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Effects of seed dispersal on *Juniperus communis* recruitment on a Mediterranean mountain

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Abstract. The recruitment of the relict shrub *Juniperus communis* on a mountain in SE Spain was studied during the period 1994-1998. The main objective was to determine both the quantitative and qualitative effects of bird dispersal on seedling establishment. Seed removal by birds, seed rain, post-dispersal seed predation, germination, and seedling emergence and survival were analysed in different microhabitats. Birds removed 53 - 89% of the seeds produced by plants. Seed rain was spatially irregular as most seeds accumulated near stones used by birds as perches and below mother plants while a few seeds were dropped in wet meadows and open ground areas. Post-dispersal seed predation by rodents affected < 10% of dispersed seeds but varied significantly among microhabitats. Only 3.6 - 5.5% of dispersed seeds appeared viable, as many seeds had aborted or showed wasp damage. Seeds germinated in the second and third springs after sowing, reaching a germination percentage of 36%. Seedling emergence was concentrated in wet meadows. Seedling mortality was high (75 - 80%), but significantly lower in wet meadows, the only microhabitat where seedlings could escape from summer drought, the main mortality cause. Seed abortion, germination and seedling mortality proved to be the main regeneration constraints of *J. communis* on Mediterranean mountains. Birds exerted a strong demographic effect, although their qualitative effect was limited by abiotic factors which caused the pattern of seed rain to differ from the final pattern of recruitment between microhabitats.

Keywords: Juniper; Microhabitat effect; Ornithochory; Seed rain; Seed viability; Seedling establishment.

Introduction

The ecological consequences of seed dispersal by animals are widely studied because of the assumed importance in the population biology of plants (e.g. Howe & Westley 1988; Stiles 1989; Willson & Traveset 2000). Seed dispersers firstly limit the number of propagules leaving the mother plant and starting the process of recruitment. Secondly, as a delayed consequence of seed-fall patterns, the dispersers partially determine seed fate. Therefore, two main types of demographic effects have been suggested for seed dispersers (Schupp 1993; Jordano 2000; Jordano & Schupp 2000): (1) a quantitative effect, related to the number and proportion of seeds that dispersers remove from mother plants; (2) a qualitative effect, related mainly to the suitability of the site where a seed is delivered. Despite this theoretical framework, few integrative studies have evaluated whether seed delivery by dispersers limits plant recruitment (Herrera et al. 1994; Rey & Alcántara 2000; Weeny 2000).

A complete evaluation of recruitment requires considering all the events subsequent to dispersal, i.e. seed mortality due to predators and pathogens, seed germination and seedling emergence and survival (Gill & Marks 1991; Jordano & Herrera 1995; Rey & Alcántara 2000; Weeny 2000). Moreover, habitat-related differences have been separately documented for seed rain, post-dispersal seed survival, germination and seedling survival (Schupp 1993, 1995; Schupp & Fuentes 1995; Russell & Schupp 1998 and references therein), but rarely integrated to provide a complete view of recruitment for a given species. In this sense, events during post-dispersal stages (and its spatial variation) are known to alter or even efface seed dispersal patterns (Herrera et al. 1994; Jordano & Herrera 1995; Rey & Alcántara 2000; Weeny 2000). Therefore, the consideration of all the stages leading to recruitment and their spatial variation becomes crucial in determining the demographic outcome of seed dispersal.

Juniperus communis (*Cupressaceae*) is a vertebrate-dispersed shrub with fleshy fruits, showing relict populations in the mountains of SE Spain. In this paper, a 4-yr field study is presented on the seedling recruitment of *J. communis* on a Mediterranean mountain in SE Spain. Seed removal by dispersers, seed rain, post-dispersal seed survival, seed germination and seedling emergence and survival were monitored. The final aim was to determine the impact of avian seed dispersal on the demography of *J. communis*. This study was designed to: (1) determine the effects of dispersers in terms of the quantity of seeds removed from mother plants and the spatial patterns of seed rain; (2) assess the losses in recruitment potential at different post-dispersal stages; (3) analyse the degree of spatial heterogeneity at different recruitment stages, by considering different microhabitats in the study site; (4) assess the qualitative effect of vertebrate dispersers on seedling establishment by integrating all stages of recruitment and their spatial variability.

Methods

Natural history

Juniperus communis inhabits the mountains of SE Spain at altitudes from 1500 to 2500 m a.s.l. It is a dominant species in shrublands above the treeline, together with the broom *Genista versicolor* and the thorny shrub *Hormathophylla spinosa* (Molero et al. 1992). These Mediterranean populations are dominated by big-sized adult and senescent individuals with a stunted structure (García et al. 1999a). *J. communis* is dioecious; female individuals produce yearly fleshy cones (galbulae) which measure circa 6.5 mm diameter and contain 1 - 4 seeds per cone. Many seeds in ripe cones are either aborted during embryo development or damaged by pre-dispersal seed predators (e.g. the chalcid *Megastimus bipunctatus*; García 1998a). Ripe cones are available to dispersers from September through the winter and spring, except when plants are covered by snow.

