basal area increment (BAI); intrinsic water-use efficiency ($_i$WUE) was estimated from tree ring carbon isotopes ($\delta^{13}C$). We compared the BAI and $_i$WUE of the last 20 years between origins (native *vs* exotic) and among species. For each species, we evaluated $_i$WUE and BAI relationships. Linear mixed-effect models were performed to identify the main environmental variables (temperature, precipitation, river flow) affecting BAI.

Main result: Native trees showed higher mean BAI than invaders, mainly due to the rising growth rate of *U. minor*. Invaders showed higher mean $_i$WUE than natives. We did not find significant correlations between $_i$WUE and BAI in any case. Warm temperatures in autumn positively affected the BAI of the natives, but negatively that of the invaders.

Research highlights: The contrasting effect of autumn temperatures on native and invasive species BAI suggests that invaders will be more hampered by the rising temperatures predicted for this century. The higher $_i$WUE found for the invaders did not translate into increased radial growth, suggesting that drought stress may have prevented them of taking advantage of increased atmospheric CO_2 for a faster growth. These findings point out that neither climate change nor rising CO_2 seem to enhance the success of study invasive species over the natives in riparian forests of central Spain. Furthermore, the low BAI of *R. pseudoacacia*, and its climate-growth model suggest that climate change may especially hamper the success of this invader.

Key words: Invasive plants; Mediterranean ecosystems; *Ulmus minor; Fraxinus angustifolia; Ailanthus altissima*; *Robinia pseudoacacia*; basal area increment.

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Introduction

The increase in temperature along the last century has resulted in increased plant-carbon uptake and in an extended growing season for some plant species (Menzel & Fabian, 1999; Peñuelas & Filella, 2001; Peñuelas & Boada, 2003), as well as changes in species distributions (Parmesan & Yohe, 2003; Lenoir *et al*., 2008). More changes are expected, considering that climatic predictions for the 21st century show an increase up to 6 °C in mean land temperature (IPCC 2013). Under climatic change, the broad environmental tolerances of invasive species may be useful attributes for outcompeting the natives, as the relative dominance of native-invasive species depends on the environmental conditions in which the species co-occur (van Kleunen *et al.*, 2010; Lamarque *et al.*, 2011; Zerebecki & Sorte, 2011). However, the literature contains contrasting results with regard to the responses of the invasive species to climate change (Stachowicz *et al.*, 2002; Bradley *et al.*, 2010; Sorte *et al.*, 2013; González-Muñoz *et al.*, 2014). Identifying the climatic conditions that favour invasive species over natives is key to solve this debate and to predict changes in the native/invasive species outcomes in a climate change context.

Currently, atmospheric CO_2 has already reached 400 ppm (Mauna-Loa Observatory 2013). Rising atmospheric CO_2 availability may increase invasive species competitiveness over co-occurring natives, if invaders are better able to take advantage of the increased CO_2 availability (i.e. Sasek & Strain, 1991; Smith *et al.*, 2000; Ziska, 2003; Dukes *et al.*, 2011). High CO_2 availability may directly favour plant growth by increasing photosynthesis capacity (Morison, 1993; Picon *et al.*, 1996; Morgan *et al.*, 2004) but also indirectly, by increasing intrinsic water-use efficiency ($_i$WUE), i.e. the ratio of carbon fixed per unit of water lost in the process of carbon fixation (Overdieck & Forstreuter, 1994). If high CO_2 leads to increased carbon uptake (Bernacchi *et al.*, 2006) while transpiration rates remain constant or even decrease, then $_i$WUE increases (Farquhar *et al.*, 1980, 1982). Then, comparing the $_i$WUE among co-occurring native and invasive species can provide useful information about their differential responses to rising CO_2 and to water stressful conditions, a relevant issue especially in Mediterranean ecosystems.

In riparian forests of central Spain, the native dominant vegetation has been severely hampered due to human activities, as the river channelization and regulation and the establishment of crops in the vicinities. These forests, dominated by the natives *Fraxinus angustifolia* Vahl. (Oleaceae) and *Ulmus minor* Mill. (Ulmaceae), are also threatened by the establishment and spread of invasive plants, as it is the case of the tree species *Ailanthus altissima* Mill. (Simaroubaceae) and *Robinia pseudoacacia* L. (Fabaceae). Both species are recognized as "invasive" in the Atlas of Exotic Invasive Plants in Spain (Sanz-Elorza *et al.*, 2004) and have been listed among the 100 worst invasive species in Europe (Inventory of Alien Invasive Species in Europe, DAISIE). Previous studies have aimed to describe which species traits and environmental characteristics are favouring these invaders over the natives (i.e. González-Muñoz *et al.*, 2011 and 2014). However, most of these works were focused on juvenile stages and information about adult stages is lacked (but see Castro-Díez *et al.*, 2014).

