

Research Article

Potential Germination Success of Exotic and Native Trees Coexisting in Central Spain Riparian Forests

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Received 18 October 2015; Accepted 15 March 2016

Academic Editor: L. M. Chu

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We compared potential germination success (i.e., percentage of produced seeds that germinate under optimal conditions), the percentage of empty and insect-damaged seeds, germinability (G_{\max}), and time to germination (T_{germ}) between the exotics *Ailanthus altissima*, *Robinia pseudoacacia*, and *Ulmus pumila* and two coexisting native trees (*Fraxinus angustifolia* and *Ulmus minor*) in the riparian forests of Central Spain. Additionally, we tested the effect of seed age, seed bank type (canopy or soil) and population on G_{\max} and T_{germ} of *A. altissima* and *R. pseudoacacia*, which are seed-banking species. Species ranked by their potential germination success were *A. altissima* > *U. pumila* > *R. pseudoacacia* > *U. minor* > *F. angustifolia*. The combination of a high G_{\max} and negligible seed insect-damage provided *A. altissima* with a potential germination advantage over the natives, which were the least successful due to an extremely high percentage of empty seeds or a very low G_{\max} . *R. pseudoacacia* showed high vulnerability to insect seed predation which might be compensated with the maintenance of persistent seed banks with high G_{\max} . G_{\max} and T_{germ} were strongly affected by seed age in the seed-banking invaders, but between-seed bank variation of G_{\max} and T_{germ} did not show a consistent pattern across species and populations.

1. Introduction

Determining what plant traits are associated with invasiveness of alien species has been a major question in invasion biology during the last decades [1, 2]. Biological invasions involve the arrival of species to regions where they have not previously occurred, followed by rapid multiplication and range expansion [3]. The quantity and quality of available propagules influence dispersal and spread in the novel environments [4]. Vegetative reproduction may promote a rapid local dominance, but reproduction by seeds is a crucial step for invasive plants to attain an efficient range expansion and establishment far beyond their introduction point [5–7]. According to Hulme and Benkman [8], seeds not only contribute to the colonization of new areas but also allow the replacement of individuals ensuring population persistence after unfavourable periods.

From seed formation until seed germination, a variety of factors are responsible for the decrease in the potential

number of new plants to be recruited. Among these factors, we can mention genetic/developmental effects, dispersal distance, seed viability, seed predation, and germinability. These factors act sequentially or in conjunction, sometimes leading to severe reproductive losses, and therefore compromise plant recruitment [8, 9]. Subsequently, only a small fraction of the seed set ends up as established seedlings. A variable proportion of seeds produced by a plant may be nonviable, either due to fruit abortion [10, 11] or due to predation during ripening [12, 13]. In some species, Crawley [14] quantified losses by predispersal seed predation which represented nearly 50% of the total seed crop. Besides, not all seeds escaping predation are able to successfully germinate. Germination is a vulnerable stage in the plant cycle [15]. It is a complex phenomenon controlled by genetic and environmental factors, such as light, temperature, moisture, and nutrient availability, which vary during the year [16–20]. Some species form banks of dormant seeds, which may germinate throughout subsequent years. Seed banks are stored genotypes produced in different

years that act as reservoirs of genetic variation [21] and affect community dynamics [22]. They allow the species to recruit in years of low seed production [23], thus spreading the chances of reproduction through time [24] and expanding the window for recruitment [25]. These facts make them particularly relevant in areas where the environmental heterogeneity in space and time is high, such as Mediterranean ecosystems [26]. Seeds from seed banks may be stored in soils (soil seed bank) or/and in plant canopies (canopy seed banks). The latter have been mostly interpreted as an adaptation to fire (seeds remain in sealed cavities of fruits until they are burned, i.e., serotiny) [27]. However, some species retaining canopy seed banks are not characteristic of fire-prone ecosystems. In this context, the extent to which germination success of invasive plants is affected by seed bank type (canopy versus soil) and seed age in seed-banking species has been largely ignored.

Floodplains are among the most vulnerable habitats for plant invasions in Mediterranean regions [28]. In Mediterranean riparian forests of central Spain, there are invasive seed-banking (i.e., *Ailanthus altissima* (Mill.) Swingle, *Robinia pseudoacacia* L.) and non-seed-banking tree species (i.e., *Ulmus pumila* L.) successfully coexisting with native species (i.e., *Fraxinus angustifolia* L. and *Ulmus minor* (Mill.)). Our intentions with this study are (1) to compare several variables accounting for potential germination success (seed viability, predispersal seed predation, germinability, and time to germination of viable seeds) among the above-mentioned coexisting invasive and native trees and (2) to examine the role of seed bank type, seed age, and provenance on the potential germination success of the seed-banking invasive trees. We hypothesize that species with greater invasive success (i.e., *A. altissima* and *R. pseudoacacia* [29–31]) will show higher potential germination success when compared with natives. Besides, on the basis of the “enemy release hypothesis” [32–34], we expect seed predation to be greater in the native than in the invasive species. Finally, we expect germinability and time to germination to be dependent upon seed bank type (canopy/soil bank) and seed age.

