

Nucleation processes in a Mediterranean bird-dispersed plant

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Summary

1. The spatial distribution of *Pistacia lentiscus*, a Mediterranean bird-dispersed plant, in abandoned orchards was found to be strongly linked to the presence of trees or shrubs that act as perches.
2. These perches not only attract seed-disperser birds but also produce favourable microenvironmental conditions for seed germination and seedling establishment.
3. Soil moisture content after a rainfall was always greater beneath perches than not beneath perches. Favourable water potentials for seed germination were maintained for a longer time beneath a perch than elsewhere.
4. After a rainfall, soil was compacted faster where not beneath perches. Seedling radicle penetration into soil was strongly associated with soil compaction.

Key-words: Abandoned fields, colonization, facilitation, perch

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Introduction

Facilitation (*sensu* Connell & Slatyer 1977) is one of the mechanisms affecting plant colonization of abandoned agricultural lands. Existing trees act as centres for the establishment of colonizing species, behaving as a nucleus for the subsequent growth of patches of other species. This facilitation process has been named nucleation because of its analogy with other physical processes, such as the growth of hailstones (Yarranton & Morrison 1974). Gill & Marks (1991) separated the facilitation model into direct and indirect components on the basis of their mechanisms. Direct mechanisms act on the later colonists through changes caused in the physical environment by earlier colonists, while indirect mechanisms act on the later colonists through the activity of animals or microbes necessarily associated with the presence of the earlier plant colonists.

The colonization of abandoned fields by bird-dispersed plants can be facilitated by existing trees both indirectly, by attracting seed-disperser birds, and directly, by improving environmental conditions. Seed-disperser birds have a marked preference for simple structures, such as stones, trees, shrubs, etc. (referred to as perches hereafter). These birds regurgitate or defecate more seeds beneath perches than in open sites or clearings, which results in higher seed

availability, beneath perches (Izhaki, Walton & Safriel 1991; Debussche & Isenmann 1994; Herrera *et al.* 1994).

Perches may also produce a microenvironment favourable for seed germination and seedling establishment. However, this direct mechanism of facilitation has received little attention. Isolated trees caused marked variations in the flora and edaphic environment under their canopy and around them (Zinke 1962; Jake & Coughenour 1990). Soils under the tree canopy are richer in nutrients and organic matter and have a macroporosity favourable to infiltration and redistribution of soil water (Montoya 1982; Escudero 1985; Joffre & Rambal 1993). This improvement of soil properties results in more water being stored in the soil beneath the canopies than elsewhere and thus more water is available for seed germination and establishment (Joffre & Rambal 1993). In addition, tree canopies protect the soil from the direct impact of rain drops, reducing surface compaction and facilitating root penetration. All these characteristics should also favour the nucleated pattern of colonizing plants around perches.

The general objective of this study was to test for the existence of a nucleated pattern in a Mediterranean bird-dispersed plant, *Pistacia lentiscus* L. (Anacardiaceae), which colonizes abandoned orchards, and to determine the mechanisms that may be responsible for this pattern. We only analysed those mechanisms that were related to changes in the germination environment, because previous work has already established

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that the density of seeds of *P. lentiscus* and other bird-dispersed plants is greater beneath the canopy of isolated trees than elsewhere (Debussche, Lepart & Molina 1985; Debussche & Isenmann 1994). The specific objectives of this study were to (1) test for the existence of a nucleated pattern in abandoned orchards colonized by *P. lentiscus*; (2) quantify the effects of the perches on soil water potential and how this affects seed germination; and (3) quantify the effects of the perches on soil compaction and how this affects seedling root penetration.

Materials and methods

STUDY SPECIES

Pistacia lentiscus is a dioecious, evergreen shrub common in Mediterranean sclerophyllous shrublands. It is wind pollinated, and usually flowers between March and May. Vegetative growth starts after the flowering period. Following pollination, the zygote remains dormant for several weeks and then, in later summer, the fruits grow quickly to their final size, ripening from August to December (Grundwag 1976; Jordano 1988, 1989). Each female produces many one-seeded drupes. Estimated average fruit production is 3764 ± 1320 ($n=28$ females from three adjacent populations; Verdú & García-Fayos 1995).

