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Seed dispersal, germination and early seedling establishment of *Populus alba* L. under simulated water table declines in different substrates

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Abstract *Populus alba* L. is an autochthonous species dominating the overstory of the floodplain forests across the Mediterranean region. In contrast to some other *Populus* spp., very little is known about its regeneration strategies. Poplars yearly disperse huge amounts of wind- and water-dispersed, non-dormant, short-lived tiny seeds that need the bare, open and moist substrates created by fluvial-geomorphic events to germinate and establish. To survive, the growing roots must keep pace with the falling water table and associated soil moisture zone. Using a greenhouse experimental facility, 9-day-old *P. alba* seedlings were subjected to five hydrological treatments (permanent saturation, drawdown rates of 1, 2.5, 5 cm day^{-1} and immediate drainage) in two different substrates (coarse and sandy), and their survival and growth were evaluated. Also, *P. alba* seed dispersal was monitored in the field, and seed germinability and longevity were tested in the laboratory. No seedlings survived the water table declines in the coarse substrate although survival was high (85%) under saturated conditions. In the sandy soil, survival was significantly greater in the permanent saturation (87%) and 1 cm day^{-1} (88%) treatments than in the 2.5 cm day^{-1} (58%), 5 cm day^{-1} (25%) and immediate drainage (22%) treatments. The lowest root and shoot growth rates occurred under the saturated and immediate drainage conditions. Seed dispersal lasted 6–8 weeks and peaked in mid-April, initial seed germinability was high (92%) and seed longevity was relatively long (half viability period, 30 days). The creation of nursery sites and release of controlled floods in mid-April, followed by water table declines of less than 1 cm day^{-1} in coarse substrates and less than 5 cm day^{-1} in sandy substrates are recommended for enhancing the initial establishment of *P. alba* seedlings.

Keywords *Populus alba* L. · Rhizopod ·
Water table decline · Seedling establishment ·
Seed dispersal · Germination · Controlled floods

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Introduction

The family *Salicaceae*, and especially the genus *Populus*, dominates most of the floodplain forests across the northern temperate zone (Karrenberg et al. 2002). The periodic recruitment of new individuals by means of either sexual or vegetative propagation is essential for the maintenance of these riparian forests (Rood et al. 1998). In particular, sexual regeneration increases genetic variation, potentially increasing population resistance to environmental change and disease (Heinze and Lefèvre 2001; Barsoum et al. 2004). Many *Populus* spp. are considered phreatophytes as they rely on the water table and associated soil moisture zone to survive and grow (Smith et al. 1998). In addition, their regeneration strategies are intimately connected to the natural hydrograph at different spatial and temporal scales

(Cooper et al. 2003). River regulation and water reclamation projects have altered the flow patterns of most rivers worldwide (Nilsson et al. 2005), thus disrupting the flow-dependent poplar life-cycle. In particular, dams and diversions modify the timing, magnitude and frequency of peak flows, reduce sediment loads, and cause abrupt water table declines, which may lead to systemic regeneration failure and overall floodplain forest decline (Johnson et al. 1976; Rood and Heinz-Milne 1989; Rood and Mahoney 1990; Johnson 1992; Rood et al. 1995; Stromberg et al. 1996; Merritt and Cooper 2000; Braatne et al. 2007).

A single mature female poplar can produce annually thousands or even millions of wind- and water-dispersed, non-dormant, short-lived tiny seeds (about 1 mm long) (Karrenberg and Suter 2003) with high viability (>90%) (van Splunder et al. 1995; Foussadier 1998; Karrenberg and Suter 2003). However, the minimal energy supply of the small seeds limits their longevity to a period of only days or a few weeks (Moss 1938; Muller and Teissier du Cros 1982; Johnson 1994; van Splunder et al. 1995; Braatne et al. 1996; Karrenberg and Suter 2003), preventing formation of long-term seed banks. Therefore, the period for seedling establishment is limited to a 'time window' defined by the period of seed dispersal and seed longevity (Mahoney and Rood 1998). Besides the timing constraint, the moisture requirements for poplar recruitment are also so restrictive that they are only occasionally satisfied (Mahoney and Rood 1998), resulting in extensive recruitment failure, sometimes for decades (Bradley and Smith 1986; Johnson 1992; Stromberg 1993).

Populus germination occurs rapidly (usually within a period of 24 h) when seeds land on moist sites (Siegel and Brock 1990; van Splunder et al. 1995). However, because they are shade-intolerant, seedlings cannot compete with established vegetation (Cooper et al. 1999). Thus, seedling colonization and early establishment rely on the fresh, open and bare new alluvial deposits formed during fluvial-geomorphic events that are exposed as floodwaters recede. Consequently, the seed dispersal period of *Populus* spp. strategically coincides with periods when floods are most likely to occur and when the most suitable conditions for seed germination and seedling establishment are present (White 1979; Stromberg 1993). Thus, *Populus* spp. have a definite and predictable seed dispersal period (Johnson 2000). However, the timing and duration of the seed release period can vary inter-annually in a range of weeks as it is basically a function of photoperiod, atmospheric temperature and precipitation (Mahoney and Rood 1998; Stella et al. 2006). Normally, within the same species, it may begin later and be shorter at higher elevations and latitudes than at lower sites (Barsoum 2001). However, Stella et al. (2006) recently found later seed release in hotter downstream sites compared to upstream sites in *P. fremontii* and *Salix gooddingii* and attributed the differences to the evolutional advantage of coordinating seed release with snowmelt spring floods at the catchment scale.

The formation of nursery sites depends on the geologic and climatic setting and the local fluvial processes (Friedman and Lee 2002; Cooper et al. 2003). Historically, either several years of channel narrowing followed by low peak flows, or moderate to high magnitude flooding events (3- to 15-year recurrence intervals) causing channel migration and scouring existing vegetation have been associated with successful recruitment (Bradley and Smith 1986; Baker 1990; Howe and Knopf 1991; Stromberg et al. 1991; Johnson 1994; Cordes et al. 1997; Scott et al. 1996, 1997; Friedman and Lee 2002; Braatne et al. 2007). However, in many regulated reaches extensive recruitment may only occur after rare, catastrophic flood events that result in overbank flooding or lead to massive geomorphic change (Yin 1998; Rood et al. 1998).