Seeds are dispersed almost exclusively by migrant thrushes, mainly *Turdus torquatus*, which overwinters in these areas from October to April, and *Turdus viscivorus*, which visits juniper shrublands from August to October (Jordano 1993; García 1998b; García et al. 1999b). During their stay in the juniper shrublands, both bird species feed almost exclusively on ripe juniper cones; seeds appear in more than 97% of the droppings (ca. seven seeds per dropping for both species, García 1998b; see also Zamora 1990). These two species show similar foraging patterns, alternating feeding on junipers with perching on stones nearby and short visits to drinking sites. After dispersal, juniper seeds are consumed by the wood mouse *Apodemus sylvaticus*, the only post-dispersal seed predator on many Mediterranean mountains (García 1998b). The wood mouse scavenges seeds from bird faeces and leaves the seed culls. No evidence of seed dispersal or caching behaviour have been reported for this species in these areas, the seeds being directly eaten in the same place where they are found (García et al. 2000b; see also Hulme 1997).

Study area

The study was carried out in Campos de Otero (2300 m a.s.l., Sierra Nevada, Granada, Spain, 37° 06' N, 3° 21' W) during the period 1994-1998. This is a well-conserved, undisturbed shrubland where common juniper is the only fleshy-fruited species. The shrubland is intermingled with boulders, stony bare ground and scattered wet meadows close to permanent streams and abandoned irrigation channels. Soils are siliceous. The climate is Mediterranean montane, with precipitation (snow) concentrated in late autumn and winter, and hot dry summers (Molero et al. 1992). Average temperature is 6.1 °C (± 0.1 SE; 1980-2000; data from a nearby meteorological station) and average total rainfall is 740 l/m^2 (± 53 SE; 1960-2000). Climatic variability between years is due primarily to differences in winter rainfall, which accounted for 80% of the variation in annual rainfall (D. García unpubl.). The summer drought is less variable (mean ± SE rainfall July-August 1960-2000 = 13.8 ± 3.4 l/m^2, ranging from 0.0 to 97.1 l/m^2; see also García et al. 1999a). During the period 1994-1999, seasonal temperatures were similar between years but winter rainfall varied from 99 l/m^2 (1998) to 723 l/m^2 (1996).

In this study, a microhabitat is defined as a distinct patch of habitat ranging from < 1 m to several m in diameter, and with a potential to influence biotic and abiotic conditions affecting groups of seeds and seedlings (Russell & Schupp 1998). Based on the pattern of habitat use by bird dispersers (Livingston 1972; García 1998b; Jordano & Schupp 2000), five microhabitat types were selected:

1. ‘Juniper’, under the canopy of stunted female junipers (14% coverage);
2. ‘Stone’, on the surface of stones or boulders > 1 m diameter (5.7%);
3. ‘Under stone’, under the shadow of stones (4.1%);
4. ‘Open ground’, open inter-spaces between woody vegetation, composed mainly of bare ground and sparse herbaceous vegetation (34%);
5. ‘Wet meadow’, dense and wet pastures close to permanent streams (7.4%).

These microhabitats accounted for 66% cover. The remaining area was covered by male *Juniperus* (16%), and *Genista* (14%), where bird dispersers were never observed perching (D. García pers. obs.). Soil moisture content was ca. 70% throughout the year in wet meadows, with no significant decrease during summer, whereas the remaining microhabitats showed values consistently below 30% and where strongly affected by summer drought (< 10% from June to August, García 1998b). Irradiance under stone and under juniper was 5.5% of the value above vegetation (García 1998b).

Seed removal and seed rain by birds

Seed removal by birds was estimated over two years, 1994 and 1995, as the proportion of the seed crop that was dispersed by birds. Hereto the density of seeds before (seed crops in plants) and after dispersal (seed rain) was calculated. First, cone density per plant was evaluated in late summer ($N = 75$ plants) by averaging the number of ripe cones counted in 10 0.04-m^2 quadrats randomly positioned on each plant. Seed density per plant was calculated by multiplying cone density by the number of seeds per cone (calculated averaging data from 30 ripe cones randomly collected). Then, seed production in the study area was calculated by extrapolating the average density of seeds per plant to the total area, considering that female junipers covered 14%. The density of dispersed seeds was calculated by extrapolating the seed density determined for the seed rain to the total area (see below), considering the accumulated coverage of all microhabitats (66%).