Frugivorous birds, mainly *Sylvia* spp., *Turdus* spp. and *Erithacus rubecula*, disperse the seeds from September to March (Herrera 1984; Jordano 1989; Verdú, Catalá & García 1989). Ants can act as secondary dispersers (Aronne & Wilcock 1994). The main pre-dispersal seed predators are chalcidoid wasps (*Megastigmus pistaciae*; M. Verdú, personal observation) and granivorous birds (*Carduelis chloris*; Jordano 1989, 1990), while the main post-dispersal seed predators are granivorous birds and rodents.

NUCLEATION PATTERN

We tested the spatial association between seedlings and adult plants of *P. lentiscus* and perches in an orchard that had been abandoned for 14 years. The orchard is located in Domeño (Valencia, east Spain), 60 km inland, at an altitude of 400 m. We divided an area 30 m wide and 250 m long into 5×5 m plots and recorded the presence and absence of both *P. lentiscus* and perches. The upper part of the studied area was in contact with the natural vegetation, a Mediterranean shrubland dominated by *Quercus coccifera*, *Juniperus oxycedrus*, *Pistacia lentiscus*, *Pinus halepensis* and *Pistacia lentiscus*. Perches were mainly *Ceratonia siliqua* (Leguminosae), the carob tree. It is an evergreen, sclerophyllous tree 4–6 m tall with 4–5 m of canopy diameter, reaching a maximum density of 50 trees ha^{-1} . It was cultivated in the past mainly for animal fodder.

WATER POTENTIAL EFFECTS

The study site was an abandoned orchard located in Porta-Coeli (Valencia, east Spain), 20 km inland at an altitude of 200 m. *Ceratonia siliqua* was also the main perch in this orchard. The Domeño and Porta-Coeli sites are 40 km apart, and have very similar climatic and ecological conditions. The climate is Mediterranean type with dry, hot summers and mild winters. Soils are developed over calcareous sediments.

We estimated soil water potentials from soil moisture content measures, extrapolating from the corresponding desiccation curves previously determined in a laboratory (Mériaux 1979). The soil under the canopies and outside them had different textures and, therefore, the desiccation curves were also different. We measured soil moisture content daily for 7 days following a rainfall of 42.91 m^{-2} , which occurred between 15 and 19 April 1994. Soil samples were taken in $6 \text{ cm} \times 2.675 \text{ cm}$ (height \times radius) cylindrical cores and the moisture content determined gravimetrically after drying at 105°C for 24 h. The first sample date was 19 April, during the rainfall; the second sample date was 36 h after, and subsequent samples were taken every 24 h. A total of 18 soil samples was taken at each sampling date (three cores \times three canopies + nine cores not under the canopies). Samples from beneath the canopies always came from the north face of the tree. Samples from outside the canopy were taken at least 5 m away from its vertical projection.

To simulate the effect of water potential on seed germination, we germinated seeds in solutions of polyethylene glycol 6000 (PEG) of known water potential. PEG forms a colloidal solution with similar matric properties to soil particles (Qi & Redmann 1993). In addition, it is metabolically inactive and does not flow into the seed because of its large molecular weight. Following the equations proposed by Michel, Wiggings & Outlaw (1983), we prepared solutions of 0 MPa, -0.02 MPa, -0.05 MPa, -0.10 MPa, -0.31 MPa, -0.39 MPa, -0.49 MPa, -0.62 MPa, -0.78 MPa and -0.99 MPa. We harvested the fruits in October 1993 in the Porta-Coeli study area, removed the pulp, and air dried and stored the seeds in the dark at room temperature for 6 months. After disinfecting the seeds with 2% sodium hypochloride for 10 min, groups of 50 seeds were placed in Petri dishes, between two filter papers, with 5 ml of PEG solution, covered with polyethylene sheets to avoid evaporation, and placed into a germination chamber (ASL, Madrid, Spain) with alternating temperatures (12 h at 25°C and 12 h at 20°C). A total of four Petri dishes was used for each water potential level. We assessed germination success for 28 days, daily during the first week and every 2 or 3 days afterwards. A seed was considered to have germinated whenever the radicle had grown at least 1 mm. When that happened, it was removed from the Petri dish. Seeds that had not germinated after 28 days were dissected in order to check their viability, to avoid including non-viable seeds in the analysis.

