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Effects of land-use and landscape structure on holm oak recruitment and regeneration at farm level in *Quercus ilex* L. dehesas

Tobias Plieninger^{a,*}, Fernando J. Pulido^b, Harald Schaich^a

^a *Institute for Landscape Management, Albert-Ludwigs-Universität, Tennenbacher Str. 4, D-79106 Freiburg, Germany*

^b *Departamento de Biología y Producción de los Vegetales, EUIT Forestal, Centro Universitario, Universidad de Extremadura, E-10600 Plasencia (Cáceres), Spain*

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Abstract

Successful regeneration of holm oaks is essential for the maintenance of biological diversity in the dehesas of Central Spain. In order to explore land-use and ecological site determinants of holm oak regeneration, we conducted a survey of oak recruitment and regeneration, physical features, and grazing impact indicators through a variety of sampling methods. Juvenile and sapling abundance was alarmingly low (51.2 ± 69.1 and 85.0 ± 85.2 plants ha^{-1}), but varied considerably within and across study sites. Statistical analysis of spatial distribution of juveniles and saplings showed that they were highly clumped ($t_N = 0.64$ and 0.61), while mature trees were dispersed uniformly ($t_N = 0.38$). The clumping of juveniles and saplings results from the tendency for regeneration to occur on safe microsites protected from browsing and radiation (shrubs and next to rock outcrops) or from the capacity of ramets to grow vegetatively underneath canopies. We developed indicators for grazing pressure, but none of these showed any relationship with vegetation variables. Crop cultivated dehesas had lower mature tree densities (18.9 ± 13.9 trees ha^{-1}) than grazed (38.6 ± 18.1 trees ha^{-1}) and shrubby (56.4 ± 27.5 trees ha^{-1}) dehesas, indicating potentially negative consequences of cultivation on holm oak demography. Abundant oak regeneration was correlated with mature tree density and size, with woody vegetation cover, and with physical features such as slope, rock cover, and paddock extent. These results suggest that holm oak regeneration in dehesas is controlled by physiognomic features and long-term human impacts rather than directly by current grazing levels.

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Keywords: Agroforestry; Cultivation; Grazing; Holm oak; Mediterranean forest; Microhabitat; Spain; Spatial patterns

*Corresponding author. Tel.: +49-761-203-3636; fax: +49-761-203-3638.

E-mail address: tobias.plieninger@landespflege.uni-freiburg.de (T. Plieninger).

1. Introduction

Holm oak (*Quercus ilex* L.) forests and shrublands are the dominant physiognomic type on the Iberian Peninsula as well as within the Mediterranean basin as a whole (Tomaselli, 1981, pp. 95–106; Blanco et al., 1997). Early 20th century botanists even used holm oak as bioindicator to define Mediterranean-type ecosystems (Blondel and Aronson, 1999). The distribution of holm oak forests, however, has been severely impacted by human transformation: today there are 20,000–30,000 km² of holm oak forests or woodlands on the Iberian Peninsula, whereas without human developments holm oaks would potentially cover 300,000 km² (Blanco et al., 1997).

In most areas, the driving forces of destruction of holm oak forests were massive cutting and burning due to population increase, extension of croplands, industrial expansion, and wars (Le Houérou, 1981, pp. 479–521). In the last few decades, human pressure on holm oak forests has decreased in the northern part of the Mediterranean basin because of land abandonment, while exploitation intensity increased in the southern and eastern parts (Romane et al., 1992, pp. 374–380). Most of the remaining holm oak forests and woodlands are disturbed and fragmented into small islands and mosaics (Blanco et al., 1997). Though, in the lowlands of Central Spain a distinct kind of land management led to the transformation of dense natural forests into extensive park-like ecosystems of *Q. ilex* ssp. *ballota* (Desf.) Samp.

These park-like lands called *dehesas* are distinguished by a systematic combination of agricultural, pastoral, and forestry uses. Most *dehesas* are divided into large estates (so-called ‘latifundios’, > 100 ha) and are held in private ownership. The land is extensively used for livestock husbandry. Previously, rotational plowing was a common management strategy for the cultivation of wheat, barley, oats, and rye and for the control of shrub encroachment (Montero et al., 1998, pp. 519–554). The motive for keeping the trees is that, in relatively poor soils, the profitability of grazing plus rotational cultivation is higher than intensive cultivation alone. Soils cannot be cultivated every year so that cultivation in *dehesas* is usually done in long rotation cycles. Areas where ecological settings or ownership structure encouraged more intensive forms of cultivation have been cleared either historically (e.g. in the so-called pseudosteppes) or relatively recently (e.g. conversion of *dehesas* to irrigated arable fields in the 1960s and 1970s). Today, most estates abandoned crop cultivation, but continue to be regularly cleared of shrubs and holm oak saplings (leaving 10–50 trees ha⁻¹) to maintain the typical vegetation structure of open oak groves, sparse shrubs, and a pronounced herbaceous layer.

Praised as sustainable exploitation system, *dehesas* are of outstanding importance for the conservation of globally endangered species, such as the Spanish Imperial eagle (*Aquila adalberti* Brehm) or Cinereous vulture (*Aegypius monachus* L.) (Pineda and Montalvo, 1995, pp. 107–122). *Dehesas* have been included in EU directive 92/43 as natural habitat type of community-wide interest, which implies the designation of special areas of conservation.

