

Recruitment and regeneration in populations of an endangered South Iberian Tertiary relict tree

Arndt Hampe*, Juan Arroyo

Departamento de Biología, Vegetal y Ecología, Universidad de Sevilla, Apdo. 1095, E-41080 Sevilla, Spain

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Abstract

The southern Iberian Peninsula is one of the most important refugia of Tertiary relict plant taxa in Europe. Under the present summer-dry climate, relict populations may experience a severely reduced regeneration. We studied the demographic structure, seed set and initial recruitment in relict populations of the endangered tree *Frangula alnus* subsp. *baetica* (Rhamnaceae) to evaluate its regeneration potential under the present environmental conditions. Populations are restricted to small riparian forests of Southwest Spanish and North Moroccan mountain ranges. The distribution of fruit crop sizes was highly left-skewed, and a few old trees produced the large bulk of the population seed pool. Bird-mediated seed dispersal appeared inefficient and post-dispersal seed predation by mice was high. Secondary seed transport by elevated creek water flow after winter rains modified the primary seed dispersal, but in consequence most seeds germinated on recently formed sandbanks where seedlings experienced reduced initial growth and survival. The most important mortality factor was desiccation, followed by herbivory. None of 1144 monitored seedlings survived for 2 years. The demographic survey through five populations indicates that drought periods may cause temporal regeneration bottlenecks. Moreover, over the last two decades populations have experienced increasing regeneration problems. Two causes are suggested: (1) browsing pressure from introduced game animals, and (2) the impact of torrential water flow peaks after heavy winter rains, exacerbated by large-scale vegetation slashing in surrounding cork oak forests. We discuss conservation strategies for this and other relict tree species that account for the peculiarities of their habitat within the Mediterranean. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The mountain areas of the Mediterranean Basin bear an extremely high floristic richness and degree of endemism among temperate regions (Cowling et al., 1996; Médail and Quézel, 1997). This diversity results from their environmental heterogeneity and historical processes, which have originated the present coexistence of Ibero-African floristic elements, Euro-Siberian Pleistocene relicts and ancient, pre-Mediterranean taxa of Actotertiary origin (Herrera, 1992; Thompson, 1999). These oldest taxa of the European vascular flora have evolved under subtropical conditions of weak climatic seasonality and little drought or temperature stress, and many became extinct with the onset of the present

highly seasonal, summer-dry climate of the Mediterranean Basin in the Pliocene (Palamarev, 1989). A particularly high diversity of Arctotertiary relicts is found today in the mountain ranges of southwestern Iberia and northern Morocco (Baetic-Rifian hotspot, sensu Médail and Quézel, 1997), whose topography and proximity to the Atlantic Ocean mitigate the summer drought of the present Mediterranean climate. The Iberian and Tingitanian coastal mountain ranges are equivalent to ecological islands for species that were formerly distributed through large parts of Europe but are currently persisting as small, disjunct populations. Under present day conditions, regeneration may be poor and they are presumably highly sensitive to human alterations of their habitats (Eriksson, 1996; García et al., 1999). However, little ecological research has yet been done to examine the persistence and viability of relict populations in the Mediterranean Basin under the current climatic constraints (but see Castro et al., 1999; García et al. 1999).

* Corresponding author. Tel.: +34-954-557056; fax: +34-954-557059.

E-mail address: arndt@us.es (A. Hampe).

The present study uses the endangered South Iberian endemic tree *Frangula alnus* subsp. *baetica* (Rev. and Willk.) Rivas Goday ex Devesa (Rhamnaceae) as a case study to assess the reproduction and regeneration problems of Arctotertiary relict trees under the present Mediterranean climate. Our study organism is restricted to riparian forests along small creeks, that are dominated by *Rhododendron ponticum* subsp. *baeticum* and shared by numerous other ancient angiosperm and fern taxa (e.g. *Laurus nobilis*, *Culcita macrocarpa*, *Pteris incompleta*; see Rivas-Goday, 1968 for further details), which highlight the peculiar climate of these refugia, considered unique in western continental Europe (Rivas-Martínez et al., 1997). A recent study on the reproductive biology of southern Spanish *F. alnus* populations (Medán, 1994) has reported a very low seed set and virtual absence of seedlings (although the latter conclusion is based on casual observations), and its recruitment biology and regeneration potential is unknown. *F. alnus* subsp. *baetica* is considered to be in rapid decline and vulnerable according to IUCN standards, and has therefore been included in the recent Red Lists of Threatened Vascular Plants of Andalusia (Blanca et al., 2000) and Spain (Anonymous, 2000). It has recently become extinct in the Sierra Nevada region (Blanca et al., 1998), and is presently known from only about 20 locations in Andalusia in addition to a few populations in northern Morocco (Fennane and Ibn Tattou, 1998; Blanca et al., 2000).

