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Seed germination and seedling survival of two threatened endemic species of the northwest Iberian peninsula

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Abstract

We examined germination and seedling survival of *Petrocoptis grandiflora* and *Petrocoptis viscosa* (Caryophyllaceae), two narrow endemic species from the northwest Iberian Peninsula. The experiments were carried out with seeds of three of eight populations of *P. grandiflora* and one of the three sole populations of *P. viscosa*. Under natural conditions, both *P. grandiflora* and *P. viscosa* produce very large numbers of seeds. However, the specific microhabitat of these species (cracks and crevices of limestone rock-faces) has very marked effects on seed germination, and subsequent seedling survival. In the present study, we examined the effects of light, cold treatment and seed weight on germination capacity. In the case of *P. grandiflora*, we also compared the germination of seeds of the different populations. In addition, we assessed seedling survival over a 1-year period. Seeds maintained in darkness showed higher germination percentages than seeds maintained with a 12:12 h photoperiod. The application of a short period of cold prior to germination had no significant effect in either species. In the case of *P. grandiflora*, population of origin had a significant effect on germination percentage. Of all the factors considered, seed weight was the most important source of variability, both in seed germination and subsequent seedling survival. In both species in the natural habitat, less than 10% of germinated seeds survived by the end of the year. Seedling survival was affected by microhabitat. Seedlings in non-rockface soil microhabitats were more likely to suffer herbivory or interspecific competition than seedlings in crevices in the rockface.

Keywords: Competency; Conservation; Microhabitat; Rare species; Seed weight

1. Introduction

Seed dispersal and germination are phases in the reproductive cycle that are typically of great importance for species fitness. Variations in seed dispersal efficacy or germination percentage are often interpreted as reflecting adaptations to specific ecological conditions (Venable and Lawlor, 1980; Grime et al., 1981; Martin et al., 1995; Nishitani and Masuzawa, 1996). Clearly, the characteristics of the microsite occupied by a seed may strongly influence its probability of germination and subsequent survival: indeed, species that live in highly specific habitats often produce seeds with highly specialized adaptations. For example, desert species may produce seeds that germinate very rapidly during the short rainy period (Venable and Lawlor, 1980; Gutterman and Agami, 1987). Similarly specialized seeds are produced by species living in wildfire-prone habitats (Grime, 1979) and by coastal halophytes (Pickart, 1988). In this connection, the responses of seeds to variations in photoperiod (reviewed by Pons, 1992) and temperature (reviewed by Probert, 1992) have been extensively studied. Furthermore, many studies have demonstrated that seed size and/or weight may be a good predictor of various performance variables, including germination capacity (Schaal, 1980; Dolan, 1984; Hendrix, 1984; Stanton, 1985; Wulff, 1986a; Marshall, 1987; Naylor, 1993), resistance to intra and interspecific competition (Wulff, 1986b; Mazer, 1989; Houssard and Escarré, 1991), dormancy period (Stamp, 1990), distance dispersed with respect to the mother plant (Augspurger and Franson, 1986) and seedling survival and/or growth (Schaal, 1980; Howe and Richter, 1982; Gross, 1984; Stanton, 1984; Weller, 1985; Wulff, 1986a; Marshall, 1987).

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Over and above these questions of theoretical interest, and as pointed out by Schemske et al. (1994), detailed information on the different stages in the reproductive cycle of endemic, rare and threatened species may contribute to improved understanding of the phenomenon of rarity, and at the same time assist conservation management decisions for the species under study (see also Menges, 1986).

