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Recruitment of two *Opuntia* species invading abandoned olive groves

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Abstract

In Europe, many agricultural areas are now abandoned and hence can be invaded by exotic species. The abundance and spatial distribution patterns of two *Opuntia* species were studied in old olive groves in the Parc Natural del Cap de Creus, Catalonia (Spain). Seedling recruitment (97.3% and 51.5% of juveniles for *O. maxima* and *O. stricta*, respectively) was higher than recruitment by cladodes. *O. maxima* had more seedlings recruited beneath olive trees and beneath *Opuntia* adults than expected. Most *O. stricta* seedlings were also located beneath *Opuntia* adult plants. However, although most seedlings were recruited beneath *Opuntia*, some (10–30%) were found away from putative parental plants. This may be due to seed dispersal by birds and wild boars. Seeds dispersed by wild boars were not significantly more viable than seeds from intact fruits. Seedlings grow very slowly but have a high survival rate. In conclusion, *Opuntia* seedling recruitment is very successful and ensures the persistence of these species within old olive groves. Consequently, it prevents restoration from an agricultural land-use back to the native community. © 2002 Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

Keywords: Cactaceae; Exotic species; Mediterranean vegetation; Microsite; *Opuntia maxima*; *Opuntia stricta*; Seed viability; Seedling recruitment and survival

1. Introduction

Invasion by exotic plant species can change the structure of the recipient community and alter ecosystem properties especially when the introduced species is qualitatively different from the native species (Chapin et al., 1995; Parker et al., 1999). Much research on plant invasions focuses on the biological characteristics of exotics and the ecological mechanisms controlling invasion (i.e. Mooney and Drake, 1986; Di Castri et al., 1990; Pyšek et al., 1995; Williamson, 1996). The first step to assess the dynamics of invasion is to describe local patterns of recruitment and thereby put forward general hypotheses to be experimentally tested.

In clonal plants, seedling recruitment is an important determinant of population dynamics and life history evolution (Eriksson, 1989, 1992). Especially for plant species known to have low sexual seedling recruitment, it is crucial to ask how they can be invaders and how seedling establishment is influenced by the native vegetation structure in a new region. For example, despite the high fruit productivity and seed dispersal of some non-columnar cacti species in Central America, seedling recruitment is rare and only occurs in safe sites under nurse plants (Turner et al., 1966; Nobel, 1988). Montiel and Montaña (2000) report that *Opuntia rastrera* can produce more than 5000 fruits/ha bearing almost 1 million seeds/ha, more than 85% of which are consumed by disperser frugivores. Seedling establishment, however, is nil.

Prickly pear cacti (*Opuntia* spp.) are one of the most well-known examples of a plant genus that has invaded different vegetation communities around the world (Cronk and Fuller, 1995). In the Mediterranean basin, several *Opuntia* species are cultivated for livestock forage and human food, and are planted as ornamentals or for fencing, increasing the chances of invasion into natural communities (Ellenberg, 1989; Inglese et al., 1995). Vegetative reproduction by cladodes (flattened segments that constitute succulent stems) of *Opuntia* spp. is an important factor in the persistence of their populations but seedling recruitment is essential for expanding the geographic range and for establishment in new areas. This study provides information about the seedling recruitment of *O. maxima* and *O. stricta* in abandoned olive groves in north-eastern Spain. The objectives of the study are: (a) to describe the main

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demographic parameters for adult plants and seedlings, (b) to analyse if there is an association between seedling establishment and vegetation cover and (c) to determine the effect of different seed sources (from intact fruit or from wild boar faeces) on seed viability.

2. Materials and methods

2.1. Study species

Opuntia spp. (Cactaceae) are non-columnar cacti (nopales) from Central America (Cronk and Fuller, 1995). The succulent stems are formed as a sequence of flattened segments, the cladodes, which generally have an elliptical base that supports the greatly enlarged, flattened upper portion. *Opuntia* has spines as leaves. The flowers, 5–10 cm in diameter, are sessile and solitary and the fruits are berries, of 4–8 cm (Castroviejo et al., 1990). Vegetative reproduction is common. Cladodes break off and root, usually near the parental ramet and form conspicuous patches. *Opuntia* resprout vigorously after above ground removal and are fire resistant.