In order to survive, seedlings must be positioned high enough to avoid being scoured by subsequent floods, buried by sediments or suffer from permanent anaerobic conditions; and low enough to maintain contact between the growing root and the falling water table and associated moisture zone (Stromberg et al. 1991; Mahoney and Rood 1998; Barsoum 2001). In fact, most of the seedlings die during the first year, mainly as a consequence of erosion and sedimentation from subsequent flood events, prolonged inundation, winter ice scour, insufficient light and drought-stress (Stromberg 1993; Scott et al. 1997; Rood et al. 1998; Cooper et al. 1999; Johnson 2000). Then, regardless of a high sexual reproductive potential, very few or no seedlings establish at most sites in most years (Braatne et al. 1996) and many of the successful recruits fail to survive to maturity (Cooper et al. 1999; Johnson 2000). In contrast, pulses of recruitment occur in favorable years (Rood et al. 1998). Although root elongation rates for first-year poplar seedlings are reported to be less than 1.3 cm day^{-1} (see summary by Mahoney and Rood 1998), it has been empirically demonstrated that poplar seedlings can survive drawdown rates of even 8 cm day^{-1} (Mahoney and Rood 1991). The drawdown rate thresholds for seedling survival and overall resistance of seedlings to low water tables are determined by the soil texture, which determines the thickness of the capillary fringe, the soil stratigraphy and the extra soil moisture provided by local precipitation (Segelquist et al. 1993; Barsoum and Hughes 1998; Cooper et al. 1999). Mahoney and Rood (1998) even proposed 2.5 cm day^{-1} as a maximum water declining rate for the optimal growth and survival of the seedlings of many *Populus* species.

Partly based on the drawdown rate, Mahoney and Rood (1998) created the 'Recruitment Box Model', a graphical technique aimed at defining the ideal characteristics of the river hydrograph (magnitude, timing and rate of

drawdown) for seedling establishment. The model was shown to be an effective tool for restoration of riparian poplar forests when it was successfully tested in the St. Mary River in Alberta, Canada (Rood and Mahoney 2000; Rood et al. 2005) and the Truckee River in Nevada, USA (Rood et al. 2003, 2005). However, specific studies on local hydro-geomorphology, seedling growth and survival and phenological analyses are needed to calibrate and import the model to other riparian species and rivers (Horton and Clark 2001; Amlin and Rood 2002), as there may be differences in the minimum flow magnitudes creating nursery sites, optimum water table decline rates, seed dispersal timing and germination in those environments.

Populus alba L., the European White Poplar, is an autochthonous species that has been present in the Central Europe and Mediterranean regions, since at least the Middle or Lower Pleistocene (Roiron et al. 2004). It belongs to the Section *Populus*, a sub-genus taxonomic group of the genus *Populus* that includes species typical of dry habitats (Karrenberg et al. 2002). In the Iberian Peninsula (SW Europe), the species occupies the riparian areas of perennial streams and large rivers at low elevations (usually <600 m) (Lara et al. 2004). In the floodplain forests of the Middle Ebro River (NE Spain), *P. alba* is one of the dominant overstory species. Mean *P. alba* basal areas of 34.2 m² ha⁻¹ and stem densities of 658 stems ha⁻¹ have been measured in gallery forests older than 50 years (González et al., unpublished data). However, the species is extremely rare within active recruitment sites and forests that originated after the 1950s (González et al., unpublished data), when the massive regulation works began to dramatically change the hydro-geomorphologic patterns in the Middle Ebro River (Ollero 2007; Cabezas et al. 2009). Although *P. alba* is a widespread tree species in Central and Southern Europe, Northern Africa and Central and Western Asia (Roiron et al. 2004), its post-dispersive sexual regeneration strategies remain totally unstudied.

In this context, the objectives of this study were twofold: (a) to determine the 'time establishment window' of *P. alba* within the Middle Ebro River by examining seed dispersal, germination and longevity traits and (b) to examine the effects of groundwater decline and substrate on survival and growth of *P. alba* seedlings using a greenhouse device for simulating alluvial water table declines. The results should help to guide future restoration plans using controlled floods.

Methods

Seed dispersal

The seed dispersal period and seed rain intensity of *P. alba* within the Middle Ebro River near Zaragoza, NE Spain

(41°39′N, 0°52′W) were determined for the period 2006–2008 using seed traps installed under the canopy of different white poplar stands within five different meanders along a 8-km long reach. A seed trap consisted of a 625 cm² wooden board hung horizontally 1 m above the soil surface by four ropes attached to nearby trees. A 400 cm² plastic sheet, coated with adhesive Tanglefoot© (Cooper et al. 1999; Gage and Cooper 2005), was attached to the upper surface of the board and changed every 3–4 days for seed counting. Seed dispersal phenology was monitored from late-March (before seed release) until mid-June (all fruits fallen). The initial 5 traps installed in 2006 were increased to 12 in 2007 and 2008, and remained at the same position each year. In order to evaluate the effectiveness of the trap sampling design, each year from 15 March to 15 June, the seed dispersal duration was confirmed by daily visual observations of seed release along the reach.

Seed collection

Seeds were collected in early-April 2007 from natural populations of *P. alba* along the reach by picking ripe catkins partially bearing opened seed capsules. The collected catkins were kept in paper bags for 24 h at ambient temperature, thus allowing the capsules to open and release their seeds (Gladwin and Roelle 1998). Later, the released seeds were separated from the abundant surrounding *pappus* by blowing air from an air nozzle through a series of sieves. Finally, the separated seeds were frozen at −20°C and stored in the dark in sealed jars containing silica gel desiccant for 9 months until they were germinated.

Seed germination and longevity

A sub-sample of seeds from three populations of *P. alba* was not frozen after collection and instead was used for germination and longevity tests. The tests consisted of weekly scattering of 50 seeds in Petri dishes (three replicate dishes per population) containing wet filter paper. The germinability (i.e., percent germination) was calculated by counting seeds with both an emergent radicle and two healthy cotyledons 5 days after sowing. The seeds were kept in paper bags in the dark at ambient temperature (since the first test was performed immediately after field collection) until no further germination was registered (12 weeks later). The germinability of the three populations was averaged weekly and the mean weekly average of the 13 tests was used as the overall *P. alba* germination rate. Seed longevity was expressed as the G_{50} (i.e., the storage time after which 50% of the seeds were still able to germinate) (Karrenberg et al. 2002) and calculated by

adjusting a sigmoidal function to the germination curve using Sigmaplot 9.0.

Greenhouse experiment

Hydrological treatments

An experimental system based on the 'Rhizopod', a device for simulating alluvial water table declines designed by Mahoney and Rood (1991), was constructed in a greenhouse to study the survival and growth of *P. alba* seedlings under five different groundwater decline scenarios. The five water treatments were: (1) permanent saturation for 64 days with the water table 2 cm below the substrate surface, (2) drawdown rate of 1 cm day^{-1} for 48 days to a water table of 50 cm below the substrate surface, (3) drawdown rate of 2.5 cm day^{-1} for 40 days to a water table of 100 cm below the substrate surface, (4) drawdown rate of 5 cm day^{-1} for 20 days to a water table of 100 cm below the substrate surface and (5) immediate and complete drainage (ID henceforth). The experimental facility consisted in a cluster of five water tanks (1.18 m diameter × 1.25 m long). Each tank represented a water table decline treatment and was filled with 24 plant growth tubes that were identical in design. The plant growth tubes were made from opaque PVC piping (10.3 cm inside diameter × 1.20 m long) capped at the bottom and cracked longitudinally. Wooden frames secured the entire assembly.