Dehesas are considered to be seriously threatened because of the absence of tree regeneration (see the seminal contribution by Rupérez Cuéllar, 1957). Although

common land management practices result in increased acorn production and quality they reduce the probability of acorn dispersal to ‘safe sites’, making seedling establishment extremely unlikely (Pulido and Díaz, 2003). The bottleneck in recruitment results in gaps in stand age distribution as has been repeatedly reported in dehesas (see Pulido et al. (2001) and Plieninger et al. (2003) for a quantitative description of this issue) and in similar oak savannas in North America (McClaran, 1987, pp. 358–360; McClaran and Bartolome, 1989; McPherson, 1997; Pulido, 2002). In some cases clonal growth of new sprouts from old stools or current roots may succeed in generating ramets capable of producing seeds and growing as self-sufficient entities (Bacilieri et al., 1993). This mechanism has been suggested to constitute an ‘escape way’ when sexual regeneration is limited, and it has been used by land managers to regenerate coppice stands in central Spain (see references in Pulido and Díaz, 2002, pp. 33–47).

Though these deficiencies in stand age structure in dehesas are now well documented, little is known about the factors influencing recruitment and about the extent to which regeneration is controlled by land-use and by the intrinsic features of dehesa stands. Several textbooks (Montoya Oliver, 1993; San Miguel Ayanz, 1994; Montero et al., 1998) have proposed underlying mechanisms related with grazing by domestic animals, but neither of these have measured any of the relevant independent variables influencing plant recruitment; in fact, no study has measured recruitment at all. The overall aim of this farm-level survey is to report ecological and anthropogenic factors affecting holm oak regeneration and other stand parameters. We analyse the relationship between regeneration and management at levels that have not been addressed in previous studies and that are critical for designing restoration plans. In particular, we compare the abundance of tree regeneration and related attributes of vegetation between three farms. Within each farm, we analyse the spatial distribution of regeneration and its likely association with certain microsites. Indicators for grazing intensity are developed and their impact on regeneration is examined. The current regeneration potential and strategies for dehesa conservation will be explored. We put special stress on vegetative propagation as a valuable, previously neglected source of regeneration.

2. Study sites

The farms studied are located in the municipality of Monroy (39°38′N, 06°02′W) in the central part of Cáceres Province in Extremadura region, Spain. Monroy is situated on an undulated plateau between the Tajo and Almonte rivers. Elevations range from 250 to 450 m and the prevailing geological formations are sedimentary cambrian and precambrian schists. Soils emerging on this ground are shallow (average depth of 20 cm), acid (pH 5.5–6.5), poor in organic matter (mean value of 2.7% in the upper 5 cm of the A horizon), nutrient-poor, and have a small water-holding capacity (Ceballos and Schnabel, 1998). Soils are classified as Entisols and Inceptisols. The climate is highly variable Mediterranean-type with mild, humid

winters and hot, dry summers. Temperature averages 27.8°C in December–February and 7.6°C in July–August; the annual average is 16.5°C. Mean annual rainfall ranges around 570 mm with a monthly maximum of 84.5 mm in December and a monthly minimum of 7.8 mm in July (CAM, 2001). According to the UNESCO aridity index, the climate of the study side is semi-arid and has a mean dry period from May to October (De León Llamazares, 1991).

Mediterranean holm oak (*Q. ilex*) is monoecious and wind-pollinated, flowering from early March to early May (Do Amaral Franco, 1989, pp. 15–36). Acorns mature and fall from November to January and lose their viability after one or two months. Acorn production in dehesas amounts to 400–600 kg ha⁻¹ yr⁻¹, but is affected by irregular crop alternances (Montoya Oliver, 1993; Siscart et al., 1999, pp. 75–87). In the study area holm oak is accompanied by sparse olive trees (*Olea europaea* var. *sylvestris* Brot.), wild pears (*Pyrus bourgaeana* Decne), and cork oaks (*Q. suber* L.). Shrub species like *Retama sphaerocarpa* (L.) Boiss., *Cytisus multiflorus* (L'Hér.) Sweet, *Phillyrea angustifolia* L. are part of the original vegetation whereas *Cistus landanifer* L., *Lavandula stoechas* ssp. *sampaiana* Rozeira, *Genista hirsuta* Vahl, *Daphne gnidium* L. and *Asparagus acutifolius* L. are elements of degenerate shrublands and rangelands (Rivas Martínez, 1987; Devesa Alcaraz, 1995).

Three dehesa estates were selected for this study. The estates 'Cerro Lobato' (CL henceforth), 'Parapuños de Doña María' (PA), and 'Pizarro' (PI), are all in private ownership and extend over 644, 797, and 561 ha, respectively. These estates are representative for lowland dehesas in Extremadura in regard to ownership regime, management schedules, and ecological settings. The surface area is subdivided into a certain number of smaller paddocks (CL: 12; PA: 10; PI: 9) by fences and stone walls in order to control grazing and keep livestock herds separated. At 'Cerro Lobato', wheat and oats are cultivated in a rotational system following these paddocks. The other farms abandoned the cultivation of their dehesas at the beginning of the 1980s. The main focus of production on these estates is raising sheep, cattle, pigs, and goats. CL has a stock of 340 ewes and 121 suckler cows, PA 1450 ewes, 150 pigs, and 150 goats, and PI 600 ewes and 100 suckler cows. So present stocking rates vary between 0.24 (CL), 0.29 (PI), and 0.30 (PA) livestock units (LU) ha⁻¹. Stocking rates of the traditional dehesa system in the 1950s are estimated around 0.10–0.15 LU ha⁻¹ (Plieninger and Wilbrand, 2001). Major changes occurred in regard to the seasonality of grazing. Livestock herds were traditionally moved from the middle of June until the beginning of October to mountain ranges in Northern Spain in order to avoid scarcity of forage on dehesa pastures due to the summer drought (Blanco et al., 1997). Nowadays livestock is kept throughout the year on the farms and is shifted in a rotational system between the paddocks. Fodder concentrates, hay, and straw are fed additionally. The period and duration of grazing within the paddocks is determined by the farm manager in individual cases and is based on his experience with the territory. Climatic and edaphic factors as well as the demands of each livestock species, paddock extent, and paddock location are influential. Wild ungulates such as red deer (*Cervus elaphus* L.) cross the three estates sporadically.

