

RESEARCH

Open Access



Rivers as a potential dispersing agent of the invasive tree *Acacia dealbata*

Daniel Zamorano^{1,2,3} , Fabio A. Labra^{2,4}, Irma Vila¹ and Claudio I. Meier^{5*}

Abstract

Background: The silver wattle *Acacia dealbata* is a fast-growing tree from Australia that has become naturalised in different regions of the world, attaining invasive status in most of them. In Chile, *A. dealbata* reaches large abundances along banks and floodplains of invaded fluvial systems, suggesting that rivers may act as a vector for seed dispersal. As hydrochory has not been documented previously in this species, the aim of this study is to evaluate the potential for water dispersal of seeds of this invasive tree along rivers.

Methods: Seed samples from rivers were collected at three sites along two *A. dealbata*-invaded rivers within the Cachapoal basin, central Chile. Number of seeds collected was contrasted versus hydraulic and local conditions within RDA. Seed buoyancy and sedimentation velocity were determined and compared between sites with an ANCOVA. Finally, the probability of seed germination after long periods of immersion in water was assessed, simulating transport conditions in the flow. Germination results were tested with a GLM.

Results: Results indicate that increasing abundance of *A. dealbata* seeds in the flow is related to the level of turbulence of the flow. Seeds display high floatability but their sedimentation velocity is high when they do sink. Finally, silver wattle seeds can germinate after long periods (many weeks) of immersion in water; however, their probability of germination depends to a large extent on whether seeds are scarified or not.

Conclusions: Based on the evidence collected, we suggest that the seeds of *A. dealbata* have the necessary traits to be dispersed by rivers, this being the first research testing this hypothesis. The success of hydrochory of *A. dealbata* would depend on river flow turbulence, and whether there are natural mechanisms for scarifying the seeds either before or during transport. The proposed methodology can be used to assess river hydrochory for any tree species.

Keywords: Chile, Hydrochory, Seed buoyancy, Seed scarification, Silver wattle, Water dispersal

Background

The silver wattle *Acacia dealbata* (Link 1822) is a tree native to southeastern Australia, occurring from Tasmania to the north of New South Wales, at elevations between 50 and 1000 m.a.s.l. [1]. This species has been declared as invasive in regions across five different continents [2], including southern Europe [1], South Africa

[3], Madagascar [4], California [5], New Zealand [6], India [7], and Chile [8–10].

Given *A. dealbata*'s status as an invasive exotic and the range of biophysical impacts it causes [11], understanding its dispersal mechanisms is particularly relevant to inform management, restoration, and prevention efforts [12–14]. The general fact that rivers are one of the most significant vectors for invasion success [15–18] suggests that hydrochory could explain the ability of this species to invade riparian ecosystems [19]. Fluvial dispersal would allow *A. dealbata* to explore the range of disturbances inherent to riparian zones, which frequently create opportunities for invasive species [20, 21], in turn

*Correspondence: cimeier@memphis.edu

⁵ Department of Civil Engineering, University of Memphis, 104 Engineering Science Building, Memphis, TN 38152, USA
Full list of author information is available at the end of the article



© The Author(s) 2022. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

increasing the potential impact of this species on invaded river corridors.

Previously documented dispersal mechanisms for *A. dealbata* include primary dispersion related to seed fall by gravity, as well as the effects of wind [22]. However, and even though its habitat range is very broad [23–26], there are multiple reports of widespread distribution of *A. dealbata* along riparian corridors. These include rivers in the species' native range [27–29], as well as locations in southern Europe, such as Portugal [30], Spain [26, 31, 32], and Italy [33], as well as in South Africa [34–36], and Chile [37]. This distribution pattern, which is shared with some other Australian acacias, coupled with anecdotal observation of seeds in rivers has prompted some researchers to suggest hydrochory for many Australian trees in the genus *Acacia* L. [38–40], in a generic way. But this hypothesis has not been tested, except for the recent discovery of hydrochory in *Acacia stenophylla* [41], a similar species which also has an ample riparian distribution and lacks a previous hydrochory background. All this evidence suggests that the seeds of *A. dealbata* may well be dispersed by rivers.

Following Schupp et al. [42], the effectiveness of seed dispersal mechanisms can be evaluated as the product of two factors: quantity (numbers of seeds dispersed) and quality of dispersal (probability that a dispersed seed produces an adult). In the case of fluvial dispersion, sequential fulfilment of the following conditions would be needed: 1) the seed reaches the river channel (or a nearby location), 2) it is transported by the flow, and 3) it germinates after depositing in the floodplain [43–45]. These three steps have been broadly evaluated in the current literature on hydrochory [19, 46] and may be checked against *A. dealbata*'s phenology and morphology. For example, some researchers have shown that seed buoyancy is a trait that determines dispersal effectiveness and is an adaptation for hydrochory [44, 47–50], while others suggest that seed buoyancy is not an important trait as regards to dispersion by rivers, as sunken seeds may also be transported in the water column (bythisochory; [45, 51–54]). Furthermore, Thompson et al. [55] describe a new type of hydrochory mediated by overland flow, where surface runoff generated during intense storms transports seeds downslope. *Acacia dealbata* forms lasting seed banks [56], allowing seeds to be transported much later than the seed fall period. However, it is not clear how frequent this transport would be, or what the potential travel distances and precise transport mechanisms (floating or in the water column) are. It is relevant to note that anemochory and hydrochory have been documented acting as sequential dispersion steps [49, 53, 57], suggesting that seed morphologies adapted to wind dispersion may be also be indirectly optimal for water

dispersion. If so, this would improve the likelihood of dispersion of *A. dealbata* by rivers [22].

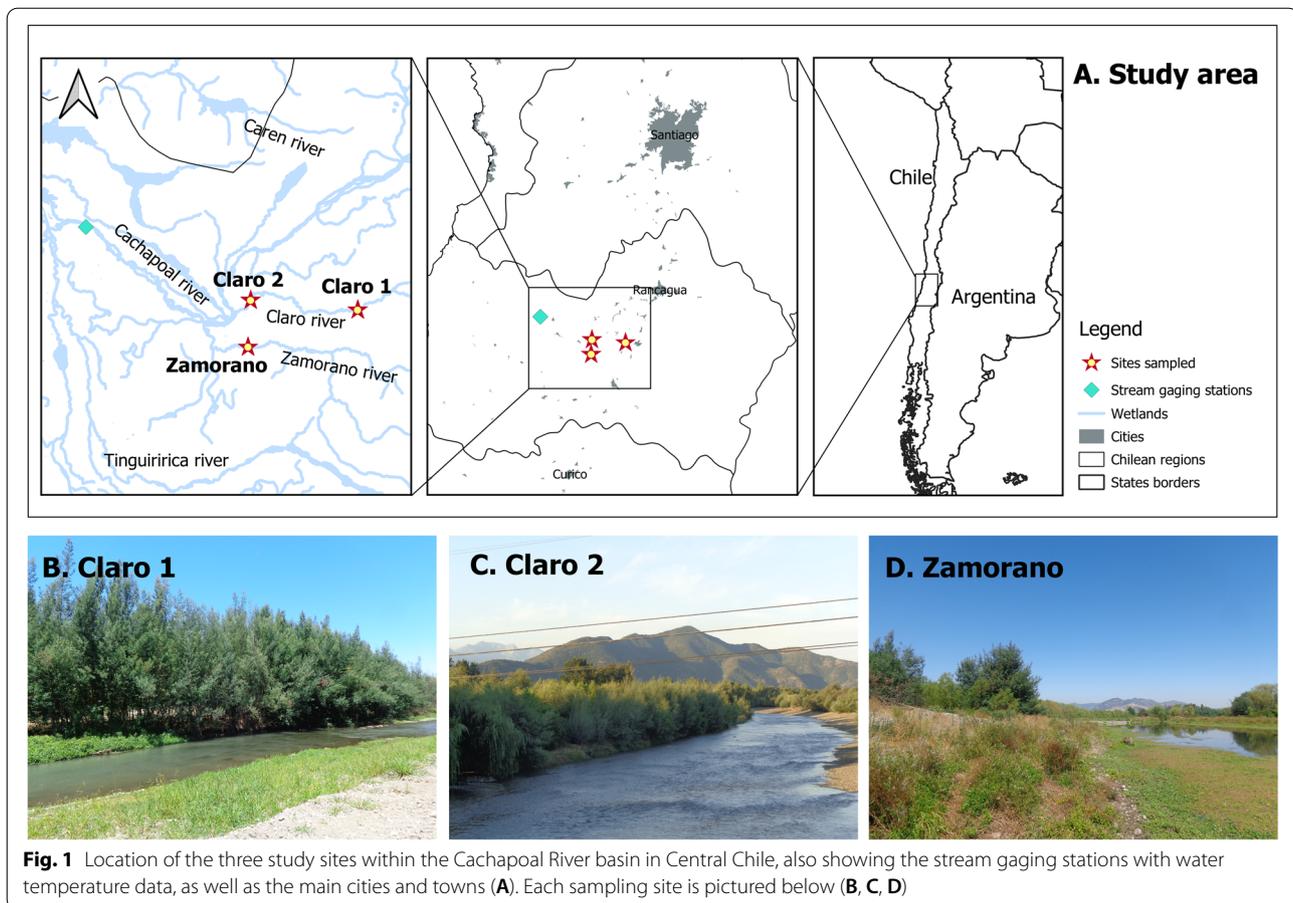
An important consideration in this discussion is the germination capacity of the seeds upon deposition on the floodplain, after of immersion. Seeds of other riparian species have been recorded to germinate after being submerged for many days [48, 53, 58, 59], in some cases with increasing germination probability [50, 60, 61]. The seeds of some riverine species are also able to germinate while floating in water [59, 60, 62]. All these traits are proposed as adaptative for hydrochory. However, with some exceptions [53, 59], previous experiments to evaluate seed germination after submergence or while floating were all conducted in still water, highlighting the need to assess the role of river flow, which is always turbulent [63]. To the best of our knowledge, there are no previously reported assessments about the potential germination of *A. dealbata*'s seeds after floodplain deposition. Given that these seeds require scarification in order to germinate, because dormancy is controlled by their seed coat [56, 64, 65], any assessment of the role of turbulence should concurrently examine seed scarification effects on the dispersal and germination process of *A. dealbata*. No other dormancy mechanism has been reported for *A. dealbata*, but other species in the Fabaceae family show two dormancy types: physiological, by controlling the production of gibberellins (GA) that stimulate germination; and physical, by waterproofing the seed coat, thus avoiding water absorption [66], as for *A. dealbata*.

