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Original article

Influence of pruning and the climatic conditions on acorn production in holm oak (*Quercus ilex* L.) dehesas in SW Spain

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Abstract – Acorn production by *Quercus ilex* L. ssp. *ballota* (Desf.) Samp. in SW Spain was assessed, and variations between years and the influence of pruning on it were examined. To this end, an experimental study was conducted at two different sites (Calañas and San Bartolomé, in the province of Huelva) where trees were subjected to traditional (light, moderate or heavy) pruning and also to a new (crown-regeneration) pruning method. Acorn yield was quantified over a period of 5 years in the Calañas plot and 4 in the San Bartolomé plot, and found to average at 95.61 ± 0.76 g DM/m^2·year, which is equivalent to 6.5 ± 0.05 kg DM/tree; however, yield figures varied markedly between years depending on the particular climatic conditions. The average acorn production was correlated with the water potential in mid summer (end of July); the annual, spring and autumn rainfall; and the actual evapotranspiration for the period from September (previous year) to August. No significant differences in acorn production between traditional pruning intensities were detected; in fact, there were only hints that heavy pruning might result in decreased acorn yields. The new pruning method used, crown-regeneration, seems promising with a view to increasing acorn yield; however, it should be tested on larger sample sizes before any final conclusions can be drawn in this respect. Based on the results, the present health status of holm oaks in southwestern Spain (a result of sustained decline) and the low value of firewood – which used to be a very important source of income from pruning a few decades ago –, the authors recommend reducing the frequency and intensity of pruning in the dehesas of the study area.

Holm oak / acorn production / pruning / masting

Résumé – Influence de la taille et des conditions climatiques sur la production de glands par le chêne vert (*Quercus ilex* L.) en dehesas dans le sud ouest de l'Espagne. La production de glands par *Quercus ilex* L. ssp. *ballota* (Desf.) Samp. Dans le sud ouest de l'Espagne a été mesurée, et l'influence de la taille sur les variations interannuelles a été examinée. Dans ce but, une étude expérimentales a été conduite dans deux sites (Calañas et San Bartolomé dans la province de Huelva) où des arbres ont été soumis à une de taille traditionnelle (légère, modérée ou forte) et aussi à une nouvelle méthode de taille (régénération de couronne). La production de glands a été quantifiée sur une période de 5 ans sur le site de Calañas et de 4 ans sur celui de San Bartolomé et était en moyenne de 95,61 ± 0,76g de matière sèche/m^2.an, ce qui équivaut à 6,5 ± 0,05 kg de matière sèche/arbre/an. Cependant la production a varié de façon marquée entre années en relation avec les particularités climatiques. La moyenne de production de glands était corrélée avec le potentiel hydrique au milieu de l'été (fin juillet) ; avec les précipitations annuelles, du printemps et de l'automne, et avec l'évapotranspiration pour les périodes allant de septembre (année précédente) à août. Aucune différence significative de production de glands n'a été détectée, entre les intensités de taille traditionnelle. La nouvelle méthode utilisée est prometteuse et permet une augmentation de la production de glands ; cependant elle devra être testée sur des lots d'arbres plus importants avant d'arriver à des conclusions définitives sur ce sujet. Sur la base de ces résultats, en prenant en compte de l'état de santé actuel du chêne vert dans le sud ouest de l'Espagne (résultat d'un déclin prolongé) et la faible valeur actuelle du bois de feu qui était habituellement une source très importante de revenus provenant de la taille il y a quelques dizaines d'années, les auteurs recommandent la réduction de la fréquence et de l'intensité de la taille dans les dehesas.

***Quercus ilex* / production de glands / taille / glandée**

1. INTRODUCTION

The Spanish dehesa constitutes an open woodland forest agroecosystem created and maintained by humans and their livestock. The Spanish dehesa ecosystem spans an area of ca. 3.2 million ha [16] that is mainly covered by *Quercus ilex* L. or *Quercus suber* L. at a density of 20–50 trees/ha. Roughly 40% of such an area is in the Andalusian region (S Spain) and 240 585 ha in the province of Huelva alone. Although the term "dehesa" is only used in Spain, similar woodlands exists in other world regions such as Portugal, North Africa and California.

Current income from dehesas is obtained mainly from livestock, hunting, fuelwood and non-timber products such as cork, mushrooms, fodder, fruits and honey. However, these open woodland forests are important in the Iberian Peninsula not only because they constitute a source of income, but also because they possess ecological and ethnological interest, and are symbols of the Mediterranean landscape. Tree-populated dehesas are listed among the habitat types protected under the European Union's Directive on Habitats.

Acorns constitute the most valuable and remunerative food resource for a number of game and non-game wild species [13]. In SW Spain, the breeding of Iberian pigs, which are fed largely on acorns from *Quercus ilex* and *Quercus suber* trees,

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has special economic significance. In other *Quercus* forests, acorn production is also very important towards regeneration [13,14] since the amount and quality of the acorns obtained are crucial factors in the development of new holm oak stands [9, 25]. However, the absence of regeneration in dehesas cannot be ascribed to a lack of acorns. Thus, Pulido and Díaz [24] found acorn production to be many times higher in dehesas than in natural oak forests. Regeneration rates, however, are far lower, which is ascribed by these authors to the inability to direct acorns to safe (shaded) sites via efficient vectors. One should also bear mind that many open woodland forests have in fact arisen from the lack of livestock control.