2. Materials and Methods

2.1. Study Site. Native floodplain forests in Central Spain have undergone a historic process of degradation, due to agriculture, farming, river regulation, and so forth. Riparian forests of the Henares River are dominated by *Populus* spp., *Salix* spp., *Ulmus minor*, and *Fraxinus angustifolia* [35]. However, during the last decades, these areas have been colonized by exotic species, which are able to displace natural vegetation [36]. Two study sites, Jadraque (Guadalajara Province, 40°56'N, 2°56'W; 808 m.a.s.l.) and Alcalá (Madrid Province, 40°29'N, 3°19'W; 600 m.a.s.l.), were selected 70 km apart along the riparian forests of the Henares River (Central Spain) (Figure 1). In Jadraque, *A. altissima* (Mill.) Swingle and *R. pseudoacacia* L. are the prevailing exotic trees, forming dense stands among a natural matrix of *Populus alba* L. and *F. angustifolia* (Vahl). In Alcalá, remnant patches of *U. minor* (Mill.) coexist with the exotic Siberian elm (*U. pumila* L.),

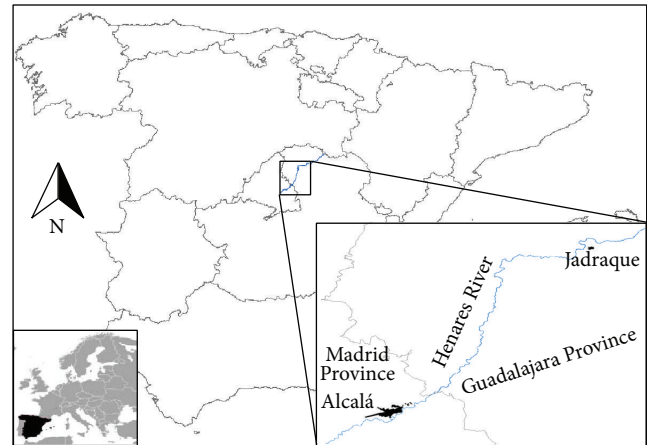


FIGURE 1: Map of the study sites (Jadraque and Alcalá) along the floodplain of the Henares River, Central Spain.

which is widely spread in this area. Here, naturalized stands of *A. altissima* and *R. pseudoacacia* are also common [37]. The climate is continental Mediterranean, with cold winters and hot and arid summers. Mean annual temperature and precipitation in each location are 10.9°C/601 mm and 13.4°C/401 mm (weather stations of Sigüenza and Alcalá de Henares; observation periods, 1933–1970 and 1931–1966, resp.) (Figure 1).

2.2. Study Species. The natives *U. minor* and *F. angustifolia* are wind-dispersed species that complete fruit set in March–April and September–October, respectively [38]. These species cooccur in our study sites with naturalized exotic trees such as *A. altissima* (wind-dispersed), *R. pseudoacacia* (barochorous), and *U. pumila* (wind-dispersed). *A. altissima* (native to SE Asia) and *R. pseudoacacia* (native to North America) are considered global invaders [31] and included in the list of the 20 most harmful alien invasive species in Spain [29]. Both were introduced during the 18th century in Spain for ornamental purposes. Nowadays, they occupy disturbed areas as well as natural and seminatural habitats, such as riparian forests, where they can displace native vegetation [36, 39]. These species are prolific seed producers [40, 41], complete fruit ripening in summer–autumn, and are able to form both canopy and soil seed banks [19, 42, 43]. Together with *A. altissima* and *R. pseudoacacia*, there is a non-seed-banking exotic tree (*Ulmus pumila*), native to relatively moist regions of East Asia. *U. pumila* was probably introduced in the 16th century in Spain and has spread throughout the Iberian Peninsula [44]. Although it is not considered as invasive by the current Spanish legislation [45], it has shown a great potential to form dense stands in the wild and to spread, both in Spain and in other countries (United States, Canada, Mexico, and Argentina) [46–48]. This species reproduces normally by seeds, which ripen in spring and disperse by wind in a few weeks, rapidly germinating [49, 50].

Seed viability in *R. pseudoacacia* has been reported to be shorter than a winter [19] or to extend up to four decades [51]. In the case of *A. altissima*, Kota et al. [43] and Hildebrand

TABLE 1: Summary of multispecies comparison germination tests indicating the native and exotic species tested within each location and the presence/absence of applied pretreatment.