Spatial pattern of seed rain by birds was quantified in 1994 and 1995. 40 permanent quadrats of 50 cm × 50 cm were established in July 1994 for each microhabitat and were monthly monitored during the autumn and snow-free period in winter and spring, collecting and counting all the seeds deposited by thrushes in droppings. The use of sampling quadrats was chosen instead of seed traps due to the open and stunted structure of the habitat, given that any kind of seed trap would have been too conspicuous for birds in most of the microhabitats (see Kollmann & Goetze 1998). No evidence of seed removal from the quadrats due to rodents or abiotic factors was detected (several quadrats were monitored before and after rain and snow melt evidencing negligible seed losses, see also next section). Seed density (no. seeds/m^2) was evaluated for every quadrat as the cumulative number of seeds for the whole dispersal event (September to April after every seed crop).

Post-dispersal seed mortality

Post-dispersal seed predation for each microhabitat was evaluated by counting the number of seeds attacked by wood mice in the seed-rain quadrats. This method can be considered as a good estimation of seed predation by rodents, as the wood mouse eats seeds without removing them from their original place and depredated seeds are easily distinguishable by teeth marks (García 1998b; García et al. 2000b). The percentage of depredated seeds was calculated for each quadrat as the cumulative number of seeds per quadrat for each year. No sign was detected of seed consumption or removal by any other potential granivorous animal.

Seed viability after dispersal was assessed in a random subsample of seed from seed-rain quadrats (3521 and 5282 seeds for 1994 and 1995, respectively), by dissecting the seeds in the laboratory and counting the number of viable seeds. These seeds contain a white embryo which entirely fills the seed locule, whereas aborted seeds bear an undeveloped embryo. Seeds damaged by chalcids show the adult wasp exit hole in their coat and the larval excrement inside. Filled seeds refer to viable seeds after a tetrazolium test (Houle & Babeux 1994; Holthuijzen & Sharik 1984).

Germination and seedling emergence

Germination was studied by sowing seeds in the field. In autumn 1995, 1200 filled seeds were randomly taken from a sample of bird-dispersed seeds collected near the study site. For each microhabitat, eight sowing stations were randomly established, each station consisting of a 15 × 15 cm surface where 30 seeds were homogeneously distributed and sown at 1 cm deep in the soil. Any external seed arriving by current dispersal to the station was removed. Sowing stations were protected by a wire cage of 10 × 30 × 30 cm and 1 cm mesh. They were monthly monitored for germination (visible radicle protrusion) and seedling emergence from spring 1996 to spring 1999.

Natural emergence of seedlings was studied from late May to late June 1996, by counting all emerging seedlings in the different microhabitats. Different patches were sampled for each microhabitat, searching for early emerged seedlings. Patches differed in number and size between microhabitats, the use of uniform and equivalent surfaces being not possible because of the different structure of microhabitats. The number of patches and the total surface sampled (between parentheses) was as follows: juniper = 10 (319 m^2), stone = 6 (266 m^2), under stone = 45 (422 m^2), open ground = 30 (115 m^2), wet meadow = 10 (177 m^2).

A germination-emergence proportion for each microhabitat was calculated by dividing the density of seedlings in spring 1996 by the density of their corresponding cohort of seeds – that is, viable seeds dispersed in 1994, after 18 months of dormancy (Livingston 1972, see also Rey & Alcántara 2000 for a similar procedure). Germination in some *Juniperus* species may occur only 3 - 4 yr after dispersal (Chambers et al. 1999). Thus, some seedlings emerging in spring 1996 could correspond to seeds dispersed before autumn 1994, however, this amount can be considered negligible, because of the extremely low filled-seed production by plants at the study site in 1992 and 1993 (García et al. unpubl.) and the fact that germination in *J. communis* concentrates mostly in the second spring after dispersal.

Seedling mortality

Every seedling found in the sampling in spring 1996 was individually labelled and monitored for mortality, by periodical surveys until spring 1997 (first-year mortality). When possible, mortality was assigned to one of the following causes: summer drought, cattle trampling, browsing. The same procedure was followed for seedlings emerging in sowing stations from spring 1997 to spring 1998. In this second group of seedlings, it was possible to identify more precisely mortality causes, as summer drought, invertebrate herbivory, flooding, hail storm and fungal attack.

Synthesis of recruitment stages

The final outcome of dispersal process in terms of actual recruitment can be determined by linking the successive stages shown above, from seed dispersal to seedling establishment. For this, a series of transition probabilities, representing the probabilities of a propagule (seed or seedling) to pass between two consecutive stages, may be combined in a stepwise manner (Gill & Marks 1991; Herrera et al. 1994; Jordano & Herrera 1995; Rey & Alcántara 2000). Both stage-specific (proportion of propagules passing through the given recruitment limitation) and stagewise cumulative recruitment probabilities (accumulated product of successive probabilities of recruitment) are respectively calculated for each microhabitat. This model is useful to: (1) identify which stage determines the highest losses of regeneration ability (i.e. that showing the lowest transition probability); and (2) compare between microhabitats the effect of different stages on final recruitment.

