

Seed dynamics of the mast seeding tussock grass *Ampelodesmos mauritanica* in Mediterranean shrublands

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Summary

1 The Mediterranean perennial grass *Ampelodesmos mauritanica* may have the potential to expand its range. We analysed temporal variability of its reproductive components (seedfall, seed bank, seed predation, seed germination, seedling emergence, survival and growth) in three microsites (open areas, beneath *Ampelodesmos* and beneath shrubs) at two sites.

2 Reproductive components prior to seedling emergence were both closely linked and very similar between microsites within a site. Seedling survival and growth differed between microsites, being lowest in open areas. Recruitment patterns cannot therefore be predicted from seedfall.

3 Abundant seed production in 1996 was followed by successful germination and high seedling survival. In the following (non-masting) year, although *Ampelodesmos* has a low-density persistent seed bank, recruitment was much lower because germination was low and post-dispersal seed predation was high.

4 Our results suggest that *Ampelodesmos* reproduction is episodic. Expansion of its distribution may be triggered by intermittent seedling recruitment following masting, but is otherwise constrained by seed limitation, post-dispersal seed predation and a loss of viability in the seed bank.

Key-words: grass expansion, microsite, post-dispersal seed predation, seed bank, spatial pattern

Journal of Ecology (2000) **88**, 479–491

Introduction

Invasions by exotic and native species are increasing in many parts of the world as a consequence of human activities (Drake *et al.* 1989; Di Castri *et al.* 1990) and there is an urgent need to identify such invasive species and the habitats they are likely to encroach upon. Although there is no single trait which can be used to predict the invasive potential of either native or exotic plant species (Thompson *et al.* 1995), success during the reproductive stage may be necessary to enable successful colonization followed by expansion into natural communities (Lodge 1993). Several traits have been proposed as being characteristic of weeds, including the production of many seeds that are widely dispersing

(D'Antonio 1990), long lived (Lonsdale *et al.* 1988) and have no special environmental requirement needed to initiate germination, and seedlings that grow rapidly (Roy 1990; Rejmánek 1995). A successful invasive species will show one or more of these characteristics (Baker 1965).

Nevertheless, to understand the mechanisms underlying plant growth and distribution and to build predictive models of plant invasion, we need to link the chain of events from seed dispersal to seedling establishment (Primack & Kang 1989; Chambers & MacMahon 1994; Schupp & Fuentes 1995; Vilà & D'Antonio 1998a). Spatial patterns of seed dispersal do not always coincide with patterns of adult establishment because different ecological factors may limit seed survival and germination compared to seedling survival (Houle 1992; Chambers & MacMahon 1994; Schupp 1995). Seed dispersal within a site may also be independent of

seedling recruitment (Houle 1992, 1994, 1998; Herrera *et al.* 1994; Jordano & Herrera 1994).

Spatiotemporal variability must be considered when reproductive characteristics are used to predict the invasive potential of species. Some studies of native species have found significant variability in seed dynamics and seed–seedling relationships on a local scale, e.g. between microsites such as open areas and under canopies (Fowler 1988; Schupp 1988). Furthermore, there is also a high temporal variability in the reproductive success when comparing seasons or years (Houle & Payette 1990; Houle 1994). Annual variability in reproductive success is extreme in mast seeding species, i.e. in populations that show synchronous seed production over long time intervals (Silvertown 1980; Kelly 1994). In invasive species, we would expect the range of suitable microsites to be very broad, temporal variability in reproductive success to be low, and a spatial relationship between seed and seedling survival to exist.

We examined the spatial and temporal reproductive dynamics of *Ampelodesmos mauritanica* (Poiret) T. Durand et Schinz (Poaceae) (*Ampelodesmos* hereafter), a perennial tussock grass that is increasing in dominance in the fire-prone sclerophyllous shrublands and pine woodlands of coastal Catalonia, north-eastern Spain (ORCA 1985), and the Balearic Islands (Castelló & Mayol 1987). The distribution range of this species may be expanding and can thus be considered expansive *sensu* Pysek (1995). We surveyed seedfall, seed germination and seedling survival at the Parc Natural del Garraf (Barcelona) for two years. Seasonal variability of the seed bank and of post-dispersal seed predation were also analysed. We addressed the following questions: (1) are there spatial and temporal differences in reproductive components of *Ampelodesmos*; (2) are the spatial patterns of different reproductive components coupled, and (3) which reproductive components are likely to control *Ampelodesmos* expansion?

Methods

STUDY SPECIES AND STUDY SITES

Ampelodesmos is a large, resprouting tussock grass found on coastal limestone soils in the Mediterranean Basin from southern Portugal to western Greece. Tussocks attain 1 m in canopy diameter and non-flowering stems reach 1 m in height. Flowering stems can be 3 m in height. Inflorescences are large panicles in which the spikelets are strongly compressed laterally. Seeds are 8–15 mm long, membranous and ciliate below and are produced from late summer to early winter. Populations seem to be expanding at several localities in north-eastern Catalonia (ORCA 1985; Montserrat 1989) and in the Balearic Islands (Castelló & Mayol 1987) due to their high fire resistance (Vilà *et al.*, in press).

Ampelodesmos may be an exotic species in Catalonia where it could have been introduced in the 18th century as equine forage from the Balearic Islands (Montserrat 1989).

Two sites, Romagosa and Piques, located 6 km apart were chosen to study the spatial and temporal variation in the reproductive components of *Ampelodesmos*. Both sites were located in Parc Natural del Garraf (Barcelona) where vegetation is mainly dominated by sclerophyllous shrublands and pine woodlands (Papió 1994). The climate is Mediterranean with cool, wet winters and warm, dry summers. The mean annual precipitation at the nearest weather station, Garraf-Begues, is 550 mm. The average annual temperature is 17 °C. The mean maximum and minimum temperatures are reached in July (28 °C) and January (0.5 °C), respectively. Soils are derived from limestone with the presence of many rock outcrops. Sites differed in geomorphology, fire history and vegetation structure as well as in the structure of the *Ampelodesmos* populations (Table 1). Romagosa is an old terraced field that has been burnt three times in the last 15 years. The high plant cover is dominated by *Ampelodesmos* which is intermingled with the grass *Brachypodium retusum* and small shrubs. Piques is located in a steep rocky valley with shrubland vegetation that was last burnt in 1982. *Ampelodesmos* cover, density and the number of stalks per plant are all lower at Piques than at Romagosa and thus they are more seeds available (Table 1).