The two study species were *O. maxima*, which presents an average height of 3 m and *O. stricta* that does not attain more than 1 m. The phenology of the two species is similar. Flowering and fruiting occur from May to July. *O. maxima* fruits have a mean length of 6.1 ± 0.1 cm and width of 4.5 ± 0.1 cm. They contain 175 ± 8 seeds per fruit and weigh 70.6 ± 2.5 g (mean ± s.e., $n = 36$ fruits). *O. stricta* fruits are 5.3 ± 0.1 cm long and 3.2 ± 0.5 cm wide, have 110 ± 6 seeds per fruit and weigh 37.1 ± 1.2 g (mean ± s.e., $n = 36$ fruits). *O. maxima* seeds are oval, are 4.07 ± 0.07 mm long and 3.18 ± 0.06 mm wide. *O. stricta* seeds have a mean length 4.20 ± 0.05 mm and width of 3.82 ± 0.03 mm (mean ± s.e., $n = 20$ seeds). When the fruits ripen, birds and wild boars consume them. In olive groves, we estimated that fruit consumption by wild boars, which disperse the seeds at long distances, was 19.4 ± 6.7% for *O. maxima* and 25.0 ± 10.9% for *O. stricta* (mean ± s.e.) (Vilà and Gimeno, unpublished). Seed dispersers at short distances are winter migratory birds, such as thrushes (*Turdus philomelos*) and starlings (*Sturnus vulgaris*).

Opuntia spp. were introduced from Central America to Europe by the Spanish conquerors between the end of the 15th century and the beginning of the 16th century (Barbera et al., 1992). *Opuntia* spp. have been used for human consumption, livestock, foraging, fencing, the production of a red dye that was obtained from a cochineal insect parasite (*Dactylopius coccus*), and as ornamentals. *Opuntia* spp. are CAM plants with a highly efficient use of water, that might explain their success in invading Mediterranean and semi-arid areas (Cortázar and Nobel, 1990). Fire is another cause of prickly pear expansion. For example, in southern California, fire has been a major factor in the ecological success of prickly pears. Dense patches of cacti are favoured by fire because only the perimeter is vulnerable to fire. They form vigorous centres which expand outward and occupy more and more space after each grass fire (Benson and Walkington, 1965). Moreover, from any living fragment, new plants may arise.

2.2. Study site

The study site was located in the Parc Natural del Cap de Creus (Catalonia, Spain). Like other European Mediterranean regions, during the last few decades, Cap de Creus has experienced great changes due to tourism, an increment in disturbances (fire, housing development), crop abandonment and a concentration of human habitation along the coast line (Debussche et al., 1999). The climate is Mediterranean with cool, wet winters and warm, dry summers. Mean monthly temperatures of the coldest (January) and hottest (August) months are 4 °C and 21 °C, respectively. Mean annual precipitation is 600 mm. The soils are acidic loamy sands (Vilà, 1996). The vegetation is mainly dominated by old terraced olive groves and vineyards, colonized by sclerophilous shrubland vegetation and planted pine woodlands (Franquesa, 1989). On average, more than 9% of the park is occupied by terraced olive groves, which have been abandoned since the 1960s due to the tourist boom (Folch, 1988).

Opuntia spp. were introduced to Cap de Creus as ornamentals in gardens and to fence fields. Their expansion in olive orchards has been favoured by the abandonment of these crops and for the high fire frequency. Cap de Creus suffered recurrent fires during the period 1975–1993 (Díaz-Delgado, 2000). Short time intervals between fires result in lower ecosystem resilience (Canadell and Lopez-Soria, 1998). Thus, when disturbance frequency is high, vegetation cover decreases, propitiating *Opuntia* invasion. The distribution range of established prickly pears that survive fire increases because their expansion is facilitated by the absence of native species competing for space. This increases the survival probability and the expansion of *Opuntia* spp. and impedes the regeneration of native species.

We studied the distribution and abundance of *O. maxima* in Selva de Mar (SM) and *O. stricta* in Port de la Selva (PS). The two study sites (3°13'E, 42°18'N) are old olive groves 3 km apart. In SM, the vegetation is dominated by *Lavandula stoechas* (31% of the vegetation cover) and *Olea europaea* (27%). In PS, the vegetation is dominated by *Brachypodium retussum* (27%) and other grasses (22%). In this site, olive trees represent 20% of the vegetation cover. *O. maxima* represents 2.3% of the vegetation cover in SM and *O. stricta* represents 5.6% in PS.