Substrates

Within each tank, 12 growth tubes were filled with a river gravel substrate (d_{50} = 8.5 mm) (Substrate G-Gravel) and the remaining 12 growth tubes with a predominantly sandy substrate with some gravel (56% by weight >2 mm, 32% >63 μm, 12% <63 μm; TOC 0.35%, TN 0.05%) (Substrate S-Sand). The 24 growth tubes were arranged randomly forming a 6 × 4 rectangle within each tank. Both substrates were taken from the floodplains of the Ebro River. We used natural substrate as previous research has shown that mycorrhizal associations may be important for *Populus* (Lodge 1989) and to ensure that they were similar in texture to some riparian substrates in the potential nursery sites of the Ebro River Basin. In all, the experimental design included five water treatments (tanks) × two substrates (G Gravel, S Sand) × 12 tubes (replicates) = 120 tubes. In order to settle down the substrate, the growth tubes were simultaneously watered from the bottom by filling the tanks with water collected in the Ebro River. The longitudinal cracks of the growth tubes allowed water circulation within the whole system. After settling, the tubes were refilled with dry substrate

and then watered again. The operation was repeated until all the tubes were topped up with substrate and no variation in the substrate level was observed for 24 h. The substrate was kept saturated by maintaining the water level 2 cm below the sediment surface during the days preceding the scattering of seeds. Small pieces of styrofoam were spread on the water surface to control algal growth and prevent water heating.

Controlled environmental parameters

The five tanks were located in a greenhouse with controlled temperature, humidity and irradiance. A 12-h day/night cycle was maintained using a set of metal halide lamps which guaranteed an approximate minimum of 3,000 lux. Temperature averaged 22°C in the daytime and 13°C at night and ranged from 11 to 35°C. The average relative humidity was 52 and 72% (day/night, respectively), and ranged from 16 to 95%. These values are similar to mid-April to mid-June climate data at the weather station in Alfranca (Zaragoza), located less than 1,000 m from the Ebro River main channel (data provided by the Regional Weather Agency, Aragon Department of Agriculture and Alimentation). Mean diurnal light intensity was 33,485 lux. Within each treatment, the soil volumetric water content at intervals of 20 cm was monitored using time domain reflectometry (TDR) by installing a cluster of probes at 10, 30, 50, 70 and 90 cm below the substrate surface in one of the 12 sandy substrate growth tubes. TDR values were recorded twice weekly. We assumed that the gravel substrate experienced minor capillary ascension compared to the sandy substrate, as it contained no fine particles. Mahoney and Rood (1992) already reported a 5 cm capillary rise within a gravel substrate with a typical particle size of 10 mm (similar to the proposed in this experiment), while it reached 70 and 50 cm within a sandy and a gravel–sand mixed substrate, respectively.

Sowing and thinning

On 13 January 2008, a total of 100 seeds (12,000 seeds m^{-2}) were scattered on the saturated substrate surface of each growth tube. Before, a thin layer (1 cm) of peat was added to the top substrate to provide a uniform surface on which the seeds were sown. The sowed seeds were regularly misted for the following 24 h to enhance imbibition and ensure contact between seeds and substrate, thus promoting germination and establishment. On 21 January 2008, the seedlings were thinned to the 20 healthiest individuals per growth tube. The water level was kept 2 cm below the sediment surface until 22 January 2008, when the five water treatments started (day 1). After that, the water levels were adjusted twice daily to the five

proposed hydrological treatments manually by either adding or draining water from the tanks.

Plant traits measurements

Seedling survival in each growth tube was recorded twice weekly until day 53. Plant height to the shoot tip (±1 mm) and number of leaves (long axis ≥ 2 mm) of the surviving seedlings were measured weekly. Root length and biomass measurements were destructive, and required harvest operations. Among the 12 tubes for each of the ten treatments (2 substrates × 5 water table declines), three were harvested on day 17 (harvest 1), three on day 38 (harvest 2) and the remaining six tubes at the end of the experiment on day 56 (harvest 3). For the harvest operations, each tube was lifted from the tank, laid horizontally, gently emptied on a table and the living seedlings were separated from the substrate by carefully watering the extracted soil column. The length of the major roots was measured to the nearest mm. The seedlings were then washed before the shoots and roots were oven dried at 60°C for 72 h, and weighed to the nearest tenth of a milligram. To prevent root breaking during the tube-emptying procedure, the substrate was kept wetted for 3 days before the day of harvest by completely submerging the selected tubes in an additional tank.

Statistical analyses

The data from week 3 (harvest 1), week 6 (harvest 2) and week 8 (harvest 3) were analyzed with two-factor analysis of variance with type of substrate (2 levels) and rate of water table decline (5 levels) as fixed factors; and (1) seedling survival, (2) shoot height, (3) number of leaves, (4) root length, (5) plant biomass and (6) root to shoot biomass ratio as the dependent variables. Growth tubes were used as replicates. Tukey post hoc range tests and t tests ($P < 0.05$) were performed to compare the treatments. As some measurements were destructive, the number of replicates (initially 12 tubes) decreased with the three successive harvests. In addition, through the course of the experiment, all the seedlings in some tubes died and, then, the number of cases could not remain the same for all variables. Therefore, the degrees of freedom of the ANOVAs varied among dependent variables and dates (Table 1).

Pseudoreplication

As each water table decline rate was implemented within a single water tank, other factors could confound the influence of water table treatments on seedling survival and growth. Then, precautions were taken to minimize the potential effects of pseudoreplication in the study and ensure all the conditions (aside from the drawdown rate) were identical among tanks. Each of the two substrates was mixed homogenously before being poured into the 120 growth tubes that were then randomly assigned to each tank. The five tanks were arranged randomly in the greenhouse with homogeneous and controlled environmental parameters and placed next to each other with only enough space to allow performing measurement and harvest operations. The collected seeds were mixed before sowing and distributed randomly among the 120 growth tubes.

Results

Seed dispersal

Populus alba seed rain in 2006–2008 began in early-April, peaked in mid-April and lasted 6–8 weeks (Fig. 1). The median cumulative seed rain density varied significantly across years, with 43,526, 18,843 and 9,120 seeds m^{-2}·in 2006, 2007 and 2008, respectively ($P = 0.018$, $df = 2$, $\chi^2 = 8.031$, Kruskal–Wallis test). Within each trap, seed rain density varied by an average of one order of magnitude from 1 year to another. The absolute minimum and maximum cumulative seed rain recorded in any trap in any year was 889 and 97,420 seeds m^{-2}, respectively. Daily seedfall differed significantly among the 3 years ($P = 0.000$, $df = 2$, $\chi^2 = 55.433$, Kruskal–Wallis test) and averaged 929, 740 and 221 seeds m^{-2} day^{-1} in 2006, 2007 and 2008, respectively. Locally in a trap, the maximum daily seedfall rate in any single measurement was 13,867 seeds m^{-2} day^{-1}.