At each site we chose a 50 × 50 m representative area where we conducted observations and experiments on three microsite types. Open areas, sites beneath *Ampelodesmos* and sites beneath shrubs were chosen to represent the range of plant cover types in the Park that may determine differences in seedling emergence and survival, and thus plant community diversity (Lloret 1998). These microsites differed in ground-level irradiance values at midday on a clear, sunny day in January. Light under the canopy of *Ampelodesmos* (425.25 ± 13.51 micromoles m⁻² s⁻¹) was more than 20 times lower than that of the open areas. However, the shrub canopy reduced light levels only by a further 4-fold. The temperature at ground level was higher in open areas (20.06 ± 1.03 °C) than beneath *Ampelodesmos* (15.67 ± 1.89 °C) or shrubs (17.57 ± 1.52 °C). Soil water content within 10 cm depth measured by the gravimetric method was significantly lower in open areas ($18.82 \pm 0.97\%$) than beneath *Ampelodesmos* ($24.09 \pm 1.42\%$) but was not significantly different from that beneath shrubs ($21.09 \pm 1.42\%$).

Twelve replicates of each microsite type were randomly located at each site.

SEEDFALL AND SEEDBANK

Plastic pots (20 cm in diameter and 15 cm deep) were used as seed traps. The pots were covered by

Table 1 Characteristics of the two study sites in Parc Natural del Garraf (Barcelona) in September 1996. Values indicate mean \pm 1 SE

	Romagosa	Piques	
Site characteristics			
Slope	Low	High	
Stone cover	< 30%	> 50%	
Aspect	SE	W	
Recent fire history	1982, 1991, 1994	1982	
Vegetation cover (%)*	121.65	80.41	
Shrub cover (%)	21.40	53.00	
Open area (%)	24.40	23.80	
Vegetation structure†	Grassland	Shrubland	
<i>Ampelodesmos</i> characteristics			
Ground cover (%)	54.20	23.20	
Plant density (plants ha ⁻¹)	14040.00 \pm 1375.55	8220.00 \pm 1369.59	$t = 2.99, P = 0.005$
Canopy diameter (cm)	81.41 \pm 5.01	92.35 \pm 6.74	$t = 0.59, P = 0.56$
Reproductive stalks per plant	13.96 \pm 1.89	5.64 \pm 0.89	$t = 3.45, P = 0.0008$

*Sum of the cover of the different species present.

†Beside *Ampelodesmos*, the main species (% ground cover) are *Brachypodium retusum* (13.4), *Coronilla minima* (10) and *Dorycnium pentaphyllum* (13.4) at Romagosa, and *Brachypodium retusum* (28), *Pistacea lentiscus* (6) and *Quercus coccifera* (22.7) at Piques.

chicken wire of a sufficiently coarse mesh (1.5 cm) to allow passage of seeds but fine enough to prevent seed predation by rodents. The bottom of the pots were pinned to the ground and holes were drilled to allow water to drain freely (Herrera *et al.* 1994). One trap was placed in each microsite in September 1996 and was surveyed six times over a period of more than 4 months until seedfall stopped. All seeds were counted and classified as 'sound', if they were whole and apparently undamaged), or 'dead' (if the seed was damaged or empty). This survey was repeated in 1997.

In November 1996, the seed bank was surveyed by taking two superficial soil cores (10 cm in diameter and 4 cm deep) in each microsite. These were mixed in the laboratory before *Ampelodesmos* seeds were counted and classified as sound or dead. This procedure was repeated in June 1997 before further seed dispersal.

VIABILITY OF 1-YEAR-OLD SEEDS

In November 1996, 12 groups of 10 sound seeds, randomly selected from a bulk collection from inflorescences in Garraf, were placed in a 5 \times 5 cm white nylon bags made from a shade cloth of a gauge sufficiently fine (0.5 mm) to retain seeds. At each microsite we placed one bag on small stones (rather than directly onto the soil surface which would not have allowed germination to occur). In October 1997, seeds were retrieved from their bags and a germination test was conducted under laboratory conditions to estimate of seed viability.

Seeds from each bag were placed in a Petri dish filled with compost (Composana, BASF®

Barcelona) and kept at 25 °C under natural daylight. Further replicates ($n = 10$) of 10 sound seeds, that had been stored in the fridge at 4 °C for a year (control seeds), were also tested for germination. Petri dishes were kept in the dark because previous germination tests showed that total germination was higher in darkness than in daylight (Vilà *et al.*, in press). Seeds were watered with deionized water to maintain soil saturation. Seeds were checked weekly for a month and were considered to have germinated if both the radicle and cotyledon had emerged from the seed coat.

SEED GERMINATION

In November 1996, at each microsite, a group of 10 seeds was placed on a 9 \times 13 \times 3 cm aluminium tray filled with soil from that site (Herrera *et al.* 1994) and covered with mesh in order to prevent the addition of falling seeds and predation by vertebrates. This allowed the fate of particular seeds to be followed and did not significantly affect ground level soil temperature as measured with a digital thermometer (t -test = $-0.15, P = 0.88$ at Romagosa, and t -test = 1.24, $P = 0.22$ at Piques). Seeds were checked approximately every 2 weeks for 4 months and were considered to have germinated if both the radicle and cotyledon had emerged from the seed coat. The procedure was repeated in December 1997.

POST-DISPERSAL SEED PREDATION

Seeds were individually glued to pieces of nylon fishing line 25 cm long and tied to a wire stake placed in the ground (Schupp 1988). The seeds ($n = 5$ per

microsite) were carefully positioned on the ground surface. In summer 1997, seeds that were placed out on 8 July were censused after 1, 3, 6, 8, 15, 28, 35 and 63 days. The experiment was repeated in autumn (30 October, counting after 3, 5, 10, 14, 21, 41, 72 and 95 days), winter (4 February, counting after 1, 4, 7, 15, 29, 49 and 53 days) and spring (30 April, counting after 1, 3, 7, 16, 22, 40, 55 and 75 days).