Our aim is to report the maternal reproductive output and the sequential stages of the early recruitment in core populations of the species. In many plant species, the largest loss of reproductive potential occurs mostly between seed and seedling establishment (Clark et al., 1999), and biotic and/or abiotic factors acting during early recruitment may have profound effects on the dynamics and spatial structure of the population (Schupp and Fuentes, 1995; Clark et al., 1999). In a second step, we examine the age structure of several populations to test if recruitment bottlenecks have occurred and if these are associated with particular environmental events (e.g. droughts) in the region. Based on the results, we evaluate the current regeneration potential and viability of the studied *F. alnus* subsp. *baetica* populations and discuss possible conservation strategies.

2. Material and methods

2.1. The study plant

F. alnus subsp. *baetica* may become three times taller and twice as old as plants of the widespread shrublike subspecies *alnus* (Hampe and Bairlein, 2000), and its treelike habit resembles rather that of *F. azorica*, an

endemic species of the laurel forests of the Azores and Madeira. The reproductive biology of *F. alnus* subsp. *baetica* has been described in detail by Medán (1994) and Hampe and Bairlein (2000). *F. alnus* resprouts well but does not reproduce nor propagate vegetatively (personal observation, Godwin, 1943, see also Hampe and Bairlein, 1999). It flowers mostly between mid-May and mid-June, fruits ripen from late-June to mid-August. The small, hermaphroditic flowers are pollinated mainly by Hymenoptera and Diptera. *F. alnus* produces blackish drupes of 9.0 ± 0.8 mm (mean \pm S.D.) diameter with usually three stones, which are eaten and dispersed by resident passerine birds (mostly *Erithacus rubecula*, *Sylvia atricapilla* and *Turdus merula*). Predation of ripe fruits by insects has never been observed during the study, while postdispersal seed predation is almost exclusively due to mice (*Apodemus sylvaticus*).

The largest populations of *F. alnus* subsp. *baetica* occur in the coastal mountain ranges of the Strait of Gibraltar area. Plants typically grow in the understorey of riparian forests 10–20 m wide and a few hundred meters to few kilometers along small, shady creeks, which are surrounded by mediterranean sclerophyllous and semideciduous forests (see Ojeda et al., 1995, 2000, for details).

2.2. Study sites

The study was carried out between May and September 1997 on three populations (Aljibe, Medio and Puerto Oscuro Gorges) located in the Sierra del Aljibe ($36^{\circ}30'N$; $5^{\circ}35'W$, Cádiz province, Spain), about 40 km NNW of the Strait of Gibraltar. Study areas were located between 1.5 and 6 km from each other and extended between 350 and 700 m a.s.l. Two additional populations (Montero and Pasada Llana Gorges), both located within a 15 km radius, were included in a demographic survey. Mean annual temperature at the closest weather station (weather station Alcalá de los Gazules, 221 m a.s.l., at ca. 10 km) is $16.7^{\circ}C$. Rainfall concentrates in the autumn and winter months and averages 880 mm/year (SinambA Difusión, 1998). However, the water supply within the gorges is considerably higher and more constant than outside due to additional humidity contributed by low clouds and fog (Arroyo, unpublished data). Extensive winter rains cause torrential water flows which produce rocky riverbeds with dispersed sandy colluvia, scarce organic matter and herbaceous vegetation. Large parts of these riverbeds (“winter riverbeds” hereafter) become dry during the summer months.

2.3. Sampling design

In June 1997 we chose a 200 m long, representative river track within each population studied in detail and

counted all *F. alnus* individuals. All trees with a diameter at breast height (dbh, at 1.4 m above ground) >0.5 cm were recorded and marked individually, while smaller juveniles and recently emerged seedlings were counted separately. We determined the height and dbh (to the nearest 1 mm) of marked trees, and estimated their fruit crop size with binoculars at the start of the ripening season. Fruit censuses carried out on 18 trees of different size and repeated after a few days showed that the species' morphology (single-layered crown, relatively sparse leaf cover, fruits exposed at branch tips) allows reasonably accurate fruit crop estimates. We took diametric wood samples of 44 marked individuals using a Pressler core. The tree age was determined in the laboratory by counting the annual growth-rings under a dissecting microscope. The relationship between tree age and stem diameter was determined by linear regression. Furthermore, we collected 30 ripe fruits from each of 10 accessible trees and determined their seed number, the number of filled (i.e. putatively viable) seeds and the seed mass (to the nearest 0.1 mg).