2.3. Plant population characteristics and spatial distribution

Olive orchard abandonment occurred in the 1960s. The oldest establishment of *Opuntia* might be 40 years old.

However, it is not possible to determine the age structure of the population. Therefore, we proceeded to determine their size structure.

In June 1998, eleven 10 m × 10 m plots of a population of *O. maxima* in SM and fourteen 10 m × 10 m plots of a population of *O. stricta* in PS were randomly placed in abandoned olive orchards invaded by *Opuntia*. In each plot, we counted the number of all *Opuntia* adult and juvenile plants. We identified if juveniles were recruited from seeds or cladodes. Seedlings were directly inserted in the soil and were smaller than juveniles from cladodes. Recruits from cladodes could be identified because they were still attached to the "parental" cladode and were more vigorous than seedlings. For all *Opuntia* we measured the height, the number of cladodes and whether they were located beneath an olive tree or not.

For each adult plant, we counted the flowers and estimated plant growth as the relative annual increment in cladode number as $(X_{t1} - X_{t0})/X_{t0}$, where X_{t1} is the number of cladodes in the current year and X_{t0} is the value in the previous year. The cladodes from the previous year were dark green in colour and with big spines in comparison to cladodes from the current year.

For each seedling, we measured the distance to the closest reproductive *Opuntia*. To evaluate the survival and growth of seedlings, in June 1998 we recorded the height and number of cladodes of 65 *O. maxima* and 58 *O. stricta* seedlings selected at random. Seedlings were tagged and were measured again 1 and 2 years later. We calculated the annual increment in height and number of cladodes to estimate seedling growth as described above for adult plants.

To quantify the spatial association between *Opuntia* seedlings and olive trees, we identified the associated cover (microsite) for each *Opuntia* seedling and classified it as: (1) beneath an olive tree, (2) beneath an *Opuntia* adult plant, (3) beneath shrubs and grasses or (4) in an open area. To compare if the observed distribution was significantly different from the expected, in each site the relative frequency of these three microsites was estimated by the point intercept method, conducted every 20 cm in eight 50 m long transects and statistically tested by χ^2 goodness-of-fit analysis (Greenlee and Callaway, 1996).

2.4. Distribution of fallen fruits and seedfall

The number of freshly fallen fruits was counted in 10 contiguous 20 cm × 20 cm quadrats along three randomly placed transects from the base of eight established adult *O. maxima* and fifteen *O. stricta*. An estimation of the seedfall beneath *Opuntia* was calculated by multiplying the density of fallen fruits by the average number of seeds per fruit. For this purpose, the number of seeds was counted in four randomly selected fruits per plant from eight randomly selected plants.

At the site invaded by *O. maxima*, plastic pots (20 cm in diameter and 15 cm deep) were used as seed traps to estimate seedfall beneath olive trees and shrubs. The pots were covered by chicken wire of a sufficiently coarse mesh to allow passage of seeds but fine enough to prevent seed predation by rodents. The bottoms of the pots were pinned to the ground and holes were drilled to allow water to drain freely. Groups of four traps beneath 10 olive trees and beneath 10 shrubs were randomly placed in June 1998. Traps were surveyed several times over 2 years (until May 2000). During these surveys, seeds from woody species or *Opuntia* spp. were removed, identified and counted.

2.5. Seed viability

Birds and wild boars that consume fruits and swallow seeds act as dispersal agents. In SM, we found several wild boar faeces that contained more than 1000 *O. maxima* seeds (Gimeno, unpublished). Therefore, we tested *O. maxima* seeds removed from wild boar faeces for seed viability and compared it to *O. maxima* seeds from intact dry fruits. Bird faeces have from one to three seeds only, they are difficult to obtain and were found in insufficient number to conduct a viability test.