We measured soil compaction beneath the canopies and elsewhere at the same locations where moisture content was measured. Using a pocket penetrometer (ELE, Hemel Hempstead, Hertfordshire, UK), we sampled a total of 60 random points at each date: 10 points \times three canopies + 30 points outside the area covered by the canopies. The penetrometer range was from 0 to 4.5 kg cm⁻², so when soil compaction was greater than 4.5 kg cm⁻², the frequency of 'out of range' points was recorded and new measurements taken until the sample size was reached.

To simulate the effect of soil compaction on the penetration of seedling radicles, we grew germinated seeds on soil compacted to different degrees. Eight 7.5-cm diameter tins with a drainage hole were filled with soil collected in the Porta-Coeli study site, and placed inside a water container to saturate the soil without compacting the topsoil. The tins were removed after 12 h and allowed to drain for 2 h. Then a pressure of 1 kg cm⁻² with a constant velocity of 50 mm min⁻¹ was applied to the soil in six of the tins with a plunger of 7-cm diameter connected to a texturometer (Model-6021; INSTRON, High Wycombe, UK). Afterwards, a 5 kg cm⁻² pressure was applied to compact the soil to 0.9 kg cm⁻². Higher compaction values were obtained by air drying the soil for several days. After 5 days, soil compaction was 1.5 kg cm⁻² and after 7 days it was 2.3 kg cm⁻².

Ten germinated seeds with a radicle of 2–7 mm were placed on the soil surface of each tin and incubated in the germination chamber. There were two tins per pressure treatment (control or 0 kg cm⁻², 0.9 kg cm⁻², 1.5 kg cm⁻² and 2.3 kg cm⁻²), which meant a total of 80 seeds (four pressures \times two tins/pressure \times 10 seeds/tin). Seedling radicle penetration success or failure was checked after 11 days, when the seedlings with roots that did not penetrate into the soil showed the first symptoms of desiccation. It was considered a success when the radicle penetrated into the soil, and a failure when the radicle could not penetrate and remained completely on the surface of the soil. To prevent any change in the moisture and compaction levels in each tin during the experiment, they were closed with a sheet of polyethylene after reaching the desired levels. Previous experiments had shown that changes in moisture and compaction were less than 3% and 25%, respectively, after 9 days. For the duration of the experiment, soil moisture content inside the tins was always higher than moisture measured in nature following the rainfall. Compaction variability within each tin was negligible.

Data were analysed with a logistic regression model, where radicle penetration was the dependent variable and soil compaction the independent variable. The Wald statistic was used to test the null hypothesis that the coefficient *B* in the logistic regres-

sion model was zero. We checked for linearity in the logit for significant continuous variables by considering the continuous variable (soil compaction) as categorical and calculating and plotting the log-odds against the observed values (Hosmer & Lemeshow 1989).

Results

NUCLEATION PATTERN

There was strong and significant spatial association between individuals of *P. lentiscus* and perches (Table 1) ($\chi^2 = 64.20$; $P < 0.00001$; 2×2 contingency table). These results confirm the existence of a nucleated pattern of *P. lentiscus* individuals tied to the presence of isolated trees and the behaviour of *C. siliqua* acting as a nucleus of colonization.

WATER-POTENTIAL EFFECTS

Following the April 1994 rainfall of 42.91 m⁻², soil moisture content and soil water potential were always greater beneath the canopies than elsewhere (Fig. 1). Figure 1 also shows three key water potentials for seed germination: -0.02 MPa (near to field capacity), -0.10 MPa and -0.99 MPa (near to permanent wilting point). The moisture content that corresponded to these key water potentials was different in the soils beneath the canopies and elsewhere, because soil structure and water-potential curves were different. Over 50% of the points beneath the canopy had water potentials lower than field capacity at every sampling date, whereas outside the area of the canopy only two points had this condition from all of the sampling dates.

The water potential had a significant effect on the percentage of seeds that germinated after 28 days of incubation ($\chi^2 = 36.54$; $P < 0.00001$; Kruskal–Wallis test). Percentage seed germination and germination velocity were not affected until the potential reached field capacity, approximately 0.02 MPa (Fig. 2). From field capacity to -0.10 MPa, percentage germination was not affected but germination velocity decreased. From -0.10 MPa to -0.10 MPa, percentage germination was not affected but germination velocity decreased dramatically. Germination was negligible at a water potential of -0.62 MPa and below.