Our aim is to assess the potential for hydrochory in this highly invasive species, using both field and laboratory experimental approaches to analyse the feasibility of fluvial dispersion of *A. dealbata* seeds. To evaluate the magnitude of seed transport, we conduct in situ measurements of the numbers of seeds transported by a river, at different reaches. To assess potential mechanisms of fluvial transport, we use field data as well as laboratory assessments of seed buoyancy and sedimentation velocity, in order to establish whether seeds will float or sink, as well as those hydraulic conditions that favour transport. Finally, to evaluate germination after deposition, we determine the probability of seed germination after long periods of water immersion in the laboratory, considering the effect of initial weight, scarification, and absence/presence of turbulence.

Methods

Study area

Three sites with abundant presence of *A. dealbata* (centered about 34°25' Lat S, 71°04' Long W) were sampled; two in the Claro River and one at Zamorano Creek, all within the Cachapoal river basin, located in Chile's Central Valley, about 115 km SSE from Santiago (Fig. 1), an



area with sub-humid Mediterranean climate [67]. Both rivers are braided-meandering (i.e., wandering) gravel-bed streams, with a median particle size in the cobble range [68]. Even though the closely located Andes range peaks at altitudes between 5000 and 6000 m.a.s.l., the hydrological regime of both rivers is markedly pluvial (i.e., rain-fed), as they drain lower-elevation Andean foothills. Mean flow maxima occur in the months between June and September, in the Austral winter, when there is an increased frequency and magnitude of storm events.

Sampling methods

At each one of the three sites, a study plot of 15 m (perpendicular to the shoreline) by 100 m (parallel to the shoreline) was randomly selected within a larger riparian patch of *A. dealbata*. All sampling was conducted on January 24 and 31, 2015, during a low-water period, within the seed-release period. All trees inside each plot were georeferenced, measuring their DBH (diameter at breast height). The height and age of each individual was then estimated from its DBH by applying a forest model for *A. dealbata* in Chile [69]. At each site, we obtained mature seeds directly from slightly closed pods in *A.*

dealbata trees, before any interaction with potential dispersal vectors. These seeds were then used to perform the experimental assessments of seed buoyancy, sedimentation velocity, and germination. In order to estimate the seed bank and degree of scarification, we collected all seeds found in 15 soil plots of size 30 × 30 cm², carrying out a stratified sampling within the larger 1500 m² study plot. To assess scarification in river-submerged seeds, we also collected sediment samples within the wet channel, immediately besides each sampling plot.

Fluvial transport of seeds and hydraulic conditions

At each one of the three sampling sites, fluvial seed transport was quantified by placing capture nets within the wet channel (i.e., in the flow), close to the shoreline. Next to each 100 m-long sampled area, seed transport was measured at five sampling points in the channel, separated from each other by 25 m. A 50 cm-diameter circular net with a mesh opening of 2.3 mm was maintained for 30 min at each point, following the methodology proposed by Kehr et al. [70]. Net dimensions and material were chosen in order to retain both seeds and pods of *A. dealbata* but were large enough to avoid any backflow

issues. The net was submerged to 60% of its diameter (i.e., 30 cm into the flow), thus collecting a combined sample of the material drifting in the water column as well as that floating at the surface. Flow depth (y) was recorded with a surveying rod at each sampling point, and current velocity was measured at five different depths over the vertical with a digital flowmeter (precision: 0.1 m/s): as close to the bottom as possible, at depths of 75%, 50%, and 25% of the total flow depth, and as close to the surface as possible. With these values, the mean flow velocity (V_m) at each measurement point was determined following a modification of the method proposed by Charlton [71]. Then, multiplying net sampling (i.e., submerged) area, sampling time, and flow velocity, we estimated sampled flow volume and seed density at each point.

With the measured flow depth y and computed mean velocity V_m at each sampling point, we estimated the Froude (Fr) and Reynolds (Re) dimensionless numbers, as in Merrit and Wohl [72]:

$$Fr = \frac{V_m}{\sqrt{g \cdot y}} \quad (1)$$

$$Re = \frac{\rho \cdot y \cdot V_m}{\mu} \quad (2)$$

where g is the standard acceleration due to gravity, μ and ρ are the dynamic viscosity and density of river water, respectively, and y is flow depth. The Froude number (Fr) quantifies the importance of inertial vs. gravitational forces in shallow flows; it is computed as the ratio of the mean flow velocity to the celerity (i.e., wave velocity) of a small disturbance. A $Fr > 1$ indicates rapid (or supercritical) flow, whereby disturbances cannot travel upstream, while $Fr < 1$ reflects a tranquil (subcritical) flow, which is by far the most common case in natural, alluvial channel.

On the other hand, the Reynolds number (Re) indexes the level of turbulence in an open-channel flow, being proportional to the ratio between inertial and viscous forces. The dynamic viscosity (μ) was obtained from a viscosity/temperature table for water [73], while water temperature was estimated by averaging data from two nearby gaging stations (Fig. 1) operated by Chile's General Water Directorate (Dirección General de Aguas, DGA).

For each sampling point, the number of seeds and fruit structures of *A. dealbata* were determined by inspecting net contents. Captured seeds were subsequently used in the scarification assessments, together with the submerged seeds that were sampled from the river sediment (details in the next section).

The seed rain in the vicinity of each net was indexed as a function of the abundance and mean DBH of adult

A. dealbata individuals located within different areas of influence, considering radii of 15 m, 30 m, and 45 m from each point where a net was placed.

In order to relate the abundance of *A. dealbata* seeds captured at each sampling point in the river (response variable) to the hydraulic conditions at, and abundance of adult trees around the point (predictor variables), a Redundancy Analysis (RDA) was performed [74]. To determine the significance of each predictor variable in the RDA, we performed a permutation analysis (1000 replicates), checking if the explanation of each predictor variable on the response variable was different from that obtained by chance.

Buoyancy and sedimentation velocity of seeds

The buoyancy index of both seeds and seed pods, as well as the sedimentation velocity of the seeds were determined in the laboratory. The seeds and pods utilized in these experiments were randomly selected from those collected from *A. dealbata*'s trees at each sampling site. The buoyancy index is the average time a sample stays on the surface of quiet water [75], while the sedimentation (or settling) velocity is defined as the mean terminal velocity at which a seed, initially placed just under the free surface, falls through a column of quiet water [53].

The buoyancy index was estimated for both seeds and pods (10 each per site, 60 in total). For these experiments, each individual seed or pod was carefully placed on the free surface of a container filled with water and left to float, until it either sank or the experiment ended (after 30 days). The time of buoyancy of the seeds was compared with those established by Romell [76] cited in Danvind and Nilsson [75], who qualified as "good floaters" those seeds that manage to float for more than two days under ideal conditions (still water, no wind or any other perturbation). To generate his index, Romell [76] floated seeds of different species, obtaining this threshold [77].

The sedimentation velocity was measured only for seeds (10 per site, 30 in total); in laboratory conditions at ≈ 20 °C, seeds were carefully dropped just below the surface of a clear, 40 cm graduated cylinder filled with water, recording the time needed for travelling a known distance. To evaluate the role of morphological traits and seed's site of origin on sedimentation velocity, we used ANCOVA considering seed weight, length, and circularity index as covariates and site origin as a way [78]. The length and circularity indices were estimated using function `coo_scalars` from `Momocs` package [79], employing the photo of each seed to obtain its outline and then compute the different indices. The circularity index, computed as P^2/A (where P and A respectively are the perimeter and the surface area of the seed as seen from above, when lying flat), is a shape factor that allows to compare

any shape against a perfect circle; the minimum result indicates a perfect circle, while increasing values reflect more asymmetrical, elongated shapes. There was no need to include other shape indices in the ANCOVA, as they all are highly correlated.