In the present study, we investigated aspects of the reproductive cycle of *Petrocoptis grandiflora* and *Petrocoptis viscosa*, two narrow endemic rupicolous species (i.e. which live in rocky habitats) from the northwest Iberian Peninsula, both falling into the IUCN category "threatened" (Izco and Guitián, 1987a,b). Both species produce large amounts of fruit and seed under normal conditions (Navarro et al., 1993; Navarro, 1996; Navarro and Guitián, 2002), with marked variation in seed weight (among populations, with the flower's position in the dichasium, with the origin of pollen, and with the moment in the flowering period). However, the highly specific microhabitat of these species (cracks and crevices in limestone rockfaces) may affect seed establishment and germination, and subsequent seedling survival. There have been no previous studies of seed germination in either species. The aim of the present study was to determine the germination and survival capacity of seeds of these species, taking into account factors including microsite type, weight and population of origin. Specifically, we studied the effects on germination percentage and survival rates of (a) exposure to low temperatures, (b) light, (c) population of origin, and (d) seed weight. In addition, we assessed the percentage survival of seedlings of the two species over a 1-year period in the natural habitat, comparing the results obtained as a function of the microhabitat occupied (soil, cracks, crevices).

2. Material and methods

2.1. The study area and species

The geographical range of *Petrocoptis grandiflora* occupies less than 80 km^2 and comprises only eight populations, while that of *Petrocoptis viscosa* occupies less than 30 km^2 and comprises only three populations. Both species have been catalogued as threatened (Izco and Guitián, 1987). Recently, both species have been synonymized with the genus *Silene* (Mayol and Rosselló, 1999). More information about the floral biology and breeding systems of these taxa is given in Navarro (1996) and Navarro and Guitián (2002).

The study was carried out in the populations of Estrecho, Covas and Vilardesilva for *Petrocoptis grandiflora* (Concello de Rubiá, Orense Province, Spain) and La Chana population for *Petrocoptis viscosa* (Concello de Borrenes, Leon Province) in the El Bierzo region of northwest Spain, in an area with a mosaic of habitats including cultivated land, small villages, limestone crags, holm oak woodland (*Quercus rotundifolia*, *Arbutus unedo* and *Quercus suber*) and Mediterranean-type scrub communities dominated by *Cistus ladanifer* on siliceous soils or *Cytisus* and spiny Rosaceae on calcareous soils. The study populations are situated on limestone rockfaces at altitudes of about 450 and 750 m. Approximately 26% of all individuals of *Petrocoptis grandiflora* are located in the Vilardesilva population, whereas Estrecho and Covas gather the 26 and 5%, respectively. In the case of *Petrocoptis viscosa* more than 60% of all individuals are located in the La Chana population. Climate in this area is Mediterranean with rainfall ranging between 528 and 650 mm and a summer drought of 3 months. The mean annual temperature ranges between 12.9 and 14.2 °C, but during the period December–February temperatures could fall to values close to 0 °C (Navarro, 1996).

Petrocoptis grandiflora Rothm. and *Petrocoptis viscosa* Rothm. (Caryophyllaceae) are perennial herbs with opposite leaves and pentamerous flowers in terminal dichotomous cymes. Each plant produces on average 70 flowers per season. Mean fruit set in the study population ranged from 64 to 75% over the period 1992–1997.

Each plant of *Petrocoptis viscosa* produces on average 41 flowers per season and mean fruit set in the study population ranged between 68 and 85% over the period 1993–1997. Supplementary pollination does not increase fruit set in either *Petrocoptis grandiflora* or *Petrocoptis viscosa*. Neither species are strictly xenogamous (i.e. species which need to receive outcross pollen for fruit production), but xenogamous pollen transfer produces seeds of higher quality (i.e. higher mean weight, higher germination percentage, and shorter mean time to germination). The position of flowers within inflorescences also has a significant effect on seed weight: seeds produced from central flowers have higher weight than those from lateral ones.

In both species, the fruit is an unilocular capsule, and the seeds (of about 1 mm diameter) are smooth, black and glossy, with a strophiole (i.e. an excrescence at the hilum composed of hairs.