Seed rain and seedling distribution patterns were recorded along 10 linear belt transects per population, that were 1 m wide and placed at 20-m intervals from the valley bottom upwards. The transects alternated between 10 and 20 m in length and were divided into 1-m² quadrats. Additionally, we randomly placed 25 1-m² quadrats, respectively, within the winter riverbeds of two creeks (Medio and Aljibe). The total sample area thus summed up 500 m², 188 of them within and 312 outside the winter riverbed. The distance of each sample quadrat to the nearest fruiting *F. alnus* canopy edge was measured. All quadrats of homogeneous substrate character (i.e. $\geq 75\%$ of the surface) were assigned to one of the four microhabitats shown in Table 1.

The seed rain was recorded in fruit traps placed in 100 randomly chosen sample quadrats. Prior to the beginning of the ripening season we installed two plastic trays of 25 cm diameter in each quadrat. The trays were fixed on the ground and covered with iron mesh (grid width 12 mm) to avoid predation by rodents. Preliminary trials had shown that predation from these seed traps was negligible. We examined traps every 2 weeks and

recorded the numbers of unripe and ripe fruits as well as bird-processed (i.e. ingested and regurgitated or defecated) filled and empty seeds.

To examine the seed predation by rodents we used fruits placed in drained Petri dishes. From the beginning of the ripening season 20 dishes, respectively, were placed either beneath or 10–15 m apart from fruiting *F. alnus* trees. They were checked weekly through the ripening season and filled each time with five fresh fruits. A dish was considered to be predated when at least three of the originally placed five fruits had disappeared (see Kollmann et al., 1998 for details of this method).

Seedling emergence within the transect quadrats was recorded between 14 and 17 June 1997. By this time virtually all seedlings had emerged while the oldest individuals were less than 2 weeks old. Identifiable dead seedlings were included in the count. Seedling survival was monitored in 16 permanently marked areas, which had been assigned to the microhabitats sandbank, forest ground and spring surroundings, respectively (total surface 9.7 m²; we did not find enough seedlings on rocky ground to include this microhabitat). The plots were censused fortnightly for 3 months. Dead individuals were classified by their presumed mortality factor (desiccation, browsing/trampling by ungulates, herbivory/infestation by invertebrates, or unknown) and removed. During the final count five seedlings per plot were chosen at random (all seedlings if less than five had survived), and their height and leaf number were recorded. In September 1999 we relocated the marked plots to search for surviving juveniles.

Finally, a demographic survey was carried out in May 2000. We recorded the age structure by measuring the dbh of all trees along a randomly chosen river track up to a number of about 130 individuals. In the smaller Pasada Llana population all trees were recorded. All dead trees were likewise recorded, while individuals smaller than 1.4 m were counted separately.

Despite a close relation between tree age and stem diameter (see later), it was impossible to calculate the exact year of germination of any individual tree by simple regression. To reduce assignment errors we

Table 1
Microhabitats covered by homogeneous sample quadrats

	Rock	Sandbank	Forest floor	Spring
Position within the winter riverbed	Yes	Yes	No	No
Litter cover	No	No (–low)	Low–high	High
Humus layer	No	No	Low–high	High
Summer soil humidity	No (–low)	No (–low)	Low	High
Number homogeneous quadrats (1 m ²)	80	17	300	2
Arriving diaspores/m ² (mean \pm 1 S.E.)	166.7 \pm 89.8	30.6 \pm 24.1	25.8 \pm 11.6	0
Emerging seedlings/m ² (mean \pm 1 S.E.)	4.2 \pm 1.5	34.6 \pm 11.1	2.2 \pm 0.4	16.5 \pm 7.5

grouped trees in 1-cm dbh size classes; for every size class we calculated then the running mean rainfall of the 2 years that were closest to the assumed germination years of the included trees. Note however that this procedure smoothes year-to-year variations of both rainfall and regeneration rates and produces a conservative measure of their variability and possible correlations.