To obtain a first estimation of the potential distance that seeds can travel downstream once they sink, we borrowed a method used in environmental engineering for the design of sedimentation (settling) tanks. By applying a vectorial composition of the sedimentation velocity in the vertical and the mean flow velocity (as measured in the field) in the horizontal, with the field-measured flow depth as an end for the displacement, we computed the distance to deposition, assuming steady-state and uniform flow conditions for sedimentation equal to those at each measurement point. As the actual flow in rivers is turbulent, instantaneous, vertical velocity fluctuations will keep the seeds in suspension for longer, so this calculation only gives a lower bound for transport distance, under the above assumptions. Moreover, downstream variations in channel shape, and corresponding flow adjustments, will either increase or decrease the travelled distance; for example, if the measurement was taken within a riffle, but a pool lies immediately downstream, settling might happen much earlier.

Germination experiments

We conducted two laboratory experiments to simulate the germination of *A. dealbata* seeds during and after fluvial transport, considering two factors: 1) Seed condition: “scarified” or “unscarified”, and 2) Immersion time: evaluating germination effects for 15, 35, and 55 days immersed in water (Graphic summary in Fig. S1). All experiments were conducted inside germination chambers keeping temperature at 20° C.

The first experiment, ‘germination in water,’ was designed to determine germination and survival of seeds (scarified or unscarified) when transported in the flow. For this, 30 seeds per treatment (10 from each site, 5 scarified, and 5 without scarification) were immersed in water for either 15, 35, or 55 days, while kept in constant motion, emulating river transport. As a control, 30 seeds (10 per site) were immersed in water at the same temperature but without movement, again including scarified and unscarified seeds (5 seeds per site of each), for 30 days. The response variable is the proportion of viable seedlings at the end of each experiment (survival rate), but we also quantified hollow seeds and rotten seedlings. The germination experiment in water was performed with a motor-powered device specifically designed to keep seeds in constant motion in a water bath (Fig. S2), attempting to simulate fluvial transport.

The second experiment, ‘germination over a substrate,’ was designed to determine the probability of germination of *A. dealbata* once a river-transported seed is deposited in the floodplain. This experiment was carried out on vermiculite substrates in Petri dishes, with one seed per dish, irrigated ad libitum (every one or two days). We utilized 15 seeds per treatment (5 per site, all unscarified) which had been previously submerged for 15, 35, and 55 days, under motion. Then, of those seeds that did complete the immersion experiment (i.e., did not rot or ended up hollow—without cotyledon), half were scarified before putting them all to germinate ($n=98$). For estimating the germination rate of seeds not subjected to fluvial transport, we made a control experiment with 30 seeds (10 per site; 15 scarified and 15 unscarified), collected from the floodplain seed bank (i.e., that never fell into the water), germinating them over the same substrate, without previous immersion. Germination was counted every 2 days over a 30 day-long period.

Since the seeds of this species germinate in autumn, the photoperiod was set to alternating 12-h periods of light and shade, to simulate a natural light environment. The scarified seeds were obtained by damaging the coat with a scalpel, at that end of the seed opposite to the location of the embryo. A seed was considered to have germinated when it exhibited both the radicle and hypocotyl.

For both experiments, results were evaluated using a GLM analysis for binomial distribution (1: seed germinated, 0: seed without germination) [80]. A two-way analysis was performed, comparing the relationship between days of immersion and condition of the seed (scarified or unscarified). In order to make a-posteriori comparisons, a permutation test was generated, which compared whether the differences in probability of germination between groups are similar to those expected by chance. To avoid Type I error, the obtained values were later corrected by an FDR (False Discovery Rate) analysis, following Benjamini & Hochberg’s (1995) formula. All statistical analyses and database processing were performed in software R v.3.2.3 [82]. All raw data and the R script to replicate statistical analyses and figures are given in supplemental material.

Results

Overall, mean seed weight was 7.3 mg and mean length was 4.3 mm. At the Claro 1 and Claro 2 sampling sites, the canopy of adult *A. dealbata* trees extended beyond the shoreline, partly covering the water surface, whereas at the Zamorano site, the closest trees were located up to 15 m inland from the shoreline (Fig. 1). The flow depth was shallower and the velocity higher at the Claro 1 (0.41 m and 0.51 m s⁻¹) and Claro 2 (0.49 m and 0.67 m s⁻¹) sites, as compared with the Zamorano site,

which was deeper (0.95 m), with a lower flow velocity (<0.1 m s⁻¹) (Table S1).

Evidence of dispersion by rivers in *A. dealbata*

Seeds were collected in the flow at all three sites sampled (Claro 1 mean: 0.8 seeds/net – 0.008 seeds/m³; Claro 2 mean: 8.2 seeds/net – 0.047 seeds/m³; Zamorano mean: 0.4 seeds/net – 0.036 seeds/m³, Table S1). Despite observing a few pods drifting in the flow and lying on the riverbed, no pods were captured by the nets. The density of seed banks was much higher at Claro sites (Claro 1 mean: 10,600 seeds/m²; Claro 2 mean: 5,760 seeds/m²) than at Zamorano (mean: 187 seeds/m²).

The RDA results indicate that only the Reynolds number is significantly related to the number of *A. dealbata* seeds collected in the flow (Table 1). The observed relationship between both variables is positive (Linear regression: R²=0.363, p=0.008), thus, the higher the turbulence of the river flow, the higher the number of seeds captured (Fig. S3).

Buoyancy and sedimentation velocity of seeds

Only seed weight was significantly correlated with sedimentation velocity (Spearman test: Weight, rho=0.54, p=0.015; Length, rho=0.20, p=0.270; Circularity, rho=-0.03, p=0.88). The ANCOVA indicates that the only morphological trait significantly related to sedimentation velocity was seed weight (Table 2). The average sedimentation velocity was 0.069 ± 0.006 m s⁻¹ (n = 30).

The buoyancy time of seeds and pods was greater than 30 days in 94% and 100% of cases, respectively, which qualifies the seed propagules of *A. dealbata* as "good floaters" [76, 77]. The minimum distance that a seed would travel while sinking, under the flow conditions at each sampled site (but without turbulence) varies with the flow velocity and depth. The lowest value was 0.49 m

Table 2 ANCOVA results on the sedimentation velocity of *A. dealbata*'s seeds. Significant results are highlighted in bold

	d.f	SS	MS	F	P
Length	1	7.06E-05	7.06E-05	2.951	0.099
Weight	1	2.28E-04	2.28E-04	9.539	0.005
Circularity index	1	7.10E-06	7.09E-06	0.296	0.591
Site	2	9.30E-06	4.67E-06	0.195	0.824
Residuals	24	5.74E-04	2.39E-05		

(Zamorano), while the maximum was 6.07 m (Claro 2) (Table S1).

Germination in water

In the 'germination in water' experiments, the survival probability of scarified seeds was very high in all treatments, with a value of about 0.95 for the 'still water,' '15 days,' and '35 days' treatments, and around 0.55 in the case of the '55 days' treatment (Fig. 2). In contrast, the germination rate of unscarified seeds in water did not exceed 16%. Rotten and hollow seeds occurred for both the scarified and unscarified cases, with a higher proportion of rotten than hollow seeds (Table 3). GLM analysis did not detect significant interactions between immersion time and seed condition (scarified/unscarified), but each factor did show significant results (Table 4). In the case of immersion time, a-posteriori pairwise analyses did not reflect any significant differences.

Germination over substrate

For the 'germination over a substrate' experiment, as in the 'germination in water' experiment, scarified seeds germinated at a much higher proportion than the unscarified ones (Table 3). GLM analysis suggests a significant interaction between immersion time and seed condition

Table 1 Results of permutation analysis to relate through RDA the number of *A. dealbata*'s seeds captured in the river with (A) presence of adult individuals of the same species at each site and (B) hydraulic characteristics at each sampled point. Significant results are highlighted in bold

Predictor variables to RDA		RDA1	P perm
(A) Seed pressure from floodplain	Abundance of individuals within 45 m	-0.015	0.978
	Abundance of individuals within 30 m	-0.117	0.759
	Abundance of individuals within 15 m	-0.164	0.644
	Median DBH of individuals within 45 m	-0.295	0.406
	Median DBH of individuals within 30 m	-0.184	0.636
	Median DBH of individuals within 15 m	0.510	0.104
(B) Hydraulic characteristics	Reynolds number	0.670	0.011
	Froude number	0.448	0.170
	Flow velocity	0.539	0.073
	Flow depth	-0.184	0.679