Germination test	Location	Species (status)	Pretreatment
March 2013	Jadraque	<i>A. altissima</i> (E)	—
		<i>R. pseudoacacia</i> (E)	—
		<i>R. pseudoacacia</i> (E)	Scarification
		<i>F. angustifolia</i> (N)	—
April 2013	Alcalá	<i>A. altissima</i> (E)	—
		<i>R. pseudoacacia</i> (E)	—
		<i>R. pseudoacacia</i> (E)	Scarification
		<i>U. pumila</i> (E)	—
		<i>U. minor</i> (N)	—

(E) exotic; (N) native.

[52] reported seed longevity of less than one year, while others reported seeds to be viable after three years of storage [20].

2.3. Experimental Design. In March 2013, we collected ripe fruits from the canopy of two exotics (*R. pseudoacacia* and *A. altissima*) and the native *F. angustifolia* coexisting in Jadraque. In April 2013 we collected ripe fruits from the three exotics (*U. pumila*, *R. pseudoacacia*, and *A. altissima*) and the native *U. minor* coexisting in Alcalá. Although seeds from the former three species ripen in autumn, they may remain in the canopy, disperse all year round, but germinate mostly in spring (personal observation). For each site and species, we pooled together harvested seeds from 10 fruiting trees. A subsample of 100 seeds per species and site was used to test seed viability. Each seed was dissected and classified as (1) empty (with malformed or no embryo), (2) insect-predated (with holes or larva inside), and (3) viable (with intact and healthy embryo).

Germination tests were performed comparing exotic and native species within each site (Table 1). Holed seeds or suspicions of containing larvae inside were discarded. Winged seeds were devoid of their wings and *R. pseudoacacia* seeds were released from their pods. Seeds were sprayed with fungicide (DITIVER; 3 mg/L), placed over three layers of filter paper (FILTER-LAB; 0.17 mm width), and moistened with 5 mL of distilled water in 90 mm Petri dishes. Filter papers were kept soaked throughout the experiment. 15 Petri dishes (10 seeds/dish) per species and site were used as replicates and placed in a germination chamber (AL658 AQUALYTIC) at $20.5 \pm 0.2^\circ\text{C}$ and 12:12 h photoperiod ($496.2 \pm 81.5 \mu\text{mol}/\text{m}^2/\text{s}$), as these conditions mimic those of the study area in spring and are optimal for germination [53]. Temperature, relative humidity, and photosynthetic photon flux density (PPFD) were recorded every hour throughout the experiment with climatic sensors connected to data loggers (HOBO model H08-006-04; Onset, Pocasset, MA, USA).

Given that *R. pseudoacacia* seeds present dormancy [19], we used two sets of seeds for germination tests, one untreated and the other pretreated, to break dormancy. Based on previous experiments and studies [54], the best pretreatment consisted of scarifying them with boiling water (90°C) for one

minute, subsequently removing them from heat and keeping them in water for 24 h. We did not pretreat *F. angustifolia* seeds because at the time of collection they had already overwintered in the crowns, and therefore they had naturally undergone cold stratification, which is considered to break dormancy in this species [55]. Petri dishes were randomly distributed in the germination chamber and rotated every 3–4 days to avoid position effects. The number of germinated seeds was recorded daily until no more germinated seeds were observed for, at least, 9 consecutive days. Protrusion of the radicle or any part of the embryo was used as germination criterion. Germinated seeds were removed from the dishes at each census. Once the germination test was concluded, nongerminated seeds were dissected to exclude nonviable ones (i.e., empty or with larvae inside) from the counting. For each replicate we assessed the cumulative germination of viable seeds at the end of the experiment (G_{max} in %) and the average time required by seeds to germinate (T_{germ} in days). Finally, we assessed the potential germination success (G_{succ} in %) by multiplying G_{max} by the percentage of viable seeds, representing the proportion of produced seeds that are able to germinate under favourable conditions ($G_{\text{succ}} = G_{\text{max}} \times \% \text{ viable seeds}$).

In late September 2011, ripe fruits of *A. altissima* and *R. pseudoacacia* were collected from 10 adult trees belonging to the same two populations as before (Jadraque and Alcalá). For each species and site, a subset of 150 healthy seeds was used for a germination test (canopy seed bank, see below) and the remaining seeds were used to simulate a soil seed bank as follows: for each species and population, 32–33 stainless metal mesh bags ($4 \times 4 \text{ cm}$; 2 mm-mesh), containing 12 seeds each, were sealed with staples and placed outdoors on the ground at the Botanical Garden of Alcalá University (Madrid Province, $40^\circ 30' \text{N}$, $3^\circ 20' \text{W}$, altitude 596 m.a.s.l.). They were covered with a layer of *A. altissima* and *R. pseudoacacia* leaf litter collected in the sampling sites and protected from the local fauna with a 4.5 mm openings plastic mesh, fixed with nails to the ground. From November 2011 to October 2012, we performed one germination test every three months, in the same conditions as described in the previous section, using 150 healthy seeds recently collected from the tree crowns (canopy seed bank) and 150 healthy seeds from the simulated soil seed bank, per species and population (15 replicates of 10 seeds per species, population, and seed bank). In the November 2011 test, only canopy seed bank was used as the soil seed bank was not available yet. For each replicate, we calculated G_{max} and T_{germ} as before.