Seed germination and longevity

Populus alba seed germinability was rather high. Almost all seeds (92%) germinated immediately after collection (Fig. 2) and most (>80%) remained viable 2 weeks after they were released from the catkins. Median seed longevity (G_{50}) was 30 days, indicating potential for survival in dry conditions well beyond 1 month. Some seeds still germinated 70 days (10 weeks) after the capsules opened.

Soil moisture changes

In the greenhouse experiment, the volumetric water content (θ_v) was continuously measured in the sandy substrate after the seeds had been sown (Fig. 3). The topsoil (0–20 cm) remained saturated for at least 18 days with a 1 cm day^{-1} water table decrease, for 7 days with a 2.5 cm day^{-1} decrease and for 1 day with a 5 cm day^{-1} decrease. In the immediate drainage (ID) treatment, the topsoil lost saturation within the first day of water table manipulations. The

Table 1 Results of two-way ANOVA for six plant traits treated with five rates of water table decline and two substrate textures at harvests 1, 2 and 3

Parameter	Harvest 1 (week 3)			Harvest 2 (week 6)			Harvest 3 (week 8)		
Source of variation	df	F test	P value	df	F test	P value	df	F test	P value
Seedling survival (%)	N = 120			N = 90			N = 60		
Water (W)	4	100	**0.000*****	4	73	**0.000*****	4	56	**0.000*****
Substrate (S)	1	793	**0.000*****	1	201	**0.000*****	1	112	**0.000*****
W × S interaction	4	62	**0.000*****	4	17	**0.000*****	4	17	**0.000*****
Error	110	MSE = 122.8		80	MSE = 202.2		50	MSE = 204.7	
Shoot height (cm)	N = 94 (26 dead of 120)			N = 63 (27 dead of 90)			N = 33 (27 dead of 60)		
Water (W)	4	5	**0.002****	4	11	**0.000*****	4	6	**0.007****
Substrate (S)	1	111	**0.000*****	1	51	**0.000*****	1	0	0.570
W × S interaction	3	2	0.155	2	10	**0.000*****	0	–	–
Error	85	MSE = 0.0		55	MSE = 0.2		27	MSE = 1.3	
Number of leaves	N = 94 (26 dead of 120)			N = 63 (27 dead of 90)			N = 33 (27 dead of 60)		
Water (W)	4	12	**0.000*****	4	13	**0.000*****	4	6	**0.002****
Substrate (S)	1	4	**0.049***	1	21	**0.000*****	1	1	0.387
W × S interaction	3	5	**0.003****	2	22	**0.000*****	0	–	–
Error	85	MSE = 0.2		55	MSE = 0.2		27	MSE = 1.0	
Root length (cm)	N = 21 (9 dead of 30)			N = 18 (12 dead of 30)			N = 33 (27 dead of 60)		
Water (W)	4	10	**0.001****	4	26	**0.000*****	4	30	**0.000*****
Substrate (S)	1	2	0.184	1	4	0.062	1	7	**0.013***
W × S interaction	1	0	0.536	0	–	–	0	–	–
Error	14	MSE = 0.8		12	MSE = 2.6		27	MSE = 13.5	
Plant biomass (mg)	N = 21 (9 dead of 30)			N = 18 (12 dead of 30)			N = 33 (27 dead of 60)		
Water (W)	4	3	**0.041***	4	13	**0.000*****	4	13	**0.000*****
Substrate (S)	1	0	0.542	1	17	**0.001****	1	1	0.821
W × S interaction	1	0	0.709	0	–	–	0	–	–
Error	14	MSE = 0.6		12	MSE = 3.3		27	MSE = 257.1	
Root:shoot ratio (mg/mg)	N = 21 (9 dead of 30)			N = 18 (12 dead of 30)			N = 33 (27 dead of 60)		
Water (W)	4	4	**0.019***	4	3	0.051	4	4	**0.007****
Substrate (S)	1	4	0.057	1	2	0.224	1	1	0.757
W × S interaction	1	4	0.057	0	-	-	0	-	-
Error	14	MSE = 0.0		12	MSE = 0.0		27	MSE = 0.1	

Note that the degrees of freedom (df) of each analysis decreased with each harvest and differed among variables as a result of destructive harvests and seedling mortality. In addition, the df of the W × S interaction declined when all replicates for some water table × substrate treatments died

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

MSE mean square error

Fig. 1 Density of seed rain (seeds·m^{-2}·day^{-1}) in 2006, 2007 and 2008. Each point represents mean of 5, 12 and 12 seed traps (2006, 2007 and 2008, respectively). The *error bars* represent ±1 standard error of the mean. Within each year, *filled triangles* and *numbers* indicate the first and last days of the seed dispersal period observed visually
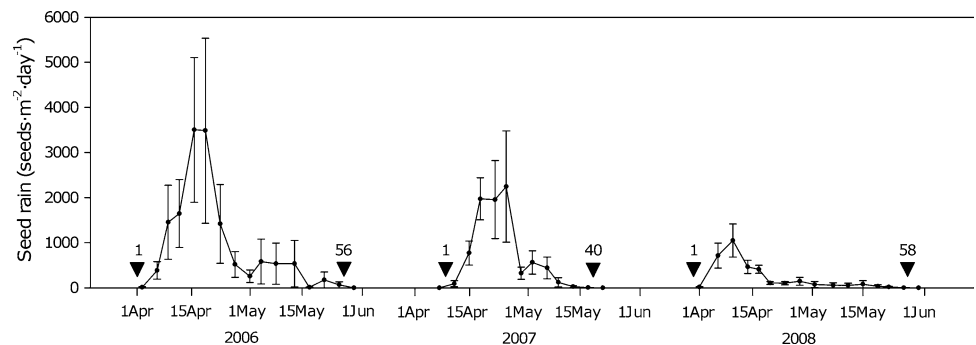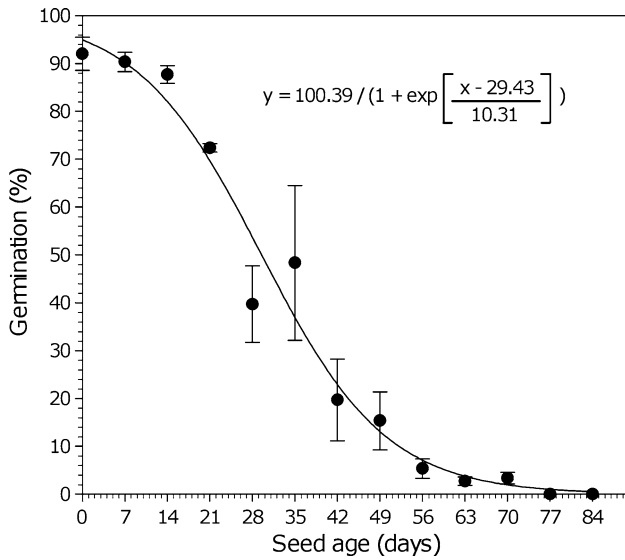
Fig. 2 Percent germination of seeds stored for increasing lengths of time. Each *point* represents the mean of three natural populations. The *error bars* represent ±1 standard error of the mean. Each population mean was obtained from three replicate Petri dishes with 50 seeds each. The *line* denotes the adjusted sigmoidal function to the germination curve