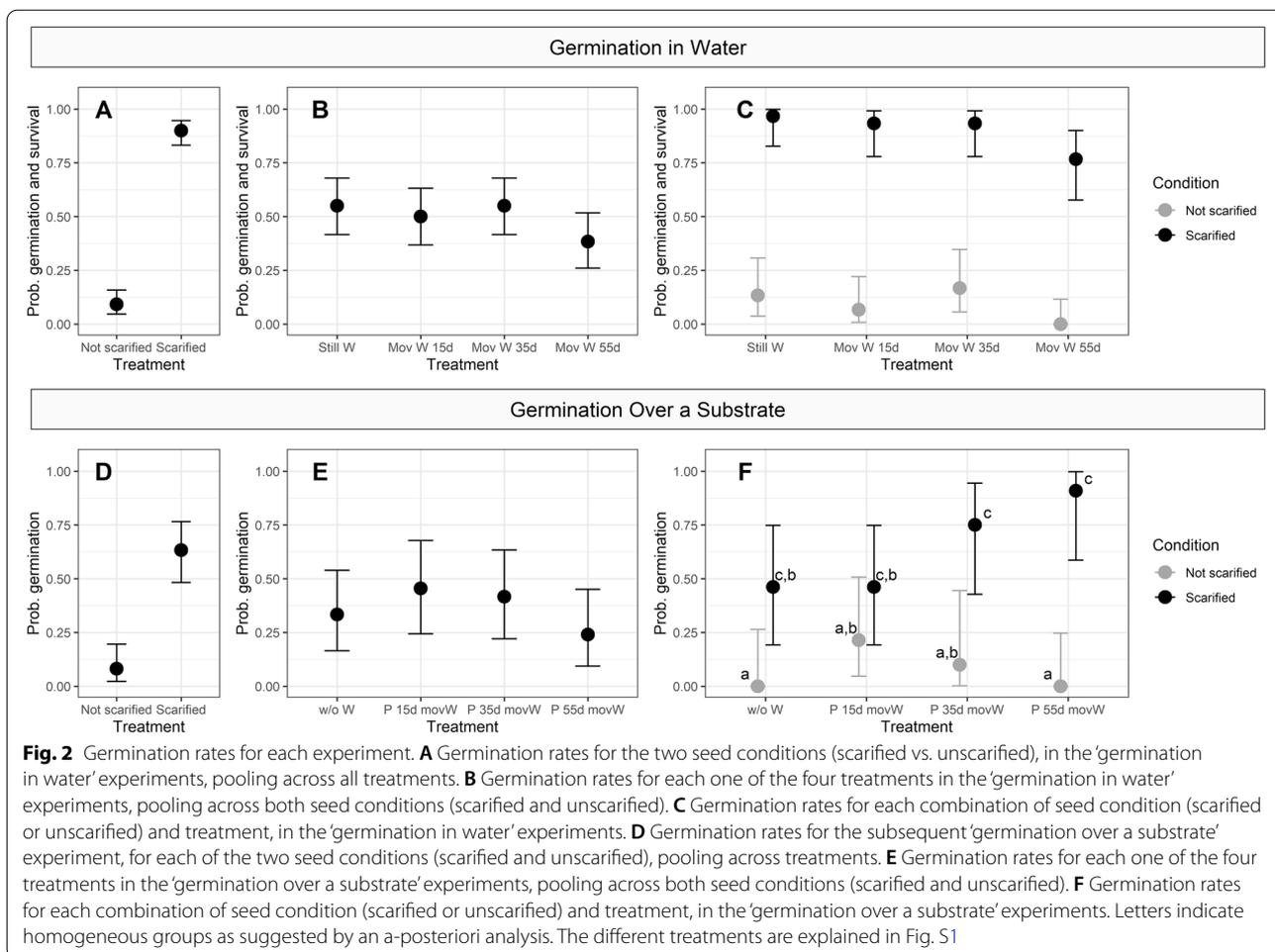


Table 3 Summary of results for the (A) 'Germination in water' and (B) 'Germination over substrate' experiments. Each seed was individually assessed after completion of each experiment, according to the following categories: "Germ", seeds that germinated during the experiment and were viable at the end; "Rot", rotten seeds at the end of the experiment; "Hollow", seeds with only tegument (no embryo) at the end of the experiment. "Control still W" is a result from a control experiment, where seeds were germinated in water without motion. "w/o W" is a result from a control experiment in which seeds were germinated without being immersed in water. More details in Fig. S1

	Scarified		Not scarified	
	Treatment	Result	Treatment	Result
(A) Germination in water	15 days	100% germ	15 days	0% germ, 20% rot
	35 days	90% germ	35 days	16% germ, 8% rot
	55 days	70% germ, 16% rot, 6% hollow	55 days	0% germ, 1% hollow
(B) Germination over substrate	Still Water (Control)	96% germ	Still Water (Control)	16% germ
	15 days	44% germ	15 days	18% germ
	35 days	75% germ	35 days	8% germ
	55 days	80% germ	55 days	0% germ
	w/o Water (Control)	44% germ	w/o Water (Control)	0% germ

Table 4 GLM analysis comparing germination rates between experiments (A) ‘Germination in Water’ and (B) ‘Germination Over a Substrate’. In both cases, GLM design is factorial: treatment (Treat, days of immersion in water) and condition (Cond, seed scarified or unscarified). Significant results are highlighted in bold

(A) Germination in Water	d.f	Deviance	Resid. d.f	Resid	P value
Intercept	239	332.69			
Cond	1	181.144	238	151.55	<2.2*10⁻¹⁶
Treat	3	13.513	235	138.04	0.004
Treat * Cond	3	1.991	232	136.05	0.574
(B) Germination over a Substrate	d.f	Deviance	Resid. d.f	Resid	P value
Intercept	97	127.744			
Cond	1	35.598	96	92.146	<2.4*10⁻⁹
Treat	3	4.587	93	87.559	0.205
Treat * Cond	3	10.421	90	77.138	0.015

(scarified/unscarified) (Table 4). A-posteriori analysis of paired comparisons suggests that the treatments ‘scarified seeds/35 days immersed’ and ‘scarified seeds/55 days immersed’ differed significantly from all treatments with unscarified seeds. It needs to be emphasized that, while the probability of germination decreases with immersion time in the case of unscarified seeds, it actually increases for scarified seeds (Fig. 2).

Discussion

Studies on riparian communities commonly assess the existence of hydrochory by evaluating seed floatability and/or fluvial transport [47–49, 57, 70]. On the other hand, studies that assess all the necessary steps for effective river dispersal, also considering the impact of river transport on germination rates, are rather scarce [e.g., 56, 57]. Our study evaluates hydrochory as a potential, previously unreported dispersal mechanism in *A. dealbata*, a species of great relevance due to its invasiveness [1, 10, 24, 26, 83].

In general, both our field and laboratory evidence strongly suggest that *A. dealbata* seeds interact with fluvial flow, allowing rivers to act as a dispersal vector. We provide field evidence that seeds are transported by river flow and, in addition, the germination experiments show that *A. dealbata* seeds are able to germinate after 15, 35, and 55 days of immersion. In what follows, we discuss how the potential relationships between the recorded seed traits and the riverscape may determine the effectiveness of river dispersal in this species. We also discuss the potential implications of riverine dispersal for invasiveness, and whether the traits recorded in *A. dealbata* would determine an adaptation for hydrochory.

Transport by rivers

Comparing our results with previous studies, we document that *A. dealbata* seeds have longer average flotation

periods than those reported for other riparian species [47, 48, 57, 60, 62]. Regarding sedimentation velocity of seeds, we only found data for the cottonwood *Populus trichocarpa*, an anemochorous/hydrochorous species that displays a mean sedimentation velocity of 0.018 m/s [53], one-third of that estimated for *A. dealbata*. Finally, observed seed density in the flow (number of seeds per unit volume of river water) was much lower than that recorded in some previous studies [70, 84, 85], but in the same order of magnitude to the densities documented by Brown and Chenoweth [86] and Meier [53]. Note though that these comparisons are not very relevant, as these authors worked with different species or groups of species; furthermore, seed density should strongly depend on the timing of seed fall interacting with the concurrent hydrologic/hydraulic conditions (such as river discharge, which locally determines flow depth and velocity, and thus the Reynolds number).

In comparison to other species in the literature [47, 76] *A. dealbata*’s seeds can be classified as “good floaters”, based on the flotation periods we observed. It should be noted though that this was mostly due to surface tension effects, so it is likely that when exposed to turbulent flow—as found in all rivers, the seeds would quickly sink. This notion is supported by the relatively high sedimentation velocity obtained in our experiments. The results of RDA, which relates numbers of seeds in the flow to turbulence (as indexed by the Reynolds number), suggest that *A. dealbata*’s seeds may be dispersed by rivers through mechanisms similar to those responsible for sediment transport, i.e., in suspension/saltation [87], where seeds are kept in suspension within the water column – with or without episodic bed contact – due to turbulence [19]. While studies that have tested this mechanism in detail are scarce, our results provide evidence that suggests such dispersal method. It should be noted that, even though the relationship between the number of captured

seeds and the Reynolds number is indeed driven mostly by a single high value at one of the sites, the upper envelope to the data points clearly displays a regularly increasing trend (Fig. S3).

Regarding the frequency of river transport of *A. dealbata*'s seeds, and the fact that the density of seeds was low, we need to consider three aspects: First, we sampled towards the end of the seed fall period [1]; second, both rivers were under low-flow conditions, with close to minimum capacities for transporting seeds; third, seed bank densities at our study sites are very high compared to other species [88, 89], only comparable to the seed banks for other *Acacia* species [90–92]. This suggests that *A. dealbata*'s seeds may be transported both during low-flow conditions (Austral summer, corresponding to the seed fall period), when seeds directly fall into the river, as well as during high-flow months (Austral winter), entrained from the seed bank by overbank flows, during flooding events.