2.4. Data Analysis. Given that data did not meet normality, we conducted generalized linear models (GLMs) to compare G_{max} , T_{germ} , and proportions of empty, insect-damaged, and viable seeds across species. As not all species were present at the two sites (Jadraque/Alcalá), analyses were performed separately for each population. Besides, given that *R. pseudoacacia* values of germination were obtained for both untreated and pretreated seeds, analyses were conducted twice, using one set of data in each case. We chose binomial error distribution and logit link function for proportions

TABLE 2: Seed mean dry weight, cumulative seed germination (G_{\max}), mean time to germination (T_{germ}), and germination success ($G_{\text{succ}} = G_{\max} \times \% \text{ viable seeds}$) of the studied species in the 2013 experiment (means \pm SE). In *R. pseudoacacia*, values in parentheses correspond to untreated seeds. In the case of *A. altissima* and *R. pseudoacacia* values for different populations (Jadraque and Alcalá) are shown.

Site	Species	Dry weight (mg)	Viable seeds	Empty seeds	Insect-damaged seeds	G_{\max} (%)	T_{germ} (days)	G_{succ} (%)
Jadraque	<i>A. altissima</i>	19.9 \pm 0.4	100 \pm 0 ^b	0 \pm 0 ^a	0 \pm 0 ^a	67 \pm 4 ^{b,A}	12 \pm 1 ^b	67
	<i>R. pseudoacacia</i>	15.8 \pm 0.2	50 \pm 6 ^a	35 \pm 5 ^{b,A}	15 \pm 4 ^b	68 \pm 4 ^{b,A} (14 \pm 3) ^{a,B,*}	7 \pm 1 ^{a,B} (7 \pm 1) ^a	33 (6)
	<i>F. angustifolia</i>	48.0 \pm 1.9	79 \pm 5 ^{ab}	19 \pm 5 ^b	2 \pm 1 ^a	14 \pm 4 ^a	14 \pm 1 ^b	11
Alcalá	<i>A. altissima</i>	24.6 \pm 0.4	98 \pm 1 ^c	2 \pm 1 ^a	0 \pm 0 ^a	97 \pm 2 ^{b,B}	12 \pm 1 ^c	94
	<i>R. pseudoacacia</i>	16.6 \pm 0.3	59 \pm 7 ^{ab}	12 \pm 3 ^{ab,B}	29 \pm 8 ^b	92 \pm 2 ^{b,B} (7 \pm 2) ^{a,A,*}	3 \pm 0 ^{a,A} (6 \pm 1) ^{b,*}	54 (4)
	<i>U. pumila</i>	9.7 \pm 0.2	73 \pm 4 ^b	27 \pm 4 ^b	0 \pm 0 ^a	99 \pm 1 ^b	2 \pm 0 ^a	73
	<i>U. minor</i>	5.1 \pm 0.2	36 \pm 5 ^a	64 \pm 5 ^c	0 \pm 0 ^a	91 \pm 3 ^b	2 \pm 0 ^a	33

Lowercase letters indicate significant interspecific differences within each site on the basis of multiple comparison post hoc test. For species present in both sites (*A. altissima* and *R. pseudoacacia*), uppercase letters indicate significant differences between populations (Wilcoxon test). * Significant differences between pretreated and nontreated *R. pseudoacacia* seeds in the same parameter, on the basis of a Wilcoxon test.

(percentages of empty, insect-damaged, and viable seeds and G_{\max}) and Poisson error and log link function for counts (T_{germ}). Whenever significant differences among species were found, post hoc Tukey's all-pairwise comparisons were conducted in R with the *glht* function in the software package *multcomp* [56].

Additionally, for species present in both sites (i.e., *R. pseudoacacia* and *A. altissima*), Wilcoxon test was performed to compare percentages of empty, insect-damaged, and viable seeds and G_{\max} and T_{germ} between populations. Similarly, we tested the effect of *R. pseudoacacia* pretreatment on G_{\max} and T_{germ} with a Wilcoxon test, comparing untreated and pretreated seeds belonging to the same population.

The effect of (i) seed age, (ii) seed bank type, and (iii) population on G_{\max} (binomial response) and T_{germ} (Poisson response) was tested separately for the species *A. altissima* and *R. pseudoacacia* using GLMs. Seed age, seed bank type, and population were used as fixed factors, and the interaction between seed bank type and population was included. The most parsimonious models were retained. All the analyses were performed with R 3.0.1 statistical package [57].