Dehesas have traditionally been the subject of tree pruning and other silvicultural practices which have changed little in the past few decades [20]. The phytopathological phenomenon known as "oak decline" has resulted in the disappearance of vast forestry areas and led to widespread weakening and vulnerability of holm and cork oaks in the southwest of the Iberian Peninsula. Products such as firewood, which has traditionally been obtained from the pruning of trees (especially holm oaks), have lost most of their value [7]. This, together with the high costs of forestry practices, led us to revise current pruning treatments in dehesas.

Traditionally, dehesa trees have been subjected to two types of pruning, namely: formative pruning, which is done only once during a tree's lifetime (typically at an age of 30–40 years, when trees are ca. 15 cm DBH) and maintenance pruning, which is done each 6–10 years and is the subject matter of this work. Pruning involves removing branches in the central and inner zones of the tree crown; this causes leaves to be displaced farther from the trunk and restricts water supply with respect to leaves in a naturally growing crown. Maintenance pruning is intended to maximize acorn yield, and forest owners generally accept that pruning has favourable effects on acorn production [7]. However, it is unclear whether it increases acorn yield as traditionally believed [26] because the actual outcome is influenced by the pruning intensity used. The economic costs of light or moderate pruning are very high in any case, and attempts at offsetting such costs by obtaining some income from firewood, charcoal or virgin cork have led producers to raise the pruning intensity. As a result, pruning is usually very intensive or even excessive [5]. Although the influence of pruning on acorn production in Mediterranean oak woodlands has long been controversial, it is poorly documented. According to Cañellas et al. [7], there is inadequate documented information to even form an objective, rational opinion about the response of trees to such an important silvicultural practice.

In this work, we examined the influence of pruning on acorn production over several years, and also changes in acorn yield between years as influenced by the particular climatic conditions. To this end, we conducted an experimental study at two sites in the province of Huelva (southwestern Spain) where trees where subjected to traditional pruning at three different intensities (low, moderate and heavy) for two years; also, we compared the results for one of the sites with those obtained using a non-traditional pruning method (crown-regeneration pruning).

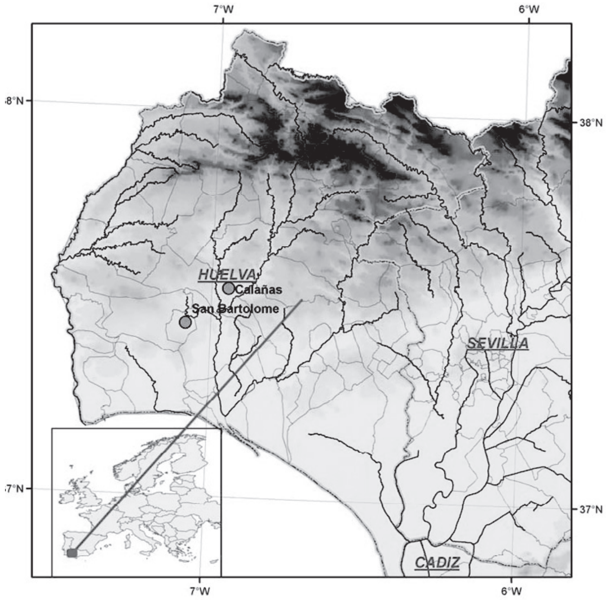

Figure 1. Location of the experimental plots (Calañas and San Bartolomé).

2. MATERIAL AND METHODS

2.1. Experimental plots

The present study was conducted in two plots located in the province of Huelva (SW Spain) (Fig. 1). One plot was on the "La Encarnación y Castilnovo" farm, in Calañas (Huelva), spanned an area of 2.9 ha and had a density of 34.5 trees/ha (UTM, zone 29: X, 681349; Y, 4156557). The other plot was on the "El Campillo" farm (San Bartolomé de la Torre, Huelva), spanned an area of 2.7 ha and had a density of 36 trees/ha (UTM, zone 29: X, 669638; Y, 4145966).

Both study areas are at the foot of the southern foothills of western Sierra Morena (Fig. 1) and feature a genuine Mediterranean climate. The Calañas area is at an altitude of 165 m, has an average annual precipitation of 727 mm, a mean annual temperature of 18.3 °C and a frost period of 4 months. The San Bartolomé area is at 128 m above sea level, has an average annual precipitation of 633 mm as rainfall, a mean annual temperature of 18.6 °C and 2 frost months. Both plots are on a substrate essentially consisting of shale and grauwacke; however, the soils in Calañas are less markedly developed (33 cm soil depth in Calañas and 67 cm soil depth in San Bartolomé) by effect of its more uneven relief. The soils range from Regosols/Leptosols to Cambisols in Calañas, and from Regosols to Luvisols in San Bartolomé; base saturation is lower than 50% in all, which are thus under a preferentially dystric regime. Both plots are structured as dehesas and covered largely by *Quercus ilex* trees of similar size and at also similar densities. The understorey in Calañas consists of heliophilic bushes (particularly *Cistus ladanifer* and *Cistus monspeliensis*). The primary uses of the Calañas farm are red deer, wild boar and partridge hunting; sheep raising and mushroom collection. The plot is affected by oak decline, and 15 trees died during the course of the study (none was among the monitored trees, so this had no impact on the experimental design). The main use of the San Bartolomé farm is fighting bull raising. Grazing and repeated tillage of the soil have

Table I. Climatic data for the Calañas and San Bartolomé plots over the period 2000/2005. Pr precipitation relative to the average value for the period 1960–2005; AR average annual rainfall (mm); SpR spring rainfall (mm); SuR summer rainfall (mm); AT average annual temperature (°C); Tm average of the lowest temperatures of the coldest month (°C); m absolute lowest temperature (°C); FD number of frost days per year; SB San Bartolomé plot; CA Calañas plot.