Fig. 3 Variation in soil volumetric water content (θ_v) in the sandy substrate throughout the course of the experiment with five water table decline treatments. The soil volumetric water content (θ_v, m³ of water per m³ of soil) was measured at 20-cm intervals with TDR probes installed 10, 30, 50, 70 and 90 cm below the substrate surface. The *white dashed line* represents the simulated water table level

drawdown rate also influenced the thickness of the capillary fringe. In the 1 and 2.5 cm day^{-1} treatments there was always a 20 cm layer of soil over the water table level where volumetric water content was greater than 20% ($\theta_v = 0.20$ m³ m^{-3}). However, the 5 cm day^{-1} treatment seemed to prevent effective capillary ascension. Unexpectedly, the immediately drained substrate retained some moisture during the first weeks, especially in the lower soil layers. In addition, moisture did not always follow a steady depth gradient, probably because of the uneven presence of gravel along the substrate column. For logistical reasons, a continuous water table decline in the treatments 2.5 and 5 cm day^{-1} was not possible for the 8 weeks of experiment. Lower soil moisture in deep soil layers would have been expectable with lower final water table levels and might have affected seedling growth. Likewise, the 3 days of submersion before harvesting, necessary to prevent root breaking, might have slightly stimulate seedling growth.

Seedling survival

Seedling survival (Fig. 4) was lower in gravel than in sand (substrate effect; Table 1), except when the substrates were saturated (water × substrate interaction; Table 1). Survival was also lower with faster water level decline rates (water effect; Table 1), especially in gravel (water × substrate interaction; Table 1). By the end of the experiment, the only surviving seedlings in the gravel substrate were those

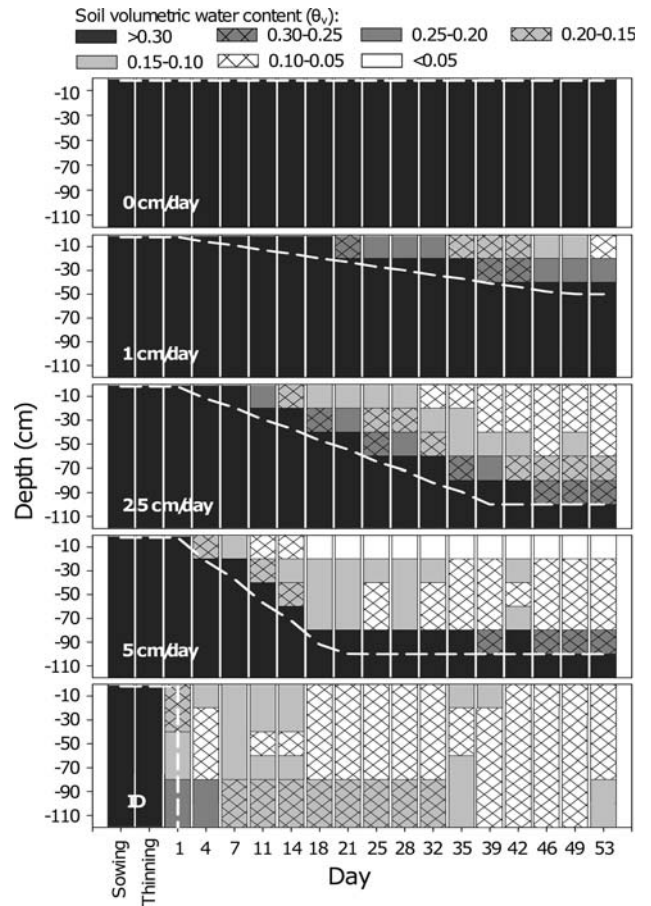grown under saturated conditions, but survival in that treatment was high (85%). In the sandy substrate, in contrast, survival was no lower in the 1 cm day^{-1} treatment than in the saturated treatment, and ~20% of seedlings survived even in the 5 cm day^{-1} and ID treatments.

Shoot height

Seedling height (Fig. 5a) did not significantly differ among substrate types at the end of the experiment (substrate effect; Table 1), although several of the treatments had no remaining seedlings in the gravel substrate, and therefore the comparison was only across the saturated treatments. Also, the decrease in degrees of freedom due to harvests and mortality provided too little power to discern water × substrate interactions (Table 1). The lowest shoot heights were observed in the ID and saturation treatments (water effect; Table 1).
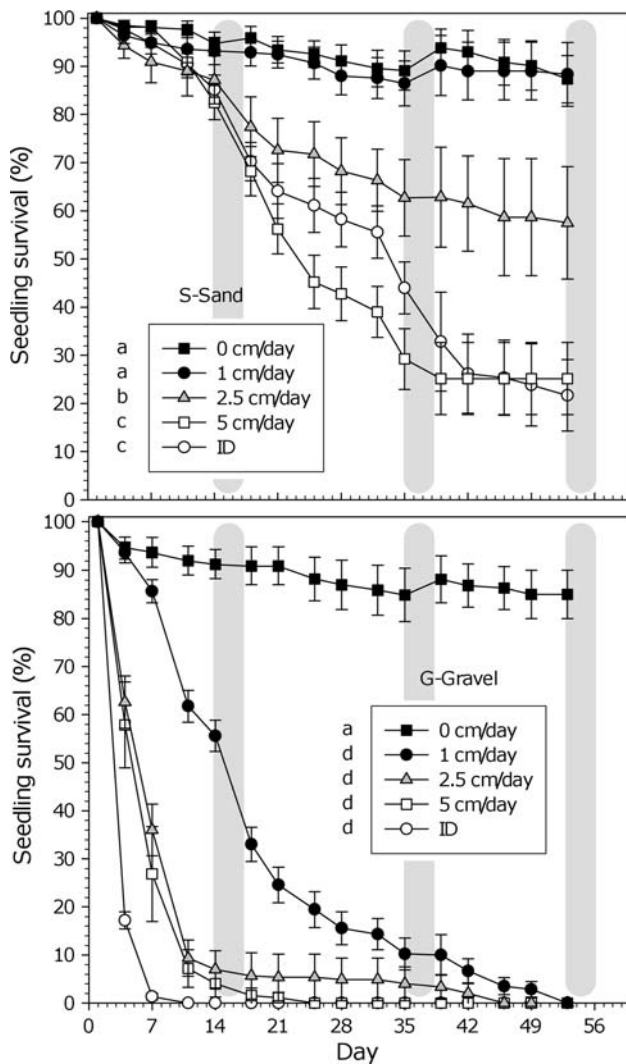
Fig. 4 Seedling survival in sandy and gravel substrates throughout the course of the experiment with five water table decline treatments. Each point represents the mean of 12 growth tubes (until day 14), 9 growth tubes (until day 35) and 6 growth tubes (until day 53). The *error bars* represent ±1 standard error of the mean. *Letters* denote significant differences between treatments at the end of the experiment (two-way ANOVA followed by post hoc *t* tests $P < 0.05$). Background *gray bands* indicate the days of harvest operations