3. Methods

3.1. Sampling design

Vegetation, physical features, and grazing impact indicators were surveyed on 31 paddocks within the three estates in spring 2002. The paddocks were mapped with a portable GPS, and their extent was calculated in ArcView 3.2. Extent was later used as a rough estimator of overall land-use intensity, assuming that small paddocks are generally managed more intensively than large ones. Three types of land-uses, cultivated ('cultivo'), grazed ('pasto' or 'majadal'), and shrubby ('matorral') dehesas, were identified by analysis of historical aerial photography (taken in 1956) and land-use maps (mapped in 1978) and by asking farm workers. We focused on long-term (1950–1980) as well as on current land-uses. A plotless sampling design was chosen for the estimation of holm oak densities as this approach is particularly apt for sparsely growing individuals (Kent and Coker, 1992). Vegetation cover data were sampled by the step-point method, a variant of line-intersect sampling (Evans and Love, 1957).

3.2. Vegetation and physical features

We inventoried three holm oak life stages that were delimited by size: juveniles, saplings, and mature trees. Size classes were preferred over chronological age classes because these can be readily determined with more precision and because consideration of growth internodes usually leads to inaccurate estimates of size. Individuals with a base diameter < 1 cm were classified as juveniles. Saplings were individuals with a base diameter ≥ 1 cm, but with a diameter at breast height (dbh) of < 10 cm. Mature trees were defined as all *Q. ilex* individuals ≥ 10 cm dbh (following Muick and Bartolome, 1987). Juveniles will be used as an indication of recent recruitment, while both juveniles and saplings will be more generally referred to as 'regeneration'. Juveniles are in a stage that is still affected by losses through herbivory, competition, or desiccation, so that effective recruitment does not guarantee successful regeneration of an existing stand (Tiver and Andrew, 1997). We delimited individuals of juveniles and saplings either as isolated shoots or as close aggregations of shoots with homogeneous height and leaf morphology that were likely to pertain to the same genetic entity (Pulido et al., 2001). A minimum distance of 25 cm between the canopy borders of shoot aggregations was defined in order to separate different aggregates. Ten sampling points were placed within each paddock by a random-walk procedure (Kent and Coker, 1992). Distance from the random point to the nearest juvenile, sapling, and mature holm oak, as well as to their respective restricted second neighbor was measured applying T-square sampling (Besag and Gleaves, 1973). For every juvenile and sapling, we mapped the microsite where it was growing (open, tree canopy, shrub canopy, rock outcrop) and noted growth morphology (isolated shoot or shoot aggregation). A total of 504 juveniles and 566 saplings were sampled at 310 points in 31 paddocks. Additionally, dbh of mature trees was recorded with tape measure. Five transects with random starting

points and directions were laid over each paddock in order to survey the relative cover of the four microsites mentioned. Young holm oaks were not included in shrub cover. One transect was 500 steps long, and the prevailing cover was noted down every fifth step. This resulted in 500 points per paddock which is considered a sufficient sample size to include the variability in a local area (Evans and Love, 1957). Cover data will be expressed in percent. Slope was determined at each sampling point with a clisimeter.

3.3. Grazing pressure

Four parameters were recorded as indicators of present grazing impact within each paddock. First, the grazing intensity of the livestock herd was estimated with fecal counts (FC) in a 25 m² circle around the 10 random points in each paddock. Dung deposits have often been used to infer grazing pressure (Puerto et al., 1990; Turner, 1999; Posse et al., 2000), and strong correlations between dung density and actual livestock presence have been experimentally confirmed for sheep by Lange and Willcocks (1978). Second and third, browsing of the sampled juveniles and saplings was estimated by a visual scheme. The percentage of severely damaged plants (defined as browsing damages at > 50% of leaf area including the apical shoot) was expressed as juvenile browsing index (JBI) and sapling browsing index (SBI) (Reimoser, 2000). Fourth, we recorded presence or absence of unpalatable plants defined by Devesa Alcaraz (1995) in a frame quadrat (0.5 × 0.5 m²) with 25 sub-units and two replicates on 10 random points within each paddock (Patón et al., 1995). Common unpalatable plants were *Carlina corymbosa* L., *Carlina racemosa* L., *Cirsium vulgare* (L.) Scop., *Asphodelus albus* Miller, and *Urginea maritima* (L.) Baker. The presence of these species was considered to reflect high grazing pressure.

3.4. Data analysis

The arithmetic means of dbh, slope, microsite cover, and the four grazing impact indicators were used for between-paddock comparison. For each paddock, mean density D of mature holm oaks, saplings, and juveniles respectively was calculated from T-square data (Diggle, 1983):

$$D = \left\{ 2\sqrt{2}/m^2 \right\} \left(\sum x_i \sum z_i \right), \quad (1)$$

where m is the number of samples, x_i equals the point-object distances in meters, and z_i equals the object-object distances in meters. The spatial distribution of individuals in different vegetation layers within each paddock was analysed by calculating t_N values (Besag and Gleaves, 1973):

$$t_N = m^{-1} \sum \left[\frac{x_i^2}{(x_i^2 + 0.5z_i^2)} \right], \quad (2)$$

where m is the number of samples, x_i equals point-object distances in meters, and z_i equals the object-object distances in meters. Spatially random distribution implies that t_N is normally distributed with a mean of 0.5 and a variance of $(12 \text{ m})^{-1}$ (Diggle, 1983). Significant deviations of t_N were tested by converting t_N to z scores and computing the corresponding p value (Kabrick et al. 1997). Points with a significantly lower t_N tend to be clumped; points significantly above 0.5 are distributed uniformly.