Hyslop and Trowsdale [45] provide a conceptual model which depicts how interactions between flow stage, river geomorphic diversity, and seed phenology, influence hydrochorous seed dispersal and deposition. According to our results, this model suggests that seeds on the floodplain (in the seed bank) may germinate, be remobilized, or drift downstream, depending on their position and the occurrence of flood events. Seeds that fall directly into the flow may be transported or not, depending on the river's diversity of hydrogeomorphic conditions. In reaches with lower turbulence levels (i.e., pools during low discharges), it is likely that most seeds will sink, given their relatively high sedimentation velocity, only to be mobilized later, during floods. On the contrary, in reaches with higher turbulence (e.g., riffles), seeds may be transported downstream as soon as they fall.

Finally, since the weight of *A. dealbata*'s seeds relates positively to their sedimentation velocity, the question arises as to whether there will be a selection of seed weights by the flow, with lighter seeds travelling longer downstream. Comparing seed weights in this work with those reported in international databases for *A. dealbata* [93–95], it is observed that our seeds have the lowest recorded weights (mean of 7 mg for sampled sites, versus 11 mg mean in other databases). This could reflect either a selection of small seed sizes in riparian sites, or else could simply be a characteristic feature of this species in Chile.

Post-transport germination

In the 'germination in water' experiment, the highest germination rate (~95%) occurred in scarified seeds, with water motion being irrelevant. On the other hand, scarified seeds that were never immersed ('germination

over a substrate' experiment control) only displayed a germination rate of around 50%. Together, these results show how relevant both water imbibition and scarification are for germination, confirming the role of the physical dormancy mechanism for this species [64, 65]. The importance of water imbibition to seed germination process has been broadly recorded [96–99]. It allows for the resumption of normal seed metabolic levels and promotes mechanisms to repair the damage occurred during drying. Furthermore, different studies have shown how seeds increase water imbibition after scarification, validating our results [99–102].

In the case of the 'germination over a substrate' results, seed immersed 35 and 55 days in water, subsequently scarified, and then germinated over a substrate, showed higher germination rates than scarified seeds that were either never immersed or were just immersed for 15 days (P 15d movW in Fig. 2F). The corresponding germination rates of unscarified seeds were close to 0 in most cases, except for the treatment "15 days water in motion-germinated over substrate" (P 15d movW), where the mean germination rate was 0.22. Both results can be explained by the possible participation of a second, physiological dormancy mechanism, besides physical dormancy due to the coat. If both mechanisms are active within the first 15 days after immersion, but physiological dormancy dominates over physical dormancy during this period, then scarification would not be as important in triggering germination; in relative terms, this would cause lower germination of scarified seeds and higher germination of unscarified seeds, as compared to the longer (35 and 55 days) treatments. On the other hand, if some stimulus or process diminished or altogether stopped physiological dormancy at some moment between 15 and 35 days of immersion, it would explain the increased germination rates after scarification, in the 35 and 55-day treatments, as well as the decreased germination of unscarified seeds. In this way, our results could be explained by the differing temporal dynamics of two dormancy mechanisms. Dessi et al. [99] observed an increase in germination rates of non-scarified seeds at 25 °C in *A. dealbata* and *Acacia mearnsii*, which is a 5° higher temperature than in our experiment, suggesting that the second dormancy mechanism could be related to water temperature. However, the metabolic controls of the different germination phases and their relationship with dormancy are still not fully understood [97, 103]. Further studies are needed for *A. dealbata*, in order to confirm or refute our proposed mechanism.

An increase in germination rates after immersion was reported by Kowarik and Säumel [50] for *Ailanthus altissima*, an anemochorous species that recorded higher germination rates after three days immersed. Lopez

[62] recorded that species such as *Pterocarpus* sp. and *Pterocarpus officinalis* (from tropical, seasonally flooded forests) showed a peak in germination after 40 days in water, while other species like *Pentaclethra macroloba* (also from flooded forests) and *Gustavia superba* (an upland tree) showed decreasing germination rates when increasing immersion times. However, none of these studies considered water motion, to simulate river transport. To our knowledge, only two studies have considered this factor. Meier [53] found that there is no effect of water movement on the seed germination rates of the cottonwood *Populus trichocarpa*, even though hypocotyl and radicle lengths were significantly shorter in the motion treatment, as compared with the control. Rouified et al. [60] showed that after four days in moving water, germination rate increased from 0 to 80% in *Fallopia x bohemica*, an anemochorous species. Summarizing, the relationship between germination rates and the duration of immersion seems to vary on a species-by-species basis, without a clear pattern.

Given the discussion about transport mechanisms in rivers and considering the results of our germination experiments, we conclude that the successful germination of a seed that has been transported by the river (effective dispersal) depends on two milestones: firstly, that the seed is scarified, and secondly, that it is deposited on the banks or floodplain, after being transported. Whether these happen, and the order in which they occur may well determine the probability of germination success for the seed. For example, if a seed is scarified during transport by the flow, our results indicate that it would probably germinate in the water; whether it succeeds or not would then depend on stochastic fluvial processes, as it would need to deposit on the floodplain within some window of time, or else sink and lose viability or be washed downstream. In turn, if a seed managed to deposit on the floodplain, it could either initiate a new dormancy process in the seed bank, or else it would probably germinate if scarified. These examples show the dynamism and complexity of the different processes, which will vary depending on the characteristics of the river (including continuously changing river discharge, and thus hydraulics), plant phenology, and seed characteristics.

A new dispersion vector for *Acacia dealbata*

This study provides strong evidence suggesting that dispersion and colonisation of *A. dealbata* along rivers is feasible, leading us to consider it as a new dispersal vector for this species. Whether our results provide evidence of adaptation to hydrochory by *A. dealbata* or they just reflect an exaptation is an open question. According to

some authors, the principal trait associated with hydrochory is phenology [44, 51, 104], but for others it is diaspore floatability [16, 47]. However, recent literature has shown how some seed phenotypes that were typically associated with a single dispersal mechanism due to their traits (e.g., “if it floats, it is hydrochorous”; “if it has winged structures, it is anemochorous”), could very well use other dispersal mechanisms for which they are apparently not adapted [49, 50, 105, 106].

In this context, we highlight the study of Planchuelo et al. [57], who show how morphological adaptations for wind dispersal may also be optimal for water dispersion. Their description fits *A. dealbata* traits that were previously described when suggesting wind dispersion for this species [22]. Thus, traits such as a low mass seed, light pods with seeds attached, or a high surface area for seeds and pods may yield positive dispersal both for wind and water transport in *A. dealbata*, suggesting that there may be a selective pressure to simultaneously improve both. In this context, Sádlo et al. [107] propose a new classification of plant dispersal strategies, classifying species as “*Phragmites* type” when they display both hydrochory and anemochory (as we are proposing for *A. dealbata*). Finally, it is important to note that even though our study contributes evidence, it does not fully resolve the question about “hydrochory or not?” in *A. dealbata*, particularly considering that the discussion about the relationship between seed traits and dispersal mechanisms is in full swing.

In general, the literature associates successful germination of *A. dealbata* with the recovery from forest fires (since heat scarifies the seeds) [26, 31], leading to displacement of competitors due to both allelopathy [108] and the fact that adults have fast seed production, reproducing after their second year [109]. In this sense, the possibility of seed dispersion by fluvial transport was generically suggested by other authors for a range of Australian acacias [38–40] but has never been tested. To the best of our knowledge this study is the first record of hydrochory in *A. dealbata*. This would increase the list of traits explaining this species’ high invasiveness, experimentally corroborating its success as an invasive species, accounting for its enormous abundances along river banks and floodplains.

The invasiveness of *A. dealbata* in central Chile has been broadly researched, allowing us to expand our discussion, pointing out potential impacts that hydrochory in this species could have in our study area. Following a climatic niche evaluation, it has been estimated that several areas with suitable conditions remain to be colonised by this species in Chile [10], with researchers suggesting that dispersal limitations of *A. dealbata* have restricted

its spread. Because of increasing land-use change in riparian ecosystems [110], high fragmentation of rivers in central Chile [111], and the short length of Chilean basins, we would not expect long dispersal processes in Chile via hydrochory. By contrast, the ability of this species to colonise areas developing high-density patches that exclude native species via allelopathy [24, 112, 113], as well as the high seed-bank densities observed, suggest a “step-by-step” dispersal process that could be broadened by fluvial transport, extending dispersal areas downstream from site scale to local scale [114]. In this way, considering available habitats to colonise, we predict that the bigger impacts of hydrochory in Chile should occur at the mesoscale.

Finally, significant differences have been documented in seed traits [115] and seed germination rate [116, 117] within populations of different *Acacia* species, including *A. dealbata*; furthermore, Chilean populations of *A. dealbata* originated by several introduction events, followed by admixture [118]. This background suggests high phenotypic and genetic variation for this species, which would impact over its seed traits, and thus how generalizable our findings are to other populations (e.g., in Australia). However, the overwhelming presence of *A. dealbata* in riparian ecosystems suggests that *A. dealbata*'s seeds should be able to interact with rivers as a dispersal agent in most of the area colonised by this species.

Conclusions

Our results, together with evidence from previous investigations, suggest that dispersal by rivers is a viable strategy for *A. dealbata*, highlighting the role of scarification for its germination success, and the importance of hydraulics in the transport and viability of the seeds. Future investigations should target the actual impacts of hydrochory on the population dynamics of *A. dealbata* by using methods specifically aimed at estimating whether river transport of seeds favours the reproduction and dispersion of this highly invasive species.