A germination test was carried out as an estimation of seed viability. Seeds were placed in Petri dishes with washed sand. Ten seeds per plate were used and 20 replicates were performed for each different seed source. The experiment was performed at laboratory room temperature (20 °C) and under natural daylight conditions. It would have been more realistic to use different temperatures during the day and the night but this was logistically impossible in our laboratory. Once a week for 4 months we counted and removed the seeds which had germinated. We considered that a seed had germinated if the radicle and cotyledon had emerged. After 110 d, we evaluated the viability of non-germinated seeds by a tetrazolium test (Ellis et al., 1985). Seeds were stained with 0.1% tetrazolium after piercing and soaking them in GA3 400 ppm at 4 °C overnight. The proportion of germinated seeds was arcsine transformed and analysed by a *t*-test to study the effect of the seed source on seed germination. Other parameters analysed were the latency time (the time elapsed until the first seed germinated) and the germination velocity (the time until 50% of the seeds germinated). The total seed viability was estimated as the percentage of germinated seeds + the percentage of viable seeds among the non-germinated seeds.

3. Results

3.1. Plant population characteristics and spatial distribution

The density of adult *Opuntia* plants was 5.92 ± 1.54 plants/100 m^2 (mean ± s.e.) for *O. maxima*

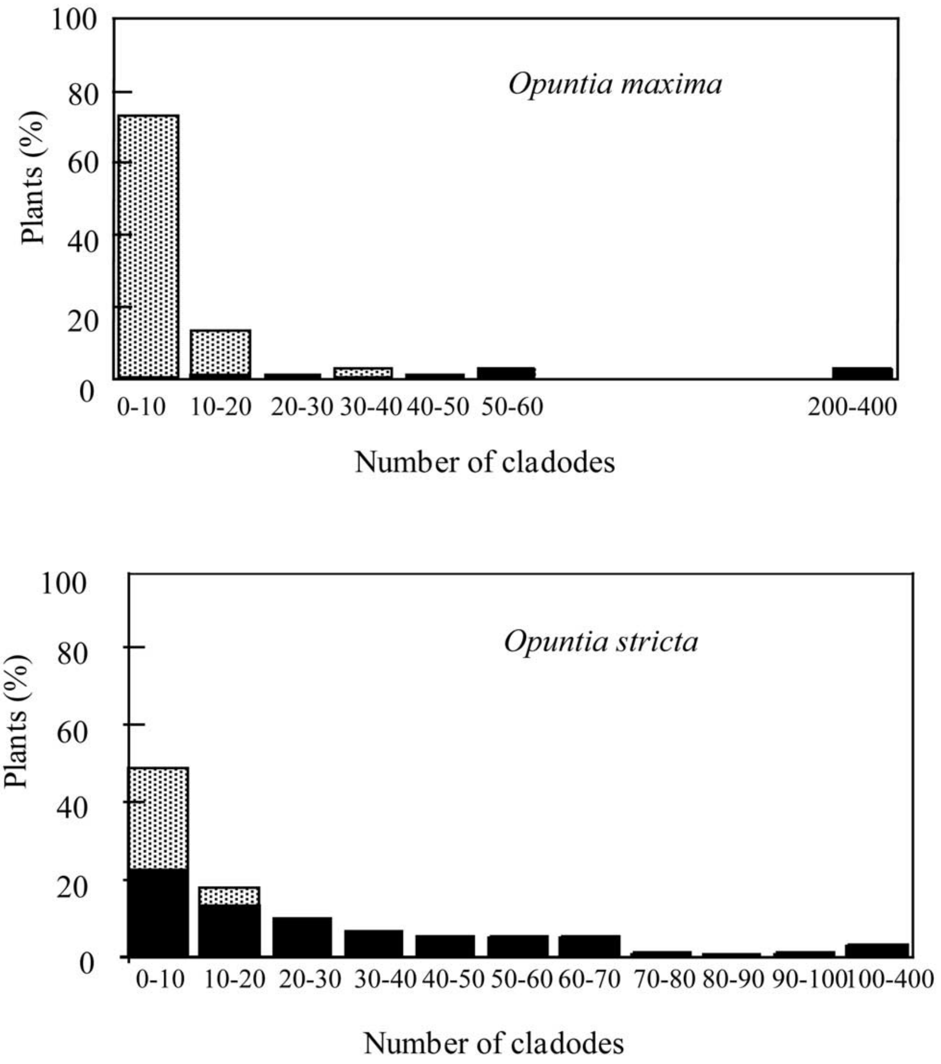

Fig. 1. Size distribution of adult *O. maxima* and *O. stricta* and percentage of reproductive plants. The black part indicates the relative percentage of plants that produced fruits.