Next we performed a χ^2 -test for goodness of fit to analyse whether juveniles and saplings showed significant positive or negative associations with the four microsites. The abundance of juveniles and saplings at each microsite was compared to their expected abundance derived from the randomly located points along the transects.

Pearson's correlation coefficients were calculated to test the internal consistency of the four indicators of grazing pressure. Those significantly correlated to at least one other grazing indicator were considered reliable. In order to account for the effect of grazing on juvenile and sapling density and for its variation between estates we included the most reliable grazing indicator as a covariate in a multivariate analysis of covariance (GLM procedure) with estate as factor and two regeneration parameters as dependent variables. We applied Principal Component Analysis (PCA VARIMAX rotation procedure) to paddock means of ten independent variables. We further performed stepwise regressions to model juvenile and sapling density as a linear function of the two gradients resulting from the PCA. We used SPSS 11.0 for all analyses.

4. Results

4.1. Variation of regeneration between farms

Juvenile density ranged from 0 to 286 plants ha^{-1} sapling density from 0 to 342 plants ha^{-1} (Fig. 1). Sapling density was significantly higher ($85.0 \text{ plants } \text{ha}^{-1} \pm 85.2 \text{ S.D.}$) than juvenile density ($51.2 \text{ plants } \text{ha}^{-1} \pm 69.1$) (paired t -test: $t_{30} = -2.30$, $p = 0.029$). The variation of both seedling and sapling density between paddocks was tremendous. Fifty-six points (18.1%) contained no juveniles and 27 (8.7%) no saplings within a 50 m radius. Only 81 juveniles (16.1%) were isolated shoots; this tendency increased in the sapling class in which the vast majority (558 individuals, 98.6%) was growing as shoot aggregates. The mean number of juveniles relative to the number of mature trees was 1.49 (± 1.99). This ratio was below 1.00 in 17 out of 31 paddocks, indicating a severe regeneration failure. Mean sapling to mature tree-ratio was higher (3.24 ± 2.53) with only six paddocks having ratios below 1.00. Correlation analysis revealed a significant positive relationship of juvenile density with sapling density ($r = 0.451$, $p = 0.011$, $N = 31$ at each case) recent tree density ($r = 0.575$, $p = 0.001$) and shrub cover ($r = 0.433$, $p = 0.015$) and a negative relationship with mature tree dbh ($r = -0.538$, $p = 0.002$). Sapling density was linearly related to the same variables as juvenile density.

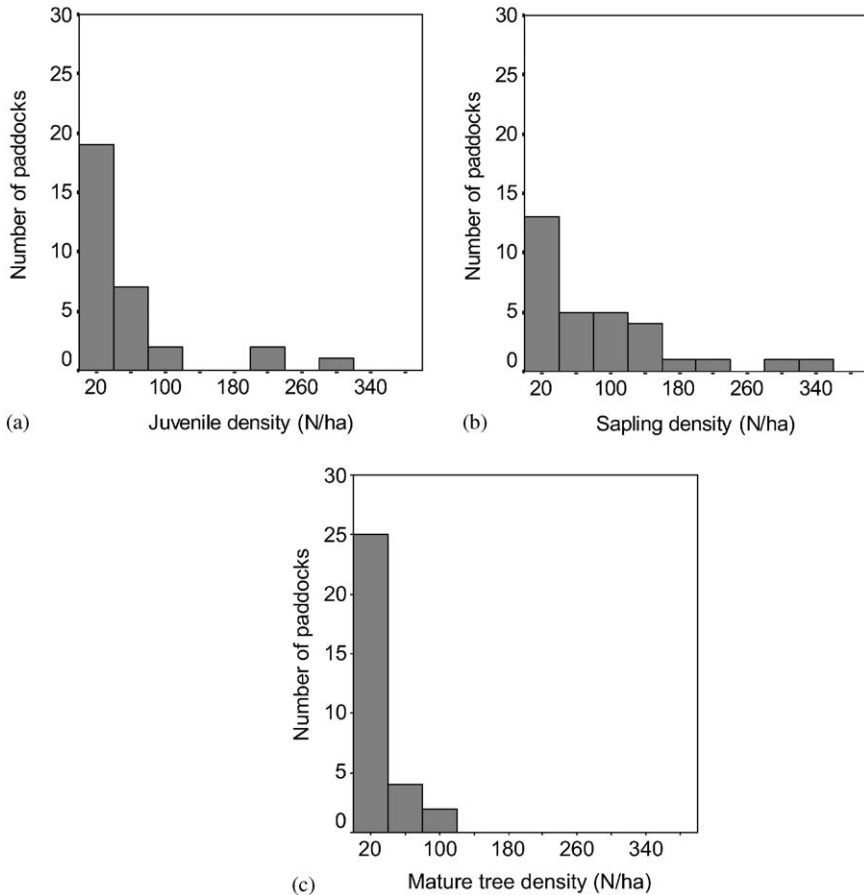


Fig. 1. Densities of (a) juveniles, (b) saplings, and (c) mature trees on the 31 paddocks.

4.2. Spatial pattern of holm oaks

Analysis of spatial patterns revealed that neither juveniles nor saplings or mature trees were distributed at random. Juveniles and saplings showed a highly clumped pattern on all estates studied. In contrast mature trees were regularly dispersed. t_N as a measure of spatial heterogeneity varied between parcels around 0.64 ± 0.11 (juveniles) 0.61 ± 0.12 (saplings) and 0.38 ± 0.08 (mature trees) (Table 1). Spatial heterogeneity (t_N) was not significantly correlated with the abundance of juveniles saplings, and mature trees.