Year	Precipitation						Pr		Temperature							
	SB			CA			SB	CA	SB				CA			
	AR	SpR	SuR	AR	SpR	SuR			AT	Tm	m	FD	AT	Tm	m	FD
2000	784.8	276.5	5.3	962.7	403.4	8.2	1.29	1.46	18.42	3.1	1	0	18.32	4.3	1	0
2001	726	20.2	76	878.9	36.1	121.1	1.19	1.33	18.68	7.5	1	0	18.43	7.1	2	0
2002	676.2	145.6	53.6	754.2	106.8	51.1	1.11	1.14	18.44	6.5	2	0	18.28	7.2	3	0
2003	871.4	112.2	29.1	861.5	115.9	25.7	1.43	1.31	18.67	5.3	0	0	18.63	5.9	1	0
2004	541.1	70.2	4.2	728.4	98.3	10.6	0.89	1.1	18.46	7.3	0	0	18.60	6.9	1	0
2005	326	30.7	0	340	47.9	1	0.53	0.51	18.35	2.6	-3.1	3	18.20	4	-2.4	2
1960–2005	611.9	97.07	27.49	660.8	125.01	34.776	1	1	18.93	5.98	-3.1	3	18.34	6.15	-2.4	2

Table II. Characteristics of the studied trees.

Parameter	*Calañas* (*n* = 100)			*San Bartolomé* (*n* = 100)		
	Min	Max	Average ± SD	Min	Max	Average ± SD
Height (m)	2.3	9.7	6.15 ± 1.68	4.5	9.5	6.54 ±1.08
Diameter (cm)	8.6	52.2	32.56 ± 10.79	15.28	57.30	35.40 ± 7.23
Crown radius (m)	1.9	6.03	3.86 ± 1.36	2.84	6.62	4.46 ± 1.07
% Crown density	20	80	53.33 ± 11.83			
% Living leaves/total crown volume	10	100	45.88 ± 14.26			

led to the virtual absence of bushes except for isolated *Chamaerops humilis*, *Asparagus acutifolius* and *Daphne gnidium* specimens at the plot boundaries or some tree foots. The plot was fenced in order to block access by cattle. Although the fungus *Phytophtora cinamommii* has been detected in this plot (a sample of soils was examined for the presence of this fungus in the province of Huelva by Tapias within the framework of research project INTERREG QUERCUS/SP5. 45), visible symptoms of oak decline are scant and no trees have died ever since it was laid out. Prior to the study, the trees in both plots had been pruned each 6–10 years since their formative pruning, which was done at an age of about 25–30 years.

It is not easy to determine the exact age of Mediterranean holm oaks owing to locally absent rings and false bands, which are quite frequent in this species [10, 15]. In any case, the trees in both plots were estimated to be 40–70 years old based on their size and on the historical knowledge of the owners, managers and forest rangers.

Table I summarizes the climatic conditions prevailing during the study and Table II the characteristics of the studied trees.

2.2. Laying out of plots and pruning of trees

A total of 100 holm oaks were marked for study in each plot. Measurements of each tree included perimeter at a height of 80 cm, total height and health status (only in the Calañas plot, where it was expressed as the percentage of living leaves with respect to total crown volume and crown density). We chose not to use breast height diameters because tree crosses were all less than 1.30 m in size by effect of formative pruning.

Trees in the two plots were subjected to traditional pruning at three different intensities (light, moderate or heavy); some, however, were left unpruned and used as controls. In addition, some trees in the Calañas plot were subjected to a new method for the studied species which we have called “crown-regeneration pruning”. This method reduces biomass in the external portion of the tree crown and removes its outermost branches, thereby shortening water transport distances to the leaves and leading to a more compact crown. The resulting modified tree hydraulic structure possibly improves the water balance in relation to traditional pruning, which causes crowns to expand and water transport distances to increase as a result. An agricultural species, *Olea europaea* L., is beginning to be subjected to a similar type of pruning in super-intensive plantations (2000 trees/ha); so far, this practice has raised fruit production (8000–13 000 kg/ha as the average for the 3rd to 6th harvesting years) [35] relative to traditional plantations; however, the outcome can be additionally influenced by density, fertilizer use or the harvesting method employed.