The transition probabilities were calculated using the data corresponding to the 1994 cohort of seeds, considering the following stages:

1. 'Predispersal', the expectancies of which were arbitrarily set at $p = 1.0$;
2. 'Dispersal', as the proportion of seeds occurring in each microhabitat of the study site, by multiplying the seed density in the microhabitat by the coverage of the microhabitat, this product being then divided by the estimated seed rain for all microhabitats together (Russell & Schupp 1998);
3. 'Post-dispersal seed predation', as the proportion of seeds depredated by rodents for each microhabitat;
4. 'Seed viability', as the proportion of viable seeds occurring in the seed rain;
5. 'Germination-emergence', estimated as above;
6. 'Seedling survival' as the proportion of seedlings surviving one year after emergence.

Statistical analysis

Repeated-Measures Analyses of Variance (R-M ANOVA), considering the sampling from seed-rain quadrats for 1994 and 1995 as repeated measures, were used to analyse the effects of microhabitat, year and their interaction on: (1) the density of dispersed seeds; (2) the percentage of seeds depredated by rodents; and (3) the proportion of viable seeds. A similar procedure was followed to check for between-microhabitats and between-year differences on germination, as this variable was repeatedly measured at the same stations for 1997 and 1998. Type III Sum of Squares was chosen when the design of data base was unbalanced (Shaw & Mitchell-Olds 1993). When necessary, variables were transformed for normality, homocedasticity and linearity, using the arcsine transformation for data expressed as frequencies, and the log-transformation for the remaining ones (Zar 1996).

Differences in the density of emerging seedlings between microhabitats were analysed with a Kruskal-Wallis test, due to the unbalanced and non-parametric nature of the data. Comparisons after this test were made using the Dunn test (Zar 1996). Finally, the mortality rate of seedlings coming from different sampling procedures (naturally emerged *vs.* sowing-station emerged) was compared between microhabitats using a Nominal Logistic Model with interaction (microhabitat and the type of sampling as main effects; Anon. 2000).

Results

Seed removal and seed rain by birds

The estimated seed production at the study site was 142 and 219 seeds/m^2 in, respectively, 1994 and 1995. Birds dispersed 127 and 117 seeds/m^2 in respective dispersal events. The rate of seed removal by birds was, thus, 0.894 and 0.534. A total of 9719 and 8929 seeds were counted in seed-rain quadrats during, respectively, 1994 and 1995. For both years, the largest accumulations of seeds were found under stones, intermediate densities of seeds appeared over stones, under junipers and in wet meadow areas, and very few seeds occurred in open-ground areas (Fig. 1A). The density of seeds dispersed by birds significantly differed between microhabitats ($F_{4,195} = 74.92$, $p < 0.0001$, R-M ANOVA) but not between years ($F_{1,195} = 3.35$, $p = 0.069$). A significant interaction term between the microhabitat and the year ($F_{4,195} = 3.18$, $p = 0.015$) indicated that the total seed rain was similar between years but the differences between microhabitats were inconsistent over time.

Post-dispersal seed mortality

Post-dispersal seed predation by *A. sylvaticus* affected less than 10% of seeds for both study years. However, more seeds were consistently eaten by rodents under stone and under juniper (Fig. 1B). Seeds dispersed to stones, open ground and wet meadow showed consistently a higher probability of escaping predation by rodents. The percentage of depredated seeds differed significantly between microhabitats ($F_{4,155}$ = 38.25, $p < 0.0001$, R-M ANOVA), with no differences between years ($F_{1,155}$ = 0.09, p = 0.768) and no microhabitat-year interaction ($F_{4,155}$= 1.58, p = 0.182).

The viability of seeds that escaped seed predation after dispersal was low, 3.6% and 5.5% of seeds appearing sound in 1994 and 1995 respectively. Remaining seeds appeared damaged by predispersal wasps (15.3% and 15.5% for 1994 and 1995, respectively) or aborted during embryo development (81.0% and 79.0% for 1994 and 1995, respectively). The proportion of sound seeds varied significantly between years ($F_{1,114}$ = 10.63, p = 0.0015, R-M ANOVA) but not between microhabitats ($F_{4,114}$= 1.37, p = 0.248, interaction term also $p > 0.05$).