Table 1. Number and percentage of plots where perches and *Pistacia lentiscus* individuals were present or absent

		Perch	
		Outside area	Beneath
<i>P. lentiscus</i>	Absent	194 (87.0%)	29 (13.0%)
	Present	31 (40.3%)	46 (59.7%)

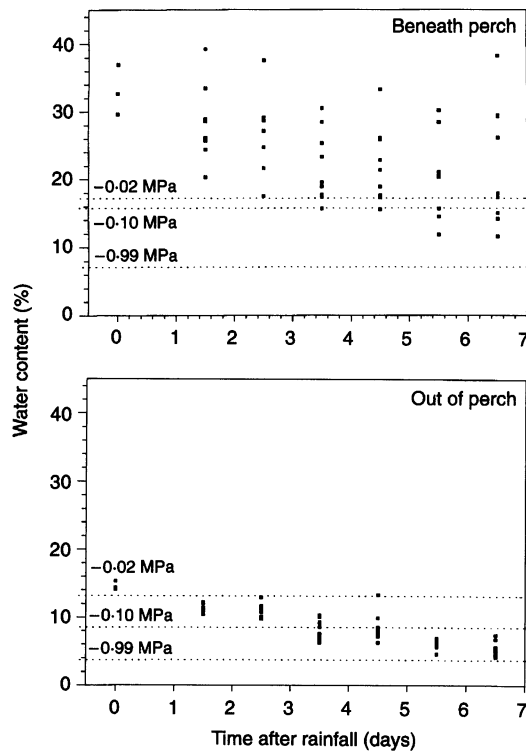


Fig. 1. Soil moisture evolution following rainfall of 42.91m^{-2} (15 to 19/4/94) beneath and outside the area of perches. Lines represent the three key water potentials for seed germination.

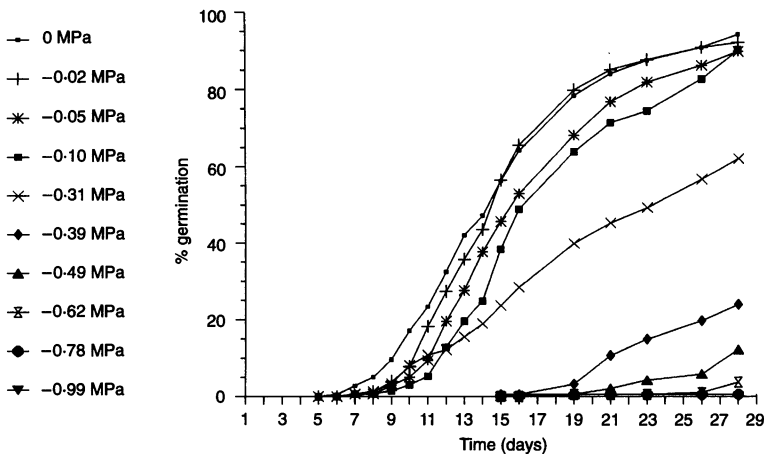


Fig. 2. Seed germination curves at different water potentials.

SOIL-COMPACTATION EFFECTS

Following the rainfall, the soil became compacted faster outside the area covered by the canopies than beneath them (Fig. 3). After 3 days, the soil outside the canopies was consistently 0.5 kg cm^{-2} more compacted than the soil beneath them. The number of points where soil was strongly compacted ($>4.5\text{ kg cm}^{-2}$) was also higher outside the canopies than beneath them (Fig. 3).

Seedling radicle penetration into the soil was strongly related to soil compaction, decreasing as soil compaction increased (Table 2 and Fig. 4).

Discussion

Our results support the hypothesis that there is a strong spatial association between bird-dispersed plants and perches. Our data also indicate that this nucleation is not only caused by higher seed availability (Debussche *et al.* 1985; Izhaki *et al.* 1991) but also by changes in the soil microenvironment that favour seed germination and survival. All the environmental properties measured beneath perches were more favourable for seed germination and seedling establishment than in the exposed soil.

Water imbibition is needed for seeds to germinate and this process depends upon soil water potential (Evans & Etherington 1990). Thus both seed germination percentage and velocity decrease at low water potentials (Williams & Shaykewich 1971; El-Sharkawi & Springuel 1977; Hegarty & Ross 1980). Our laboratory data also provides evidence that germination velocity decrease when water potential decreases. The germination percentage decreased from -0.10 MPa to -0.99 MPa , where *P. lentiscus* seeds did not germinate.