4.3. Microhabitat niches

The analysis showed a close association of holm oak juveniles and saplings to specific microhabitats. Juveniles grew significantly more often than expected for a

Table 1

Test for the spatial distribution of juveniles, saplings, and mature trees. t_N -values >0.5 indicate aggregation, $t_N < 0.5$ regularity

	Juveniles				Saplings				Mature trees			
	<i>m</i>	t_N	<i>z</i>	<i>p</i>	<i>m</i>	t_N	<i>z</i>	<i>p</i>	<i>m</i>	t_N	<i>z</i>	<i>p</i>
C. Lobato	104	0.62	4.40	<0.001	118	0.61	4.04	<0.001	120	0.36	-5.16	<0.001
Parapuños	83	0.64	4.27	<0.001	95	0.66	5.25	<0.001	100	0.40	-3.62	<0.001
Pizarro	63	0.72	6.18	<0.001	70	0.58	2.42	0.016	90	0.38	-3.88	<0.001

Table 2

Association of holm oak (a) juveniles and (b) saplings with open, tree canopy, shrub and rock outcrop habitats determined by χ^2 -test

Juveniles	Open	Tree canopy	Shrub	Rock outcrop	df.	χ^2	<i>p</i>
(a) Association of juveniles with Microhabitats							
Cerro Lobato							
Obs.	86	118	11	—	2	313.40	<0.001
Exp.	177	79	9	—			
St. res.	-7	4	1	—			
Parapuños							
Obs.	38	67	40	47	3	162.69	<0.001
Exp.	122	29	21	20			
St. res.	-7	7	4	6			
Pizarro							
Obs.	36	75	3	34	3	498.03	<0.001
Exp.	113	32	0	3			
St. res.	-7	8	—	18			
(b) Association of saplings with Microhabitats							
Cerro Lobato							
Obs.	114	90	—	—	1	111.69	<0.001
Exp.	201	33	—	—			
St. res.	-6	10	—	—			
Parapuños							
Obs.	82	58	18	50	3	82.16	<0.001
Exp.	132	31	23	21			
St. res.	-4	5	-1	6			
Pizarro							
Obs.	70	51	3	37	3	439.10	<0.001
Exp.	122	35	0	3			
St. res.	-5	3	—	20			

Standardized residuals (= St. res.) larger than two indicate a significant deviation of the observed from the expected value. Obs. = observed values; Exp. = expected values.

random distribution below tree canopies, beneath shrubs, and close to rock outcrops (Table 2(a)). Saplings were likewise associated with tree canopies and rock outcrops (Table 2(b)), but not with shrubs. Juveniles and saplings both were negatively associated with open sites. This pattern was found on all three estates (Fig. 2).

4.4. Impact of grazing and cultivation

The frequency of unpalatable plants was not correlated with any of the other parameters. Correlation analysis, however, revealed a close relationship between FC, JBI and SBI (Pearson's $r = 0.44$, $p = 0.013$ for FC-SBI, $r = 0.68$, $p < 0.001$ for FC-JBI and $r = 0.70$, $p < 0.001$ for SBI-JBI, $N = 31$ each). JBI was correlated most closely to the other indicators and was hence selected as the most reliable grazing indicator. MANCOVA results showed however that JBI had no significant effect on juvenile sapling density (Wilks' $\lambda = 0.95$, $F_{1,27} = 0.68$, $p = 0.51$). Likewise no significant effect of overall management schedules was found (Wilks' $\lambda = 0.769$, $F_{2,27} = 1.83$, $p = 0.14$).

Vegetation parameters, physical variables, and grazing impact indicators showed marked differences between cultivated, grazed, and shrubby dehesa types (Table 3). Given small sample size and lacking statistical analysis, these differences should rather be considered trends than confirmed facts. Matorral dehesas had by far the highest levels of juvenile density, sapling density, mature tree density, woody vegetation cover, paddock extent, slope, and rock cover, while dbh was lowest. Cultivated and grazed dehesas had low juvenile sapling densities, and a low vegetation cover, and a small paddock extent in common. Mature tree density and the three grazing impact indicators were distinctly lower in cultivated than in grazed dehesas.

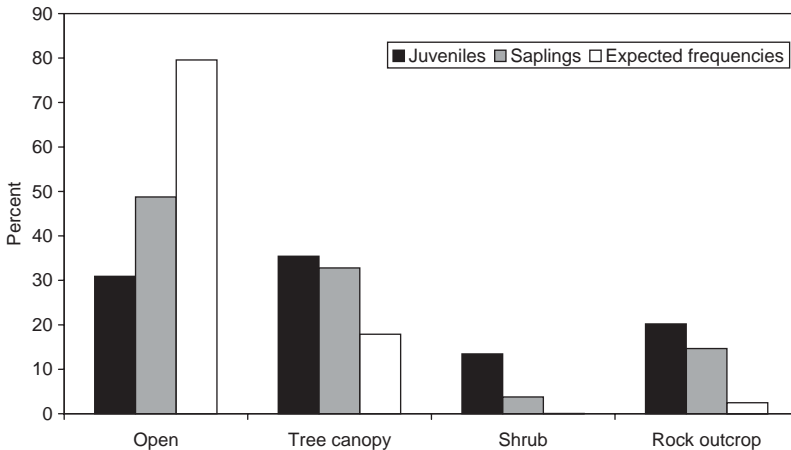


Fig. 2. Juvenile and sapling abundance at different microhabitats.

Table 3

Differences in vegetation parameters, physical variables and grazing indicators between cultivated, grazed, and shrubby dehesa types (means \pm S.D.)