2.2. Laboratory germination trials

In mid August 1992, once the fruiting period had finished, seeds were collected from *Petrocoptis grandiflora*. To ensure that the seeds were fully mature, they were collected on successive visits to three populations: Estrecho, Covas and Vilardesilva, with 600 seeds. One year later we collected another 600 seeds from the La Chana *Petrocoptis viscosa* population. The seeds were in all cases collected from all positions in the inflorescence, from at least 20 plants per population. In both species experiments were carried out approximately a week after collection of seeds. In the meantime the seeds were stored at environment temperature in glass vials.

Experiments were performed to investigate the effects on germination rate and germination percentage (a) of light (since in the natural microhabitat for germination of both species, i.e. cracks and crevices in limestone rockfaces, the amount of light received is practically zero) and (b) of cold treatment (to investigate whether a short period of cold is required to break dormancy. The germination of seeds of both species generally occurs early in the spring, just after the cold period which takes place between December and February. During this period in the study area is usual that temperatures fall close to 0 °C for a few days (Navarro, 1996).

For these experiments, half of the seed sample from each population ($n=300$) was maintained at 4–5° C for 5 days (i.e. cold treatment). Half of these seeds ($n=150$) were left to germinate in the dark, while the other half were left to germinate under artificial light (12:12 h light:dark). Prior to the experiments, all seeds were surface-sterilized by immersion in a 1% sodium hypochlorite solution for 5 min, then washed several times with distilled water. The seeds were then placed in Petri dishes on filter paper that was periodically wetted with distilled water. The temperature in the germination chamber ranged between 20 and 24° C. Photosynthetically active radiation (PAR) in the germination chamber was 184.8 μmol m^{-2} s^{-1}; for darkness, the dishes were covered with aluminium foil. The dishes were inspected daily over a 30-day period for both species, with daily counting and removal of germinated seeds. A seed was considered to have germinated when radicle length exceeded two times seed length. Finally, with the obtained data we calculated final germination percentage.

2.3. Effect of seed weight on seedling survival and germination

During August 1992 we collected 1020 seeds of *Petrocoptis grandiflora* from the Covas population. One year later, in the La Chana population, we collected 1051 seeds of *Petrocoptis viscosa*. In both cases, each seed was weighed with a precision balance (Sartorius model 2045), and assigned to one of three groups depending on weight. For each species, the groups were defined in view of the proximity of the seed to the mean weight for seeds of that species. For *Petrocoptis grandiflora*, the mean seed weight was 545±143 μg (Navarro, 1996) and the three groups were: (1) <450 μg; (2) 450–50 μg; and (3) >650 μg. For *Petrocoptis viscosa*, the mean seed weight was 491±105 μg (Navarro and Guitián, 2002), the three groups were: (1) <400 μg; (2) 400–600 μg; and (3) >600 μg.

The seeds were left to germinate in the dark, and on germination were transferred to seed-trays in potting compost. The seedlings in seed-trays were watered daily during the fourth month. Germination percentage was calculated after transferring to seed-trays and seedling survival after 4 months for each weight group.

2.4. Seedling survival in the natural habitat

At the beginning of spring, very small recently germinated seedlings of both species can be found in the natural habitats, in cracks and crevices in the rockface, in soil-bearing ledges, or on the ground beneath the wall. During March 1994, we found and marked *Petrocoptis grandiflora* seedlings in the Vilardesilva population, and *Petrocoptis viscosa* seedlings in the La Chana population, in each case recording microhabitat (soil, soil-bearing ledge, or crevice). Table 1 details the number of plants marked in each microhabitat. To avoid damage of seedlings, marking was done with an indelible marker and pencil on the rockface, washing the rock first when necessary (seedlings located in ledges or crevices), or with "flagpost" labels pegged into the ground (seedlings in soil). Each population was subsequently visited about once a month, with the aim of determining survival over the first year.

2.5. Data analysis

The incidence of the different treatments (light/dark and cold/no-cold) on the probability that a seed will germinate was analysed by log-linear analysis of variance, using the Catmod procedure in the statistics package SAS (SAS Institute, 1988). In the case of *Petrocoptis grandiflora*, the influence of population of origin was also analysed.