3. Results

3.1. Reproduction and seed set

Stem diameter and plant age were highly correlated (linear regression: $y = 0.76x - 8.44$, $R^2 = 0.89$; $n = 44$; $P < 0.001$). Trees started to reproduce at an age of about 20 years (equivalent to a dbh of 6.0 cm). We recorded a total of 2794 seedlings, 57 juveniles with a stem diameter < 0.5 cm, 80 larger saplings and 154 adults within the three river tracks studied in detail. In 1997, 82% of the adults set fruit and each produced 2689 ± 4893 (mean \pm S.D.) fruits, which lead to an estimated total of 339 567 fruits within the three studied 200-m tracks. Fruits contained 2.9 ± 0.2 seeds, of which 76% were filled (i.e. putatively viable), resulting in an estimated total of 748 405 potential offspring within the studied total 600-m river track. However, most measured fruit traits experienced considerable among-plant variation (Table 2). The crop size was significantly correlated with tree age (linear regression: $R^2 = 0.42$, $F = 99.42$, $P < 0.001$, $n = 141$) and height ($R^2 = 0.17$, $F = 30.49$, $P < 0.001$, $n = 141$). The distribution of crop sizes was highly left-skewed with the three largest trees contributing as many fruits to the population seed pool as the smallest 90 adults (Fig. 1).

3.2. Seed dispersal and recruitment

The seed traps caught a total of 853 diaspores (i.e. entire fruits and bird-processed seeds, see Fig. 2). Assuming an average number of 2.9 seeds per fruit

(see above), the ratio between entire ripe fruits and bird-processed seeds found indicated that about 36% of the produced fruits had been consumed by birds. Compared to the abundance of ripe fruits, the percentage of ingested seeds decreased from July to September ($\chi^2 = 29.5$; $df = 4$; $P < 0.001$, Fig. 2). Seventy-two percent of all bird-processed seeds were recorded within a 1-m radius of the nearest fruiting *F. alnus* canopy, and only 9% were caught more than 2 m away. Since entire fruits fell up to 2 m away from the nearest canopy, birds transported only about 3% of all produced seeds to sites that were not reached by entire fruits. Both the total diaspore and the bird-dispersed seed rain were not randomly distributed among microhabitats ($\chi^2_{\text{all diaspores}} = 1288.6$; $df = 3$; $P < 0.001$; $\chi^2_{\text{bird-dispersed seeds}} = 79.0$; $df = 3$; $P < 0.001$, Fig. 3). Considerably more diaspores fell into the riverbed than expected by chance ($\chi^2 = 35.5$; $df = 1$; $P < 0.001$); however, this tendency was found to be only marginally significant when exclusively the bird-dispersed seed rain was considered ($\chi^2 = 3.63$; $df = 1$; $P = 0.06$).

Seed losses due to predation averaged 72.9 ± 14.2 % per week. The rate did not vary throughout the study period (Kolmogorov–Smirnov test: $Z = 1.15$; $P = 0.14$; $n = 12$). Neither the position of the dishes within or outside the winter riverbed nor their placement under or far from fruiting trees affected the predation rate (Mann–Whitney U test: $Z_{\text{riverbed}} = -0.85$; $P = 0.4$; $n = 24$; $Z_{\text{tree}} = -1.51$; $P = 0.13$; $n = 24$).

We recorded a total of 863 seedlings (maximum per m^2 : 163). The spatial patterns of seed rain and seedling emergence were not correlated (Spearman: $r_s = 0.07$; $n = 100$; $P = 0.46$). Seedlings emerging within the winter riverbed were located at a considerably greater mean distance (3.4 ± 3.3 m) from the nearest *F. alnus* canopy than the primary seed rain of filled seeds (distance: 0.4 ± 1.3 m; t -test: $t = -14.8$; $P < 0.001$). Many more seedlings were counted on recently formed sandbanks and around springs than might be expected from the primary seed rain (Fig. 3; $\chi^2 = 448.3$; $df = 3$; $n = 934$; $P < 0.001$).