Germination and seedling emergence

Seeds sown in the field stations in fall 1995 started to germinate in late April 1997, reaching a percentage of germination of 24.50 ± 2.38% (n = 40 stations) in late June, evenly distributed between the different microhabitats (Fig. 1C). In spring 1998, no seeds germinated in wet meadows but a variable proportion of seeds germinated in the remaining microhabitats, mainly under stones and in open ground (Fig. 1C), the accumulated percentage of germination reaching to 35.9 ± 2.6% (n = 40 stations). No germination was recorded in spring 1999. Accumulated germination proved to be significantly different between years ($F_{1,35}$ = 43.68, $p < 0.0001$, R-M ANOVA) but not between microhabitats ($F_{4,35}$ = 1.28, p = 0.298). A significant interaction term between microhabitat and year indicated that microhabitat differences appeared only in 1998 ($F_{4,35}$ = 6.24, p = 0.0007).

Seedling density in spring 1996 averaged 0.23 (± 0.05 SE) seedlings/m^2, unequally distributed in the different microhabitats (H = 35.96, $p < 0.0001$, df = 4, Kruskall-Wallis test, Table 1). Seedling density was highest in wet meadows and lowest in open ground. Emergence in wet meadows was five-fold higher than in the remaining microhabitats (Table 1).

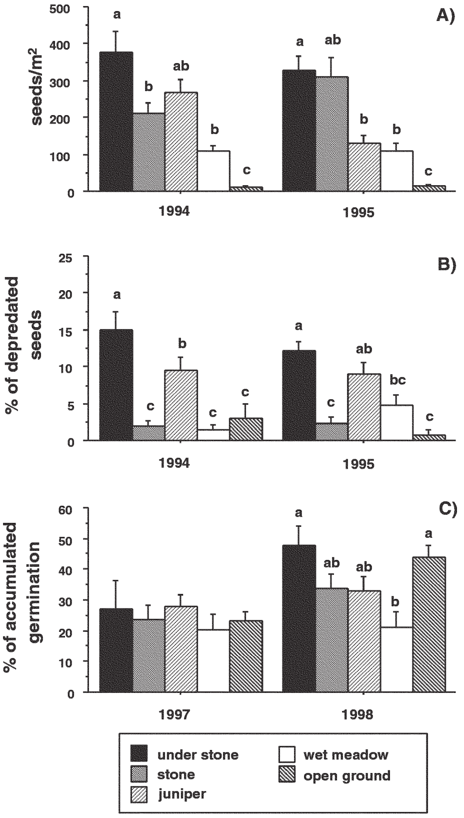

Fig. 1. Mean values (+ SE) of (**A**) the density of seeds dispersed by birds; (**B**) the percentage of seeds eaten by rodents after dispersal; (**C**) the percentage of seeds germinating in sowing stations, for different microhabitats and years. Values with different superscript letters are different between microhabitats, within year, at $p < 0.05$ (after Bonferroni-Dunn).

Seedling mortality

The percentage of seedlings dying during the first year was 80.14% for natural seedlings (N = 255) and 74.74% for seedlings established in sowing stations (N = 269). No differences in mortality rate were found between the two kinds of sampling (Wald χ^2 = 0.07, p = 0.790, Nominal Logistic Model), but significant effects

Table 1. Density (mean ± SE) of seedlings in different microhabitats in spring 1996 (values with different superscript letters are different at $p < 0.05$; Dunn test). The estimated percentage of emergence (see Methods) for each microhabitat is also shown.

	Seedlings/m^2	% emergence
Under stone	0.14 ± 0.03^b	1.11
Stone	0.10 ± 0.04^{bc}	1.07
Juniper	0.22 ± 0.03^b	4.41
Wet meadow	1.24 ± 0.36^a	36.10
Open ground	0.04 ± 0.02^c	6.20

Table 2. Mortality rates and causes for first-year seedlings in different microhabitats and samplings (% mortality = percentage of emerged seedlings dying; N = no. of seedlings; values with different superscript letters are different at $p < 0.05$ after partial χ^2). The percentage of mortality corresponding to specific causes (calculated for seedlings for which the mortality cause was known) is also shown.

	Under stone	Stone	*Juniperus*	Wet meadow	Open ground
Natural emergence					
% mortality (N)	92.75^{a} (69)	84.21^{a} (38)	87.23^{a} (94)	56.58^{b} (76)	100.00^{c} (5)
Drought	66.67	83.33	80.00	26.92	25.00
Trampling	25.93	12.50	20.00	34.62	75.00
Browsing	7.41	4.17	0.00	38.46	0.00
Sowing stations					
% mortality (N)	64.62^{a} (65)	98.25^{b} (57)	71.64^{ac} (67)	47.73^{a} (44)	87.50^{bc} (56)
Drought	85.37	90.91	91.31	0.00	95.92
Herbivory	4.88	0.00	0.00	33.33	2.04
Other	9.70	9.09	8.69	66.66	2.04

appeared for the microhabitat (Wald $\chi^2 = 43.34$, $p < 0.0001$) and for the interaction between microhabitat and sampling type (Wald $\chi^2 = 14.44$, $p = 0.006$). The lowest mortality was consistently found in wet meadows (Table 2). For naturally emerged seedlings, mortality was invariably > 84% in the remaining microhabitats, and up to 100% for open ground seedlings. For seedlings emerging from sowing stations, the highest mortality rates appeared at open ground and on stones.