Ant predation was also studied during the summer experiment. An open glass tube 7 cm long and 1.5 cm wide containing an *Ampelodesmos* seed was placed in each microsite at Piques and in five randomly selected microsites of each type at Romagosa. Care was taken to place tubes horizontally in the ground and to fix them with small stones to prevent rolling. Tubes were set up on 8 July and checked for seed removal on the same dates as for vertebrate predation (see above).

SEEDLING EMERGENCE, SURVIVAL AND GROWTH

In April 1997, the density of seedlings that had emerged in late 1996 and early 1997 was estimated in a randomly selected 20 × 20 cm area in each microsite. Ten randomly selected seedlings in each Romagosa microsite were marked and survivorship was recorded once a month for a year (Houle 1992; Lloret 1998). Each group of seedlings was covered by chicken wire in order to protect them from vertebrate herbivory. The survey was not conducted at Piques because seedling density was extremely low at this site. The number of living seedlings was counted for the last time in September 1998 and the total number of leaves and the length of the longest leaf per seedling was measured to the nearest mm.

ESTIMATION OF SEEDLING RECRUITMENT

We defined seedling recruitment as the number of seeds that developed into seedlings in 1997 and survived for at least one further year (September 1998). We calculated the recruitment of new individuals at Romagosa for different microsites using an equation modified from Aguiar & Sala (1997):

$R_i = \text{Seedfall}_i \times \text{Germination}_i \times \text{Survival}_i \times \text{Microsite}_i$, where R_i is the estimated recruitment density in microsite type i (number of individuals per m²), Seedfall_i is the density of seeds trapped between September 1996 and January 1997 in microsite type i , Germination_i is the proportion of seeds that germinated when placed in microsite type i (data from 1996 sowing), Survival_i is the proportion of emerged seedlings that survived two dry seasons (summers of 1997 and 1998) in microsite type i , and Microsite_i is the proportion of the area covered by microsite type i at Romagosa (Table 1). Recruitment expectancies for the different microsites are therefore equivalent

to those presented in Herrera *et al.* (1994) and Vilà & D'Antonio (1998a).

STATISTICAL ANALYSIS

Differences between microsites within a site with respect to a single reproductive parameter (i.e. seed-fall density, seed bank density, percentage seed germination, seedling emergence density, and percentage seedling survival) were analysed by ANOVA. Differences between the mean number of leaves per seedling and the mean length of the longest leaf per seedling were also analysed by ANOVA.

Differences between sound and dead seed density in the seed bank and differences between dates (November 1996 and June 1997) in the density of sound seeds and the percentage of dead seeds in the seed bank within a microsite were analysed by paired *t*-tests (or by the sign test, if data did not fit the assumptions of parametric analysis).

We compared the survival of seeds after post-dispersal seed predation and the survival of seedlings between microsites at the end of the experiment by χ^2 tests. Heterogeneity between microsites within a site in curves showing seedling survival and seed persistence following predation were also tested by the Gehan-Wilcoxon test (Pyke & Thompson 1986; Fox 1993).

Programs obtained from Abacus Concepts (1989, 1992) were used for the computation of ANOVAs and survival analyses, respectively. When necessary, data were transformed to meet the assumptions of parametric analysis. The Scheffé test was used for pairwise comparisons (Zar 1984). Throughout the paper, means are shown (± 1 SE) unless otherwise indicated.

Differences between seedfall density in autumn 1996, density of sound seeds in the seed bank in November 1996, and seedling emergence in April 1997 within a microsite at each site were compared by the Friedman two-way analysis of variance by ranks followed by multiple comparisons between the three reproductive components.

Results

SEEDFALL

Flowering of adult *Ampelodesmos* was ubiquitous and large amounts of seed were produced in 1996, but no plants flowered at either site during 1997. Few plants in the 50 × 50 m study area flowered in 1998 (4 and 9 at Piques and Romagosa, respectively) and the number of stalks per plant was very low (1.56 ± 0.24 and 1.5 ± 0.29). Overall, seedfall at Romagosa during the autumn of 1996 was greater than 1000 sound seeds m⁻², 7.7 times higher than the value for Piques (Table 2). We did not find significant differences between microsites at either site

Table 2 Mean density (\pm SE) of reproductive components (number m^{-2}) of *Ampelodesmos* within a microsite at Romagosa and at Piques. Values within a row followed by different lower-case letters are significantly different between microsites at a site. Values within a column followed by different capital letters (i.e. for seedfall in autumn 1996, seed bank in November 1996 and seedling emergence in April 1997) are significantly different within a microsite

	Open areas	Beneath <i>Ampelodesmos</i>	Beneath shrubs
Romagosa			
Seedfall autumn 1996	994.62 \pm 92.9 a, A	1169.3 \pm 227.22 a, A, B	1110.2 \pm 162.52 a, A, B
Seed bank Nov. 1996	4031.2 \pm 541.84 a, B	2979.2 \pm 565.72 a, A	3056.8 \pm 684.93 a, A
Seedling emergence April 1997	770.83 \pm 85.27 a, A	602.08 \pm 111.90 a, B	822.91 \pm 177.75 a, B
Seed bank June 1997	160.26 \pm 52.56 a	182.05 \pm 65.38 a	202.56 \pm 57.69 a
Seedfall autumn 1997	0	0	0
Seedfall autumn 1998	0	0	0
Piques			
Seedfall autumn 1996	110.21 \pm 28.19 a, A	212.35 \pm 42.26 a, A	102.15 \pm 33.16 a, A, B
Seed bank Nov. 1996	145.83 \pm 57.23 a, A, B	958.33 \pm 350.64 b, A	572.92 \pm 139.72 b, A
Seedling emergence April 1997	22.92 \pm 16.70 a, B	2.08 \pm 20.8 a, B	45.83 \pm 25.87 a, B
Seed bank autumn 1997	202.56 \pm 105.13 a, b	288.46 \pm 84.61 a	150.00 \pm 85.90 b
Seedfall autumn 1997	0	0	0
Seedfall autumn 1998	0	0	0

($F_{2,33}=0.09$, $P=0.91$ at Romagosa; $F_{2,33}=3.40$, $P=0.05$ at Piques). No dead seeds or seed remains were found in the seedfall traps. In 1996 and 1997 we did not record any seeds in the seedfall traps.

SEED BANK

In November 1996, the seed bank at Romagosa was not significantly different between microsites (sound seeds: $F_{2,32}=1.24$, $P=0.30$; dead seeds: $F_{2,32}=0.67$, $P=0.52$) and only 8% of seeds were dead (Fig. 1).