Number of leaves

Like shoot height, the number of leaves (Fig. 5b) was not significantly different among substrates (substrate effect; Table 1) at the end of the experiment. Similarly, widespread mortality in the gravel substrate limited the comparison among substrates to saturated conditions and reduced power to discern water × substrate interactions (Table 1). Again, the ID, and to a lesser extent, the seedlings subjected to the saturation treatments produced significantly less leaves than the seedlings subjected to the 1, 2.5 and 5 cm day^{-1} treatments (water effect; Table 1).

Root length

In the first and second harvest, root length (Fig. 6a) was lower in the drier treatments (water effect; Table 1). At the end of the experiment, roots grew significantly longer in the 1, 2.5 and 5 cm day^{-1} treatments than in saturation and ID conditions (water effect; Table 1). Root length was lower in saturated sand than in saturated gravel (substrate effect; Table 1), but widespread mortality in gravel made impossible to discern water × substrate interactions (Table 1). Some of the longest roots reached the 60 cm depth (growing rate ~ 1 cm day^{-1}).

Biomass

Although significant differences in total biomass were observed between treatments in the first and second harvest, they were difficult to interpret (Fig. 6b; Table 1) and may have been due to the difficulties of precisely washing and weighting the tiny harvested shoots and roots. However, at the final harvest, seedling biomass was greater in the 1, 2.5 and 5 cm day^{-1} treatments than in the ID and saturation treatments (water effect; Table 1). There were no significant differences in biomass among substrate types (substrate effect; Table 1). Like biomass, root to shoot ratios had no clear trends in the first and second harvest (Fig. 6c). However, at the end of the experiment, the seedlings subjected to permanent saturation had lower root:shoot ratio than the other four treatments (water effect; Table 1). In particular, the seedlings subjected to permanent saturation conditions allocated less biomass to roots than to shoots (root:shoot ratio <1), while the seedlings subjected to the four declining treatments concentrated more resources to the root system (root:shoot >1). In all cases, there was no effect of substrate type on total biomass and root to shoot ratios (substrate effect; Table 1), but, as mentioned before, comparisons could only be made across saturated conditions due to widespread mortality in gravel.

Discussion

Seed dispersal periods reported in the literature range in duration from 2 to 9 weeks for *P. nigra* L., 4 to 9 weeks for *P. fremontii*, 3 to 12 weeks for *P. deltoides* Marsh and 6 weeks for *P. balsamifera* L., depending on the study area (see summary by Guilloy-Froget et al. 2002). A long seed dispersal period should be especially favorable for seedling establishment in a Mediterranean river such as the Ebro River, characterized by a considerable intra- and interannual flow discharge variability (Ollero 2007). Thus, the 6- to 8-week seed dispersal period we observed for *P. alba*, which is somewhat above the average duration period of

Fig. 5 **a** Plant height to the shoot tip (±1 mm) (cm) and **b** number of leaves (long axis ≥2 mm) of the seedlings growing in sandy and gravel substrates throughout the course of the experiment with five water table decline treatments. Each *point* represents the mean of surviving seedlings in the growth tubes at each date. The *error bars* represent ±1 standard error of the mean. *Letters* denote significant differences between treatments at the end of the experiment (two-way ANOVA followed by post hoc *t* tests $P < 0.05$). Background *gray bands* indicate the days of harvest operations
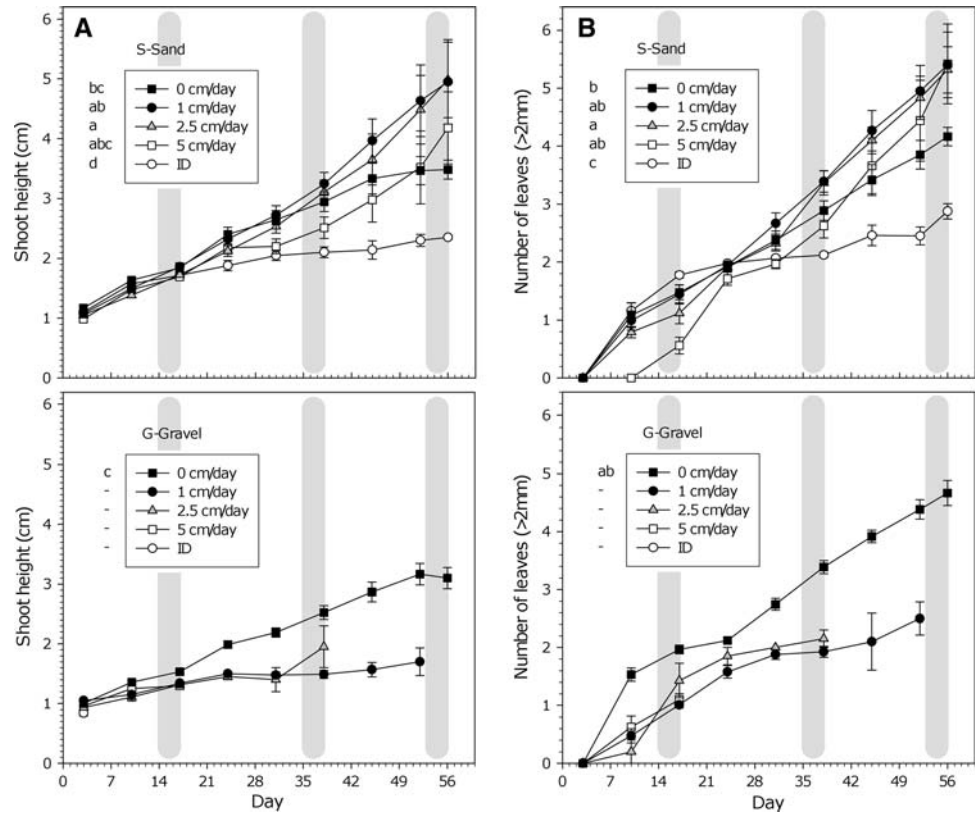
Populus spp., might partly explain the historical common presence of *P. alba* along the Middle Ebro River (González et al. unpublished data). In addition, the early spring seed release coincides with the period when floods are more likely to occur within the Middle Ebro River, as a result of rainfall and snowmelt in the bordering mountain ranges. Indeed, peak seed dispersal was close to mid-April, i.e., earlier than other *Salicaceae* spp. in other regions of the world (Guilloy-Froget et al. 2002). The timing of seed release did not vary greatly from 1 year to another, only hastened or delayed by 1 or 2 weeks. Although the photoperiod, air temperature and precipitation do not vary greatly within the Middle Ebro River (a 346 km reach), our results should be taken with caution when applying to other sections of the river and to other watersheds, as the study reach was relatively small (8 km). In this sense, future studies aimed at modeling the *P. alba* seed dispersal timing as a function of temperature and other climatic factors are recommended (Stella et al. 2006).