3. Results

3.1. Germination trials

In the *Petrocoptis grandiflora* germination trials, seeds germinated up to 21 days after the start of the trial; after day 21 no seeds germinated. The overall mean germination percentage of *Petrocoptis grandiflora* seeds under laboratory conditions was high (81%, $n=1800$). However, the response of seeds showed great variability depending on treatment and population of origin. Considering the three populations together, the seeds that

Table 1
Number of plants of each species marked in each of the three microhabitats studied

Species	Soil	Ledge	Crevice
Petrocoptis grandiflora	108	46	40
Petrocoptis viscosa	112	44	53

were left to germinate in the dark showed higher germination percentages (86.4 and 85.3% with and without cold treatment, respectively) than seeds that were left to germinate under a 12:12 h light:dark cycle (79.8 and 72.4% with and without cold treatment, respectively). Furthermore, germination rate was higher for seeds maintained in the dark (see Fig. 1). The results of the analysis of variance shown in Table 2 (factor *light regime*) confirm these observations. Exposure to a short period of cold had no significant effect on final germination percentage. However, population of origin did have a significant effect (see Table 2). Specifically, and considering all of the treatments together, 90.2% of seeds collected from the Covas population germinated. This value was not much higher than that obtained for the seeds from the Estrecho population (85.3%), but markedly and significantly higher than that obtained for the seeds from the Vilardesilva population (67.5%).

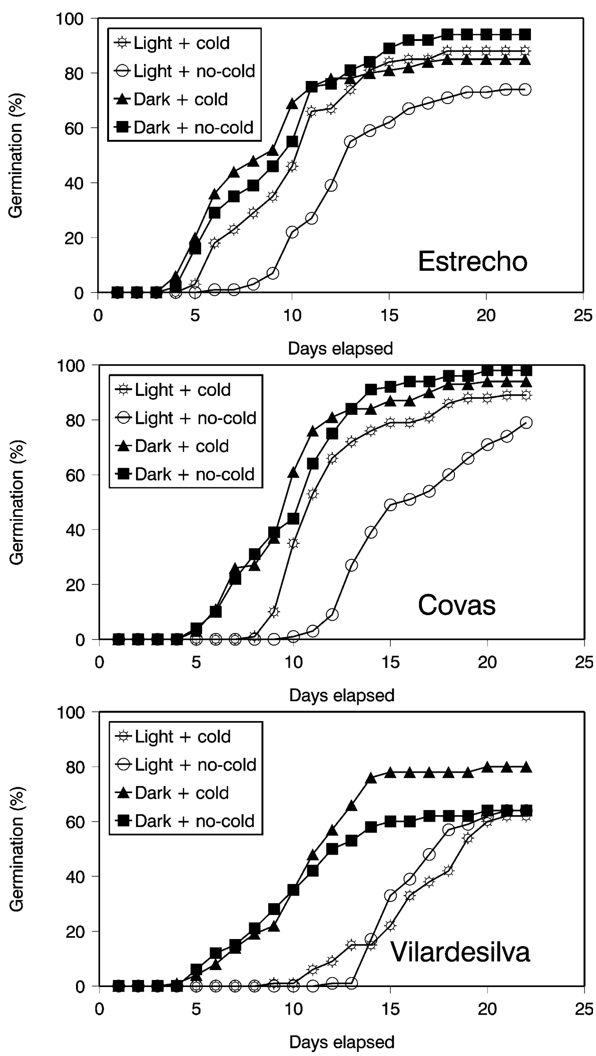

Fig. 1. Cumulative germination percentages for *Petrocoptis grandiflora* seeds collected in the three study populations, under each of the four light/temperature combinations tested (see text for details).

As can be seen from Fig. 1, the response of *Petrocoptis grandiflora* seeds to the different treatments varied significantly among the populations of origin. The seeds from the Estrecho and Covas populations that were maintained in the dark and not subjected to prior cold treatment showed the highest germination percentages (>90%); the seeds from the Vilardesilva population subjected to the same treatments showed lower germination percentages, similar to those reached by seeds exposed to artificial light. In this population, the highest germination percentage was obtained when the seeds were maintained in the dark after cold treatment (see Fig. 1).