3. Results

Seed viability differed largely among species, the ranking being *A. altissima* \geq *F. angustifolia* \geq *R. pseudoacacia* in Jadraque and *A. altissima* $>$ *U. pumila* \geq *R. pseudoacacia* \geq *U. minor* in Alcalá (Table 2). This fact was the consequence of the proportion of empty seeds, except for *R. pseudoacacia* of Alcalá, whose low proportion of viable seeds was due to a relatively high proportion of insect-damaged seeds. The native *U. minor* exhibited a very high proportion of empty seeds (64%). Insect-damage was irrelevant in all species except for *R. pseudoacacia* (Table 2). The percentage of insect-damaged and viable seeds did not differ between populations in *A. altissima* or in *R. pseudoacacia* (Table 2). The percentage of empty seeds was also similar between populations in *A. altissima*, but in *R. pseudoacacia* it was higher in Jadraque than in Alcalá ($W = 90.5$; $P = 0.002$) (Table 2).

In Jadraque, G_{\max} was similar between *A. altissima* and pretreated *R. pseudoacacia* and higher than that of *F. angustifolia* (Table 2). In Alcalá, G_{\max} was similar across species and higher than 90% in all of them (considering pretreated seeds in *R. pseudoacacia*) (Table 2 and Figure S1 available online at <http://dx.doi.org/10.1155/2016/7614683>). G_{\max} of pretreated *R. pseudoacacia* was superior to untreated seeds in both populations (Table 2, $W = 225$; $P < 0.001$). G_{\max} widely varied between populations of the two invaders, being higher in Alcalá (Table 2). After multiplying G_{\max} by the proportion of viable seeds (i.e., G_{succ}), *A. altissima* was the species with the most successful potential germination in the two sites, followed by *U. pumila* in Alcalá and by *R. pseudoacacia* in Jadraque. The two native species showed the least G_{succ} in Jadraque (*F. angustifolia*) and in Alcalá (*U. minor*).

F. angustifolia and *A. altissima* were the species that required longer time to germinate ($T_{\text{germ}} = 14$ days and 12 days, resp.). *R. pseudoacacia* showed an intermediate T_{germ} and the *Ulmus* gender was the fastest in germinating (2 days). *R. pseudoacacia* seeds from Alcalá germinated faster when pretreated, but the same was not true for Jadraque, where both pretreated and untreated seeds took the same time to germinate (Table 2, Figure S1).

Although we are aware of some *A. altissima* trees retaining seeds in their canopies for more than a year (Figure S2), it was not the case for those from the studied populations, so we could perform germination tests on seeds from the canopy bank neither in August 2012 (Jadraque) nor in October 2012 (Jadraque and Alcalá). Nevertheless, seeds from the soil bank retained high viability after one year ($>65\%$) (Figure 2). Seeds of *R. pseudoacacia* remained in the canopy during the whole monitored year (Figure 2).

Seed age and population were the factors that contributed the most to explaining the variation of G_{\max} in both species (Table 3). In *A. altissima*, G_{\max} increased rapidly until May (94.4%) and then slowly declined until October (72.2%) (Figure 2). In *R. pseudoacacia*, G_{\max} ranged from 32.3% to 93.4%, peaking in August, except for the seeds of the canopy bank of Jadraque, which showed erratic dynamics (Figure 2(b), Table S1). Seeds from Alcalá showed higher G_{\max}

TABLE 3: Generalized linear models assessing the importance of seed age, seed bank type, and population on cumulative seed germination (G_{max}) and mean time to germinate (T_{germ}) in *A. altissima* and *R. pseudoacacia* in the 2011-2012 experiment.

Species	<i>A. altissima</i>								<i>R. pseudoacacia</i>								
	G_{max}				T_{germ}				G_{max}				T_{germ}				
Response variables	df	D	RD	P	df	D	RD	P	df	D	RD	P	df	D	RD	P	
Explanatory variables																	
Seed age (SA)	4	263.913	330.46	<0.001	4	149.826	249.72	<0.001	4	91.864	790.66	<0.001	4	140.983	469.72	<0.001	
Seed bank type (SBT)	—	—	—	NS	1	70.299	179.42	<0.001	1	4.093	786.57	0.04	1	7.932	461.79	0.005	
Population (POP)	1	23.766	306.70	<0.001	1	2.692	176.73	NS	1	29.579	756.99	<0.001	1	125.783	336.01	<0.001	
SBT × POP	—	—	—	NS	1	6.767	169.96	0.01	1	4.784	752.21	0.03	—	—	—	NS	

(df) degrees of freedom; (D) deviance; (RD) residual deviance; (P) P value of χ^2 test used to evaluate if selected predictors explain a significant fraction of the deviance; NS, not significant).