In this work, we aimed to identify some of the species traits and environmental factors that are leading *A. altissima* and *R. pseudoacacia* to success. To do so, we measured and compared the radial growth and $_i$WUE among the dominant natives *F. angustifolia* and *U. minor* and the two invasive species. Radial growth was evaluated by measuring tree-ring width and converting it to Basal-Area Increment (BAI); $_i$WUE was estimated from the ratio of carbon isotopes in tree rings ($\delta^{13}C$). We also evaluated the relationship between $_i$WUE and BAI. Finally, we performed growth models to identify the environmental variables with a largest impact on the species BAI. Considering that 1) high growth rates have been previously related to invasive species success (van Kleunen *et al.*, 2010; Lamarque *et al.*, 2011); and 2) invasive plants are recognized as opportunistic, able to take advantage of available resources (as increased atmospheric CO_2 can be) (Pyšek *et al.*, 1995; Rejmánek & Richardson, 1996), we hypothesized that: i) the two invaders will have higher BAI than the natives; ii) the invaders will show higher $_i$WUE than the natives, as well as a positive relationship between $_i$WUE and BAI, related to a fertilization effect of rising atmospheric CO_2. We also expected differences in the environmental variables boosting/hampering the BAI of studied species, as they are original from very different geographic areas: the natives from riparian areas of Mediterranean ecosystems of inner Spain; *A. altissima* from a wide region of China and *R. pseudoacacia* from humid areas of North America. Among them, we expected that summer precipitation should especially enhance the BAI of *R. pseudoacacia*, given that it is original from areas without a recurrent summer water stress (Sanz Elorza *et al.*, 2004). The compendium of results will contribute to provide insights about the consequences of ongoing global change on these tree species.

Methods

Site and species description

The trees selected for this study grew in the river floodplains of the Manzanares and Henares rivers, in the provinces of Guadalajara and Madrid (central Spain, Table 1). The regional climate is continental Mediterranean, with hot and dry summers and cold winters. Mean annual temperature and precipitation are 14.2 °C and 333.1 mm, respectively (data from Torrejón de Ardoz weather station, National Institute of Meteorology, 1961-2011; Figure 1). Soils are luvi and fluvisols (Monturiol & Alcalá, 1990).

Table 1. Origin, number of trees sampled (N. trees), locality names, mean altitude (m), mean tree height (m), mean DBH (cm), mean age at sampling height (years) and δ^{13}Cwood (‰)± SE for each species. AH: Alcalá de Henares (40°28′54.65″N, 3°21′51.32″W); Ch: Chiloeches (40°34′27″N, 3°9′41″W); M: Mejorada del Campo (40°23′48″N, 3°29′3″W); RV: Rivas-Vaciamadrid (40°20′22″N, 3°31′5″W).

	Ailanthus	***Robinia***	***Fraxinus***	***Ulmus***
Origin	Invasive	Invasive	Native	Native
N. trees	11	9	10	10
Localities	AH, Ch, M	AH	AH	RV
Altitude (m)	716	607	600	590
Tree Height (m)	11.03±0.79	13.30±1.15	7.04±0.48	21.72±1.17
DBH (cm)	41.31±4.64	36.33±3.85	23.08±3.15	64.62±3.73
Age at sampling height	44.18±4.08	54.44±1.44	21.87±1.56	45.43±2.63
δ^{13}Cwood (‰)	–23.44±0.09	–23.89±0.13	–25.36±0.14	–24.93±0.10