In the *Petrocoptis viscosa* germination trials, seeds germinated up to 23 days after the start of the trial; after day 23 no seeds germinated. The overall mean germination percentage of *Petrocoptis viscosa* seeds under laboratory conditions was likewise high (80.8%, $n = 600$). Of the different treatments tested (light/dark and cold/not-cold), only light had a significant effect on germination percentage (Fig. 2, Table 2). By contrast with the 85.3% germination obtained for seeds that were maintained in the dark, only 76.3% germination was obtained for seeds that were maintained under a 12:12 h photoperiod.

3.2. Effects of seed weight on seed germination and seedling survival

Seed weight influenced germination capacity and seedling survival in both species. The germination percentage for *Petrocoptis grandiflora* seeds weighing less than 450 μg was 54.9%, versus 84.6% for seeds weighing 450–650 μg, and 99.1% for seeds weighing more

Table 2
Effects of the different treatments (light or dark; cold or no cold; see Methods) and of population of origin (*Petrocoptis grandiflora* only) on germination percentage. The analysis was performed with the CATMOD procedure of the statistics package SAS (1988)

Source of variation	Degrees of freedom	Chi-square	*P*
Petrocoptis grandiflora			
Intercept	1	479.09	<0.0001
Light	1	34.75	<0.0001
Cold	1	3.11	0.0777
Population	2	107.11	<0.0001
Light×Cold	1	10.80	0.0010
Light×Population	2	8.42	0.0148
Light×Cold×Population	2	26.39	<0.0001
Likelihood ratio	3	4.39	0.2220
Petrocoptis viscosa			
Intercept	1	190.50	<0.0001
Light	1	7.73	0.0054
Cold	1	0.88	0.3478
Likelihood ratio	1	0.00	0.9460

than 650 µg (Table 3). Similarly, seedling survival (to age 4 months) was only 3.6% for seeds weighing less than 450 µg, versus 51.8% for seeds weighing 450–650 µg, and 87.4% for seeds weighing more than 650 µg (Table 3). Similar results were obtained for *Petrocoptis viscosa*: both germination percentage and seedling survival increased with increasing seed weight (Table 3).

Of the total of 1020 *Petrocoptis grandiflora* seeds used in these experiments, 48.7% germinated and survived to age 4 months. In *Petrocoptis viscosa* this percentage was markedly lower (24.2%, $\chi^2 = 135.1$, $P < 0.0001$). This difference is largely attributable to the small proportion of germinated *Petrocoptis viscosa* seeds that produced seedlings. In *Petrocoptis grandiflora*, 57.5% of germinated seeds (in all three weight groups) reached the 4-month-old seedling stage. In *Petrocoptis viscosa*, by contrast, only 28.7% reached this stage ($\chi^2 = 67.4$, $P < 0.0001$). However, germination percentage did not differ significantly between the two species ($\chi^2 = 0.2$, $P > 0.05$).

3.3. Seedling survival in the natural habitat

In both species, late spring and particularly early summer were the periods of highest seedling mortality; from August to September onwards, mortality rates were much lower (Fig. 3). In the case of *Petrocoptis grandiflora*, seedling survival in crevices and in soil-bearing ledges one year after germination was very similar to that observed after 4 months (10.9% versus 12.5%, $\chi^2 = 0.048$, $P > 0.05$). During spring, mortality increased as a result of herbivory by domestic goats and juvenile snails (*Helix aspersa*). One-year survival of seedlings in non-rockface soil was only 2.8%. This percentage survival did not differ significantly from that obtained for seedlings in soil-bearing ledges ($\chi^2 = 2.802$, $P > 0.05$), but did differ significantly from that obtained for seedlings situated in crevices in the rockface ($\chi^2 = 3.662$, $P < 0.005$).