The percentages of seedlings dying by identified causes is shown in Table 2. For natural seedlings, summer drought was the main mortality cause in all microhabitats except in the wet meadows (trampling or browsing by ungulates) and in open ground (trampling). Mortality causes differed between microhabitats ($\chi^2 = 35.66$, $p < 0.0001$, df = 8). Among the seedlings from the sowing stations, summer drought accounted for > 85% of the mortality in all microhabitats except in wet meadows where many seedlings died because of flooding and invertebrate herbivory.

Table 3. Summary of stages leading to recruitment of *J. communis* in the Sierra Nevada. Shown are the stage-specific (proportion of seeds or seedlings passing through the given recruitment limitation) and stagewise cumulative recruitment probabilities (accumulated product of successive probabilities of recruitment) for 1994 dispersal.

Stage	Stage-specific probability	Stagewise, cumulative probability
Seed removal by birds	0.894	0.894
Post-dispersal seed predation	0.906	0.810
Seed viability	0.036	0.029
Germination-emergence*	0.098	2.84E-3
Seedling survival 1st year	0.199	5.65E-4

*Average of observational estimation of different microhabitats (see Methods)

Additional causes included hail storms (under and above stones, open ground), fungal attack (under *Juniperus*) and invertebrate herbivory (under stones, open ground). Also in this case, mortality causes differed between microhabitats ($\chi^2 = 114.52$, $p < 0.0001$, df = 8).

Synthesis of recruitment expectancies

Table 3 shows the stage-specific and stagewise cumulative recruitment probabilities obtained for *J. communis*, from the 1994 data. Although the probabilities to be dispersed by birds and to escape from post-dispersal seed predators were high ($p > 0.89$), seedling survival, germination-emergence and, especially, seed viability stages showed very low transition probabilities. The final recruitment probability was lower than 6E-4.

A synthesis of recruitment expectancies for *J. communis* seeds and seedlings in different microhabitats is represented in Fig. 2. The probability of finding a seed after dispersal was highest below mother plants but lowest in open ground (Fig. 2A). This pattern of seed dispersion is different from those directly derived from seed rain due to the differences in coverage between microhabitats. In this sense, the higher cover of plants compensates the slightly lower density of seeds in these areas, compared to stones. This arrangement of microhabitats along the gradient of probability of recruitment varied in the subsequent stages, where the highest percentages of recruitment appeared in wet meadow areas (Fig. 2A). In terms of the cumulative probability of recruitment (Fig. 2B), the pattern of differences between microhabitats appearing at the 'dispersal' stage strongly changed after the 'germination-emergence' stage. As a result, the final probability of recruitment for juniper seedlings was highest in the wet meadow and lowest in the open ground.

Discussion

Seed removal by frugivorous birds

Thrushes dispersed a large proportion of the juniper seeds every year. The values of seed removal reported here are high compared to other data for the Mediterranean area (e.g. Debussche & Isenmann 1994; Herrera et al. 1994; Alcántara et al. 1997). This is probably a consequence of the high abundance of birds, their almost strictly frugivorous diet at the study site and the long period for frugivore-plant interactions, as many cones remain attached to junipers and birds stay in the shrublands from late summer to winter (Zamora 1990; Jordano 1993; García 1998b). Proportional seed removal decreased in 1995 compared to 1994. This decrease coincided with a strong increase in juniper seed crop, but no apparent change in bird density (no statistical differences from census data between 1994 and 1995; D. García unpubl.) nor dispersal activity (similar quantities of seed rain between years). Therefore, differences reported here in seed removal may be the result of disperser saturation (Herrera et al. 1994).

Spatio-temporal patterns of seed rain

The spatial pattern of seed deposition by birds was highly irregular, as some microhabitats received many seeds (stones and their immediate vicinity, and mother plants) but other habitats (wet meadow, open ground) were scarcely visited by birds. This high spatial heterogeneity in dispersal is common among many frugivorous birds, owing to post-foraging habitat selection (Jordano 2000; Schupp 1993, 1995). In the case reported here, the seed-rain pattern was clearly determined by the availability of stones, used by birds as perches for vigilance and shelter (Livingston 1972; Holthuijzen & Sharik 1985a; Chávez-Ramírez & Slack 1994; Debussche & Isenmann 1994; Kollmann 1995). In addition, thrushes spent a substantial proportion of time in junipers, feeding on cones. Large accumulations of seeds under mother plants seem to characterize simple plant-frugivore systems, where a given plant species is the only, or at least the most important, resource (Salomonson 1978; Holthuijzen et al. 1987; Alcántara et al. 2000a). On the other hand, seed presence in wet meadows appears to result from their use as drinking sites (see also Holthuijzen & Sharik 1985b). Finally, thrushes rarely dropped seeds on open ground, as found for other avian-dispersal systems in the Mediterranean (Debussche & Isenmann 1994; Herrera et al. 1994; Alcántara et al. 2000a).