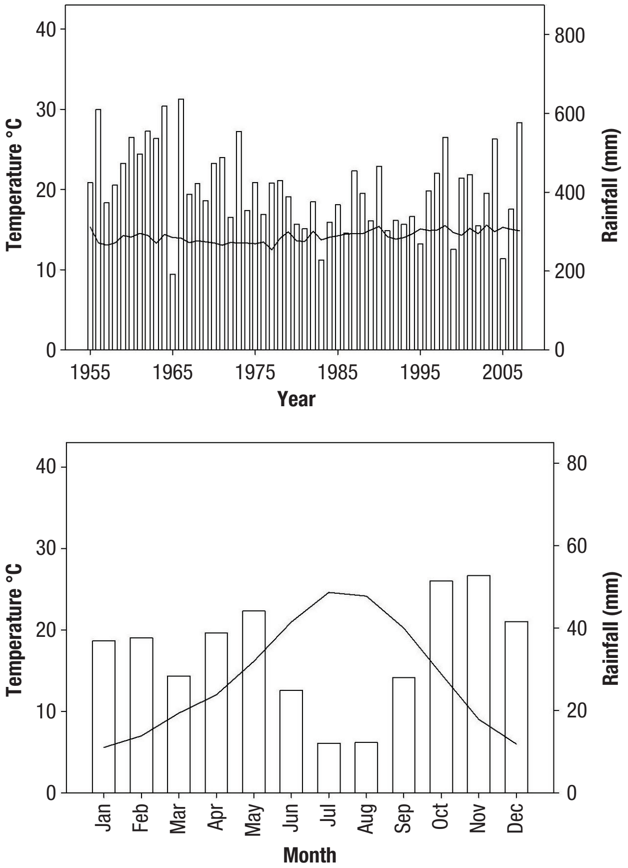

Figure 1(a). Annual precipitation (mm) and mean temperature (°C) from 1955 to 2007. Figure 1(b). Mean monthly precipitation (mm) and temperature (°C) during the same period (data from Torrejón de Ardoz weather station, Instituto Nacional de Meteorología, AEMET, Government of Spain). Precipitation is represented with bars and temperature with lines. In Figure 1a, see the positive trend in the mean temperature and the slight negative trend in the annual precipitation along last decades.

The dominant native tree species in the study area are *Fraxinus angustifolia* and *Ulmus minor*, together with *Populus alba* L., *Populus nigra* L. and different species of the genera Salix and Tamarix (Blanco *et al.*, 2005). The most abundant exotic tree species are *Ailanthus altissima* and *Robinia pseudoacacia*. *Ailanthus altissima* is native to southeastern Asia and was introduced in the Iberian Peninsula in the end of the 18th century. In its native range, climate is characterized by a long and warm growing season and by annual precipitation over 500 mm (Kowarik & Säumel, 2007). In contrast, *R. pseudoacacia* is native to central and eastern North America, where the climate is temperate humid or even hyper-humid (Huntley, 1990). It was introduced in the Iberian Peninsula during the 19th century (Sanz Elorza *et al.*, 2004). *Robinia pseudoacacia* and *A. altissima* have been previously described as pioneer, shade intolerant, fast growing species (Knapp & Canham, 2000; Sanz Elorza *et al.*, 2004; Kowarik & Säumel, 2007). In contrast, *F. angustifolia* and *U. minor* are able to establish successfully under a wide range of light and soil moisture conditions (González Muñoz *et al.*, 2011; González Muñoz *et al.*, 2014).

Sampling protocol and dendrochronological methods

We selected 10-12 dominant adult trees per species. Trees were chosen following 4 criteria: they should not show evidences of growth suppression by competition along the tree ontogeny; should show straight and regularly shaped stems (to avoid any tension on the rings) and should have a large DBH (to obtain long chronologies). Trees following the last requirement were difficult to find. Native riparian forests are largely impacted by human activities. Moreover, the frequency of adult individuals of *U. minor* has been severely reduced by the Dutch elm disease in the study area (Brasier *et al.*, 2004; Martín *et al.*, 2006). Similarly, the invasive trees are frequently cut-off when they reach a certain size. As a consequence, we had to sample trees placed at certain distances in some cases. However, our sampling procedure aimed to ensure the maximum habitat homogeneity in any case (trees not close to river courses, roads, paths, crops or populated places).

In each selected tree, we extracted one increment core, measured the perimeter at breast height (PBH, 130 cm above the base) and estimated the tree height (TH, m, from the angle between the distance observer-tree base and the distance observer-tree top) (Table 1). Increment cores were glued on wooden holders and dried and surfaced with a microtome to make tree rings clearly visible. All four study species are deciduous and form clear ring boundaries of ring-porous wood (http://insidewood.lib.ncsu.edu). Cores with rotten segments, knobs or unclear boundaries were rejected. In total, cores from 40 trees were considered for analysis. All samples were visually cross-dated following Yamaguchi procedures (1991). Total ring width (RW) was measured with an accuracy of 1/100 mm using a LINTAB measuring table and the software TSAP (Rinn, 1996). Dating errors of the individual series were corrected using the program COFECHA (Grissino-Mayer, 2001).