However, at Piques the density of sound seeds was lower in open areas than beneath *Ampelodesmos* (Scheffé test, $P < 0.006$) or beneath shrubs (Scheffé test, $P < 0.04$), but the density of dead seeds was again very low (5%) and not significantly different between microsites ($F_{2,33}=0.26$, $P=0.77$).

The density of sound seeds decreased with time while the density of dead seeds increased. The density of sound seeds decreased significantly in the 7 months between samples, except in open areas at Piques (Fig. 1). By June 1997 the percentage of dead

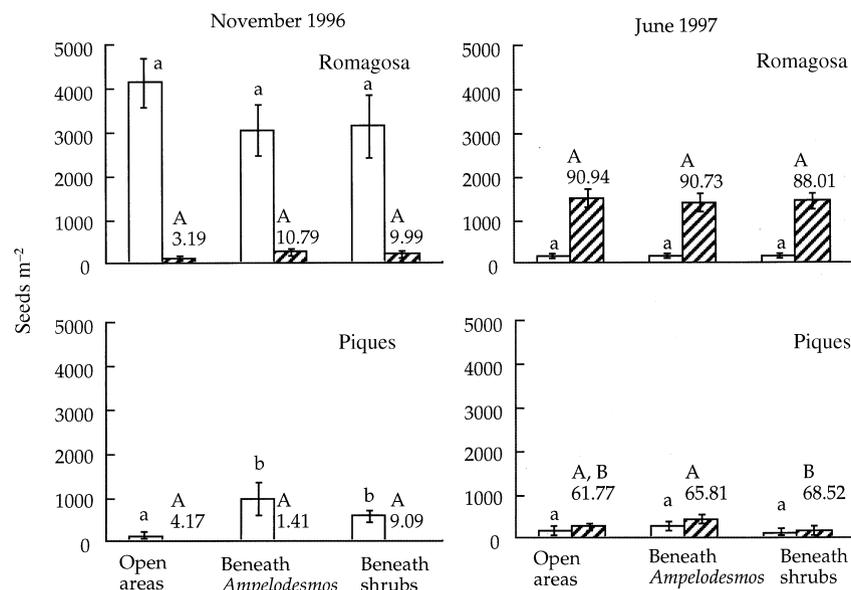


Fig. 1 Seed bank (mean \pm SE) of *Ampelodesmos* at Romagosa and Piques in November 1996 and June 1997. Shaded bars represent dead seeds (with percentage given above). Bars with different lower-case or upper-case letters show significant differences between microsites within a site for sound and dead seeds, respectively.

seeds was almost 90% at Romagosa and 65% at Piques. There were no significant differences between microsites except for a lower density of dead seeds beneath shrubs than beneath *Ampelodesmos* at Piques ($F_{2,33} = 3.62$, $P = 0.038$, Scheffé test, $P = 0.04$).

VIABILITY OF 1-YEAR-OLD SEEDS

Stored (control) seeds had a higher germination total than seeds left on the ground for a year ($F_{3,42} = 33.54$, $P = 0.0001$ at Romagosa, $F_{3,42} = 94.37$, $P = 0.0001$ at Piques) (Fig. 2). In Romagosa more than 30% of seeds left beneath *Ampelodesmos* or shrubs germinated while only 2.5% of the seeds from open areas did (Scheffé test, $P = 0.001$ and $P = 0.004$, respectively). The germination of seeds (mean percentage \pm SE) from Piques was very low (8.33 ± 4.05 beneath shrubs, 6.67 ± 2.84 open areas, 0 beneath *Ampelodesmos*) and was not significantly different between microsites (Scheffé test, $P > 0.2$).

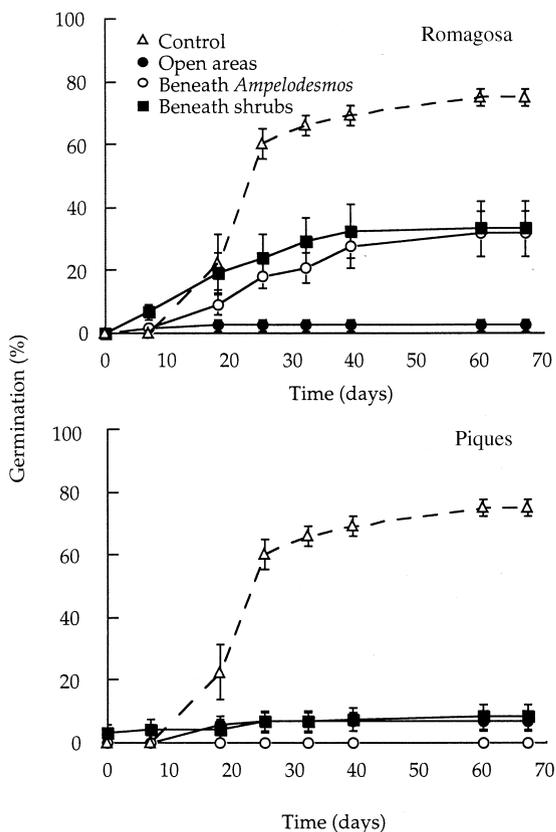


Fig. 2 Cumulative total laboratory germination (mean \pm SE) of *Ampelodesmos* seeds exposed for 1 year at each microsite at Romagosa and Piques. Control seeds had been stored in the fridge at 4 °C for 1 year.

SEED GERMINATION

In 1996–97, total germination in the field was very high (Fig. 3a). On average 85.75% of seeds germinated and there were no significant differences in total germination between microsites at either site ($F_{2,33} = 0.90$, $P = 0.41$ at Romagosa; $F_{2,33} = 1.43$, $P = 0.25$ at Piques). In 1997–98, total germination averaged only 47.22% and differences were marginally significant between microsites ($F_{2,33} = 3.11$, $P = 0.06$ at Romagosa; $F_{2,33} = 2.96$, $P = 0.06$ at Piques). In both seasons, germination started after the first winter rain and cumulative germination followed the same pattern as cumulative precipitation (Fig. 3).