(n = 11 plots) and 20.20 ± 6.40 plants/100 m^2 for *O. stricta* (n = 14 plots). The *O. maxima* adult plants (n = 75) were on average 84 ± 8 cm tall and had 15 ± 5 cladodes (mean ± s.e.). *O. stricta* plants (n = 123) were shorter (58 ± 3 cm) but had a higher number of cladodes (22 ± 3). The majority of *O. maxima* adult plants (73%) and half the *O. stricta* plants had less than 10 cladodes (Fig. 1). There was a higher proportion of reproductive plants for *O. stricta* than for *O. maxima*. *O. stricta* plants start to reproduce at a smaller size than *O. maxima*. The production of new cladodes in *Opuntia* adult plants is positively correlated to the number of old cladodes.

Vegetative recruitment was lower than recruitment by seeds. Seedling recruitment represented 97.3% of juveniles for *O. maxima* and 51.5% for *O. stricta*. The seedling density of *O. stricta* was lower than that of *O. maxima*. Seedlings grew very slowly but they had a high survival rate (Table 1). The annual increment in cladode number for *Opuntia* seedlings was similar for the two species and varied between periods. The annual increment in height during the second period (1999–2000) was higher for *O. stricta* (n = 58) than for *O. maxima* (n = 65) (Table 1) but the estimated growth was not significantly different between species. For adult plants, the absolute annual increment of the cladode number, during the period 1998–1999, was 3 ± 1 for *O. maxima* (n = 75) and 2 ± 0.5 for *O. stricta* (n = 123) (mean ± s.e.). The growth in height of both species was similar (0.18 ± 0.02 cm for *O. maxima* and 0.12 ± 0.01 cm for *O. stricta*).

Although olive cover was less than 30%, many *Opuntia* adult plants were located beneath olive trees (36.6% for *O. maxima* and 15.8% for *O. stricta*). Seedling distribution in different microsites does not correspond to the expected distribution, considering the vegetation cover type at the study sites (χ^2 = 1740.68, $P << 0.001$ for *O. maxima*; χ^2 = 177.88, $P << 0.001$ for *O. stricta*) (Table 2). Similar to the situation for adult plants, there were more *O. maxima* seedlings (36.6%) located beneath olive trees than expected. Both species had a higher proportion of seedlings beneath *Opuntia* adults than expected (39% for *O. maxima* and

Table 1
Demographic characteristics of *O. maxima* ($n = 65$) and *O. stricta* ($n = 58$) seedlings. Values are given as means ± standard error (s.e.)

Seedling characteristics	*Opuntia maxima*	*Opuntia stricta*	t-value	P-value
Density (seedlings/100 m^2)	17.8 ± 9.50	3.70 ± 1.60	1.63	0.115
Mean distance to an adult (m)	2.67 ± 0.17	1.38 ± 0.24	3.99	< 0.0001
Annual increment of height (cm)				
Period 1998–1999	2.54 ± 0.30	2.20 ± 0.30	0.40	0.688
Period 1999–2000	4.08 ± 0.80	5.80 ± 1.30	– 5.15	< 0.0001
Annual increment of cladodes				
Period 1998–1999	0.59 ± 0.07	0.57 ± 0.07	0.35	0.724
Period 1999–2000	0.20 ± 0.10	0.20 ± 0.07	0.53	0.599
Height growth				
Period 1998–1999	0.18 ± 0.02	0.15 ± 0.02	0.99	0.326
Period 1999–2000	0.20 ± 0.02	0.23 ± 0.03	– 0.626	0.533
Cladode growth				
Period 1998–1999	0.20 ± 0.03	0.18 ± 0.02	0.34	0.737
Period 1999–2000	0.07 ± 0.02	0.05 ± 0.02	1.02	0.310
Survival (%)	100	94.83		

35.8% for *O. stricta*). Most of them were located 1 m away from an adult. But a few were 10 m away from the closest adult plant (Fig. 2). Although shrubs and grasses represent 50% and 60% of plant cover at the *O. maxima* and *O. stricta* site, respectively, fewer seedlings than expected were recruited beneath this cover type (11.3% for *O. maxima* and 38.9% for *O. stricta*).

3.2. *Distribution of fallen fruits and seedfall*

Most fruits fall at a distance less than a metre from the base of the mother plant (Fig. 3). Some *O. maxima* fruits, as the plants are taller than *O. stricta* plants, were further away from the mother plant than the fruits of *O. stricta*. The estimated seedfall beneath the mother plant was 2218 seeds/m^2 for *O. maxima* ($n = 8$ plants) and 1666 seeds/m^2 for *O. stricta* ($n = 15$ plants).