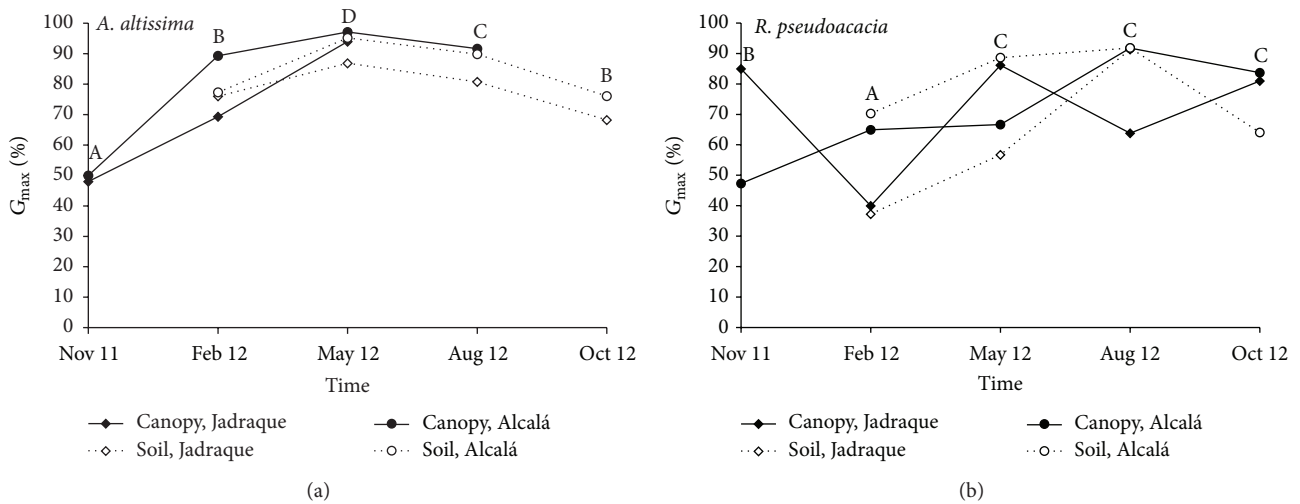


FIGURE 2: Maximum proportion of germinated seeds (G_{max}) from the canopy and soil seed banks of *Ailanthus altissima* and *Robinia pseudoacacia* from two populations (Jadraque and Alcalá) throughout a year ($N = 150$). Uppercase letters represent significant differences ($P < 0.05$) in G_{max} among seeds of different age (i.e., at different moments of the year).

in both species (Figure 2). Finally, seed bank type did not have any effect on G_{max} in *A. Altissima* seeds but somewhat affected G_{max} in *R. pseudoacacia* ($P = 0.043$) (Table 3), seeds from the soil bank showing a slightly higher G_{max} than those from the canopy.

Seed age and seed bank type played an important role in determining T_{germ} both for *A. altissima* and *R. pseudoacacia* (Table 3). *A. altissima* seeds germinated faster (lower T_{germ}) in May (10.5 days) and October (9.5 days) than in the remaining months, whereas *R. pseudoacacia* showed its fastest germination in August (3 days) (Figure 3; Table S1). Seeds from the canopy bank of *A. altissima* emerged 6 days later than those from the soil bank (Figure 3). By contrast *R. pseudoacacia* seeds from the soil bank germinated later than those of the canopy, although this difference was only relevant in Jadraque (Table 3, Figure 3). Population was a more influential factor than seed bank type on T_{germ} for *R. pseudoacacia* (seeds from Alcalá germinating faster than seeds from Jadraque) but it did not have an effect on T_{germ} for *A. Altissima* (Table 3, Figure 3).

4. Discussion

Our results show that exotic species benefited from several characteristics that helped them increase the potential germination success over natives. It was the combination of various features that led exotics to outperform natives in terms of potential germination success. Among the studied species, *A. altissima* was the most successful in terms of G_{succ} . This species showed a low proportion of empty seeds, virtually no insect attack, and very high germinability. These properties, along with the prolific seed production [40] and the long-distance seed dispersal by wind and water [58–60], provide this species with a very high potential to quickly spread far beyond the introduction point, which is the condition of naturalized exotic plants to be considered as invasive [3]. Besides, this species also attains a high degree of dominance at local scale due to its profuse resprout [61]. Altogether, these properties help explain why *A. altissima* is considered as one of the top invaders, both in Spain [29] and in the world [31].