Pruning was done in January 2001 in Calañas and in February 2003 in San Bartolomé in order to more accurately compare the effect of this practice aside the influence of the particular climatic conditions of the pruning year. All trees had been pruned before such a time; those in the Calañas plot were pruned in 1994 (seven years before 2001) and those in the San Bartolomé plot in 1996 (seven years before 2003). The number of trees under each treatment was 20 in Calañas (20 trees × 5 treatments = 100 trees per plot) and 25 in San Bartolomé (25 trees × 4 treatments = 100 trees per plot). Treatments were randomly assigned to trees at both sites.

The pruning operation was performed by workers hired by the forest owners. In the absence of previous criteria, the pruning intensity was established as follows: light pruning involved removing sucker and dead branches only; heavy pruning coincided with the usual practice in the area; and moderate pruning was in between the previous two. In order to ensure homogeneity in treatment intensity, each worker was assigned a single treatment type and supervised by a member of the research group.

Once work was completed, pruning intensity was estimated as a function of the weight of pruned branches and tree diameter. Pruning treatments were discriminated in terms of intensity by using the

Table III. Pruning quantification for the two plots and three pruning intensities. FM: average fresh matter weight (kg) per tree, DM: average dry matter weight (kg) per tree, DM/d: average dry matter weight per tree divided by the average diameter for the treatment.

Plot	Pruning	N	FM (kg) ± SD	DM (kg) ± SD	DM/d ± SD
Calañas	Light	20	13,71 ± 10,71	10,44 ± 8,05	0,31 ± 0,18
	Moderate	20	66,82 ± 57,86	50,76 ± 43,05	1,36 ± 0,76
	Heavy	20	167,64 ± 150,24	127,13 ± 114,15	3,22 ± 2,12
San Bartolomé	Light	25	45,81 ± 48,20	34,72 ± 36,04	0,75 ± 0,68
	Moderate	25	64,38 ± 27,65	49,40 ± 21,11	1,46 ± 0,57
	Heavy	25	137,88±88,14	105,63 ± 67,26	2,87 ± 1,26

branch dry weight (DW) to tree diameter (D) ratio; thus, DW/D was less than 0.8 for light pruning, greater than 1.7 for heavy pruning and in between these two levels for moderate pruning [2]. Every holm oak harvested for acorns was classified into its original group, so no tree was changed to a different pruning treatment. The data obtained from pruning quantification are summarized in Table III.

2.3. Estimation of acorn production

The trees used to estimate acorn production were selected by stratified sampling as a function of stem diameter. All trees were assigned to one of the following three diameter classes: diameter < 25 cm, 25 cm < diameter < 40 cm and diameter > 40 cm. One tree per treatment and diameter class was randomly selected for acorn harvesting in the Calañas plot (3 trees per treatment and 15 trees per plot). Four trees per treatment (16 trees per plot) were randomly selected in San Bartolomé plot; one belonged to the higher diameter class, another to the lower class, and the other two to the intermediate class.

Acorns were harvested by using a trapping method (containers) (see [6, 12, 13]). Four containers 0.45 m in diameter at the top were placed under the selected trees following the north, south, east and west directions at three-quarters of the crown radius distance from the base of the trees. The production figure for each was the average of the four containers used for harvesting.

The container method allowed us to sample a fraction of the projection of the crown surface where acorns were assumed to fall. In order to ensure correct results, we collected all acorns fallen from 9 trees in the two plots (one tree per treatment and plot randomly selected between the 31 trees monitored for acorn production). Predation by higher herbivores was avoided by fencing the perimeter of the selected crowns in the Calañas plot; no similar precaution was necessary in San Bartolomé as the plot was already fenced.

Acorns were harvested during the 2001/02, 2002/03, 2003/04, 2004/05 and 2005/06 dissemination periods (i.e. the first five years following pruning) in the Calañas plot, and during 2002/03, 2003/04, 2004/05 and 2005/06 (i.e. the first year before and three years following pruning) in San Bartolomé. In each period, acorns fell from the trees from September–October to January–February and were harvested on a fortnightly basis in each plot. In what follows, we will assume the year 2001 to include acorns fallen from September 2001 to February 2002, and subsequent years to encompass production over the equivalent periods.

All acorns collected in the containers were transferred to the laboratory on the day of harvesting and stored refrigerated at 3 °C overnight. Then, they were counted and their individual fresh weights (FM) measured to within ± 0.001 g on a precision balance. In order to determine the water content, WC, of the acorns, 90 fruits (from the 9 trees used for total acorn harvesting, ten fruits per tree) were randomly chosen each month and cut in half to measure their dry weight (DM) following drying to a constant weight at 65 °C in a stove. The percent water content was estimated from the expression WC (%) = 100(FM – DM)/FM.

The physiological condition of the trees in the most unfavourable season (summer) was estimated from their photosynthetic activity and water potential. Measurements were made at the beginning (June 16–21), middle (July 27–30) and end (September 17–21) of the summer, while both plots were fully operational (in 2003, 2004 and 2005). The Calañas plot was subject to additional measurements of this type in July 2002. On each date, five trees per treatment type and plot (including the selected trees chosen for acorn harvesting in both plots) were subjected to two different determinations, namely: xylem water potential (Ψ), which was measured in twigs of the year by using a Model 1000 pressure chamber from PMS Instruments (Corvallis, OR) immediately after sunrise; and photosynthetic activity, which was measured on adult leaves with an Lci Portable Photosynthesis System from ADC BioScientific (Hoddesdon, UK) between 10 and 12 am (local time) in order to obtain an estimate of the maximum daily rates at the time (especially in mid-summer, when the drought was at its peak) [33].