In order to remove the trend of decreasing RW with increasing tree size, we converted the data of raw RW into basal area increment (BAI, cm^2 $year^{-1}$), as follows:

$$BAI = \pi \left(r^2_t - r^2_{t-1}\right) \qquad \text{(Eq. 1)}$$

where r is the tree radius and t is the year of tree-ring formation.

This value is a reliable indicator of the progressive depletion of carbohydrate stores, as secondary growth has lower carbon allocation priority than that of primary growth (i.e., stem and root elongation; see Waring, 1987). In addition, it can be used as a surrogate for net carbon gain, assuming that basal area increment is correlated with the whole-tree carbon budget (e.g. Litton *et al*., 2007; McDowell *et al*., 2010, 2011).

Wood isotopic analyses and water-use efficiency

In each wood sample, we identified the last 25-30 annual tree rings and separated them into wood segments containing 5 contiguous rings with a razor blade. Wood segments were ground to a particle size <1 mm (PM100, Retsch Haan, Germany). We did not extract cellulose as both whole wood and cellulose isotope time-series show similar long-term trends related to atmospheric CO_2 and climate (Saurer *et al*., 2004; Taylor *et al*., 2008). The isotopic ratio $^{13}C/^{12}C$ of each wood sample was determined from tin capsules containing aliquots of 0.5-0.7 mg on a mass spectrometer (Thermo finningan Delta Plus XP, UC Davis Stable Isotope Facility, Davis, California, USA).

According to Farquhar *et al*., (1982), the total discrimination against ^{13}C during carbon fixation is expressed as:

$$\Delta(‰) = a + (b - a)\, C_i/C_a \qquad \text{(Eq. 2)}$$

where a is the fractionation against $^{13}CO_2$ during CO_2 diffusion through the stomata; b is the fractionation associated with carboxylation and C_i and C_a are the CO_2 concentrations in the leaf intercellular space and in the ambient air, respectively.

The linear relationship between C_i/C_a was used to calculate intrinsic water-use efficiency or $_i$WUE, which is defined as the ratio of net photosynthetic assimilation (A) to stomatal conductance for water (g_w) ($_i$WUE=A/g_w). According to Fick´s law, C_i/C_a reflects the balance between net assimilation (A) and stomatal conductance for CO_2 (g_c):

$$A = g_c(C_a - C_i) \qquad \text{(Eq. 3)}$$

The stomatal conductance for CO_2 (g_c) and water vapour (g_w) are related by a constant ($g_w = 1.6g_c$), which links the leaf-gas exchange of both CO_2 and water. By combining Equations 2 and 3 with the Fick´s law we obtain the following expression to estimate $_i$WUE (Ehleringer *et al*., 1993):

$$_iWUE = A/g_w = (C_a - C_i)1/1.6\ (\mu molCO_2/molH_2O) \qquad \text{(Eq. 4)}$$

(See Suppl. Table S1 [pdf on line] for the average $_i$WUE showed by each species in each 5-year period of the last 20 years of tree growth).

Environmental data

Climate data were provided by the National Institute of Meteorology (AEMET, Government of Spain). Among the existing climate stations, we selected Torrejón de Ardoz (40°29´00´´N 3°27´12´´W), as it has the longest and most complete record available and was located close to all the sampled trees. As *F. angustifolia* and *U. minor* trees were located closer to river courses than the invaders, we also evaluated groundwater effects on their BAI, using river flow data (m^3/s) as an indicator of the groundwater water availability. We used river flow data provided by the Government of Spain (www.cedex.es) from the Espinillos station for *F. angustifolia* (40°27´40´´N 3°25´13´´W) and the Vaciamadrid station for *U. minor* (40°19´15´´N 3°30´32´´W).

We used monthly and seasonal average data of the current and previous years for the following parameters: average, maximum, and minimum temperatures (T, Tmax and Tmin), precipitation, number of days with frost (DF) and river flow (RF). Seasonal data were calculated as the average (temperature and RF) or sum (precipitation and DF) of winter (December$_{(t-1)}$-February$_{(t)}$), spring (March$_{(t)}$-May$_{(t)}$), summer (June$_{(t)}$-August$_{(t)}$) and autumn (September$_{(t)}$-November$_{(t)}$).