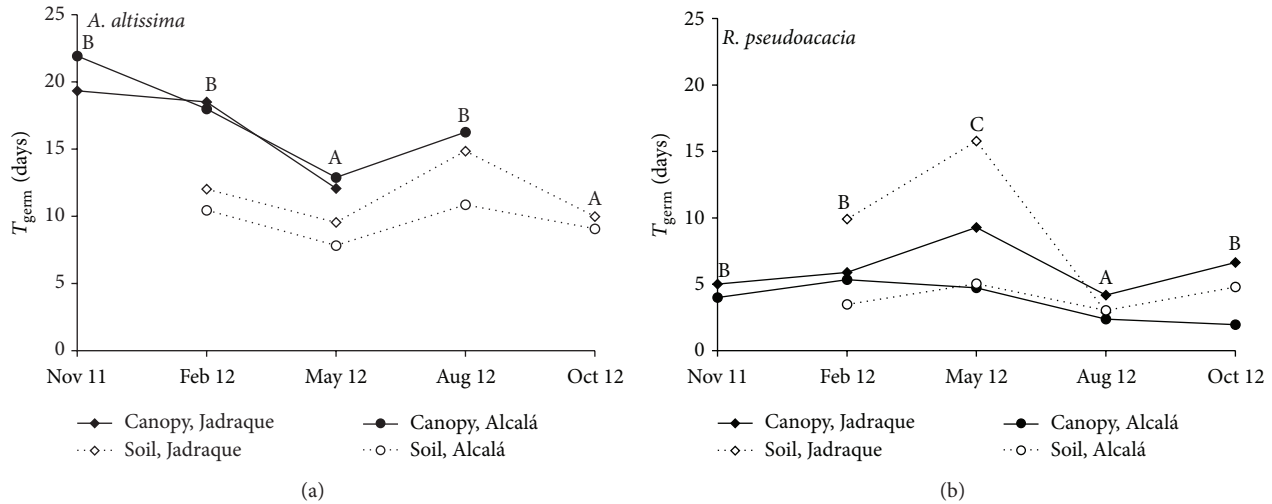


FIGURE 3: Time to germinate (T_{germ}) of *Ailanthus altissima* and *Robinia pseudoacacia* seeds from the canopy and soil seed banks from two populations (Jadraque and Alcalá) throughout a year. Uppercase letters represent significant differences in T_{germ} among seeds of different age (i.e., at different moments of the year).

Despite the fact that *U. pumila* is not considered an invasive species in Spain [45], we found that it had a high potential germination success (only overcome by *A. altissima*) because of its high germinability (nearly 100%), negligible predispersal insect attack, and moderate proportion of empty seeds. In addition, *U. pumila* seeds may present a relatively high longevity, as Dulamsuren et al. [62] found seeds from the previous growing season retaining 92% of germinability. Like *A. altissima*, this species also produces large quantities of wind-dispersed seeds [63]. This makes *U. pumila* also a good candidate for a quick spread from the introduction point. In fact, we have observed a high recruitment of this species in abandoned fields, crop and road borders, and even riparian forests of Central Spain. Therefore, we suggest that its “noninvasive” status should be revised.

Although *R. pseudoacacia* is also considered as a top invader in several sources [29, 31], in terms of potential germination success, we find it to be far below *A. altissima* and even *U. pumila*. A relatively high proportion of empty and insect-damaged seeds contributed to this low success. However, unlike *A. altissima* and *U. pumila*, *R. pseudoacacia* seeds present dormancy, which can be broken by natural processes, such as the passage through the digestive track of animals, fires, or abrasion with soil particles [64]. Even if dormancy depresses germination success of a seed cohort in the short term, at longer time scales it may increase reproductive success by extending the temporal window for germination [22]. Furthermore, the formation of long-lasting seed banks associated with seed dormancy represents a challenge to attain long-term eradication [65–67].

The two native species showed the lowest potential germination success: in the case of *U. minor* due to the high proportion of empty seeds and in the case of *F. angustifolia* due to its low germinability. These results match those of Gérard et al. [68] reporting germinability of 2–20% for *F. angustifolia*. However, other authors have shown stratification to largely

increase germinability of this species [69, 70]. Given that our seeds underwent stratification in the wild (they overwintered in the trees), our low germination rate may be attributed to a secondary dormancy induced by constant temperatures of 20°C during the germination assay [69, 71, 72]. In any case, literature also indicates a relatively high proportion of empty seeds for this species [72].

Against our hypothesis 2, we did not find seed predation to cause higher seed losses in native than in invasive species. Indeed, the invasive *R. pseudoacacia* was the most affected by insect seed predation. Many seed traits may affect the choice of fruit species by animals, such as morphology, weight, size, chemical composition, or fruiting phenology [73–75]. The null predation of *Ulmus* seeds may be partly explained by the fact that they were collected within 3–5 weeks since fruit set, while seeds of the remaining species had been exposed to predators for a fairly long period (9 to 11 months since the beginning of fruit set). However, only one known insect, the larva of *Cirrhia gilvago*, feeds on elm samara, and it is quite infrequent in Europe [76]. In the case of *A. altissima*, a high content of bitter-tasting quassinoid compounds [77] may explain the negligible predation of its seeds. Accordingly, Kelbel [78] also found that *A. altissima* seeds were not damaged by predators in a multispecies experiment. On the other hand, the high predation of *R. pseudoacacia* seeds may be attributed to their high protein and sugar content (unpublished data), as these compounds have been positively associated with fruit infestation [74, 79, 80]. Producing empty seeds may also contribute to reduce pre- and postdispersal seed predation [81–83]. This is a common phenomenon in wind-dispersed trees, for which animals mainly act as seed predators, rather than dispersers [84]. Given that, for a seed predator, the cost of seed-handling increases as the proportion of full seeds decreases, possessing empty seeds may contribute to overall plant fitness by discouraging animals to search for full seeds [11, 84]. This argument matches with the results