Abbreviations

RDA: Redundancy Analysis; GLM: General Linear Model; ANCOVA: Analysis of covariance; Treat: Experimental treatment, days of immersion in water; Cond: Seed condition for experiment, scarified or unscarified; Still W: Experimental treatment, seed germination in still water; Mov W 15d: Experimental treatment, seed germination in motion water for 15 days; Mov W 35d: Experimental treatment, seed germination in motion water for 35 days; Mov W 55d: Experimental treatment, seed germination in motion water for 55 days; w/o W: Experimental treatment, seed germination without include water; P 15d movW: Experimental treatment, seed germination after 15 days in motion water; P 35d movW: Experimental treatment, seed germination after 35 days in motion water; P 55d movW: Experimental treatment, seed germination after 55 days in motion water.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40693-022-00109-7>.

Additional file 1: Table S1. Geographic location of each sampled point (WGS 84 UTM zone 19S), with its hydraulic characterization, captured pods and samples, and other estimated variables. **Figure S1.** Summary of germination experiment. A, Firstly, to evaluate the probability of germination while drifting in the river's flow, we conduct 'germination in water' experiments. Using the immersion device shown in Fig. 2, we simulate transport by the river of both scarified and unscarified seeds. We assess the effect of immersion duration (15, 35, and 55 days). As a control treatment, we germinate seeds in water without any movement. B, Secondly, to assess germination post river transport (post deposition), we perform a 'germination over substrate' experiment with those unscarified seeds previously used in the 'germination in water' experiments with motion (Fig. 2), scarifying half of them. Again, we evaluate the effect of immersion duration in water in movement (15 days, 35 days, and 55 days). Some seeds rotted during the 'germination in water', which was quantified; this decreased the number of samples for the 'germination over a substrate.' As control treatment, seeds that were previously not immersed in water were also tested. **Figure S2.** Schematic drawing of the device used for continuous immersion and motion of the seeds, in the 'germination in water' experiments. A) A small electrical motor with a gearbox and a propeller is attached to a wooden support. B) Each seed is placed in a pocket, which is suspended from a wooden frame that is attached to the propeller. C) The frame is placed atop a plastic container filled with water. The circular motion of the electrical motor generates a vertical up-and-down movement, maintaining the seeds in continuous motion. **Figure S3.** Relationship between the Reynolds number and *A. dealbata*'s seeds caught in the river flow (seed/min), at each sampling site. Linear regression is significant ($R^2 = 0.363$, $p = 0.008$).

Acknowledgments

This project was carried out with no funding and therefore it was possible because of the support and enthusiasm of around twenty-five colleagues and friends who collaborated receiving nothing in return. To all of them, thanks. I am particularly grateful to my coauthors, Irma, Fabio and Claudio, who supported this project during so many years wholeheartedly, to my mom Verónica Castillo and my sister Carolina Zamorano, who helped developing fieldwork material and processing samples, and to my wife Diana Lillo and friends Manuel Badilla, Felipe Rojas, and Faviola González, who participated on field work. I am eternally grateful to them.

Authors' contributions

D.Z., I.V. and C.I.M. conceived the ideas and designed the methodology. D.Z. collected field data and carried out experiments. D.Z. and F.A.L. analyzed data. D.Z. and C.I.M. led manuscript writing with contributions of I.V. and F.A.L. The authors read and approved the final manuscript.

Funding

Personal funding.

Availability of data and materials

The datasets supporting the conclusions of this article are available in the Figshare repository, <https://doi.org/10.6084/m9.figshare.19199774> Digital repository including raw data and R code: <https://doi.org/10.6084/m9.figshare.19199774>

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

None.

Author details

¹Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Santiago, Chile. ²Centro de Investigación e Innovación para el Cambio Climático, Facultad de Ciencias, Universidad Santo Tomás, Santiago, Chile. ³Department of Zoology, University of Otago, Dunedin, New Zealand. ⁴Doctorado en Conservación y Gestión de la Biodiversidad, Facultad de Ciencias, Universidad Santo Tomás, Santiago, Chile. ⁵Department of Civil Engineering, University of Memphis, 104 Engineering Science Building, Memphis, TN 38152, USA.

Received: 14 March 2022 Accepted: 3 June 2022

Published online: 07 July 2022

References

- Lorenzo P, González L, Reigosa MJ. The genus *Acacia* as invader: the characteristic case of *Acacia dealbata* Link in Europe. *Ann For Sci*. 2010;67:101–101.
- Richardson DM, Rejmánek M. Trees and shrubs as invasive alien species—a global review. *Divers Distrib*. 2011;17:788–809.
- Gouws AJ, Shackleton CM. A spatio-temporal, landscape perspective on *Acacia dealbata* invasions and broader land use and cover changes in the northern Eastern Cape. *South Africa Environ Monit Assess*. 2019;191:74.
- Kull CA, Tassin J, Rangan H. Multifunctional, Scrubby, and Invasive Forests? *Mt Res Dev*. 2007;27:224–31.
- Bossard C, Brooks M, DiTomaso J, Randall J, Roye C, Sigg J, Stanton P, Warner P. California invasive plant inventory. Berkeley: Calif Invasive Plant Council; 2006.
- Wandrag EM, Sheppard AW, Duncan RP, Hulme PE. Pollinators and predators at home and away: do they determine invasion success for Australian *Acacia* in New Zealand? *J Biogeogr*. 2015;42:619–29.
- Bhat JA, Kumar M, Negi AK, Todaria NP (2012) *Acacia dealbata* Link. (Silver Wattle), an invasive species growing in high altitudes of the Himalaya. *Curr Sci* 103:130
- Becerra PI. Invasión de árboles alóctonos en una cuenca pre-andina de Chile central. *Gayana Botánica*. 2006;63:161–74.
- Teillier S, Figueroa JA, Castro SA. Especies exóticas de la vertiente occidental de la cordillera de la Costa, Provincia de Valparaíso, Chile central. *Gayana Botánica*. 2010;67:27–43.
- Langdon B, Pauchard A, Bustamante RO. *Acacia dealbata* invasion in Chile: Surprises from climatic niche and species distribution models. *Ecol Evol*. 2019;9:7562–73.
- Le Maitre DC, Gaertner M, Marchante E, et al. Impacts of invasive Australian acacias: Implications for management and restoration. *Divers Distrib*. 2011;17:1015–29.
- Sheley RL, Krueger-Mangold, Jane (2003) Principles for restoring invasive plant-infested rangeland. [https://doi.org/10.1614/0043-1745\(2003\)051\[0260:PFRIPI\]20CO;2](https://doi.org/10.1614/0043-1745(2003)051[0260:PFRIPI]20CO;2) 51:260–265
- Soomers H, Karssen D, Soons MB, Verweij PA, Verhoeven JTA, Wassen MJ. Wind and Water Dispersal of Wetland Plants Across Fragmented Landscapes. *Ecosystems*. 2013;16:434–51.
- Albers HJ, Hall KM, Lee KD, Taleghan MA, Dietterich TG. The Role of Restoration and Key Ecological Invasion Mechanisms in Optimal Spatial-Dynamic Management of Invasive Species. *Ecol Econ*. 2018;151:44–54.
- Thebaud C, Debussche M. Rapid Invasion of *Fraxinus ornus* L. Along the Herault River System in Southern France: The Importance of Seed Dispersal by Water. *J Biogeogr*. 1991;18:7.
- Nilsson C, Gardfjell M, Grelsson G. Importance of hydrochory in structuring plant communities along rivers. *Can J Bot*. 1991;69:2631–3.
- Pysek P, Prach K (1994) How important are rivers for supporting plant invasions. In: *Ecol. Manag. invasive riverside plants*. John Wiley & Sons Ltd., pp 19–26
- Tabacchi E, Planty-Tabacchi A-M, Roques L, Nadal E. Seed inputs in riparian zones: Implications for plant invasion. *River Res Appl*. 2005;21:299–313.
- Nilsson C, Brown RL, Jansson R, Merritt DM (2010) The role of hydrochory in structuring riparian and wetland vegetation. *Biol Rev* 85:no-no
- Holmes PM, Richardson DM, Esler KJ, Witkowski ETF, Fourie S (2016) A decision-making framework for restoring riparian zones degraded by invasive alien plants in South Africa. *S. Afr. J. Sci*.
- Poff B, Koestner KA, Neary DG, Henderson V. Threats to Riparian Ecosystems in Western North America: An Analysis of Existing Literature. *JAWRA J Am Water Resour Assoc*. 2011;47:1241–54.
- Fu Z, Zhang C, Zheng Y, Wang Z, Duan F. Invasive potential of two introduced tree species: *Acacia mearnsii* and *Acacia dealbata*. *Sci Silvae Sin*. 2006;42:48–53.
- Hunt MA, Unwin GL, Beadle CL. Effects of naturally regenerated *Acacia dealbata* on the productivity of a *Eucalyptus nitens* plantation in Tasmania, Australia. *For Ecol Manage*. 1999;117:75–85.
- Fuentes-Ramírez A, Pauchard A, Cavieres LA, García RA. Survival and growth of *Acacia dealbata* vs. native trees across an invasion front in south-central Chile. *For Ecol Manage*. 2011;261:1003–9.
- González-Muñoz N, Costa-Tenorio M, Espigares T. Invasion of alien *Acacia dealbata* on Spanish *Quercus robur* forests: Impact on soils and vegetation. *For Ecol Manage*. 2012;269:214–21.
- Hernández L, Martínez-Fernández J, Cañellas I, de la Cueva AV. Assessing spatio-temporal rates, patterns and determinants of biological invasions in forest ecosystems. The case of *Acacia* species in NW Spain. *For Ecol Manage*. 2014;329:206–13.
- Abernethy B, Rutherford ID. Does the weight of riparian trees destabilize riverbanks? *Regul Rivers Res Manag*. 2000;16:565–76.
- Simkin R, Baker PJ. Disturbance history and stand dynamics in tall open forest and riparian rainforest in the Central Highlands of Victoria. *Austral Ecol*. 2008;33:747–60.
- Daley EA, Kirkpatrick JB. Native riparian vegetation in Tasmania. *Cunninghamiana*. 2004;8:409–30.
- Aguar FC, Ferreira MT, Moreira I. Exotic and native vegetation establishment following channelization of a western Iberian river. *River Res Appl*. 2001;17:509–26.
- Vazquez de la Cueva A. Case studies of the expansion of *Acacia dealbata* in the valley of the river Miño (Galicia, Spain). *For Syst*. 2014;23:3.
- Valero E, Picos J, Álvarez X. Characterization of riparian forest quality of the Umia River for a proposed restoration. *Ecol Eng*. 2014;67:216–22.
- Nucci A (2011) Distribution patterns of riparian plant species across river of Sardinia and Tuscany. Università degli Studi di Cagliari
- Myburgh WJ, Bredenkamp GJ. Macro-channel riparian vegetation of the Olifants River System in the Grassland Biome, Mpumalanga. *Koedoe*. 2004;47:41–54.
- Slabbert E, Jacobs SM, Jacobs K. The Soil Bacterial Communities of South African Fynbos Riparian Ecosystems Invaded by Australian *Acacia* Species. *PLoS One*. 2014;9: e86560.
- Hirsch H, Castillo ML, Impson FAC, Kleinjan C, Richardson DM, Le Roux JJ. Ghosts from the past: even comprehensive sampling of the native range may not be enough to unravel the introduction history of invasive species—the case of *Acacia dealbata* invasions in South Africa. *Am J Bot*. 2019;106:352–62.
- Pauchard A, Maheu-Giroux M (2007) *Acacia dealbata* invasion across multiple scales: Conspicuous flowering species can help us study invasion pattern and processes. In: *Sourceb. Remote Sens. Biodivers. Indic. Secr. Conv. Biol. Divers. Montr. Tech. Ser.* p 203
- Milton SJ, Hall AV. Reproductive biology of Australian acacias in the south-western Cape Province, South Africa. *Trans R Soc South Africa*. 1981;44:465–87.
- Wilson JR, Gairifo C, Gibson MR, Arianoutsou M, Bakar BB, Baret S, Celesti-Grapow L, DiTomaso JM, Dufour-Dror J, Kueffer C. Risk assessment, eradication, and biological control: global efforts to limit Australian acacia invasions. *Divers Distrib*. 2011;17:1030–46.
- Richardson DM, Kluge RL. Seed banks of invasive Australian *Acacia* species in South Africa: role in invasiveness and options for management. *Perspect Plant Ecol Evol Syst*. 2008;10:161–77.
- Murray BF, Reid MA, Capon SJ, Thoms M, Wu S (2019) Gene flow and genetic structure in *Acacia stenophylla* (Fabaceae): Effects of hydrological connectivity. *J Biogeogr* jbi.13566
- Schupp EW, Jordano P, Gómez JM. Seed dispersal effectiveness revisited: a conceptual review. *New Phytol*. 2010;188:333–53.