Statistical analyses

We evaluated differences between origins (native or exotic) and species (nested in origin) on the average BAI and $_{i}$WUE of the last 20 years of tree growth (1987-2007) with two-way nested ANOVAs. We only considered the last 20 years for this comparison because it was the period in which we had the highest replication. Trees were used as replicates. *Post-hoc* Tukey tests were applied for multiple comparisons among species. We checked for homoscedasticity and for normality of the residuals using the Bartlett and Shapiro-Wilk tests respectively.

For each origin and species, we examined the relationship between BAI and $_{i}$WUE along the last 20 years of tree growth, with simple Pearson correlations. To perform these correlations, we averaged the BAI in five-year periods, as our values of $_{i}$WUE were estimated from segments of five contiguous rings.

We used linear mixed-effect models to identify the effects of environmental variables on the species BAI. In these models, the environmental variables were fixed factors and the tree the random factor. We modelled the period comprises between 1963 to 2007 for *A. altissima* and *R. pseudoacacia*, 1967 to 2007 for *U. minor*, and 1981 to 2007 for *F. angustifolia*. For *F. angustifolia* and *U. minor*, river flow was also included in the model. The selection of climate and river flow variables to include in the model and the random factor structure were performed manually using backward stepwise regression, beginning with variables and then removing progressively less significant variables to minimize the value of Akaike Information Criterion (AIC; Burnham & Anderson, 2002). The first order autocorrelation structure of BAI (the growth in the previous year or BAIp) was modelled using the non-climate/river flow residuals (i.e., difference between observed and predicted values) as a response variable. Thus, part of the unexplained variance in the climate-growth model was accounted with the individual autocorrelation structure. The same procedure was carried out for accounting the tree-age effects. As trees were not dated, we used tree age at sampling height (number of rings contained and measured in each core) as an indirect estimate of tree age. We used the Akaike information criterion corrected for small sample size (AIC$_{c}$) for multi-model selection. The model with the lowest AIC was selected (Burnham & Anderson, 2002). Models with ΔAICc between 0 and 2 were considered to have equivalent empirical support. In the case of equivalent models, we selected the model explaining the highest variance. If the explained variance was also equivalent, the simplest model (i.e., the model with less explanatory variables) was selected.

All statistical analyses were performed using R software (R Development Core Team 2013).

Results

Differences in radial growth and $_{i}$WUE between native and invasive species

Significant differences were found in the 20-year mean BAI between origins ($F_{1,35} = 13.66$, $p < 0.001$)

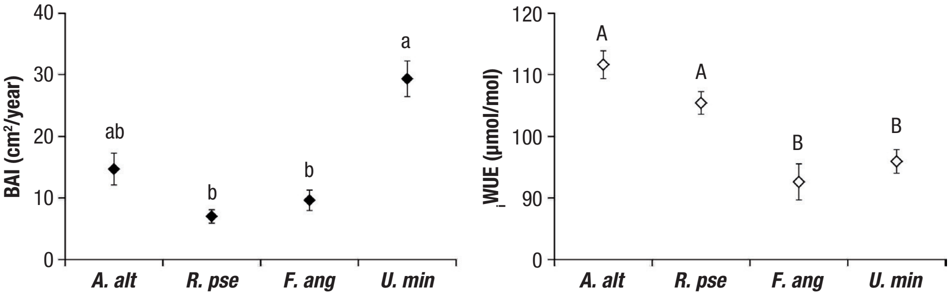

Figure 2(a). Mean basal area increment (BAI, cm^2/year^{-1}) for each studied species from 1987-2007 (20 years). Figure 2(b). Mean water-use efficiency (iWUE, µmol CO_2/mol H_2O) for the same period. Different small letters represent significant differences in BAI among species whereas different capital letters mean significant differences between origins in $_{i}$WUE, according to *post-hoc* Tukey tests. *Ailanthus altissima* –A. alt-, *Robinia pseudoacacia* –R. pse-, *Fraxinus angustifolia* –F.ang–, *Ulmus minor* –U.min–.

and species ($F_{3,35}$ = 15.56, <0.001) (Figure 2a). However, the average highest BAI of the natives was mostly due to *U. minor* (approximately 29 cm^{2}year^{-1}) (Figure 2a). Significant differences were also found among origins in the last 20-year mean $_{\mathrm{i}}$WUE ($F_{1,35}$ = 41.20, $p < 0.001$), with invaders showing higher $_{\mathrm{i}}$WUE on average than natives (Figure 2b).