found for the anemochorous species *U. pumila*, *U. minor*, and *F. angustifolia*, which showed a relatively high proportion of empty seeds and a low proportion of seed predation. We should also note that, in the particular case of *U. minor*, the extremely high proportion of empty samaras (64%) agrees with results reported by Laguna [85], Cogolludo-Agustín et al. [44], and López-Almansa and Gil [86] and may be due to either seed abortion [87] or inbreeding depression undergone by *U. minor* population caused by Dutch Elm Disease (DED) (present in Spain since the beginning of the 1930s [88]). DED induces canopy decay of large trees, which are the most prolific. Although trees may profusely resprout after infection, juvenile resprouts have scarce sexual reproduction, leading to a genetic impoverishment of populations [89].

Overall, our results show that all the three exotics species (*A. altissima* > *U. pumila* > *R. pseudoacacia*) could potentially outperform natives, especially when colonizing open sites by seeds. For instance, *A. altissima* and *R. pseudoacacia* recruit better under high levels of irradiance, contrary to the natives *U. minor* and *F. angustifolia* which recruit better under moderate levels of irradiance [90].

Finally, as we expected, there was a clear effect of seed age on germination parameters (G_{\max} and T_{germ}). However, the influence of seed bank type varied depending on the studied species and population. Seed germinability (G_{\max}) was found to be strongly dependent on seed age in both species, peaking in May–August and slightly declining until the following autumn. The fact that germinability peaked in or near the beginning of the arid summer agrees with the humid/subhumid origin of these species [91, 92] and suggests a lack of adaptation to the Mediterranean environment. This contributes to explaining why, in Spain, these species invade habitats where summer drought is somehow mitigated (floodplains, crop borders, road sides, etc.) [36]. Our findings also emphasize the importance of accounting for age-dependent variations in germination tests when comparing species. For instance, our cross-species experiment comparing seeds collected in March–April may have underestimated the potential germination of *A. altissima* and *R. pseudoacacia*, which reach their maximum later.

Although we found G_{\max} to be slightly superior in the soil seed bank of *R. pseudoacacia*, no differences were found between seed banks in *A. altissima*. T_{germ} varied across seed banks in different ways for each species. Therefore, there does not seem to be a consistent superiority of one seed bank over the other. Alternatively, the advantage might be possessing both seed banks, rather than only one. Some species have tried to counterbalance environmental pressures through certain mechanisms aiming at spreading the risk of sexual reproduction failure through time [24], for example by spreading germination along the year or along several years. This prevents parental fitness from dropping in years of unfavourable conditions for germination or seedling survival [93]. Possessing two seed bank types may further contribute to spreading the risk of germination failure, for instance, by splitting the risk of predation between soil and canopy seed-eaters.

The fact that the between-seed bank variation of G_{\max} and T_{germ} did not show a consistent pattern across species and populations suggests that the optimal environmental

conditions for a successful germination differ between seed banks. However, although significant, differences in time to emergence between seed banks are of few days; therefore, they might not be ecologically meaningful. Overall, variation across populations in germination traits may reflect genetic differences between populations or local adaptations of the species to different conditions, as reported previously for invasive populations of *R. pseudoacacia* [19] and *A. altissima* [20].

5. Conclusions

Our results suggest that the combination of certain characteristics such as high germinability and seed viability provides the exotic trees *A. altissima* and *U. pumila* with a higher potential germination success than cooccurring natives. Furthermore, the ability of *A. altissima* and *R. pseudoacacia* to maintain at least one seed bank type, viable during more than one year, brings about a large temporal window for recruitment, and more chances for a successful germination under heterogeneous conditions. Finally, seed age should be accounted for when studying germination responses (i.e., G_{\max} or T_{germ}) in seed-banking species. All these factors should be considered in management strategies to eradicate or control populations of these invasive trees.

Competing Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

Acknowledgments

This study was supported by Project CGL2010-16388/BOS of the Spanish Ministry of Economy and Competitiveness, POIII0-0179-4700 of the Junta de Comunidades de Castilla-La Mancha, and REMEDINAL network S2009/AMB-1783 of the Comunidad de Madrid. Isabel Cabra-Rivas was supported by a grant from the Spanish Ministry of Education, Culture and Sport (FPU Fellowship, AP2010-1513) and by a grant from Alcalá University. The authors acknowledge Rosendo Elvira and the staff of the Alcalá University Botanical Garden for their support to perform this experiment. The authors also thank Guillermo Valle Torres and Alejandra Blánquez Moya for their valuable help during field sampling and laboratory work.

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