POST-DISPERSAL SEED PREDATION

Seed predation was very intense at both sites but significantly different between microsites and seasons within a site (Fig. 4, Table 3). Almost half of the seeds were predated on the same day as they were placed in the field. On average, seed predation was significantly higher at Romagosa (91.25%) than at Piques (67%) ($\chi^2 = 38.79$, d.f. = 1, $P < 0.001$). During all seasons at Romagosa, seed predation in open areas was faster than beneath *Ampelodesmos* or shrubs, and there were no significant differences between seed removal beneath *Ampelodesmos* and beneath shrubs (Table 3). However, at Piques, patterns of seed predation between microsites were not consistent between seasons (Table 3). In summer, seeds were removed slower in open areas than beneath *Ampelodesmos*, but there were no significant differences in other seasons. Seed removal was faster beneath shrubs than beneath *Ampelodesmos* in summer and spring but not significantly different during autumn and winter.

A high proportion of seeds (73.87%) had been removed, presumably by ants, from the glass tubes by the end of the summer. There were no significant differences between microsites in the survival time of these seeds at either Romagosa ($\chi^2 = 4.17$, d.f. = 2, $P = 0.13$, mean survival time = 16.93 days) or Piques ($\chi^2 = 3.91$, d.f. = 2, $P = 0.14$, mean survival time = 37.06 days).

SEEDLING EMERGENCE, SURVIVAL AND GROWTH

Seedling emergence was not significantly different between microsites within a site ($F_{2,33} = 0.78$, $P = 0.47$ at Romagosa; $F_{2,33} = 1.51$, $P = 0.24$ at Piques) (Table 2). In Romagosa, seedling mortality was greatest during summer (from July to September) after which it tended to decline (Fig. 5). A year and a half after emergence, 29% of the seedlings were still alive and survival was significantly different between microsites ($F_{2,33} = 9.89$, $P =$

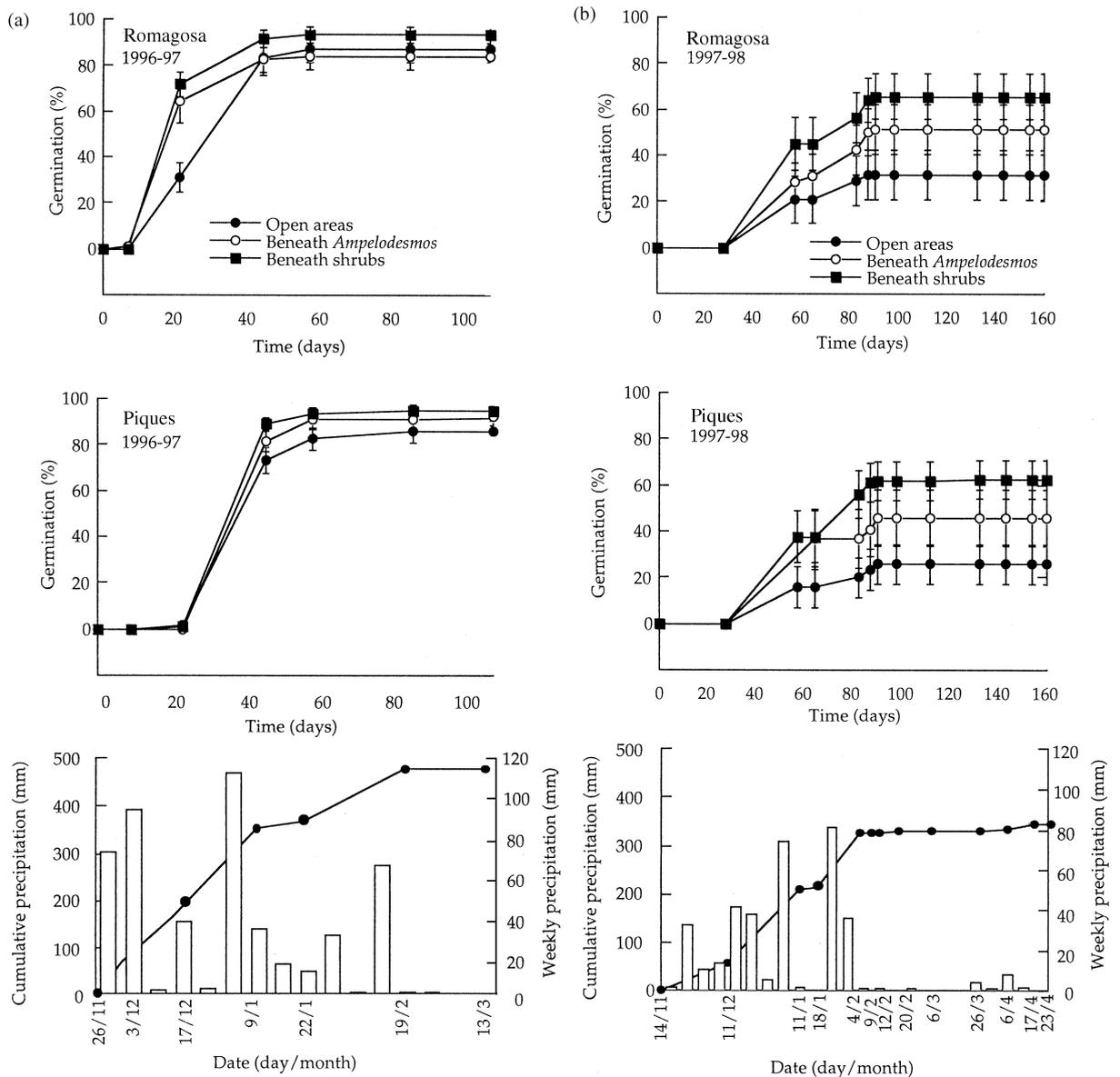


Fig. 3 Cumulative total germination (mean percentage \pm SE) of *Ampelodesmos* seeds in trays at Romagosa and Piques and cumulative rainfall at each site (a) from November 1996 to March 1997 and (b) from December 1997 to April 1998.