43. Cousens R, Dytham C, Law R. Dispersal in plants. A population perspective. 1st ed. USA: Oxford University Press; 2008.
44. Boedeltje G, Bakker JP, TenBrinke A, Van Groenendael JM, Soesbergen M. Dispersal phenology of hydrochorous plants in relation to discharge, seed release time and buoyancy of seeds: the flood pulse concept supported. *J Ecol*. 2004;92:786–96.
45. Hyslop J, Trowsdale S. A review of hydrochory (seed dispersal by water) with implications for riparian rehabilitation. *J Hydrol (New Zealand)*. 2012;51:137–52.
46. Vogt K (2006) Hydrochory, seed availability and species diversity in riparian landscapes. Christian-Albrechts-Universität zu Kiel
47. Johansson ME, Nilsson C, Nilsson E. Do rivers function as corridors for plant dispersal? *J Veg Sci*. 1996;7:593–8.
48. van Leeuwen CHA, Sarneel JM, van Paassen J, Rip WJ, Bakker ES. Hydrology, shore morphology and species traits affect seed dispersal, germination and community assembly in shoreline plant communities. *J Ecol*. 2014;102:998–1007.
49. Sämel I, Kowarik I. Propagule morphology and river characteristics shape secondary water dispersal in tree species. *Plant Ecol*. 2013;214:1257–72.
50. Kowarik I, Sämel I. Water dispersal as an additional pathway to invasions by the primarily wind-dispersed tree *Ailanthus altissima*. *Plant Ecol*. 2008;198:241–52.
51. Fenner M, Thompson K. The ecology of seeds. Cambridge University Press; 2005.
52. Groves J, Caitcheon G, Norris R, Williams D (2007) Prediction of fluvial seed dispersal and long-term sustainability of riparian vegetation using sediment transport processes. In: Aust. Rivers Mak. a Differ. Proc. 5th Aust. Stream Manag. Conf. Charles Stuart Univ. Thurgooona, New South Wales. pp 121–126
53. Meier CI (2008) Cottonwood establishment in a gravel-bed river. *ProQuest*
54. Sarneel JM. Effects of experimental snowmelt and rain on dispersal of six plant species. *Ecohydrology*. 2016;9:1464–70.
55. Thompson SE, Assouline S, Chen L, Trahthenbrot A, Svoray T, Katul GG. Secondary dispersal driven by overland flow in drylands: Review and mechanistic model development. *Mov Ecol*. 2014;2:7.
56. Royal Botanic Gardens Kew (2018) Seed Information Database (SID). In: Version 7.1. <http://data.kew.org/sid/>. Accessed 1 Jun 2016
57. Planchuelo G, Catalán P, Delgado JA. Gone with the wind and the stream: Dispersal in the invasive species *Ailanthus altissima*. *Acta Oecologica*. 2016;73:31–7.
58. Goodson JM, Gurnell AM, Angold PG, Morrissey IP. Evidence for hydrochory and the deposition of viable seeds within winter flow-deposited sediments: the River Dove, Derbyshire, UK. *River Res Appl*. 2003;19:317–34.
59. Mao R, Nguyen TLT, Osunkoya OO, Adkins SW. Spread pathways of the invasive weed *Parthenium hysterophorus* L.: The potential for water dispersal. *Austral Ecol*. 2019;44:1111–22.
60. Rouifed S, Pujalon S, Viricel M-R, Piola F. Achene buoyancy and germinability of the terrestrial invasive *Fallopia x bohemica* in aquatic environment: A new vector of dispersion? *Écoscience*. 2011;18:79–84.
61. Coops H, Van der Velde G. Seed dispersal, germination and seedling growth of six helophyte species in relation to water-level zonation. *Freshw Biol*. 1995;34:13–20.
62. Lopez OR. Seed flotation and postflooding germination in tropical terra firme and seasonally flooded forest species. *Funct Ecol*. 2001;15:763–71.
63. Dingman SL (1984) Fluvial hydrology. WH Freeman and Company, New York, NY
64. Danthu P, Ndongo M, Diaou M, Thiam O, Sarr A, Dedhiou B, Ould Mohamed Vall A. Impact of bush fire on germination of some West African acacias. *For Ecol Manage*. 2003;173:1–10.
65. Kheloufi A, Mansouri L, Aziz N, Sahnoune M, Boukemiche S, Ababsa B (2018) Breaking seed coat dormancy of six tree species. *Reforesta* 4–14
66. Finch-Savage WE, Leubner-Metzger G. Seed dormancy and the control of germination: Tansley review. *New Phytol*. 2006;171:501–23.
67. Di Castri F, Hajek ER. Bioclimatología de Chile. Chile: Vicerrectoría Académica de la Universidad Católica de Chile Santiago; 1976.
68. Rodrigues S, Moatar F, Claude N (2013) Sediment Transport Based in part on the article “Sediment transport” by Alec E. James, which appeared in the Encyclopedia of Environmetrics. *Environmetrics*. <https://doi.org/10.1002/9780470057339.vas010.pub2>
69. Pinilla J, Molina M, Gutiérrez B, Gutiérrez J (2003) Acacia En El Desarrollo Forestal Productivo De Chile: Avances De Investigación. Acta del XII Congr. For. Mund.
70. Kehr JM, Merritt DM, Stromberg JC. Linkages between primary seed dispersal, hydrochory and flood timing in a semi-arid region river. *J Veg Sci*. 2014;25:287–300.
71. Charlton R (2007) Fundamentals of fluvial geomorphology. Routledge
72. Merritt DM, Wohl EE. Processes governing hydrochory along rivers: hydraulics, hydrology, and dispersal phenology. *Ecol Appl*. 2002;12:1071–87.
73. Streeter VL, Wylie EB, García-Rejón GA, Fuentes Zurita GA, Soria López A (1988) Mecánica de fluidos. McGraw-Hill
74. Legendre P, Legendre L (2012) Numerical ecology. Elsevier
75. Danvind M, Nilsson C. Seed floating ability and distribution of alpine plants along a northern Swedish river. *J Veg Sci*. 1997;8:271–6.
76. Romell L-G (1938) Växternas spridningsmöjligheter. In: Skottsberg C (ed) Växternas liv IV. Nordisk Familjeboks Förlag AB, Stockholm, pp 279–448
77. Nilsson C, Andersson E, Merritt DM, Johansson ME. Differences in Riparian Flora between Riverbanks and River Lakeshores Explained by Dispersal Traits. *Ecology*. 2002;83:2878.
78. Chambers JM, Freeny A, Heiberger RM (1992) Analysis of variance; designed experiments. *Stat Model* 5 145–193
79. Bonhomme V, Claude J, Bonhomme MV (2020) Package ‘Momocs’
80. Venables WN, Ripley BD. Modern applied statistics with S. New York: Springer New York; 2002.
81. Benjamini Y, Hochberg Y. Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. *J R Stat Soc Ser B*. 1995;57:289–300.
82. R Core Team (2019) R: A language and environment for statistical computing.
83. Rodríguez J, Lorenzo P, González L. Different growth strategies to invade undisturbed plant communities by *Acacia dealbata* Link. *For Ecol Manage*. 2017;399:47–53.
84. Merritt DM, Wohl EE. Plant dispersal along rivers fragmented by dams. *River Res Appl*. 2006;22:1–26.
85. Greet J, Cousens RD, Webb JA. Flow regulation affects temporal patterns of riverine plant seed dispersal: potential implications for plant recruitment. *Freshw Biol*. 2012;57:2568–79.
86. Brown RL, Chenoweth J. The Effect of Glines Canyon Dam on Hydrochorous Seed Dispersal in the Elwha River. *Northwest Sci*. 2008;82:197–209.
87. Parsons AJ, Cooper J, Wainwright J. What is suspended sediment? *Earth Surf Process Landforms*. 2015;40:1417–20.
88. Dalling JW, Swaine MD, Garwood NC. Soil seed bank community dynamics in seasonally moist lowland tropical forest, Panama. *J Trop Ecol*. 1997;13:659–80.
89. Kalamees R, Zobel M. The role of the seed bank in gap regeneration in a calcareous grassland community. *Ecology*. 2002;83:1017–25.
90. Goets SA, Kraaij T, Little KM (2018) Seed bank and growth comparisons of native (*Virgilia divaricata*) and invasive alien (*Acacia mearnsii* and *A. melanoxylon*) plants: implications for conservation. *PeerJ* 6:e5466
91. Strydom M, Veldtman R, Ngwenya MZ, Esler KJ. Invasive Australian Acacia seed banks: Size and relationship with stem diameter in the presence of gall-forming biological control agents. *PLoS One*. 2017;12: e0181763.
92. Holmes PM. Implications of alien Acacia seed bank viability and germination for clearing. *South African J Bot*. 1988;54:281–4.
93. Dent TV. Some records of extreme longevity of seeds of Indian forest plants. *Indian For*. 1942;68:617–31.
94. Dent TV (1948) Seed storage with particular reference to the storage of seed of Indian forest plants. Manager of Publications