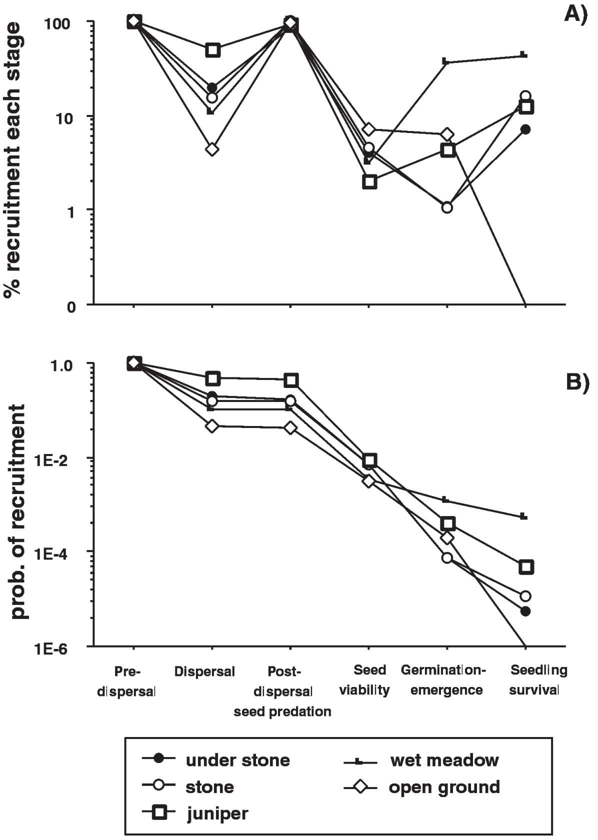

Fig. 2. Synthesis of recruitment expectancies for *Juniperus communis* seeds and seedlings in different microhabitats of the study site (1994 data, note logarithmic vertical scale). **A.** Relative recruitment at each stage expressed as percentage of individuals (seeds or seedlings) passing through different recruitment limitations, i.e. seeds dispersed by birds, seeds surviving postdispersal seed predation, viable seeds after dispersal, emerging seedlings from germination (observational estimation), and first year surviving seedlings (naturally emerged). **B.** Probability of recruitment through the end of each stage (accumulated product of successive probabilities of recruitment). 'Predispersal' expectancies have been arbitrarily set at 100% (**A**) and 1.0 (**B**).

Post-dispersal events

Post-dispersal seed predation was low, compared to findings in other Mediterranean areas, where *Apodemus sylvaticus* is the main seed predator (Herrera et al. 1994; Schupp 1995; Hulme 1997; Castro et al. 1999; Alcántara et al. 2000b). These differences are probably related to the lower density of rodents above the treeline (D. García pers. obs.), but also to the different methodology adopted in different studies (Alcántara et al. 2000b). Despite low general values, the spatial pattern of seed predation was consistent over time. Seed predation was concentrated under stones and under junipers, the probability of escaping from rodents being higher in stones, wet meadows and open ground. Lower seed predation in open areas is frequent (Hulme 1993; Kollmann 1995) as such habitats leave rodents vulnerable to predators (Bowers & Dooley 1993). Nevertheless, in Mediterranean habitats, seed predation by *A. sylvaticus* can be positive (Schupp 1995; Hulme 1997; Alcántara et al. 2000b; this work) or negatively (Herrera et al. 1994) affected by shrub presence, or may be even independent (Castro et al. 1999).

The viability of seeds surviving predation was consistently very low and large numbers of empty seeds appeared in the seed rain, due to predispersal seed predation and seed abortion. This high abortion rate is a typical feature of *Juniperus* populations on Mediterranean mountains of SE Spain, apparently related to climatic and genetic constraints in pollination and embryo development (García et al. 2000a).