Table 3 Product-limit (Kaplan-Meier) estimations of mean (\pm SE) survival time (days) of seeds at Romagosa and Piques for each season. Values followed by different lower-case letters are significantly different between microsites within a season at a given site (Gehan-Wilcoxon test)

	Summer	Autumn	Winter	Spring
Romagosa				
Open areas	1.97 \pm 0.29 a	3.40 \pm 0.22 a	1.48 \pm 0.26 a	1.63 \pm 0.12 a
Beneath <i>Ampelodesmos</i>	6.53 \pm 1.44 b	5.47 \pm 0.66 b	5.13 \pm 1.43 b	8.30 \pm 2.03 b
Beneath shrubs	6.25 \pm 1.27 b	7.55 \pm 2.23 b	9.07 \pm 2.13 b	5.40 \pm 1.13 b
Gehan-Wilcoxon test	$\chi^2 = 24.49^{***}$	$\chi^2 = 7.93^*$	$\chi^2 = 13.67^{**}$	$\chi^2 = 5.89^*$
Piques				
Open areas	22.61 \pm 3.31 a	14.35 \pm 3.63 a	5.68 \pm 1.58 a	22.08 \pm 3.18 a
Beneath <i>Ampelodesmos</i>	12.77 \pm 2.32 b	8.25 \pm 2.36 a	7.97 \pm 1.42 a	21.88 \pm 3.12 a
Beneath shrubs	6.57 \pm 1.23 c	7.95 \pm 2.04 a	4.00 \pm 0.64 a	13.77 \pm 2.86 b
Gehan-Wilcoxon test	$\chi^2 = 12.27^{**}$	$\chi^2 = 3.53$ NS	$\chi^2 = 4.46$ NS	$\chi^2 = 7.74^*$

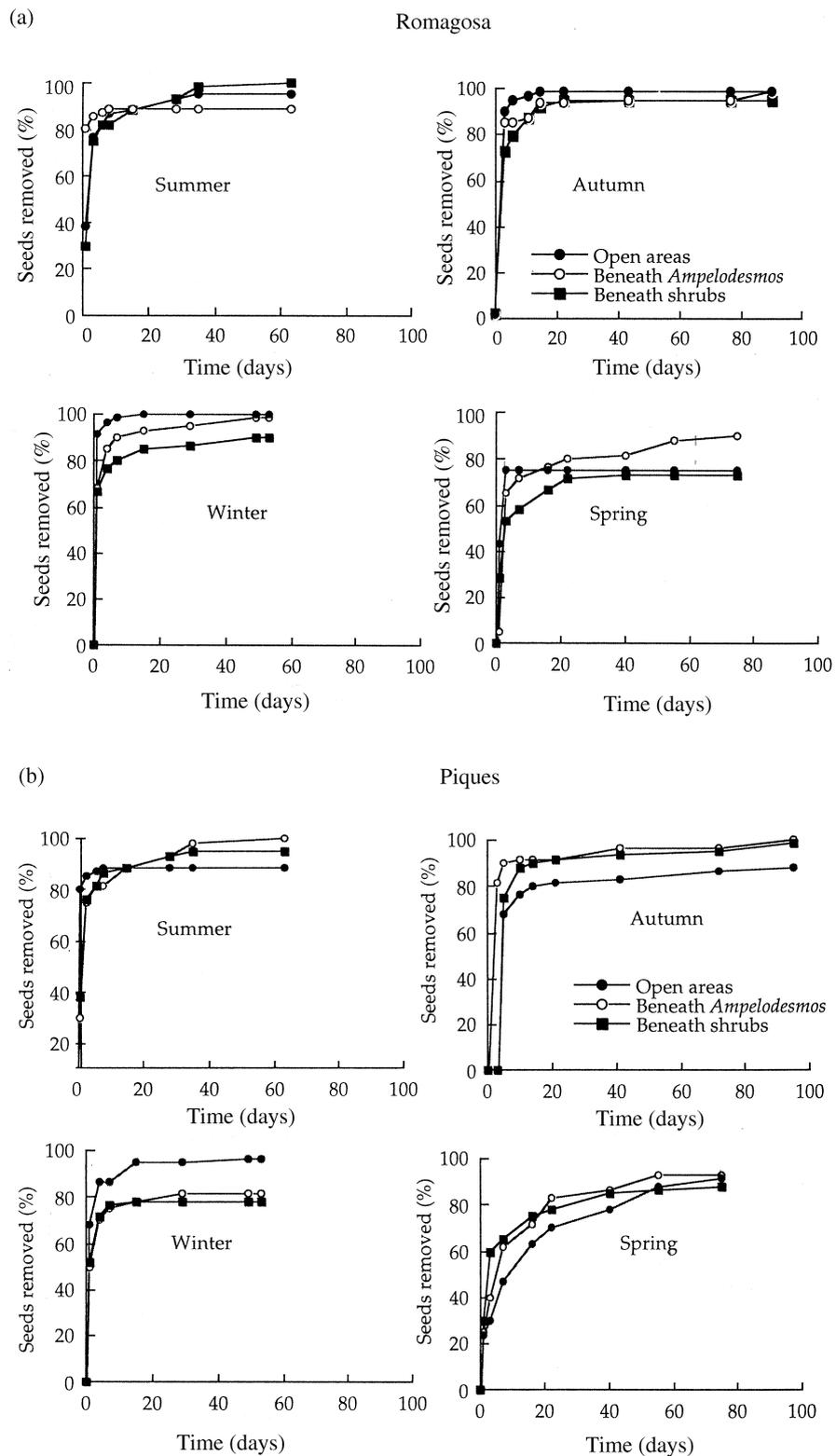


Fig. 4 Post-dispersal seed predation curves for different seasons for *Ampelodesmos* at (a) Romagosa and (b) Piques. The total initial number of seeds per microsite type and per season was 60.

0.0004), with lower values in open areas (Scheffé-test, $P = 0.0005$). Mortality rates were also significantly different between microsites ($\chi^2 = 20.97$, d.f. = 2, $P < 0.0001$, Gehan-Wilcoxon test), being fastest in open areas and slowest beneath shrubs.