In contrast, *Opuntia* seedfall due to bird dispersal beneath olive trees and shrubs was negligible. During the 2 years of survey, we only found 11 (two beneath shrubs and nine beneath olive trees) *Opuntia* seeds in the traps. More seeds from three different species were found in the traps: *Olea europaea* (299 seeds), *Celtis australis* (73 seeds) and *Pistacea lentiscus* (46 seeds). More seeds were collected beneath olive tress than beneath shrubs (t-value = 4.11, $P = 0.0007$).

3.3. *Seed viability*

Although seeds from faeces germinated more quickly during the first days of germination, the germination velocity was only marginally different between seed sources ($F_{1,38} = 4.54$, $P = 0.05$). Seeds from intact fruits had a higher germination rate ($F_{1,15} = 4.695$, $P = 0.037$) and a lower latency time ($F_{1,38} = 30.140$, $P < 0.001$) than seeds from wild boar faeces (Fig. 4). There were no significant differences in total seed viability (93% from intact fruits and 97.4% from wild boar faeces).

4. Discussion

Opuntia spp. invade abandoned olive groves in the Cap de Creus. Our findings differ from the low cacti seedling recruitment found in native areas (Turner et al., 1966; Nobel, 1988; Mandujano et al., 1996). The two species, *O. maxima* and *O. stricta*, had higher seedling recruitment than vegetative recruitment by cladodes, an opposite trend

Table 2
Observed and expected *O. maxima* and *O. stricta* seedling distribution in different microsites in Selva de Mar and in Port de la Selva, respectively

Study area	Cover type	Relative frequency	Number of *Opuntia* seedlings	
			Observed	Expected
Selva de Mar[a]	Beneath olive tree	27.1	107	79
	Beneath *O. maxima*	2.3	114	7
	Open area	20.9	38	61
	Beneath shrub and grass	49.7	33	145
Port de la Selva[b]	Beneath olive tree	19.4	15	18
	Beneath *O. stricta*	5.6	34	5
	Open area	13.6	9	13
	Beneath shrub and grass	61.4	37	59

[a] For this site, $n = 292$, $\chi^2 = 1740.68$, df = 3 and $P << 0.001$.
[b] For this site, $n = 95$, $\chi^2 = 177.87$, df = 3 and $P << 0.001$.

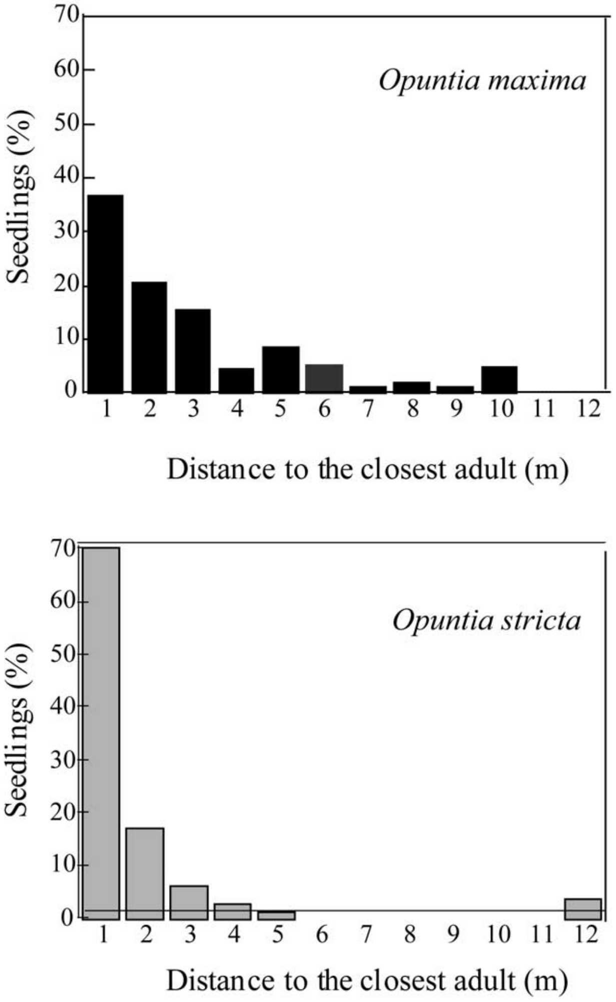

Fig. 2. Distance distribution of *O. maxima* and *O. stricta* seedlings from the closest *Opuntia* adult plant.