2.4. Analysis of data

The container-based method used to estimate acorn production was validated by subjecting the results to linear regression analysis, using fallen acorn biomass, Ps (g/m^2), as dependent variable (Ps = Pt/Sc, where Pt was the total amount of acorn biomass harvested from soil, in grams, and Sc the area of the vertical projection of the tree crowns, in m^2) and container harvested biomass (Pc (g/m^2)) as independent variable. The relationship between acorn production and pruning intensity was assessed jointly in both plots by using a repeated measurements General Linear Model with acorn production (g/m^2) as dependent variable, and treatment and site as fixed factors. The analysis was also conducted by using the annual production (g/m^2) per tree divided by the average production per plot per year. Because it was only used in Calañas, crown-regeneration pruning was excluded from this analysis and examined separately, and so was the production data for San Bartolomé in 2002 as it was obtained prior to pruning.

The influence of the number of years elapsed after pruning was examined by using a Univariate General Linear Model with the annual acorn production per tree (g/m^2) and annual acorn production per tree divided by the average production for the year concerned in each plot as dependent variables, and pruning treatment and the number of years after pruning – with provision for the fact that pruning

Table IV. Average distribution of container harvested fresh biomass (acorns) during the dissemination period in the two plots. (n = 15 for Calañas and n = 16 for San Bartolomé).

Period	Calañas (2001/05)		San Bartolomé (2002/05)	
	g/m^2	% Production	g/m^2	% Production
Sep 15–Oct 15	12.64	6.60	19.46	7.77
Oct 15–Nov 15	72.29	37.75	105.39	42.07
Nov 15–Dec 15	78.12	40.80	86.26	34.43
Dec 15–Jan 15	25.14	13.13	29.59	11.81
Jan 15–Feb 15	3.29	1.72	9.80	3.91

was done in January 2001 in Calañas and February 2002 in San Bartolomé – as fixed factors. Only the first, second and third years after traditional pruning in the two plots were included in this analysis.

The potential advantages of crown-regeneration pruning as regards acorn production were established by comparing its results with those of the other pruning treatments, using a General Linear Model with repeated measurements and acorn production relative to average annual production as independent variable

A correlation matrix was constructed from production variables (acorn production in g/m^2, acorn number per m^2, and acorn weight and size), climatic variables (annual rainfall, seasonal rainfall, average annual temperature, average of highest temperatures of the hottest month, average of lowest temperatures of the coldest month, extreme temperatures), edapho-climatic variables (actual evapotranspiration for the periods September–August, January–August, August–December, January–December as obtained from the water balance where potential evapotranspiration was estimated using the method of Thornwaite (1948), in addition to some humidity and aridity rates), and tree physiological variables (water potential at sunrise as measured in mid-summer). The values used for the analysis where no specific period is stated were always annual averages per plot.

All statistical analyses were performed with the aid of the software SPSS v. 14, and all significance figures are given at the $p < 0.05$ level.

3. RESULTS

3.1. Acorn production

Acorn production as measured with the container method was quite consistent with the total acorn yield divided into the crown surface: Ps (g/m^2) = 16.04 + 0.729Pc (g/m^2), with R^2 = 0.82 (n = 45, p = 0.000, F = 99.853).

Acorns fell from September to February (77.5% between October 15 and December 15) (Tab. IV). Their average water content was 47.01% in Calañas and 44.34% in San Bartolomé (the combined figure was 45.67%) (Tab. V). Such a content decreased throughout the acorn fall period and peaked in October – by exception, contents in 2005 were higher than all other years and increased near the end of the mast period. Worth special note here is the abrupt decrease in WC observed in San Bartolomé and, especially, Calañas, in February 2004, which was followed by a shortage of fruits that year.

The average acorn production for the Calañas plot in the studied period was 74.61 ± 1.26 g DM/m^2 and 3.97 ± 0.07 kg DM/tree (n = 76); that for the San Bartolomé plot was significantly higher (120.56 ± 1.78 g DM/m^2 and 9.67 ± 0.13 kg DM/tree, n = 64, p = 0.006, F = 7.71). A multiple-comparison test provided two homogeneous subsets consisting of the years with the lowest production results (2001, 2004 and 2005) on the one hand, and of the two with the highest (the consecutive years 2002 and 2003) on the other. The combined production of both plots was 95.61 ± 0.76 g DM/m^2 and 6.50 ± 0.055 kg DM/tree (n = 140). The year × site interaction was significant and production was higher in San Bartolomé except in 2004, where it was slightly lower (Fig. 2).