In Romagosa, the only site where it was analysed, seedling growth was very slow. Two year old seedlings had on average 2.24 leaves of 3.68 cm in length. There were significant differences between microsites in the mean length of the longest leaf per

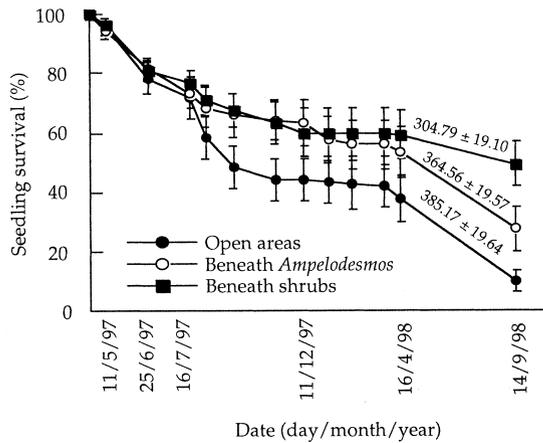


Fig. 5 Seedling survivorship curves of *Ampelodesmos* at Romagosa. Values are mean (\pm SE) product-limit (Kaplan-Meier) survival times at each microsite. Total initial number of seedlings per treatment was 120.

seedling ($F_{2,30} = 9.007$, $P = 0.0009$). Seedlings in open areas (20.92 ± 2.34 mm) were shorter than beneath *Ampelodesmos* (39.82 ± 5.01 mm) and shrubs (49.59 ± 5.44 mm) (Scheffé test, $P = 0.029$ and $P = 0.001$, respectively).

VARIABILITY AMONG REPRODUCTIVE COMPONENTS

There were significant differences between values for each of the three reproductive components within a microsite type at a site (Table 2). The seed bank was not significantly different from seedfall except in open areas at Romagosa where the seed bank was more than four times larger than seedfall. Seedling emergence was not significantly different from seedfall at any Romagosa site but was significantly lower than seedfall in open areas and beneath *Ampelodesmos* at Piques. A low density of seeds remained in the bank until June 1997, probably due to residual dormancy of seeds produced in 1996.

We estimated that there was a decline of three orders of magnitude from the number of seeds present in the seedfall to those that became established seedlings at the end of the recruitment process (Fig. 6). Although germination and emergence were very high, survival of seedlings was low. Adjusting for the proportion of the site occupied by each microsite type decreased seedling recruitment still further. The lowest overall seedling recruitment occurred in open areas (19 seedlings m^{-2}) where seedling survival was lowest and area represented only 24.4% of the total. The highest seedling recruitment occurred beneath *Ampelodesmos* (147 seedlings m^{-2}) mainly as a result of the high *Ampelodesmos* cover. Recruitment beneath shrubs (109 seedlings m^{-2}) is also high because of the highest seedling survival rate.

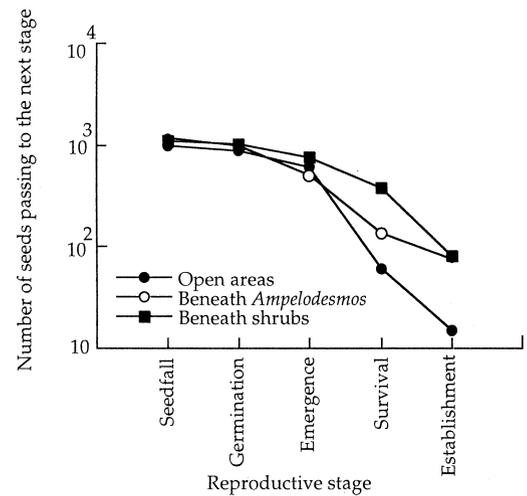


Fig. 6 Recruitment expectancies (m^{-2}) for *Ampelodesmos* seedlings at Romagosa. Reproductive stage: Seedfall (January 1997), seeds trapped on the ground; Germination (March 1997), seeds that germinate in the field; Survival (September 1998), seedlings that survived two dry seasons; Establishment, seedlings recruited adjusting for the proportion of the area covered by each microsite. Note log-scale on vertical axis.

Discussion

TEMPORAL AND SPATIAL VARIABILITY OF REPRODUCTIVE COMPONENTS

There was annual variability in both seed production and germination of *Ampelodesmos*. High seed production occurred synchronously within the populations in 1996 followed by a null crop in 1997 and very low production in 1998. The high level of seed production recorded in 1996 is within the range observed for other perennial grasses (Peart 1989). Germination was also higher in 1996 than in 1997 and was associated with periods of high precipitation that supplied the soil with the necessary moisture.

Mast seeding may be associated with years in which environmental conditions are favourable for recruitment. Such years may provide optimum conditions for germination (Silvertown 1980; Kelly 1994) and may occur following favourable weather during the preceding growing season (Waller 1993). Precipitation from January to August in the mast year 1996 (677 mm) was higher than in the following non-mast years 1997 (549 mm) and 1998 (237 mm). Moreover, precipitation during May, the month when there is much vegetative growth before the floral structures start to develop, was more than twice as high in 1996 (118.3 mm) as it was in 1997 (52.9 mm), and it was extremely low in 1998 (16.2 mm). An association between masting and high precipitation has also been found for the perennial tus-

sock grass *Stipa tenacissima* in semi-arid regions of southern Spain (Hasse *et al.* 1995).

Although it is widely stated that soil moisture stimulates both seed production and germination (Baskin & Baskin 1998), masting may also be a response to other environmental conditions such as fire which increases soil nutrients and light availability at the individual level and reduces competition (Daubenmire 1968; Kelly 1994). *Ampelodesmos* produces higher crops and higher seedling recruitment in burnt than in unburnt sites (Vilà *et al.*, in press). This may also partially explain the higher seed production per plant and seedling emergence at Romagosa compared to Piques, as the sites were last burnt 2 and 14 years before the study commenced, respectively.

Differences in reproductive components between the two sites may also be due to seed limitation or lack of safe sites. Lower adult density and inflorescence density, and thus lower seed production, at Piques may lead to seed limitation. However, higher seedfall than seedling emergence in open areas and beneath *Ampelodesmos* at Piques suggests that the lack of safe sites may also contribute to lower seedling emergence there. As seed germination in trays was very high at both sites, we think that the large number of surface rocks at Piques could constrain seedling emergence (as was found for short-lived species in the same area; Lloret 1998) because they reduce root-soil contact (Chambers *et al.* 1991). Seed emergence was not significantly different from seedfall beneath shrubs because shrub litter may provide good conditions for seed germination despite the rocky soil surface.

Seedfall, seed germination and seedling emergence were fairly homogeneous among microsites, whereas seed and seedling mortality and seed predation were significantly higher in open areas than beneath *Ampelodesmos* and shrubs at Romagosa. Other studies have both found differences in reproductive components between microsites and the requirement of grass species to have safe sites (Fowler 1988; Cheplick 1998). For example, in the Patagonian steppe, although seedfall is very homogeneous within a site, vegetated microsites recruit more grass seedlings compared to open areas (Aguilar & Sala 1997).