Structural modifications in the soil produced by perches favour a greater water availability beneath them than elsewhere. Water content measurements following rainfall showed that favourable germination conditions, as defined by the laboratory experiments, were maintained for a longer time beneath perches than elsewhere. The range of water potential where seed germination percentage was negatively affected (between -0.10 MPa and -0.99 MPa) was quickly reached outside the area of perches, while beneath them it lasted for at least 5 days. The increased water availability beneath trees has been documented extensively (Escudero 1985; Joffre & Rambal 1988, 1993; Ovalle & Avendaño 1988). In Mediterranean sites, water loss due to surface runoff and deep drainage is negligible beneath perches when annual rainfall is lower than 540 mm, whereas water loss outside the area of perches is negligible only up to 250 mm (Joffre & Rambal 1993). These authors have also shown that water availability beneath perches is greater throughout the entire year. Therefore, it is expected that perches not only improve seed germination but also seedling establishment and growth because these processes require more water than germination (Evans & Etherington 1990).

Another modification produced in soil beneath perches is an increase in macroporosity (Joffre & Rambal 1988). This effect is favourable to seedling establishment. Macroporosity is strongly related to soil resistance to penetration. This resistance limits seedling radicle penetration into soil (Barley, Farrel & Graecen 1965). The probability of a *P. lentiscus* seed penetrating soil decreased as soil compaction increased. After rainfall, the soil was compacted faster outside the area of perches than beneath them and,

Table 2. Effect of soil compaction on seedling radicle penetration

Variable	B	SE	Wald	df	Exp(B)
Pressure			11.35*	3	
0 kg cm ⁻²	0.40	0.46	0.79 ^{NS}	1	0.37
0.9 kg cm ⁻²	-1.02	0.65	2.45 ^{NS}	1	0.36
1.5 kg cm ⁻²	-2.08	0.78	7.16**	1	0.12
2.3 kg cm ⁻²	-2.97	1.13	6.86**	1	0.05

* $P < 0.05$; ** $P < 0.01$. NS, not significant.

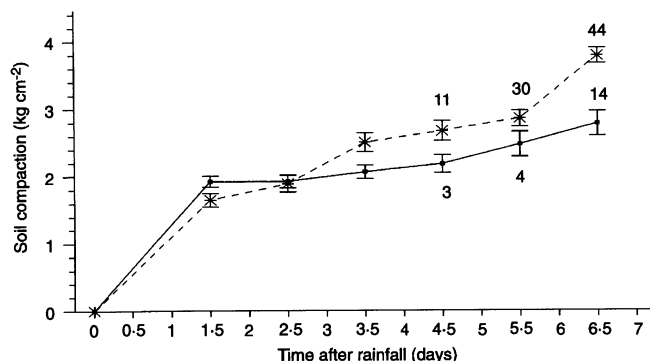


Fig. 3. Soil compaction changes beneath and outside the area of perches following a rainfall of 42.9 l m⁻² (15 to 19/4/94) (solid line = beneath perch; dashed line = outside perch). The numbers inside the graph are the number of soil points with a compaction higher than 4.5 kg cm⁻².

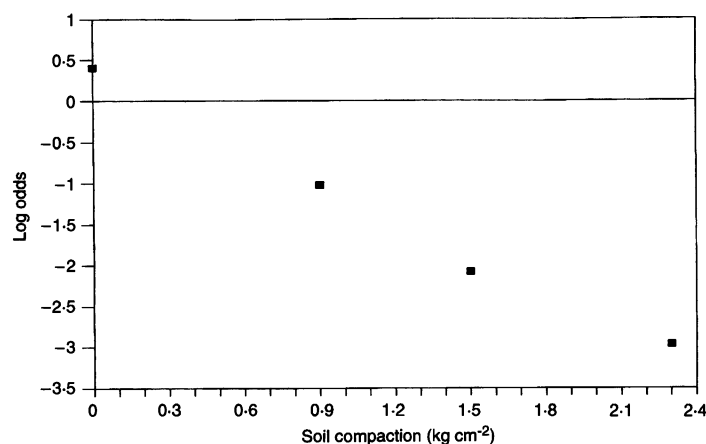


Fig. 4. Plot of the logits of seedling penetration under different soil compactations.

therefore, seedling establishment would be easier beneath perches than elsewhere.

In summary, nucleation of bird-dispersed plants around perches is favoured both indirectly by the higher probability of a seed being dispersed to there and directly by the microenvironmental effects produced beneath that perch.

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