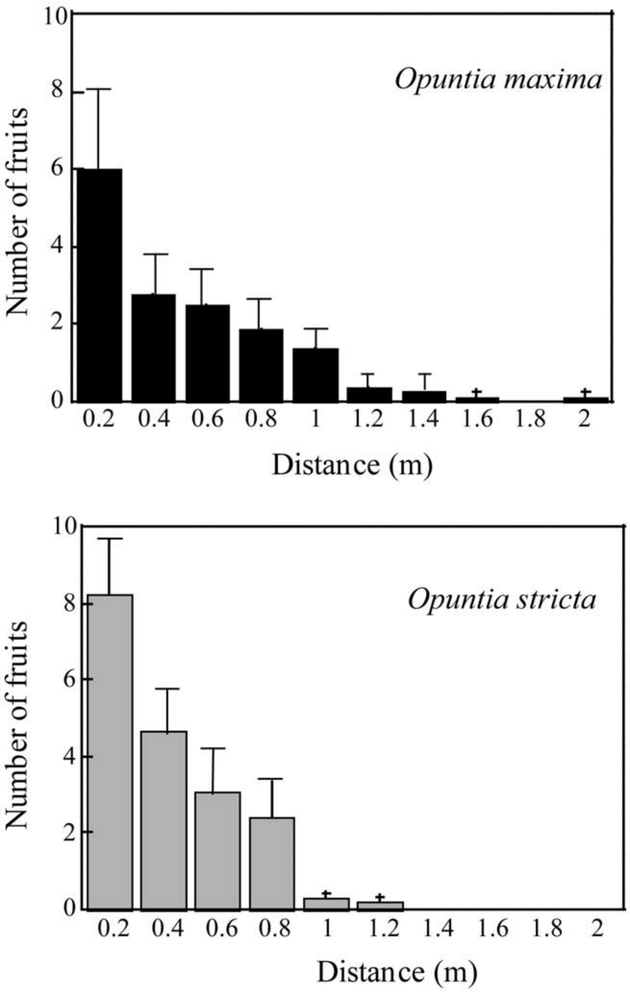

Fig. 3. Spatial distribution of fallen fruits around mother plants. Number of fruits per plot ± s.e. (plot = 20 × 20 cm).

compared to some non-columnar *Opuntia* in their native range (Mandujano et al., 1998). The advantages of this sexual reproduction include the expansion of the distribution area, the colonization of new sites and the increase of genetic variability within the population.

The expansion of a species range is influenced by biological differences between species and their interaction with the habitat (Thébaud et al., 1996). Seedling recruitment varied depending on *Opuntia* species. Although *O. stricta* plants are smaller than *O. maxima* plants, they produce more fruits and are at higher densities than *O. maxima*. However, seedling recruitment is less for *O. stricta* than for *O. maxima*.

Adult plant and seedling spatial distribution did not correspond to fruit fall distribution near adult plants. If we compare the seedling recruitment pattern between species, we observe that *O. maxima* seedlings were most abundant beneath olive trees (37%) while few (16%) *O. stricta* seedlings were found in this microsite. Eriksson and Ehrlén (1992) suggested two alternatives for recruitment limitation: availability of seeds or availability of suitable microsites. In our study, the causes of the different seedling recruitment between species or the factors limiting this process could be the seed dispersal, seed predation, seedling emergence, seedling predation, seedling competition with neighbouring plants and disturbances by humans or wild boars.

The association of plants to vegetation cover has been described for some cacti species in arid and semiarid ecosystems (Yeaton, 1978; Valiente-Banuet and Ezcurra, 1991). Some observations show that establishment of cladodes was less dependent on vegetation associations than that of seedlings (Mandujano et al., 1998). These associations may be related to better environmental conditions (temperature, reduced evapotranspiration) beneath vegetation than in the open (Pugnaire and Callaway, 1999). For example, seed germination and seedling establishment beneath olive trees may be favoured by lower soil compression in these sites (Verdú and García-Fayos, 1996). *O. maxima* seedling distribution was not associated with the most dominant vegetation cover (shrubs and grasses) but it was associated with adult *Opuntia* plants and olive trees. This seedling recruitment beneath *Opuntia* may be due to the existence of an abundant seed bank beneath adult plants.