Mean seed rain rates in *P. alba* were two orders of magnitude higher than those described for *P. deltoides* by Cooper et al. (1999), who also used Tanglefoot© coated traps. This difference could be due to the fact that Cooper et al. (1999) installed seed traps in potential seedling establishment sites instead of directly beneath the seed sources. Nevertheless, the extremely dense seed rain reported here suggests that seed production is not a limiting factor for *P. alba* recruitment, even though the spatial and temporal variabilities in seed rain intensity were notable. Gage and Cooper (2005) also reported high inter-annual and spatial variability in seed production by six *Salix* spp. in the Fall River and Big Thompson River, Colorado, USA.

As expected, initial germinability of *P. alba* was almost complete (92%). Seed longevity ($G_{50} = 30$ days) was longer than reported for *P. nigra* by van Splunder et al. (1995) and Karrenberg and Suter (2003) ($G_{50} = 15$ and 23 days, respectively) but much shorter than the $G_{50} = 85$ reported for *P. deltoides* by Fenner et al. (1984). However, seeds germinate as soon as they contact a moist surface and then, weathering forces (i.e., rainwater, air humidity, dewdrops, etc.) probably substantially reduce seed longevity under field conditions (Karrenberg and Suter 2003). Thus, the 'time window' for establishment may be determined by seed dispersal timing (Karrenberg et al. 2002) and local hydrological conditions (Mahoney and Rood 1998) rather than seed germinability or longevity.

The results of the greenhouse experiment show that the substrate type and water table level can influence *P. alba* seedling survival and growth substantially. Overall, seedlings responded best (in terms of both seedling survival and growth) to the sandy substrate and the 1 cm day^{-1} water table decline treatment. The absence of fine particles within the gravel substrate apparently prevented effective capillary ascension of water, resulting in widespread mortality
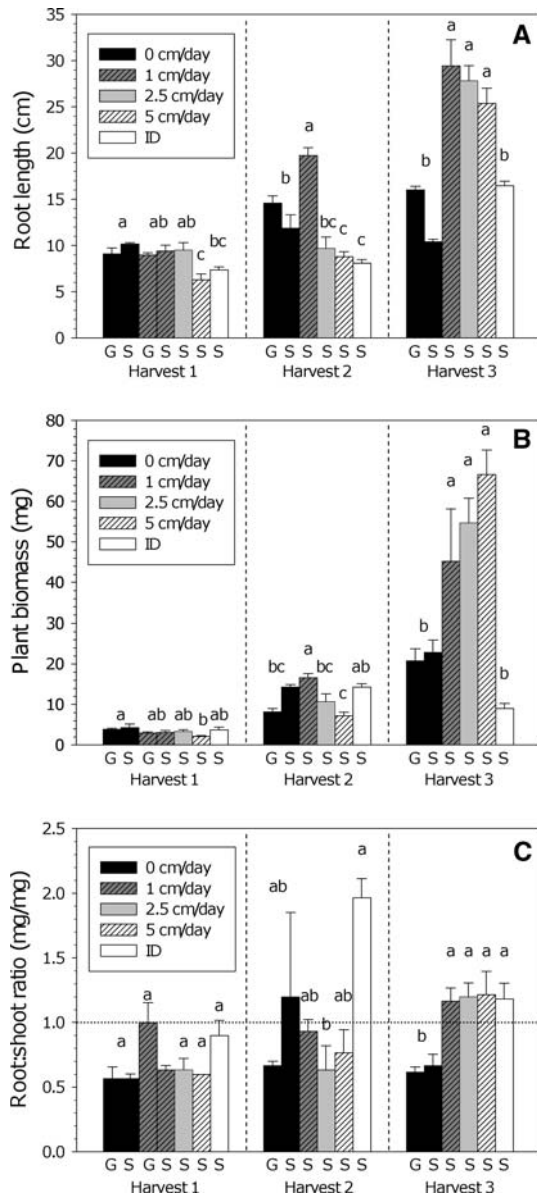
Fig. 6 a Root length (cm), **b** total plant biomass (mg) and **c** root to shoot ratios (mg/mg) at harvest on days 17, 38 and 56. *Vertical bars* represent the mean of each plant measurement. The *error bars* represent ±1 standard error of the mean. *Lowercase letters* denote significant differences between treatments (two-way ANOVA followed by Tukey post hoc range tests $P < 0.05$) (*S* sand, *G* gravel)

in the declining and ID treatments, as roots could not maintain contact with the falling water table. The highest mean root growth rates ranged from ∼4 mm day^{-1} (sand, 5 cm day^{-1}) to ∼5 mm day^{-1} (sand, 1 cm day^{-1}), which are similar to those reported by Mahoney and Rood (1991) for the natural poplar hybrid *P. deltoides* × *P. balsamifera* and close to the 6 mm day^{-1} proposed by Fenner et al. (1984) for *P. fremontii*. But even the highest root elongation rates recorded in this experiment (∼1 cm day^{-1}) were insufficient to cope with the water table declines

(≥1 cm day^{-1}) in gravel. However, the fact that there were no significant survival and growth differences between the substrates under saturated conditions (aside from root length) suggests that the gravel substrate per se is not limiting when enough water is available. Within the finer substrate, the capillary fringe provided the necessary soil moisture to support considerable percentage of seedlings (including in the ID treatment). By the end of the experiment, the surviving seedlings in the 2.5, 5 cm day^{-1} and ID treatments were rooted in soil layers with volumetric water content (θ_v) <0.10 m^3 m^{-3}, similar to the results of Segelquist et al. (1993), who suggested that 2% soil moisture ($\theta_v = 0.02$ m^3 m^{-3}) is the minimum water requirement for seedling survival and growth.