Table 2
Results of morphometric fruit analyses of ten *Frangula alnus* individuals ($n = 30$ fruits per plant)^a

Fruit trait	Mean \pm 1 S.D.	<i>P</i>
Diameter	9.0 \pm 0.8	***
Fresh weight (mg)	404.7 \pm 94.8	***
Total seed number	2.96 \pm 0.25	*
Number of filled seeds	2.26 \pm 0.80	***
Number of empty seeds	0.69 \pm 0.81	***
Single seed weight (mg)	36.9 \pm 10.0	***
Total seed weight (mg)	108.7 \pm 30.3	***

^a Test results indicate differences among individuals (by one-way ANOVA or Kruskal–Wallis H test).

* $P < 0.05$.

*** $P < 0.001$.

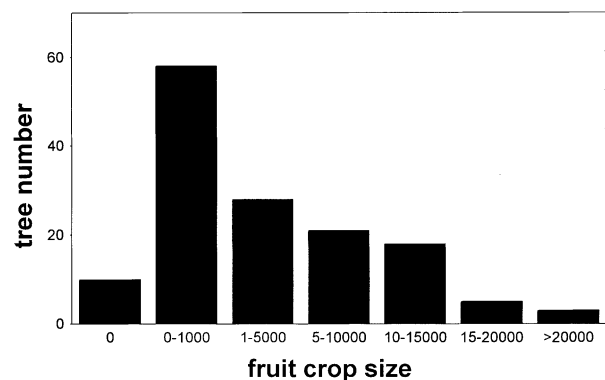


Fig. 1. Distribution of fruit crop sizes in the studied *Frangula alnus* populations; only flowering, adult trees are included ($n = 143$).

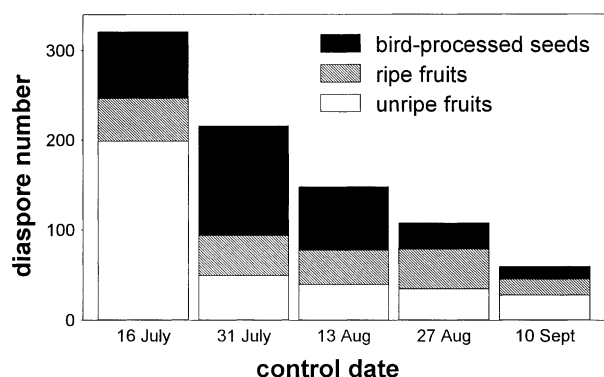


Fig. 2. Proportions of primary diaspore rain deposited throughout the ripening season.

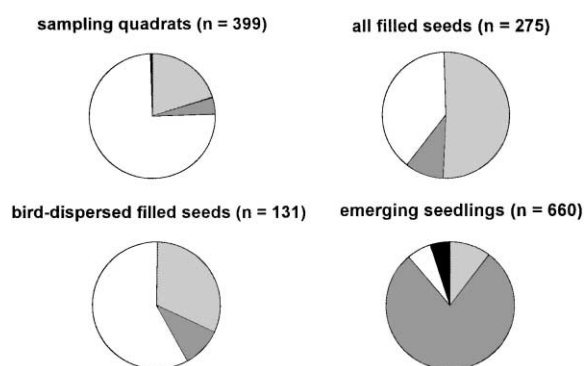


Fig. 3. Ground surface of different microhabitats and distribution of total seed rain, bird-mediated seed rain and seedling emergence amongst them. Microhabitats: rock (light grey), sandbank (dark grey), forest floor (white) and spring (black).

The seedling survival through the first three months was considerably higher on ground irrigated by spring water than on the forest floor or on sandbanks (Table 3). The most important mortality factor was desiccation, followed by herbivory (Fig. 4). Seedlings on sandbanks were significantly smaller and had fewer leaves than in other microhabitats (Table 3). None of 1124 monitored individuals survived from June 1997 to September 1999.

3.3. Population demographic structure

Results of the demographic survey of five *F. alnus* populations are summarized in Table 4. The mean dbh and presumable age varied significantly among populations (Kruskal–Wallis H test: $H=40.1$, $df=4$, $n=613$, $P<0.001$), and likewise did the distributions of 2-cm dbh classes ($\chi^2=92.71$; $df=52$, $n=613$, $P<0.001$), since some populations counted with higher percentages of young trees than others (Table 4). However, since former dendrological analyses had shown that the stem growth rate did not differ among the three populations studied in detail (One-way ANOVA: $F=0.51$; $df=2$, $n=44$; $P=0.60$), we pooled all recorded trees to search for regional age structure patterns (Fig. 5). The resulting