3.2. Influence of climatic conditions on acorn production

The water potential in the most unfavourable period (mid-summer) in San Bartolomé was never below –3.51 ± 0.14 MPa. It amounted to –2.7 ± 0.08 MPa in the year 2003, which was wetter than usual. During the summer, gas exchange rates reduced to 30–40% of the spring values; net photosynthesis rates, however, retained positive values – at least during the morning hours. By contrast, holm oaks in Calañas were severely affected by the drought of 2005 (the water potential was –4.10 ± 0.05 MPa), and also, substantially, in the late summer of 2004 (with a water potential of –3.97 ± 0.004 MPa). Gas exchange rates fell to 15% of the highest spring levels in 2004, and reached negative values in 2005. Differences in these respects between pruning treatments were not significant for any plot or year (p > 0.150). However, there was a slight relationship (R^2 = 0.89, p = 0.02, n = 7) between the average acorn production value per plot per year and the water potential in mid-summer (end of July) per plot per year (Fig. 3). As can be seen from the variation ranges in Figure 3, correlation between variables increased with decreasing water potential below –3.5 MPa. Acorn production and water potential were correlated with annual rainfall (p = 0.037), spring rainfall (p = 0.015) and autumn rainfall (p = 0.04), and also with the actual evapotranspiration for the period from September (previous year) to August (p = 0.04)

Acorn production (g/m^2) was more strongly dependent on the number of acorns harvested (p = 0.0008) than it was on their average weight (p = 0.2809), and such a number was dependent on water potential in mid-summer (p = 0.01) and autumn rainfall (p = 0.006), among other variables. Acorn weight was correlated with actual evapotranspiration (January–August) (p = 0.01) in both plots, and also with summer rainfall (p = 0.0098) in the Calañas plot.

3.3. Influence of pruning type on acorn production

The joint analysis of both plots revealed the absence of significant differences in acorn production, both in absolute (g/m^2 per tree, n = 140, p = 0.692, F = 0.491) and in relative terms (g/m^2 per tree divided by the average acorn production per plot per year, n = 140, p = 0.819, F = 0.309), as a function of pruning type. Differences in production between pruning types were less marked in Calañas than in San Bartolomé (Fig. 4).

Table V. Percent water content of acorns harvested in different months and years in the two plots. CA Calañas plot (*n* = 50), SB San Bartolomé plot (*n* = 40).

Month	2003			2004			2005		
	CA	SB	Average	CA	SB	Average	CA	SB	Average
September	*	43.76	43.76	*	*	*	*	*	*
October	49.56	51.14	50.35	48.81	49.65	48.51	61.60	46.09	53.84
November	48.41	42.13	45.36	44.80	39.97	45.63	*	47.33	47.33
December	46.58	42.02	44.30	37.64	37.48	40.23	*	54.94	54.94
January	34.97	41.42	38.19	28.31	36.73	35.52	*	58.79	58.79
February	41.61		41.16	16.55	24.15	20.35	*	59.06	59.06
Average	44.22	43.10	43.85	35.22	37.59	36.51	61.60	52.34	54.79

* Blanks correspond to the months where no acorns were harvested in the plot concerned.

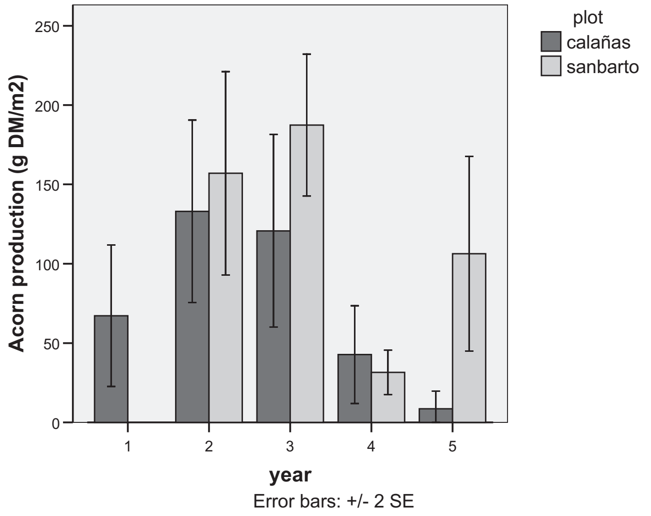

Figure 2. Average acorn production (g DW/m^2) in the two plots during the studied period. Year: 1, 2001; 2, 2002; 3, 2003; 4, 2004; 5, 2005 (*n* = 15 for Calañas and *n* = 16 for San Bartolomé).

Table VI shows acorn production for the different treatments and years in San Bartolomé, which were examined separately because they included data obtained prior to pruning. As can be seen, production was higher the year following pruning, decreased after 2 years and again increased in the third; the trend was identical with all treatments. Because annual production exhibited significant differences, we used the average annual production for each plot as the independent variable in the statistical analysis. A comparison of the results for the control, lightly pruned and moderately pruned oaks revealed an increase in production from 2002 (i.e. prior to pruning) to 2005 (i.e. 3 years after pruning). The opposite held for heavily pruned trees.

In order to assess the effect of crown-regeneration pruning on acorn production, we examined the results for the Calañas plot, which exhibited significant differences ($p = 0.025$, $F = 4.40$) in acorn production between pruning treatments; thus, production with crown-regeneration pruning exceeded the average figure for traditionally pruned and control oaks by 96.7% (Fig. 5).