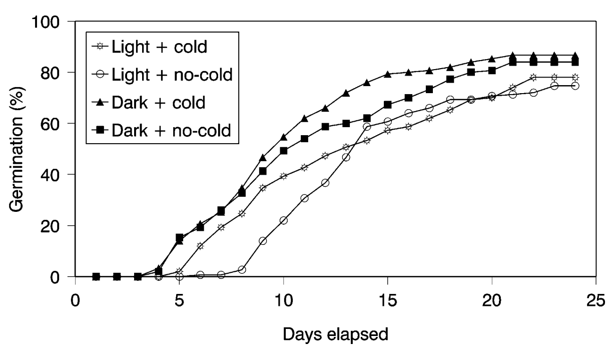

Fig. 2. Cumulative germination percentages for *Petrocoptis viscosa* seeds under each of the four light/temperature combinations tested (see text for details).

Finally, the scarcity of water from June onwards appears to be a major constraint on seedling survival in all three microhabitats, since during this period a large number of drought-killed seedlings were observed. However, seedlings situated in crevices in the rockface were the most severely affected by the summer drought (see Fig. 3).

In the case of *Petrocoptis viscosa*, 1-year survival of seedlings in soil-bearing ledges and in crevices was 9.1 and 11.3%, respectively ($\chi^2 = 0.0006$, $P > 0.05$). Seedlings located in the soil showed lower one-year survival (5.4%), though the differences are not statistically significant ($\chi^2 = 0.2436$ for the comparison ledge-soil). In this species we did not observe evidence of herbivory: seedling mortality was almost exclusively due to competition with other species for substrate space, and to lack of water. On non-rockface soil, interspecific competition was even more marked, the chief competitors being the creeper *Bryonia cretica* subsp. *dioica* (Jacq.) (Cucurbitaceae) and the fern *Pteridium aquilinum*. As with *Petrocoptis grandiflora*, a large proportion of seedlings died during the summer because of water shortage (Fig. 3). In accordance with this, laboratory experiments have shown that seedlings of this species are highly sensitive to water shortage (Navarro, unpublished data).

Table 3
Results of the germination trials for *Petrocoptis grandiflora* and *Petrocoptis viscosa*, showing results obtained for the different seed-weight groups

Seed-weight class (µg)	No. of seeds (NS)	No. of seeds germinated (NG)	Germination percentage	No. of seedlings surviving	Seedling survival (wrt NS) [%]	Seedling survival (wrt NG) [%]
Petrocoptis grandiflora						
<450	102	56	54.9	2	2.0	3.6
450–650	702	594	84.6	308	43.9	51.8
>650	216	214	99.1	187	86.6	87.4
Total	1020	864	84.7	497	48.7	57.5
Petrocoptis viscosa						
<400	265	181	68.3	6	2.3	3.3
400–600	527	442	83.9	128	24.3	29.0
>600	259	259	100	119	45.9	45.9
Total	1051	882	83.9	253	24.1	28.7