	Dehesa with		
	Cultivation ($N = 19$)	Pasture ($N = 8$)	Matorral ($N = 4$)
Juvenile density ($N \text{ ha}^{-1}$)	36.9 \pm 47.5	33.1 \pm 36.9	154.8 \pm 121.1
Sapling density ($N \text{ ha}^{-1}$)	70.3 \pm 69.4	70.8 \pm 72.6	183.1 \pm 128.8
Tree density ($N \text{ ha}^{-1}$)	18.9 \pm 13.9	38.6 \pm 18.1	56.4 \pm 27.5
Tree dbh (cm)	38.4 \pm 5.4	36.7 \pm 11.4	27.9 \pm 8.8
Shrub cover (%)	5.0 \pm 6.2	0.9 \pm 1.3	15.7 \pm 23.7
Woody vegetation cover (%)	20.1 \pm 10.5	25.8 \pm 7.8	46.6 \pm 20.7
Paddock extent (ha)	69.5 \pm 43.2	24.8 \pm 25.3	127.8 \pm 105.6
Slope (deg)	3.7 \pm 1.6	3.7 \pm 1.3	7.8 \pm 2.4
Rock cover (%)	1.8 \pm 3.5	4.7 \pm 6.4	18.4 \pm 8.6
Juvenile browsing index (%)	27.8 \pm 32.8	65.1 \pm 35.5	56.7 \pm 24.0
Fecal counts ($N \text{ ha}^{-1}$)	8.3 \pm 6.3	29.6 \pm 14.2	12.1 \pm 10.7
Sapling browsing index (%)	57.4 \pm 35.2	74.0 \pm 31.6	87.5 \pm 21.8

4.5. Multivariate analysis of environmental attributes

Ten independent environmental attributes on the 31 paddocks were reduced to two variables using PCA. The eigenvalues (λ) for the first two axes were 4.52 and 2.44, explaining 69.55% (45.17%, axis I; 24.38%, axis II) of the total variation. The plot of eigenvector scores (Fig. 3) showed a strong correlation between axis I and rock cover, slope, tree density, woody vegetation cover, paddock extent, and shrub cover. Negative correlations existed between axis I scores and dbh. Axis II was related to the three grazing impact indicators and to a minor degree to paddock extent. The first principal component mainly reflected stand parameters and physical factors, whereas axis II corresponded to a grazing intensity gradient. Individual factor loadings are given in Table 4.

4.6. Determinants of regeneration

Stepwise regression found a highly significant correlation between juvenile density and axis I ($r = 0.763$, $p < 0.001$, $N = 31$), while axis II was discarded as it did not generate a better fit. Sapling density was likewise related to axis I ($r = 0.852$, $p < 0.001$, $N = 31$) and not to axis II. This demonstrates that environmental attributes like rock cover, slope, woody vegetation cover, tree density, paddock extent, tree dbh, and shrub cover are powerful determinants of juvenile and sapling abundance. In contrast, the three grazing impact indicators (represented by axis II) did not have any relationship with the dependent variables.

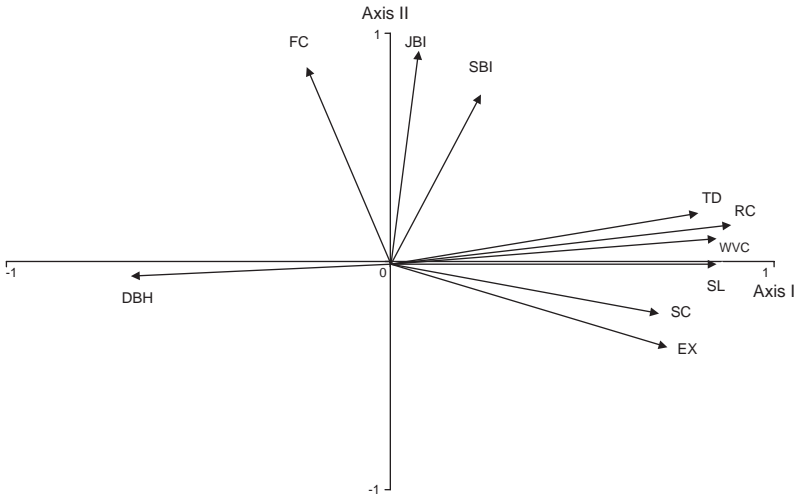


Fig. 3. PCA of independent woody vegetation, physical and grazing impact parameters. Variables are DBH (Diameter at breast height), EX (Paddock extent), FC (Fecal counts), JBI (Juvenile browsing index), RC (Rock cover), SBI (Sapling browsing index), SC (Shrub cover), SL (Slope), TD (Tree density).

Table 4
Factor loadings on the first two principal components

	Eigenvectors	
	Axis I	Axis II
Rock cover	0.897**	0.165
Slope	0.865**	-0.006
Woody vegetation cover	0.864**	0.148
Tree density	0.795**	0.208
Paddock extent	0.726**	-0.361*
Tree dbh	-0.674**	-0.059
Shrub cover	0.704**	-0.210
Juvenile browsing index	0.075	0.917**
Fecal counts	-0.219	0.858**
Sapling browsing index	0.239	0.769**

*Indicates a significance level of $p < 0.05$.