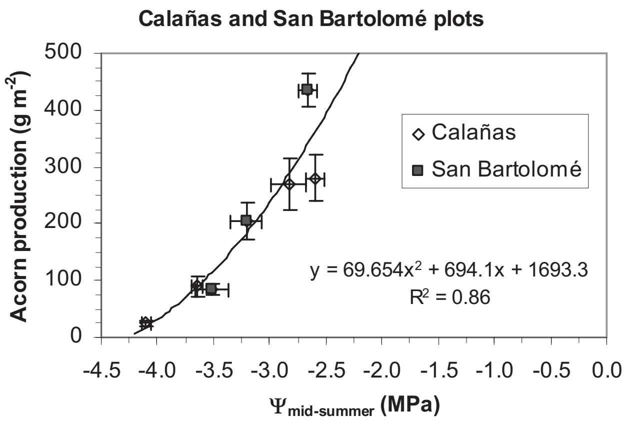

Figure 3. Relationship between acorn production (DM) and xylem water potential in mid-summer as measured immediately after sunrise. The graph shows the average values (± SE) for each plot and year (*n* = 25 for Calañas and *n* = 20 for San Bartolomé).

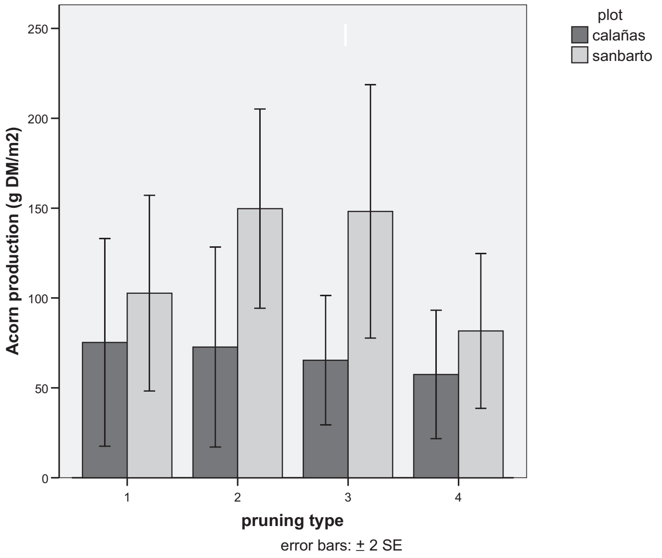

Figure 4. Average acorn production (g DW/m^2) as a function of pruning type during the studied periods (2001/05 in Calañas, *n* = 15, and 2003/05 in San Bartolomé, *n* = 16). Pruning type: 1 control, 2 light, 3 moderate, 4 heavy.

Table VI. Acorn production in the San Bartolomé plot, expressed in g /m^2, during the studied period. AP/YP ratio of the production for each pruning type to the average overall production for the same year

	Production (g/m^2)				AP/YP			
Pruning type	2002	2003	2004	2005	2002	2003	2004	2005
Control	270.51	362.93	66.54	213.44	0.75	0.83	0.78	1.04
Light	398.63	541.60	163.86	249.87	1.11	1.24	1.92	1.22
Moderate	524.22	413.53	60.67	310.89	1.46	0.94	0.71	1.52
Heavy	233.99	425.29	49.80	43.51	0.65	0.97	0.58	0.21
Average	356.84	435.83	85.22	204.43				

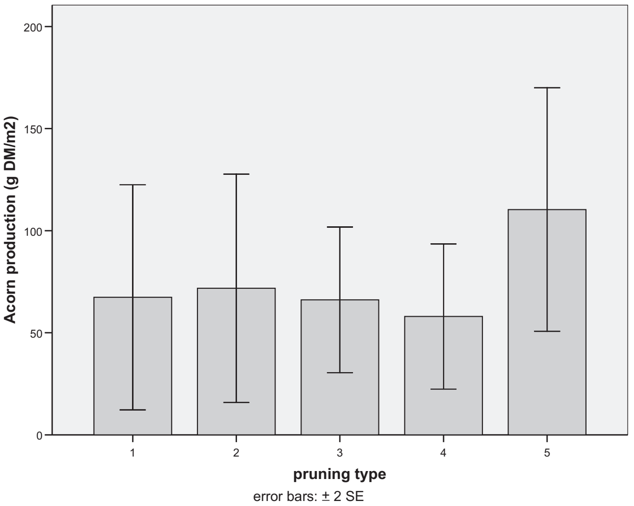

Figure 5. Variation of acorn production (g DM/m^2) in the Calañas plot ($n = 75$) over the period 2001/05. Pruning type: 1 control, 2 light, 3 moderate, 4 heavy, 5 crown- regeneration.

4. DISCUSSION

The average acorn production of our plots, 95.61 g DM/m^2 (or 6.50 kg DM/tree), is in between the 11.6 and 285.8 g/m^2 and between 1.3 to 42.1 kg DM/tree previously reported for Andalusian dehesas[18]; also, it falls within the range for *Quercus suber* reported by Cañellas et al. [6]: 0.7–332.8 g/m^2. Carbonero et al. [8] obtained an average production of 363 g FM/m^2 (peak 1383 g FM/m^2); our respective figures were 256.44 g FM/m^2 as average and 1016.41 g FM/m^2 as peak value. Alvarez et al. [3] harvested an average production of 10.45 kg DM/tree from Salamanca dehesas with a tree density of 25 trees/ha on the assumption of a water content of 45% for the fruits. Poblaciones et al. [22] estimated the average acorn production over a two-year period in five dehesas in Extremadura (W Spain) to be 600–830 kg DM/ha and found large differences between individual dehesas; these levels are higher than the average production values for our plots (227.5 kg DM/ha).