No significant correlations were found between BAI and $_{\mathrm{i}}$WUE in all cases ($p > 0.05$) (Suppl. Figure S1 [pdf on line]).

Model selection for the radial growth of the native and invasive species

The invasive species showed a relatively steady temporal pattern in BAI. *Ailanthus altissima* BAI showed a slight decline since the beginning of the 1990s (Figure 3). In contrast, the native species showed higher temporal variance in BAI (Figure 3). *Fraxinus angustifolia* had a very slow growth rate during its juvenile phase (approximately 5 cm^{2}year^{-1}), increasing after the 1990s to relatively steady values (about 15 cm^2). In contrast, *U. minor* showed a relatively slow growth rate until the onset of the 1980s and then reached a maximum between 1978 and 1993 (Figure 3).

For the invader *A. altissima*, the selected model explained the 67.92% of the variance and indicated a negative effect of TmaxOct on BAI, whereas positive effects of TminFeb and PJul (Table 2). TmaxOct accounted for the highest relative weight of the variance (42.50%, table 2). For *R. pseudoacacia*, the selected model explained the 67.53% of the variance and indicated a negative effect of TminOct and a positive effect of PApr on BAI (Table 2). BAIp, closely followed by TminOct, explained the highest amount of the variance (32.09 and 26.70%, respectively) (Table 2). For *F. angustifolia*, the selected model explained the 67.69% of the variance and indicated a positive effect of TmaxSep (31.34%), TminPrevApr, RFAug, RFMar and TminJan (Table 2). For *U. mino*r, the selected model explained the 57.89% of the variance. This model indicated positive effects of TSep, TmaxDec, TmaxNov, RFPrevMay and PApr and negative effects of DFMay and DFOct (Table 2). BAIp explained the highest proportion of the variance of BAI of *U. minor* (38.73%), whereas environmental variables explained very little in this species (19.17% in total) (Table 2). The tree age at coring height was not significant in any case.

(See Suppl. Table S2 [pdf on line] for the model selection procedures)