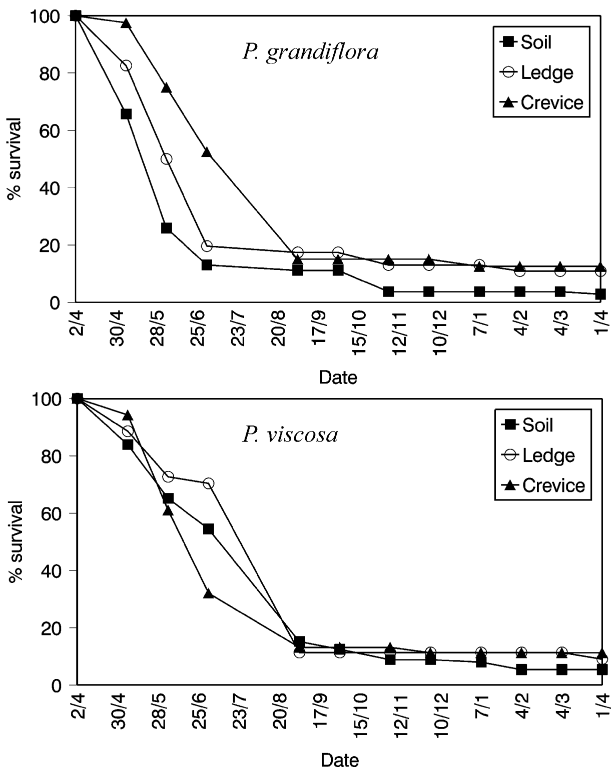

Fig. 3. Percentage survival of *Petrocoptis grandiflora* and *P. viscosa* seedlings in various microhabitats, during their first year of life.

4. Discussion

The two species studied here showed similar germination patterns. In both cases, the final germination percentage was high, and was significantly influenced by one or more of the treatments applied. For example, germination was favoured in all populations by darkness. This behaviour has been described for other species (see Martin et al., 1995; Nishitani and Masuzawa, 1996; though see also Baskin et al., 1995), and has been related to the control of germination by phytochromes (Probert et al., 1985). The fact that the germination percentage is greater in the absence of light could favour seeds that fall into cracks or crevices in the rockface. By contrast, the application of a short period of cold did not have any effect on the final germination percentage. Nishitani and Masuzawa (1996) have shown that the application of different periods of cold treatment has different effects on the final germination percentage.

Taking into account that we have only one year's data the present results suggest significant variation in germination percentage among populations of *Petrocoptis grandiflora*. Similar results have been described previously for other species (see review in Baskin and Baskin, 1973), and have often been ascribed to genetic factors (see Martin et al., 1995). However, examination of the interactions between populations and treatments indicates that the three populations did not respond in the same way to the different treatments. In some previous studies, it has been suggested that variability in the responses of seeds of different populations to germination treatments may be due to environmental differences between the populations, ultimately responsible for corresponding genotypic differences (see Maruta, 1994; Martin et al., 1995; Nishitani and Masuzawa, 1996). It will be very interesting in future works to analyse the variability in the response of seeds collected on all populations of these two endemic species to that treatments.

Studies of numerous species have shown that seed weight and/or size very often have significant effects on final germination percentage, germination rate, seedling survival and/or seedling growth, and even on resistance to intra or interspecific competition. Harper (1977) suggests that the poorer performance of lighter seeds is due to their lower endosperm content. Our results are in accordance with this hypothesis, in that in both species heavier seeds showed significantly greater germination and subsequent seedling survival than lighter seeds.

Little is known about mechanisms of seed dispersion in this genus. During the period 1992–1995 censuses were carried out in order to know if there was a biotic seed disperser for any of those species. Not one was observed, so zoochory can probably be ruled out (Navarro, 1996). One possible mechanism might be anemochory, taking advantage of the strong air currents characteristic of the rockfaces on which these species live (García, 1993). However, seeds of the species of the genus *Petrocoptis* have a strophiolar tuft of claviform hairs, which have hygroscopic properties and become mucilaginous on wetting. This characteristic (myxospermy sensu Grubert, 1974) can be expected to facilitate adherence within damp crevices. This probably reduces the risk of dispersal to more distant sites (which are likely to be less suitable), and is in accordance with a strategy of remaining within existing habitats. García (1993) has suggested that this characteristic, not observed in other Caryophyllaceae, may be an adaptive character of the genus *Petrocoptis*, originating as a consequence of its ecological specialization for rupicolous habitats. In this sense, it is interesting that seedling distribution in both species does not correspond with adults distribution. Seeds that are dispersed out of the limestone rockfaces into a habitat less suitable than those closer to mother plants still germinated, but were killed before the next reproductive season. Natural selection might therefore lead to the loss of characters that increase dispersal (e.g. elaiosomes), and the reinforcement of characters that increase maintenance in rocky, wet microsites (e.g. strophiole; see Thomson et al., 1996).