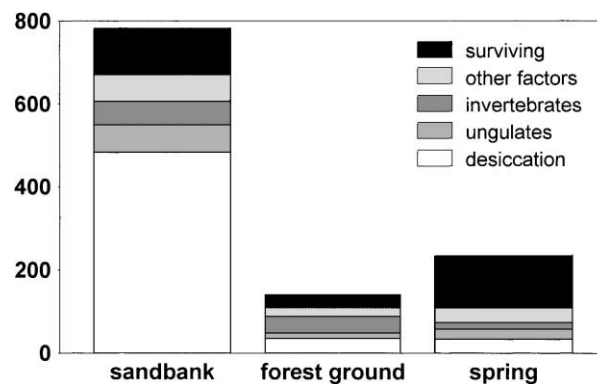


Fig. 4. Factors causing seedling mortality during the first three months in different microhabitats.

Table 3
Seedling survival and growth in June–September 1997 in different microhabitats^a

	Sandbank	Forest floor	Spring
n_{survival}	742	148	234
Survival after 3 months [%]	17 ^{**}	24 ^{***}	52 ^{***}
$n_{\text{measurements}}$	36	15	24
Height after 3 months [cm] ^b	5.4±1.0 ^{***}	7.1±2.1 ^{**}	7.5±1.7 ^{**}
Leaf number after 3 months ^b	3.6±1.1 ^{***}	4.5±1.5 ^{**}	4.9±1.1 ^{**}

^a Significant differences are indicated by different letters (one-way ANOVA with Student–Newman–Keuls post hoc test).

^b Mean±1 S.D.

^{**} $P<0.01$.

^{***} $P<0.001$.

size distribution peaked around a dbh of 8–10 cm, which corresponds to an age of 25–30 years. Younger trees were less abundant, and especially juvenile plants (dbh < 2 cm) were scarce. A positive relationship existed between annual rainfall and tree abundance up to a dbh of 8 cm ($R^2=0.53$, $F=6.8$, $n=8$, $P=0.04$).

4. Discussion

4.1. Seed production

According to a recent study (Medán, 1994), South Iberian relict populations of *F. alnus* show an exceptionally poor maternal reproductive output (1.42% of the produced ovules) and virtually no recruitment. In contrast to this previous study, our populations fruited for markedly longer (approximately 2.5 versus 1.5 months), and produced fruits with more filled seeds and only half of the seed abortion rate (24 versus 50%) reported by Medán. The difference in rainfall between the years of Medán's study (1993: 775 mm) and our study (1997: 990 mm) may contribute to explain the first observation. However, the differences in seed set and abortion may be due at least partly to the fact that we worked in large

Table 4

Demographic parameters of five *Frangula alnus* populations, determined from all individuals along a river track of variable length^a

	Puerto Oscuro	Aljibe	Medio	Montero	Pasada Llana
<i>n</i>	135	134	128	127	92
dbh (cm) ^b	7.0±4.4 (27.5)	7.8±5.8 (39.8)	9.9±5.4 (27.5)	10.4±5.4 (25.5)	9.8±6.9 (25.2)
Height (m) ^b	5.9±1.7 (11)	6.6±2.4 (14)	7.5±2.3 (13)	8.9±2.7 (16)	6.3±2.5 (13)
% adults (dbh ≥ 6 cm)	57.1	51.5	78.5	78.0	67.4
% subadults (dbh < 6 cm)	37.0	41.8	17.7	17.3	27.2
% juveniles (< 1.4 m tall)	5.9	6.7	3.8	4.7	10.9

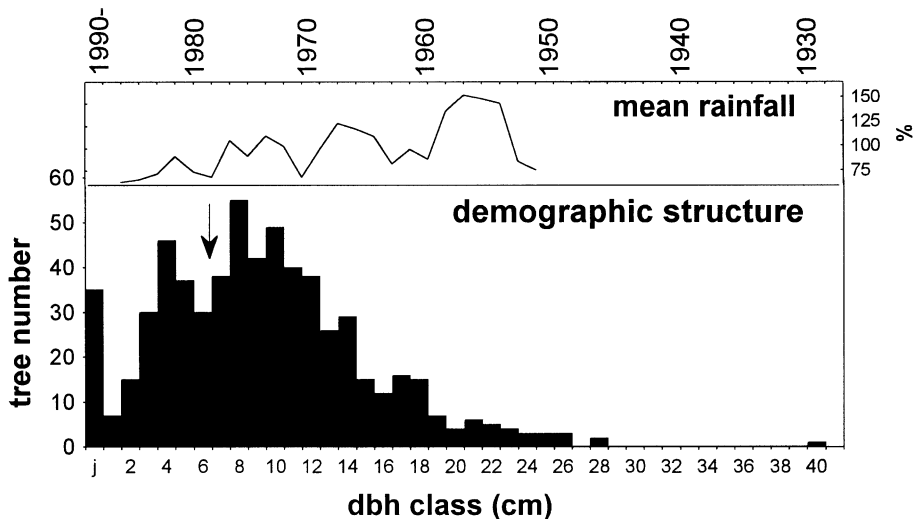
^a The Pasada Llana population was sampled completely.^b Mean ± 1 S.D.; in parentheses: maximum.