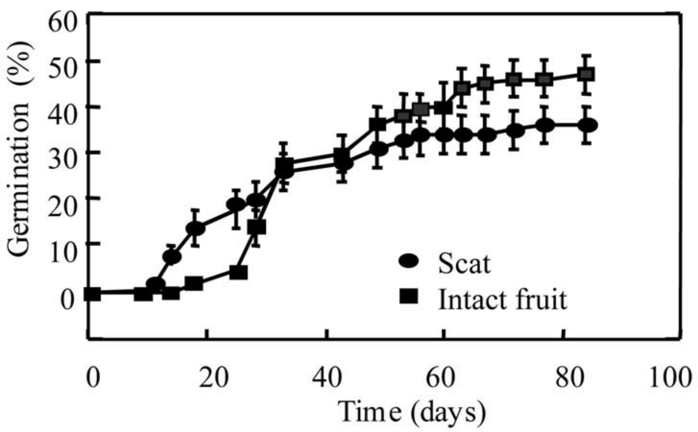

Fig. 4. Germination curve of *Opuntia* spp. seeds from fresh fruits and wild boar faeces. Values represent the mean percentage ± s.e. of seeds which germinated.

Even so, some seedlings were found away from parental plants. Seed dispersal by birds or wild boars may be the cause of this spatial distribution. Debussche and Isenmann (1985) studied the role of *Turdus philomenos* in seed dispersal in southern France and they found that these birds consumed fleshy fruits and disseminated their seeds. The association of *O. maxima* seedlings to the presence of olive trees might be due to seed disperser birds that have a preference to perch on these trees. A comparative study of seed rain and the soil seed bank between forested sites and grasslands demonstrated the major influence of perch sites on deposition patterns of bird-dispersed seeds (Ferguson and Drake, 1999). Beneath perches, the seed availability is higher than in open sites because birds defecate or regurgitate more seeds in these microsites (Debussche and Isenmann, 1994). However, the results of seedfall test below olive trees suggest that seed dispersal in this microsite is slow. Furthermore, seed removal by birds might also be low. Janzen (1986) estimated that in their native range, only 1–5% of seeds are dispersed by birds. In the case of *O. stricta*, we found seedlings associated to adult *Opuntia* but the spatial association between olive trees and *O. stricta* is not so evident as for *O. maxima*.

The observed seedling distribution could also be due to other plant–animal interactions such as seed predation. This factor reduces plant population recruitment and together with microsite characteristics (e.g., distance to reproductive adult, seed density), fruit production and the accompanying satiation of seed predators determine seed mortality (Janzen, 1971). The satiation effect for predators near *Opuntia* plant induced by the high seed density in this microsite could explain the distribution of *O. stricta* seedlings. The total density of seeds beneath *O. stricta* in the study area is high (the estimated seedfall was less than that of *O. maxima* but the density of reproductive *O. stricta* plants was greater than for *O. maxima*). This abundance of seeds might cause the satiation of predator agents and so the low seed predation intensity could generate a high proportion of seedlings in this microsite. Seed predation could determine the seedling distribution at other microsites where predators are not satiated.

Seed dispersal by vertebrate frugivores of fleshy-fruited plants may be very important for seedling recruitment (Montiel and Montaña, 2000). The capacity of seeds to germinate after ingestion by frugivores is important for the population dynamics of some plant species (Traveset, 1998). Some seeds germinate better after passage through an animal digestive tract. Most intact seeds in wild boar faeces were viable and their germination was similar to seeds from fruits. The plant–frugivore relationship is mainly unbalanced: the plant rewards dispersers with many fruits but the benefit of frugivores to plants is low. As Montiel and Montaña (2000) describe for *Opuntia rastrera*, there is an asymmetric interaction with frugivores because there is high fruit production but the rate of recruitment is very low. However, we found *O. maxima* seedlings far away from the population, suggesting that the plant benefits from seed dispersal by frugivores.

This study suggests that seed germination, seedling emergence and recruitment, the mean distance of seedlings from their putative parental origin and the shape of the distribution of these distances depend on the interaction between the exotic plant and the recipient community and are critical for understanding the significance of biotic factors in plant invasion dynamics.

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