It seems that both immediate drainage and permanent saturation conditions are not compatible with *P. alba* seedling establishment, but that the species tolerates a broad range of water table declines of up to 5 cm day^{-1} rather than just an optimal decline rate, at least if the substrate allows effective capillary ascension. On the one hand, although seedling survival was surprisingly not different between the 5 cm day^{-1} and ID treatments, poor seedling growth in the ID treatment suggests that the seedlings might have failed to survive to maturity under those conditions. On the other hand, saturation limited shoot and especially root growth, which is consistent with previous studies. In particular, Fenner et al. (1984) and Segelquist et al. (1993) described greater root elongation with declining water tables than under saturated conditions in *P. fremontii* and *P. deltoides*, respectively. Mahoney and Rood (1992) detected slower growth rates in *P. balsamifera* × *P. deltoides* hybrids growing under a constant water table and attributed that to root anaerobiosis. Surprisingly, while seedling survival decreased progressively with steeper water table declines, seedling growth (shoot height, number of leaves, biomass and root length) did not significantly differ between the 1, 2.5 and 5 cm day^{-1} water table treatments among surviving individuals. This paradox may reflect an increasingly positive stress response with regard to growth as the water table decline rates increased. An alternative explanation might be that only the seedlings that could achieve certain growth rates could survive the more abrupt drawdown rates.

River regulation has dramatically altered geomorphic dynamics in the Middle Ebro River. The change in geomorphic patterns has occurred sequentially in three main periods: (1) pre-regulation period until ca. 1950, with braided-meandering channel and unstable riverbanks; (2) regulation period until ca. 1980, with progressive degree of stabilization in the meandering channel and riverbanks, large reservoirs and numerous defenses built and (3) stabilization period until present time, with very reduced channel migration, restricted meandering channel and

stable riverbanks (Ollero 2007; Cabezas et al. 2009). As a result, the area covered by barren sites (potential nursery sites) has decreased from 13.2 to 1.8% of the 10-year floodplain in the period 1946–2003 (Cabezas et al. 2009). Regulation has also notably decreased the frequency and magnitude of overbank floods (Cabezas et al. 2009). However, the drawdown rates from April to June have not changed significantly with regard to the pre-regulation period (Fig. 7). They correspond to a median drawdown rates of 3.1, 2.6 and 2.3 cm day^{-1} in the pre-regulation, regulation and stabilization period, respectively ($P = 0.432$, $df = 2$, $\chi^2 = 1.679$, Kruskal–Wallis test). Apparently, the observed low recruitment of P. alba might be due to the reduction in the frequency of high floods and to the severe loss of geomorphic dynamism but not to too abrupt drawdown rates.

Many restoration projects have difficulties in providing nursery sites for phreatophyte recruitment and instead approach restoration by planting cuttings, saplings or adult
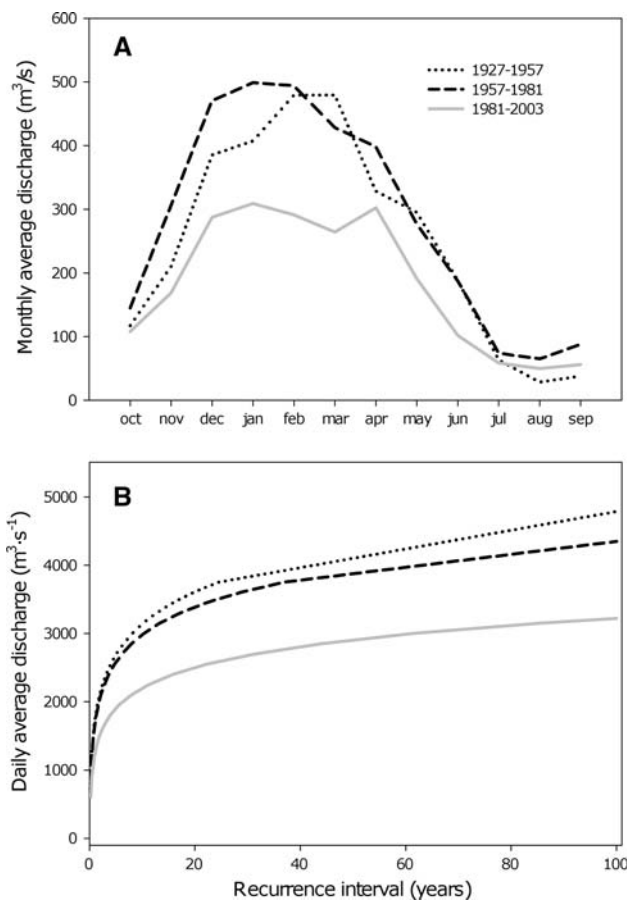

Fig. 7 a Monthly average discharge and b magnitude–frequency plots illustrating reduced frequency of high-discharge events in the unregulated period (1927–1957), regulation period (1957–1981) and stabilization period (1981–2003) at the gauging station of Zaragoza, Middle Ebro River

stems (Rood et al. 2003). Nevertheless, this study shows that P. alba is a potentially valuable species for restoration based on patterns of sexual recruitment, i.e., long seed dispersal periods with peaks coinciding with early spring floods, high initial seed germinability and longevity and tolerance of early seedlings to a relatively broad range of water table decline rates. In particular, the promotion of fluvial-geomorphic events occurring in mid-April, followed by smooth water table declines of less than 1 cm day^{-1} in gravel substrates and less than 5 cm day^{-1} in sandy substrates might enhance early recruitment of P. alba seedlings. In cases where the geomorphological dynamics are highly constrained by regulation and the release of catastrophic floods is not socially admissible (e.g., the Middle Ebro River), the creation of nursery sites for P. alba might be achieved by mechanically disturbing the substrate and removing the competing vegetation on potential recruitment sites directly before seed release peaks (from late-March to early-April in the Middle Ebro River). Later, the created barren sites would need to be locally flooded to disperse the seeds and provide adequate moisture for seeds germination and seedlings establishment (Barsoum 2001), and then would need to be drained according to the proposed drawdown rates. The recruitment zones would also need to be protected from grazing, as livestock has been shown to trample seedlings (Rood et al. 1998) and prefer Populus spp. over other, less palatable species such as Tamarix spp. (Stromberg 1998).

However, this restoration approach may not always be effective as sexual recruitment is a complex process. Other factors such as post-colonization floods (Johnson 1994, 2000; Dixon and Turner 2006), inter-specific competition (Sher et al. 2000; Roelle et al. 2001), shade tolerance (Sacchi and Price 1992; Cooper et al. 1999), short-term climatic fluctuations (Baker 1990) and herbivory (Andersen and Cooper 2000) have not been addressed in this study and may determine the fate of initially established seedlings. It would also be interesting to examine the potential of vegetative recruitment of P. alba, and its relative importance compared to sexual recruitment. Legionnet et al. (1997), Gom and Rood (1999) and Barsoum et al. (2004) described important vegetative propagation in some Populus species, but, to our knowledge, there is no study on P. alba vegetative reproduction in the existing literature. Moreover, in the context of global warming, P. alba may increase in abundance within temperate Northern river floodplains where it is only poorly represented today. To fully understand P. alba regeneration strategies and better inform future restoration efforts, studies are needed that monitor seedling survival and growth in natural settings and that relate historical recruitment events to hydrologic regimes and geomorphological processes. In the meantime, additional greenhouse and laboratory studies may provide

further insights into the regeneration strategies of this riparian tree species.

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