Fig. 5. Pooled age structure of five South Iberian *Frangula alnus* populations. Size class *j* refers to juveniles aged ≥ 1 year old but lower than breast height (1.4 m); note that it spans over more years than other size classes. Seedlings were not recorded. The age of first fruit production is indicated by an arrow. The running mean rainfall of the two closest years to the assumed year of germination of each dbh class is given above. (See Section 2.3 for further details.) Rainfall data are shown as the percentage of the long-term mean at the weather station Alcalá de los Gazules.

core populations, whereas Medán studied small, sparse and rather peripheral stands. Given the need to cross-pollinate (Medán, 1994), seed set in small and dispersed populations might be pollen-limited. Moreover, despite the obligate outcrossing breeding system of *F. alnus*, Medán (1994) reported a negative correlation between tree density and seed set, and attributed this to compatibility problems among closely related individuals. His observations and the divergent results of the two studies suggest that small *F. alnus* populations may be highly susceptible to inbreeding depression and are currently suffering reduced fitness, a process widely documented in the literature (Ellstrand and Elam, 1993; Hedrick and Kalinowski, 2000). Conservation strategies should account for this fact, since in large parts of its range *F. alnus* subsp. *baetica* populations are typically sparse, small (< 100 individuals; Hampe, unpublished data) and progressively declining (Anonymous, 2000). Additionally, even in our large populations a very few trees produced the bulk of viable seeds, and the peculiar linear spatial population structure may have further restricted

gene flow within the studied populations. In general, our observations suggest that the effective population size of *F. alnus* subsp. *baetica* is actually much smaller even than the low number of individuals recorded in many populations (Ellstrand and Elam, 1993).

4.2. Seed dispersal and recruitment

Compared to trees in other Mediterranean habitats (Herrera, 1995), *F. alnus* fruit removal rate was low and the bird-mediated seed dispersal appeared ineffective. However, the differing spatial distribution of primary seed dispersal and seedling emergence indicates that secondary seed transport by elevated water flow after winter rainfall rearranges and overwhelms the seedfall pattern produced by bird dispersal. The weak effect of bird-mediated seed dispersal on spatial recruitment patterns contrasts with most studies on vertebrate-dispersed plants (see Schupp and Fuentes, 1995; Rey and Alcántara, 2000 for references). While secondary seed dispersal by abiotic agents is a widespread and

commonly studied phenomenon (e.g. Chambers and MacMahon, 1994), a switch from a bird-mediated to largely water-mediated seed dispersal has to our knowledge not been reported previously.

The water flow dynamics also affect subsequent recruitment stages, as they create germination sites by moving the riverbed substrate and protect seeds from predation by burying them. This latter factor may assume considerable significance, since the observed post-dispersal seed predation by mice is amongst the highest reported for Mediterranean woody plants (Hulme, 1997; Rey and Alcántara, 2000). However, these beneficial effects on seed survival and germination are counteracted by other water flow-mediated processes: Many seeds appear to be physically destroyed or carried away from suitable habitats, since numerous seedlings were found up to more than one kilometer downstream from mature *F. alnus* stands (Hampe, personal observation). Preliminary results of seed bank analyses and experiments with coloured artificial seeds (Hampe, unpublished data) also indicate a considerable seed loss. Furthermore, seed transport by water deposits large seedling agglomerations on sandbanks, where they are exposed to desiccation, nutrient scarcity and strong intraspecific competition. Finally, many sandbanks are removed or destroyed by water flow peaks during subsequent winters (Hampe, personal observation). The water flow dynamics, though largely beneficial for seed dispersal and survival, thus leave few stable sites for the seedling establishment. As a result, *F. alnus* subsp. *baetica* suffers high mortality during early recruitment (Schupp, 1995).