The moment of seed germination may have a very important influence in those environments in which there is at least a short unfavourable period (Marks and Prince, 1981; Kachi and Hirose, 1990). One possible explanation of why germination in these two species is delayed until next spring and does not take place in the autumn, like most Mediterranean species, could be the incapacity for both species of achieve sufficient biomass to survive the winter if seed germination take place in autumn. The results obtained for the two species of *Petrocoptis* showed that seedling's early-summer mortality was very high (see Fig. 3). A possible cause of this very high mortality is the absence of a well-developed root system. If this is the case, seeds that germinate in late spring may had have a lower probability of survival than seeds that germinate in early spring (see Nishitani and Masuzawa, 1996). To survive the winter, seedlings must achieve sufficient biomass by the end of the growth period (see Maruta, 1983, 1994). Germination at the beginning of the following spring, after the cold period, is probably the best option for these plants.

Other factors mitigating against the successful establishment of seedlings of these two species are competition with individuals of other species, and— in the case of some *Petrocoptis grandiflora* populations—herbivore pressure (Navarro, 1996). The pressure exerted by these competing species or by herbivores is greatest for seeds germinating in non-rockface soil. In this connection, our field observations showed that plants of *Petrocoptis grandiflora* and *Petrocoptis viscosa* are generally displaced by other species in these microsites, in accordance with the hypothesis that ''rare'' taxa are typically weaker competitors (McNaughton and Wolf, 1970). Drury (1974) suggests the existence of two extreme adaptive types: (1) strong general competitive ability at the cost of incapacity to grow in specialization-requiring habitats, and (2) physiological adaptations for the utilization of resources in specialization-requiring habitats, at the cost of general competitive ability. According to this model, the lack of general competitive capacity shown by *Petrocoptis grandiflora* and *Petrocoptis viscosa* is a reflection of the high ''evolutionary cost'' of specialization for life on limestone rockfaces. In a study of *Viola cazorlensis*, Herrera (1989) maintains that, despite the fact that this species shows a similar capacity for vegetative growth in both soil and rockface microsites, it generally occurs in rockface microsites where its ''reproductive efficacy'' is greater. Herrera suggests that the observed current distribution of plants of *V. cazorlensis* is attributable to the greater reproductive value of rockface microsites than non-rockface soil microsites, rather than to such microsites being a better habitat per se. In the case of the two species of *Petrocoptis* considered in the present study, the pressure exerted by other plant species and herbivores on plants growing in ledges or in non-rockface soil may be the most direct causes of the observed current distribution (i.e. they are almost exclusively restricted to rockface crevices (Navarro, 1996), essentially ''enemy-free spaces'' (Jeffries and Lawton, 1984).

From our results we can conclude that seeds are programmed to ''wait'' until the following spring before germinating. Heavier seeds (1) germinate earlier, improving their chances of developing an adequate root system before the summer drought period, (2) will be more resistant to intra- and interspecific competition, and (3) will achieve a greater biomass by winter. Finally, seeds that reach a rockface crevice will have a greater chance of germinating, and will do so more rapidly (in view of the absence of light), and seedlings growing in such microsites will be subject to less herbivore pressure and less competition from other plant species than seedlings growing in the soil. Although both species seems not to be intrinsically endangered, its narrow distribution makes them very vulnerable to habitat destruction. In this sense, the current proliferation of limestone quarries in their area of distribution clearly constitutes the most important short-term threat to these species. As seed quality for both species is improved by outcrossing (Navarro, 1996; Navarro and Guitián, 2002) any restoration plan must contemplate seed production by outcrossing, seed germination in dark conditions, and seedling sowing in crevices of the limestone rockfaces. Nevertheless, it is quite easier to conserve the existing populations than to restore them once they are lost. Thus, the survival of the remaining populations of these Tertiary relicts is thus entirely dependent on the commitment and effective responses of the relevant local, regional and national authorities.

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