95. O'Dowd DJ, Gill AM (1986) Seed dispersal syndromes in Australian Acacia. *Seed dispersal* 87–121
96. Bewley JD. Seed germination and dormancy. *Plant Cell*. 1997;9:1055–66.
97. Ayuso M, Landín M, Pablo Gallego P, Esther Barreal M. Artificial Intelligence Tools to Better Understand Seed Dormancy and Germination. *Seed Dormancy Germination*. 2020. <https://doi.org/10.5772/intechopen.90374>.
98. Terskikh VV, Feurtado JA, Ren C, Abrams SR, Kermode AR. Water uptake and oil distribution during imbibition of seeds of western white pine (*Pinus monticola* Dougl. ex D. Don) monitored in vivo using magnetic resonance imaging. *Planta*. 2005;221:17–27.
99. Dessi L, Podda L, Brundu G, Lozano V, Carrouée A, Marchante E, Marchante H, Petit Y, Porceddu M, Bacchetta G (2021) Seed Germination Ecology of *Acacia dealbata* Link and *Acacia mearnsii* De Wild.: Two Invasive Species in the Mediterranean Basin. *Sustainability* 13:11588
100. Puteh AB, Aris EM, Sinniah UR, Rahman MM, Mohamad RB, Abdullah NAP. Seed anatomy, moisture content and scarification influence on imbibition in wild banana (*Musa acuminata* Colla) ecotypes. *African J Biotechnol*. 2011;10:14373–9.
101. Marler TE. Temperature and Imbibition Influence Serianthes Seed Germination Behavior. *Plants*. 2019;8:107.
102. Kestring D, Klein J, de Menezes LCCR, Rossi MN. Imbibition phases and germination response of *Mimosa bimucronata* (Fabaceae: Mimosoideae) to water submersion. *Aquat Bot*. 2009;91:105–9.
103. Allen PS, Benech-Arnold RL, Batlla D, Bradford KJ (2018) Modeling of seed dormancy. In: *Annu. Plant Rev. online*. Wiley Online Library, pp 72–112
104. Kubitzki K, Ziburski A. Seed Dispersal in Flood Plain Forests of Amazonia. *Biotropica*. 1994;26:30.
105. Römermann C, Tackenberg O, Poschlod P. How to predict attachment potential of seeds to sheep and cattle coat from simple morphological seed traits. *Oikos*. 2005;110:219–30.
106. Kaproth MA, McGraw JB. Seed Viability and Dispersal of the Wind-Dispersed Invasive *Ailanthus altissima* in Aqueous Environments. *For Sci*. 2008;54:490–6.
107. Sádlo J, Chytrý M, Pergl J, Pyšek P. Plant dispersal strategies: a new classification based on the multiple dispersal modes of individual species. *Preslia*. 2018;90:1–22.
108. Lorenzo P, Palomera-Pérez A, Reigosa MJ, González L. Allelopathic interference of invasive *Acacia dealbata* Link on the physiological parameters of native understory species. *Plant Ecol*. 2011;212:403–12.
109. Gibson MR, Richardson DM, Marchante E, et al. Reproductive biology of Australian acacias: important mediator of invasiveness? *Divers Distrib*. 2011;17:911–33.
110. Stella JC, Rodríguez-González PM, Dufour S, Bendix J. Riparian vegetation research in Mediterranean-climate regions: common patterns, ecological processes, and considerations for management. *Hydrobiologia*. 2013;719:291–315.
111. Díaz G, Arriagada P, Górski K, Link O, Karelovic B, Gonzalez J, Habit E. Fragmentation of Chilean Andean rivers: expected effects of hydro-power development. *Rev Chil Hist Nat*. 2019;92:1–13.
112. Fuentes-Ramírez A, Pauchard A, Marticorena A, Sánchez P. Relación entre la invasión de *Acacia dealbata* Link (Fabaceae: Mimosoideae) y la riqueza de especies vegetales en el centro-sur de Chile. *Gayana Botánica*. 2010;67:188–97.
113. Aguilera N, Becerra J, Guedes LM, Villasenor-Parada C, Gonzalez L, Hernandez V. Allelopathic effect of the invasive *Acacia dealbata* Link (Fabaceae) on two native plant species in south-central Chile. *Gayana Botánica*. 2015;72:231–9.
114. Domisch S, Jähniig SC, Simaika JP, Kuemmerlen M, Stoll S. Application of species distribution models in stream ecosystems: the challenges of spatial and temporal scale, environmental predictors and species occurrence data. *Fundam Appl Limnol / Arch für Hydrobiol*. 2015;186:45–61.
115. Daehler CC, Yorkston M, Sun W, Dudley N. Genetic variation in morphology and growth characters of *Acacia koa* in the Hawaiian Islands. *Int J Plant Sci*. 1999;160:767–73.
116. Ginwal HS, Gera M (2000) Genetic variation in seed germination and growth performance of 12 *Acacia nilotica* provenances in India. *J Trop For Sci* 286–297
117. Broadhurst LM, Young AG, Forrester R. Genetic and demographic responses of fragmented *Acacia dealbata* (Mimosaceae) populations in southeastern Australia. *Biol Conserv*. 2008;141:2843–56.
118. Hirsch H, Richardson DM, Pauchard A, Le Roux JJ. Genetic analyses reveal complex introduction histories for the invasive tree *Acacia dealbata* Link around the world. *Divers Distrib*. 2021;27:360–76.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Ready to submit your research? Choose BMC and benefit from:

- fast, convenient online submission
- thorough peer review by experienced researchers in your field
- rapid publication on acceptance
- support for research data, including large and complex data types
- gold Open Access which fosters wider collaboration and increased citations
- maximum visibility for your research: over 100M website views per year

At BMC, research is always in progress.

Learn more biomedcentral.com/submissions