**Means $p < 0.01$.

5. Discussion

5.1. Spatial patterns of regeneration and stand structure

Considerable concern has been expressed about low oak regeneration and the sustainability of dehesa management (Hernández Díaz Ambrona, 1996;

Plieninger et al., 2003). Results of this first regeneration survey revealed that juvenile and sapling abundance is generally low, but varies considerably. There were no statistically significant differences between farms. Most paddocks had an alarmingly low regeneration capacity, some having fewer juveniles than mature trees. A preliminary survey in a nearby dehesa had led to similar results, with 89% of seedlings found on only one out of nine plots and no seedlings or ramets older than 1 year (Díaz et al., 1997, pp. 178–209). Vegetation structure on the three estates studied corresponded to common dehesa descriptions (Díaz and Pulido, 1995, pp. 103–111). Stands were generally open, with densities between 4 and 91 mature trees ha^{-1} , and shrub cover was low. This situation is in contrast to other, less intensively used holm oak forests (mainly coppices) in Northern Spain, where *Q. ilex* ssp. *ilex* seedlings occurred in densities between 200 and 3800 stems ha^{-1} (Lookingbill and Zavala, 2000). However, management and climate of holm oak coppices are different to that of dehesas so that a direct comparison cannot be made.

In contrast to most *Q.* species in Mediterranean California (Standiford et al., 1991, 1997), holm oak regeneration showed larger numbers of saplings than juveniles. So unsuccessful holm oak recruitment seems to be limited not by transition to the sapling stage but by failures of seedling emergence and establishment. Pulido and Díaz (2003) identified these as the most critical stages in the regeneration cycle of holm oaks in dehesas. Higher sapling than juvenile densities could furthermore indicate that regeneration failure has accelerated in recent years, although data for a temporal comparison are lacking.

5.2. Microhabitat specificity of sexual and asexual regeneration

The spatial distribution of holm oak individuals changed over life stages: Juveniles and saplings were found highly clumped. This observed pattern could be explained by two complementary, not mutually excluding, mechanisms: First, that there are specific microhabitats in the dehesas where regeneration from seed origin is bound to occur (regeneration niches sensu Grubb, 1977), and second, that vegetative propagation operates around mature trees.

Juveniles were found more often than expected underneath mature trees, shrubs, and next to rock outcrops. Saplings showed the same preferences, with less certainty concerning association with shrubs. This could be interpreted as the result of directional dispersal by rodents or birds, which usually scatter-hoarded acorns in these microhabitats (Borchert et al., 1989; Díaz et al., 1993), and/or facilitation of seedling establishment (Pulido and Díaz, 2003). Another advantage is shelter from browsing by livestock through ‘associated resistance’ (Briske, 1998, pp. 37–67; Olf et al., 1999). The phenomenon of ‘nurse plants’ is widespread in range ecosystems and has been documented e.g. for *Q. lobata* Nee and shrubs of *Salvia leucophylla* Greene and *Artemisia californica* Less. (Callaway, 1992). Concentrations around rock outcrops have also been observed at *Q. agrifolia* Nee in California (Snow, 1972) and might be attributable to a beneficial microclimate and certain protection from browsing. Sites underneath tree crowns offer shade, have enhanced water storage capacity (Joffre and Rambal, 1988), and represent ‘islands of fertility’ (Owens et al., 1995) with

increased nutrient and organic matter levels (Gallardo et al., 2000). Though, these beneficial effects are counteracted by livestock browsing (Pulido and Díaz, 2003) and by intraspecific competition through auto-allopathy (Bran et al., 1990; Romane et al., 1992). Concentration of juveniles and saplings underneath mature trees is therefore indicative rather of an asexual origin of most regeneration than of favorable conditions of *Q. ilex*.

San Miguel Ayanz (1994) and Montero et al. (1998) consider aggregated growth of holm oak sprouts an adaptation to herbivore consumption. As soon as the horizontal extension of the stools is wide enough, a central shoot can gain height without being penetrated by browsing livestock.

Mature trees had a highly uniform dispersion. This finding has been related to anthropogenic selection and thinning in order to bring up wide crowns with a high acorn productivity (Pulido et al., 2001).

5.3. Influences of land-use

Three of four factors tested as indicators for present grazing pressure were positively correlated and thus internally consistent. Still, we did not detect any relationship of these indicators with regeneration densities. This is in contrast to other range ecosystems where higher levels of herbivory showed significantly negative effects on regeneration (Hall et al., 1992; Tiver and Andrew, 1997). But light livestock grazing may also have beneficial effects on past recruitment by removing herbaceous competition and reducing fire frequencies (Jackson et al., 1998). Our results support recent studies suggesting that the regeneration failure of holm oaks is a widespread phenomenon and does not vary across prevalent grazing regimes (Montero et al., 1998). Though, the survey considered current grazing levels, while regeneration and stand structure might rather be influenced by past grazing regimes acting over decades. Study of the long-term impact of grazing is difficult, and ‘oak establishment is more complicated than the presence or absence of livestock’ (McClaran, 1987). Another factor that has shown influential on oak seedling damage and survival is the grazing season. In an experimental study by Hall et al. (1992), summer grazing, i.e. grazing at a time in which biomass production has stopped due to drought, caused far higher seedling mortality than winter or spring grazing. Seasonal grazing up to the desiccation of the herbaceous layer might have beneficial effects on oak seedling survival due to reduced water competition (Standiford et al., 1996). In contrast, summer grazing can cause massive damages as oak seedlings provide the only usable fresh biomass in this period. Unfortunately the role of the once common, nowadays abandoned seasonal livestock movements for the regeneration of holm oaks has not been studied so far.

Browsing and acorn consumption by livestock are important factors limiting acorn germination and seedling establishment (Pulido and Díaz, 2003). A lack of safe sites can prevent oak recruitment in grazed dehesas although holm oak is adapted to grazing by resprouting and vegetative regeneration. Cultivated dehesas additionally suffer from high mortality due to plowing, and from intensive clearings that are targeted to alleviate tilling, though availability of acorns surviving predation and

conditions for early establishment are presumably enhanced (Pulido and Diaz, 2003). Increased mortality might explain that mature tree densities are lower than in grazed dehesas. Field impressions of long-term ploughed dehesas make us fear that cultivation and brushing might be an even more significant constraint for regeneration than livestock grazing.