Our study indicates that winter rainfall and the resulting water flow strongly influence the early recruitment of *F. alnus* subsp. *baetica* (and of other woody plant species sharing its habitat; Hampe et al., 2000). The overall effect on recruitment success presumably varies according to the highly variable amount of rainfall, and is therefore difficult to predict. However, periodic extreme water flows after heavy rainfall have obviously deleterious effects on seedling and sapling survival.

4.3. Demographic structure

The demographic survey revealed a size structure that indicates two underlying processes. First, a positive correlation between the yearly precipitation and the abundance of dbh classes up to an age of 25–30 years suggests that recruitment bottlenecks related to drought periods may actually affect the demographic structure of *F. alnus* subsp. *baetica* populations over several years. Unfortunately, the temporal resolution of the recorded data precludes us from determining the effect of single years of drought. It is likewise impossible to determine the impact of periodic, unusually high flood peaks, since these presumably kill offspring of several consecutive

years and do therefore not leave distinctive “traces” in the demographic structure. Second, the observed size distribution showed a remarkable decline in the abundance of young trees through the last two decades. We suggest two mutually non-exclusive explanations for this trend. First, the abundance of game animals (mainly Roe Deer, *Capreolus capreolus*, and the introduced Red Deer, *Cervus elaphus*) has greatly increased since the late 1970s due to the exploitation of the area for hunting (Felipe Oliveros, director of the “Los Alcornocales” Nature Park, personal communication). The deer presumably exert heavy browsing pressure, which concentrates on riparian vegetation during summer and affects particularly seedlings and young saplings. Second, large-scale mechanical scrub slashing in the surrounding cork oak (*Quercus suber*) forests has continually increased during the last 15–20 years. While riparian vegetation has to remain untouched in a belt of 3 m around the creeks (Anonymous, 1994), and this fringe is usually broadened up to 6 m (F. Oliveros, personal communication), almost the entire shrub cover is removed every few years from the adjacent cork oak forests in order to improve the cork production and remove inflammable material. This practice may greatly reduce the water retaining capacity of the area, increase its per se high erodability (Jordán, 2001), and promote extreme water flow peaks after heavy winter rains, which may in turn have the documented effects on the recruitment of *F. alnus* and other relict woody plant species (e.g. *Rhododendron ponticum* subsp. *baeticum*, *Laurus nobilis*; see Hampe et al., 2000).

4.4. Conservation

Partly due to their significance for the presence and survival of relict plant and animal species, many South Iberian riparian forests have recently been protected and therefore experience little direct interference by man (whereas in Morocco they do not have any legal protection and are usually heavily exploited). However, the results of the present study suggest that successful conservation strategies have to go beyond the current spatial limitations: A strict protection of additional, several (i.e. 10–20) meters broad vegetation belts adjacent to the riparian forests appears necessary to improve the low recruitment success of *F. alnus* and other riparian species which experience similarly high seedling mortalities (Hampe and Arroyo, unpublished data). Belts of intact scrub vegetation might have several favourable effects. First, they would help to mitigate effects of the summer drought within the riparian forests by increasing local water retention. Second, they would reduce the impact of short-term water flow peaks after heavy rains. Finally, they would help to reduce the herbivore pressure, since game species would rely less on the riparian vegetation for food.

Finally, restoration efforts should focus on the uppermost creek tracks as key areas for population persistence. Trees there may contribute most to the reproductive output and genetic structure of the population, since their seeds are potentially dispersed by water through the entire area. Contrastingly, the colonization of high tracks relies mostly on inefficient seed dispersal by birds, while many seeds produced in situ are washed downhill by the water flow. Therefore most effective conservation measure would be to improve particularly the plant recruitment in the highest tracks. This might be achieved by seed sowing or planting young trees in areas fenced over some years against herbivores. Plantations might moreover be used as starting points for a natural restoration of extinct populations along entire gorges. These measures, together with a strict and effective protection against human interceptions, might help to improve the long-term perspectives of *F. alnus* subsp. *baetica* and other relict species (e.g. *Laurus nobilis*, *Rhododendron ponticum* subsp. *baeticum*) in their Mediterranean refugia during future climate changes (Bennett et al., 1991; Hewitt, 2000).

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