Ampelodesmos seeds are homogeneously dispersed by wind throughout a site. The rough ground and the presence of hairy caryopses may facilitate anchorage of seeds onto the ground surface (Peart & Clifford 1987) resulting in a relatively homogeneous pattern of seedfall and seedling emergence. Nevertheless, high light radiation and water stress may reduce the longevity of those seeds in open areas that fail to germinate, while also reducing seedling survival there. However, a previous study in this Mediterranean shrubland did not find differences in seedling emergence, survival and growth

between open and vegetated areas for short-lived woody species (Lloret 1998).

To summarize, spatial patterns of the different reproductive components were only partially coupled. At both sites there was an initial correspondence between seed germination and seedling emergence that could be predicted from seedfall. However, ecological factors that operate at the seedling stage obscured the initial relationship because seedling survival was favoured when protected by vegetation. Such an absence of relationship between seed and seedlings within a site has also been found for bird-dispersed species (Herrera *et al.* 1994) and other wind-dispersed species (Houle 1992, 1998) in temperate communities.

CAUSES OF SEED LOSS

Seed predation and seed mortality in the seed bank were two important causes of *Ampelodesmos* seed loss. Post-dispersal seed predation may limit recruitment of *Ampelodesmos* because it was very intense and occurred all year round.

Seeds were removed from the tied lines in various ways, and thus we think that several animal agents were involved in post-dispersal seed predation. These include quails and small rodents, which may have been the predators when seeds were totally removed from the tied lines. Ants were also efficient seed predators. In 1996 we observed the granivorous ants *Mesor barbatus* and *M. bouviery* harvesting large quantities of *Ampelodesmos* seeds from the ground and taking them to their nests. Large amounts of *Ampelodesmos* seed chaff were present on ant refuse piles.

Our results do not support the escape hypothesis which predicts a disproportionately high seed and seedling mortality beneath parent species (Janzen 1970; Connell 1971; Schupp 1988; Schupp & Frost 1989). At Romagosa, seed removal was generally highest in open areas but at Piques the pattern depended on the season. The absence of a consistent post-dispersal seed predation between microsites and between sites could be explained if several processes are operating at the same time (Díaz 1994; Verdú & García-Fayos 1996). As our post-dispersal seed predation experiments were conducted in a non-mast year and the seed bank was not significantly different between microsites, our results were independent of seed density and differences between microsites could not be explained by the influence of predator satiation. Seed predation patterns in different microsites and sites may depend on the types of predators and their response to habitat structure and plant cover. Faster seed predation in open areas may be related to seeds being easier to find (Getty & Pulliam 1993). On the other hand, lower seed predation in open areas may be due to the higher vulnerability of granivores to their predators and to the

presence of granivore refuges beneath the canopy of vegetated areas (Hay & Fuller 1981).

Mortality in the seed bank, due to senescence, environmental stress or pathogen attack, may also cause loss of *Ampelodesmos* seeds. Differences in loss of seed viability between sites may be due to variability in ground cover that may determine differences in the soil microclimate and microflora, both of which interact with seeds in the seed bank. Seeds of many grasses form persistent seed banks (Baskin & Baskin 1998). *Ampelodesmos* has a low-density persistent seed bank (Type III) because most seeds germinate soon after they are released, although a proportion of them do become incorporated into a persistent seed bank (Thompson & Grime 1979).

POTENTIAL FOR RANGE EXPANSION

Increase in the abundance and distribution range of exotic invasive and native expansive species (as defined by Pysek 1995) is not necessarily due to exceptional reproductive traits. Like most species, invasive and expansive plants face ecological constraints that are spatially and temporally variable (Parker 1997; Vilà & D'Antonio 1998b). Our results are consistent with some predictions of attributes of the ideal invader but contradict others. During a mast year, *Ampelodesmos* produces a large seed crop and seed germination and seedling emergence is very high in a wide range of microsites. However, most seeds that fail to germinate soon after dispersal will die because seed viability is short-lived and post-dispersal seed predation is very intense. Furthermore, *Ampelodesmos* does not produce seeds every year, which implies a potential loss of opportunities for reproduction. Thus, episodes of population growth through seedling recruitment are restricted to years of favourable weather and periods after fire (Vilà *et al.*, in press).

As stated by Houle (1998), spatiotemporal heterogeneity in plant recruitment complicates the modelling of population dynamics. There is both temporal and spatial variability in the reproductive components of *Ampelodesmos* and the consequences of this for the long-term dynamics are not known. However, as found in the exotic invasive *Mimosa pigra* in Australia by Lonsdale & Abrecht (1989), even if short-term seed and seedling survival is poor, invasion can occur through prolific seed production aided by years when good timing of abundant rain favours seedling recruitment.

In conclusion, sporadic pulses of resources such as high precipitation or release from competition and increase in resource availability after fire may increase *Ampelodesmos*'s seed crop, seed germination and seedling recruitment. However, two main ecological factors may control the expansion of *Ampelodesmos*'s distribution range within

Mediterranean shrublands. First, natural enemies are involved in seed loss. Secondly, in Mediterranean environments water availability is low, so reducing allocation to reproductive structures and decreasing germination of seeds in the seed bank. Overall, lack of (or low) *Ampelodesmos* seed availability can be understood as an 'episode of scale', meaning that occasional large episodes of reproduction are more efficient in terms of successful recruitment than regular small ones (Norton & Kelly 1988).

Acknowledgements

We thank E. Ogheri, U. Gamper, I. Gimeno, Y. Meggaro, A. Casanovas, A. Aragay, A. Ballés and J. Broncano for field and laboratory assistance. P. Jordano, M. Aguiar and two anonymous referees provided critical comments on an earlier version of the manuscript. We thank the Servei de Parcs de la Diputació de Barcelona and in particular S. Llacuna for permission to work in the Parc Natural del Garraf. Partial financial support was provided by the European Union project LUCIFER, the Ministerio de Educación y Ciencia DGICYT (AG97-533) and the Comissionat per a Universitats i Recerca de la Generalitat de Catalunya.

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Received 22 April 1999

revision accepted 30 November 1999