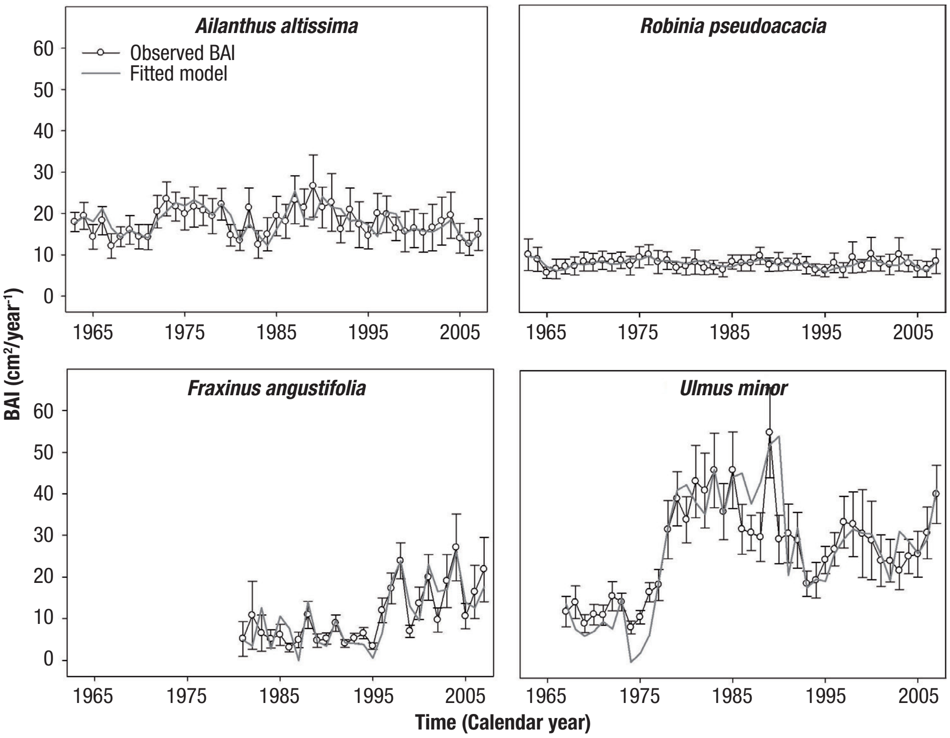

Figure 3. Basal-area increment (BAI, dark line) ± SE measured in the trees of each studied species (invasive species above, natives below). Linear mixed-effect models (grey line) based on environmental variables (climatic variables and river flow) and BAIp (first-order autocorrelation) (see table 2 and supplementary 2). Remarkable drought periods in the study area were 1990-1991 and 2004-2005 (AEMET, Government of Spain).

Table 2. Regression coefficients of the best supported linear mixed-effect model explaining basal area increment (BAI). For each variable, the relative weight in the model (RGM) and the explained variance (VE) are indicated. Variables are defined as follows: BAIp (previous year BAI); Variables are defined as follows: Tmax (average maximum temperature); Tmin (average minimum temperature); T (average temperature); RFJul (river flow); DF (days with frost) and P (precipitation) in a certain month (Jan, Feb, Mar, Apr, Jun, Jul, Aug, Sep, Oct, Nov, Dec). Prev: value of a variable in that month of the previous year.

Species (Origin)	Variable	Value	Std.Error	RGM (%)	VE
Ailanthus altissima	TmaxOct	–0.53	0.23	62.28	42.50
(Invasive)	TminFeb	0.77	0.30	6.59	4.48
	PJul	0.08	0.03	6.08	4.13
	BAIp	0.53	0.04	24.74	16.81
	Total VE (%)				**67.92**
Robinia pseudoacacia	TminOct	–0.30	0.13	39.54	26.70
(Invasive)	PApr	0.02	0.01	12.95	8.75
	BAIp	0.66	0.04	47.51	32.09
	Total VE (%)				**67.53**
Fraxinus angustifolia	TmaxSep	0.96	0.38	46.46	31.34
(Native)	TminJan	0.83	0.37	0.76	0.51
	TminPrevApr	2.28	0.63	23.38	15.77
	RFMar	0.19	0.09	3.66	2.47
	RFAgo	0.67	0.31	5.29	3.57
	BAIp	0.42	0.03	20.45	13.80
	Total VE (%)				**67.69**
Ulmus minor	TmaxDec	2.31	0.99	7.76	4.49
(Native)	TSep	1.96	0.61	12.28	7.11
	TmaxNov	1.71	0.73	7.71	4.46
	RFPrevMay	0.27	0.09	3.28	1.90
	PApr	0.13	0.05	1.58	0.91
	DFMay	–6.79	3.51	0.24	0.14
	DFOct	–6.58	1.95	0.27	0.16
	BAIp	0.62	0.03	66.90	38.73
	Total VE (%)				**57.89**

Discussion

Do invasive species grow more than natives?

We hypothesized a higher BAI in the invaders than in the natives, as high growth rates have been previously related to invasive species success. Instead, the native *U. minor* showed the highest average BAI, mostly due to an increase in growth between 1978 to 1993 (Figure 3). This could be attributed to: 1) long-term warming trends (discussed below); 2) a reduction in stand density occurred due to the Dutch elm disease (Martín *et al*., 2006). The stand where we collected *U. minor* samples is one of the best preserved elm forests of the Iberian Peninsula. However, since 1956, some events of stand reduction have been detected from aerial photographs and related to peaks of this disease (Martín *et al*., 2006). Also in contrast to our hypothesis, the invasive *R. pseudoacacia* showed a very low BAI (Figures 2a and 3), perhaps as a result of the dry conditions imposed by the Mediterranean climate (also discussed below).

What explains radial growth in invaders and natives?

Climate significantly and differentially influenced the BAI of all study species. However, despite the differences among species, it is possible to point out some general trends in climate-growth patterns for natives and invaders (see Table 2). For instance, we did not find any negative effects of warm temperatures on the BAI of the natives. Moreover, warm autumns yielded opposite effects on native and invasive trees, enhancing BAI in natives but hampering it in invaders (Table 2). High temperatures in autumn can extend the length of the growing season, by extending the canopy lifespan and favoring plant growth. In this sense, Peñuelas & Filella (2001) suggested that the accelerated tree growth observed throughout Europe is caused by the extended growing season consequent to global warming, together with atmospheric N deposition and increased CO_2. Therefore, the negative effect of warm autumn temperatures on both invaders was surprising, especially in the case of *A. altissima*. The native distribution of this invader presents warm conditions and, in the coldest areas of its invaded range, it is confined to the mild conditions of urban areas (Kowarik & Böcker, 1984; Gutte *et al*., 1987). The negative effect of warm autumns on the BAI of *A. altissima* may be related to an extension of summer drought stress or to a decrease in the amount of stored reserves for the next year (Atkin & Tjoelker, 2003).