Germination, emergence and seedling survival

Seed sowing evidenced a minimum dormancy of 18 months for *J. communis* in the Mediterranean high-mountain. A long dormancy is common for the genus *Juniperus*, as embryos complete their development long after cone ripening (Johnsen 1962; Chambers et al. 1999). Germination concentrated during the two springs after this dormancy and no seeds germinated thereafter, probably because the seeds lost their viability in the field after this 2-yr germination period (Holthuijzen & Sharik 1984; Owens & Schliesing 1995). Microhabitat showed an effect on germination after the second year, as no seeds germinated in wet meadows in 1998. These differences were probably related more to a higher long-term seed mortality in wet meadows (fungal attack) than to differences in dormancy-breaking conditions. However, the observational proportion of germination emergence was substantially higher in wet meadows than in the remaining microhabitats. The fact that seeds in sowing stations were found 1 cm below the surface might account for this discrepancy, as between-microhabitat differences in light and water probably vary when considering surface laying seeds instead of uniformly buried seeds. For instance, juniper seed germination was found to be favoured in wet substrates which allow a complete imbibition of the seed coat (Young et al. 1988; Chambers et al. 1999).

Seedling mortality

Emerged seedlings registered a high mortality rate during their first year, mainly due to summer drought (see Arista 1994; Herrera et al. 1994; Rey & Alcántara 2000 for a similar pattern for other Mediterranean species). In the case of naturally-emerged seedlings, additional mortality was due to trampling or browsing by cattle. Sowing stations also evidenced some seedling mortality due to other abiotic factors. When excluded from herbivores, seedling survived better under stones and under junipers, probably because the shade lessened the effect of drought (Meagher 1943; Breshears et al. 1998; Chambers et al. 1999). In any case, wet meadows proved to be the best microhabitat for survival, because of their higher water availability even during summer. Lower light availability under junipers and under stones may also account for the seedling survival differences compared to wet meadows (Grubb et al. 1996).

Synthesis of recruitment stages

Only 0.06% of all seeds produced by mother plants were able to produce a seedling surviving its first year. This percentage of final recruitment is considerably lower than those for other avian-dispersed, Mediterranean montane plant species (0.12 - 0.21% for *Phillyrea latifolia*, Herrera et al. 1994; 0.89% for *Olea europaea* var. *sylvestris*, Rey & Alcántara 2000). On the other hand, the comparison between stage-specific probabilities suggest that recruitment is not limited by disperser activity, as dispersal probability is higher than for other stages (see also Rey & Alcántara 2000). Conversely, constraints on germination, seedling mortality and, especially, seed viability, constitute the key factors limiting juniper recruitment. Thus, regeneration of *Juniperus communis* is limited by the availability of microsites for recruitment but also, due to seed abortion, by the availability of seeds (see also Eriksson & Ehrlén 1992).

The recruitment expectancies for *J. communis* seeds and seedlings showed high variability in space during most stages of recruitment. The microhabitat strongly influenced recruitment, but each microhabitat showed different effects for different stages. For example, areas under stone received many dispersed seeds but were suboptimal sites for seedling emergence and survival. On the contrary, the few seeds dispersed to wet meadows had a high probability of escaping predation, germinating, and producing seedlings that could survive. Thus, this different suitability of a given microhabitat throughout recruitment represented conflicts between the respective requirements of seeds and seedlings at the microhabitat scale (*sensu* Schupp 1995).

In terms of cumulative recruitment probability, the spatial pattern created by seed dispersers on seed rain is maintained after post-dispersal seed predation and seed viability losses. However, differences in microhabitat-specific suitability for germination and seedling establishment offset the initial variation in seed rain. As a result, wet meadows, a microhabitat scarcely selected by frugivorous birds, become the optimal microhabitat for juniper recruitment because of their beneficial effects for seedling emergence and survival. This effect of wet meadows, considered over a longer period and in a wider spatial scale, leads to the establishment of populations characterized by higher proportions of seedlings and juveniles (García et al. 1999a).

Concluding remarks

This study offers a comprehensive, sequential picture of the recruitment of *J. communis* on a Mediterranean mountain. The main conclusion is that abiotic factors acting in late recruitment stages (germination, emergence and seedling establishment) uncouple the patterns of seed rain from the final pattern of recruitment between microhabitats. Thus, the qualitative effect of dispersers on juniper recruitment is strongly limited. However, the quantitative effect of dispersers (i.e. the removal of huge numbers of seeds in masting years) becomes necessary for some sound seeds to reach wet meadows, the relatively scarce microhabitat where recruitment is comparatively higher.

The pattern of recruitment described here is probably consistent in time, despite the climatic variability typical of Mediterranean environments, because the main recruitment factors (i.e. seed viability, and microhabitat water availability for seedling emergence and survival) seem to be unaffected by annual weather variation. Firstly, low seed viability on Mediterranean mountains is a trait determined more by macro-ecological factors than by local weather factors (García et al. 2000a). And secondly, the contrast between microhabitats appears both in rainy and dry years, as it is imposed mainly by summer drought. As a consequence, constraints on seedling recruitment lead to the current situation of regenerative collapse for juniper populations on Mediterranean mountains (García et al. 1999a).

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