5.4. Dehesas—oak orchards or natural forests?

An important question for the management of oak regeneration is whether the semi-natural dehesa system should be considered as an artificial orchard or as a natural forest. Depending on this view, age structure will be assessed differently and silvicultural treatment will be different. Historically seen, there is no doubt that the large surface of holm oak dehesas in Extremadura and especially in the area studied is the result from manipulation of the native Mediterranean hardwood forest, mainly from the 18th to the beginning 20th century (Sánchez Marroyo, 1993; Linares-Luján and Zapata-Blanco, 2002, pp. 13–25). A historical analysis of holm oak management in dehesas (Plieninger, in preparation) provides evidence that holm oaks have never been planted in the study area before the 1990s. Today's dehesas resulted from the process of *adehesamiento*, a combined action of shrub removal, selective thinning, and intensive pruning, and the holm oaks we see today are mainly remnants from the original forest (Martín Galindo, 1966; Pulido et al., 2001). This forest was not necessarily completely undisturbed before dehesa creation, but management operations in that time did not result in such massive changes in vegetation and forest age structure like those in the dehesa system (see a detailed description in Martín Bolaños, 1943). Initial practices could include apiculture, extensive goat and sheep grazing, or firewood extraction. Regions included in the dehesa range were highly marginal and scarcely populated, so that people hardly could have altered forest structure far from human settlements. Due to the relatively young age of most dehesas active regeneration management has not yet evolved traditionally (e.g. documented by one senior farm manager who stated about oak management in the 1950s: 'We did not care for oak regeneration, as there were abundant trees').

As common in agroforestry research (Ashton and Ducey, 2000, pp. 207–228) we decided to study the growth and development of holm oak stand in dehesas in analog to the natural dynamics of holm oak forests where a balanced, inverse-j-shaped age distribution guarantees that old or dying individuals will be replaced by trees from younger age classes (as described quantitatively for a nearby natural holm oak forest by Pulido et al., 2001). However, we can address this question only qualitatively, as no effort has been made to build up demographic models for oak replacement. For this reason we used the negatively exponential size structure as a minimum safe criterion for successful regeneration. One of the reasons for the great ecological value of dehesas is that they act as natural ecosystem mimics (Joffre et al., 1999). We consider a deeper understanding of natural regeneration processes under different dehesa situations fundamental for the development of management tools that imitate natural processes in dehesas. Alternatively, one could decide to establish a more artificial system of oak regeneration as we know it from orchards. For this, a

minimum of tree densities desired, the population structure, and the longevity of holm oaks would have to be estimated, and the number of trees to be planted per hectare to maintain a sustainable population would be determined from that. A simple replacement model for landowners was developed, e.g. for California's hardwood rangelands by Standiford et al. (1996).

6. Conclusion: practical approaches for dehesa regeneration

Juvenile and sapling densities were highly coincident with other vegetation parameters and physical features but were completely unrelated to grazing levels. Altogether, regeneration seems to be controlled by ecological features and long-term land-uses rather than directly by the grazing pressures measured. However, this study analysed relative differences in grazing intensity, but did not include ungrazed sites (that were not available on the three estates). It has been documented already that ungrazed and unmanaged holm oak forests (Pulido and Díaz, 2003) are abundant in holm oak seedlings. So threshold grazing levels for successful regeneration are probably low, and additional human impacts on vegetation, especially regular brushing and soil tillage, seem to be influential barriers to regeneration. True seedlings being assumed to be virtually nonexistent, most regeneration in dehesas stems from asexual reproduction that is better adapted to cope with grazing. Growth pattern of ramets, however, is different from that of seedlings (Montero et al., 1998; Espelta et al., 1999, pp. 61–73). In the face of lacking alternatives, we consider vegetative reproduction a valuable solution for stand regeneration, but studies on the consequences on dehesa structure, acorn productivity, and oak vitality are needed. Regeneration depends on safe microsites, especially shrubs, that are mostly unavailable in the present dehesa system, but are present in ungrazed and unmanaged forests. Thus the challenge is to find out the management practices that promote spatial heterogeneity of dehesa attributes linked to regeneration.

Potential strategies to implement regeneration in dehesas are to either mimic or restore these missing structural components. First, naturally grown sprouts, sown acorns, or planted seedlings could be protected by mesh cages. This option would allow continuing uses and thus show economic benefits. However, experiences about these techniques, especially about afforestation, are limited as these measures were not started in Extremadura before the 1990s. Plantation of holm oak seedlings with mesh protectors but without shading has led to great failures in the area (Plieninger, personal observation). The second option comprises the restoration of the conditions of the dense Mediterranean hardwood forests where regeneration success is about 70 times higher than in dehesas (Pulido and Díaz, 2003). Field evidence has shown that dehesas are resilient enough to establish a shrub layer and abundant holm oak regeneration after a set-aside of 20–30 years (Plieninger et al., 2003). This implies total exclusion of uses on small parcels (e.g. 5% of an estate), not only of grazing, but of all forms of vegetation management, during a time period that varies according to starting conditions and grazing species (Montero et al., 1998). To our

knowledge, there have not been any practical experiments with long-term monitoring that could serve as a reference to predict the ecological and economic results of set-aside or grazing regulation. Field experiments in a wide array of ecological situations and technical demonstration projects are necessary to put dehesa regeneration into practice. Additional future research, possibly starting from available regeneration data from the Spanish National Forest Inventory, is needed to link holm oak regeneration with climatic, edaphic, and management variation on a regional or even national scale.

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