The effect of precipitation on BAI was smaller than that of temperature. July precipitation had a positive effect on *A. altissima* BAI (Table 2). In our study site, the maximum leaf area of *A. altissima* coincides with the driest period (July), as this species has a delayed leaf budburst (González-Muñoz *et al*., 2013). Therefore, summer precipitation may compensate for evapotranspiration losses associated with high summer temperatures. However, in contrast to our initial hypothesis, spring (April) and not summer precipitation boosted *R. pseudoacacia* radial growth (Table 2). The positive effect of spring precipitation, together with the high effect of BAIp on the secondary growth of this species, suggest a mobilization of stored carbohydrates and an enhanced sap flux at the beginning of the growing season, which may contribute to the fast and early leaf bud-burst of *R. pseudoacacia* in our study area (González-Muñoz *et al*., 2013). The low BAI achieved by this species suggests a short growing season, which is confirmed by the short leaf lifespan of *R. pseudoacacia* (González-Muñoz *et al*., 2013). Koretsune *et al*., (2009), in a study conducted with adult trees of *R. pseudoacacia* in China, found that high precipitation during the early growing season increased *R. pseudoacacia* earlywood formation. However, they also found a higher average ring width than us. This suggests that *R. pseudoacacia* has a higher growth potential in a more humid climate, which cannot be expressed in our study area.

Regarding the natives, spring river flow and spring precipitations increased *F. angustifolia* and *U. minor* BAI, respectively. High water availability in early spring may favor a high sap flux at the beginning of the growing season. Besides, summer river flow also favored *F. angustifolia* radial growth, likely due to an effect of water stress alleviation through a high water table during the dry summer. Nevertheless, it was BAIp and not climate which explained the most of the variance of *U. minor* BAI, suggesting that its secondary growth may be highly dependent on the carbohydrates stored during the previous growing season, a low climate sensitivity, or both (Fritts, 1976).

Our models explained from the 57.89 to the 67.92% of the BAI variance of studied species. Other factors not evaluated here can be responsible of the rest of the variance, as micro-environmental conditions, groundwater availability, management activities or stand structure (competition or stand reductions by pathogens) (Fritts, 1976). In addition, we indirectly estimated the tree age as the number of rings measured in each core. Despite it was not significant, still some signal due to ontogenetic differences between species can remain in our growth models. All these are common limitations of dendrochronology studies. However, our sampling procedures and modelling approach still provide robust conditions about the climatic factors affecting the BAI of studied species and allow us to evaluate differences in their growth strategies.

Do invaders take advantage of atmospheric CO_2?

We expected to observe a fertilization effect of atmospheric CO_2 on the secondary growth of invasive species, as invaders are generally considered opportunistic, and then able to quickly take advantage of available resources. However, our results do not support this hypothesis, as we did not find a significant correlation between the BAI and the $_i$WUE. Then, although the invaders had higher $_i$WUE than natives, this higher $_i$WUE did not translate into increased radial growth. Higher $_i$WUE can be achieved by increasing carbon uptake or by decreasing water loss due to lower stomatal conductance (Francey & Farquhar, 1982). For the invaders, drought stress may have reduced stomatal conductance, and thus prevent them of taking advantage of increased atmospheric CO_2 for a faster growth.

Pulling all together: Will studied exotic species win in a global change scenario?

Our results suggest that neither climate change nor rising CO_2 will enhance the success of study invasive species over the natives in riparian forests of central Spain. Firstly, the contrasting effect of autumn temperatures on native and invasive species BAI suggests that study invaders will be more hampered by increasing temperatures. Secondly, we did not find a fertilization effect of CO_2 on the BAI of the invasive species. Moreover, these findings, together with the low BAI of *R. pseudoacacia*, suggest that higher temperatures may especially hamper this invader, limiting its presence to areas where water stress is less severe.

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