The sampled plots exhibited significant differences in acorn production between years; thus, 2002 and 2003 were quite productive in relation to 2001, 2004 and 2005. Climatic conditions during the reproductive stages from bud initiation to acorn ripening have been shown to account partly for the variability in acorn production by some oak species [1, 11, 19, 31]. Precipitation in 2002 and 2003 exceeded that in 2004 and, especially, 2005, which was a very dry year (Tab. I). Although precipitation in 2001 was also high, the spring was drier, which may have influenced the formation and maturation of female flowers. In species adapted to the changeable Mediterranean climate, the advantages of investing in mast years increase in years with favorable weather conditions [10, 29, 30].

There was indeed some synchronicity as regards production increase or decrease in both plots; however, production was invariably higher in San Bartolomé. Also, all types of pruning led to the same trends in production in different years. Only in 2005 was the trend broken: production in San Bartolomé was greater than the previous year, whereas that in Calañas was markedly lower – 2005 was the worst year in this respect at this site. The year 2005 was very dry (precipitation was 53–56% of the mean value for the period 1960–2005, Tab. I), with heavy frosts in the first quarter that were more influential on the trees in the Calañas plot as revealed by the physiological measurements. These frosts could have led to bud freezing [10] and to a considerably decreased xylem hydraulic conductivity [34, 36]. Notwithstanding the unfavourable climatic conditions of that year, the water potential of the oaks never fell below –3.70 MPa in San Bartolomé, but reached –4.10 MPa in Calañas. This may have been a result of a better edaphic and tree status in San Bartolomé. When the water potential falls below –4 MPa, the ensuing reduced hydraulic conductance of twigs can severely hinder water supply to leaves. In fact, *Quercus ilex* has been found to lose more than 50% of its initial hydraulic conductance below that water potential level [34]. A comparison of hydraulic conductance measurements made in both plots in 2004 revealed that cavitation in the conducting system of the oaks in Calañas in mid-summer was 40% higher than in San Bartolomé. Also, the conducting system of trees at the former site was 20% less efficient than in the latter [21]. The differences in hydraulic conductance between the two plots probably increased over the summer of 2004 and throughout 2005. In fact, the water potential in Calañas in the late summer of 2005 was below –4.1 MPa and the maximum photosynthetic rates in the early morning were negative, which is suggestive of net consumption of reserves and the absence of a surplus for vegetative growth or fruit production at the time. The correlation between acorn production and the xylem water potential observed in this work suggests that, below –3.5 MPa, water stress is severe enough to become a limiting factor for acorn production. Above –3.2 MPa, however, water stress has a much less marked effect on acorn production relative to other internal and external factors.

Based on the relations between variables, the critical factors for fruiting are spring rainfall (flowering) and autumn rainfall (ripening). Summer is no doubt a critical period; because of the scarce, irregular precipitations, trees must live on soil reserves. García-Mozo et al. [10] found temperature, relative humidity and rainfall in January, March and September to be the most influential climatic variables. Key events in the phenological cycle occur in spring. The final stage in catkin development occurred in the first half of March, and the availability of water in a dry Mediterranean area could increase the rate of final pollen production and hence acorn production [10]. Acorn production and actual evapotranspiration of the year before fruit ripening (September–August) are correlated and dependent on the existing photosynthetic ability. In most species, cell division before the anthesis and cell expansion after it determine how much fruits grow and their final size. In mid-summer, clearly after anthesis, little fruits will fatten if their water status (cell turgor) is suitable. When the water potential falls below –3.2 to –3.5 MPa, which is close to the turgor loss point for holm oak [32], the lack of cell turgor and the accumulation of abscisic acid and ethylene can stop the development of fruits and cause them to fall [4].

Assessing the effect of pruning on acorn production is complex as it requires using long data series obtained prior to and after pruning [11]. This has so far hindered research into this topic. Carbonero et al. [8] found no significant differences in production between pruning treatments – they examined a single pruning intensity, however. We found no significant differences in this respect, either; however, heavily pruned trees were found to exhibit lower production than were lightly pruned trees. According to Gea-Izquierdo et al. [11], most authors have found production to decrease the first year after pruning. Thus, Carbonero et al. [8] identified a statistically unconfirmed trend in production to improve the fifth year after pruning and Porras [23] concluded that pruned trees only start to produce more fruits than unpruned trees after three years; the trend, however, does not persist subsequently and these results were not supported by a statistical analysis confirming the significance of differences. Cañellas et al. [6] found moderate pruning – which is the pruning treatment traditionally used in cork oak dehesa systems – of *Quercus suber* to have no effect on the amount of acorns produced per unit area of crown during the first three years following pruning; also, they found the mast year to have a strong effect on acorn yield in both pruned and unpruned trees. Our data expose an increasing trend in absolute and relative production the year following pruning and a decrease in subsequent years for heavily pruned trees, a slight increase for control and lightly pruned trees, and no substantial change in moderately pruned trees; these trends, however, were not statistically significant owing to the high variability between trees.

The increased productivity derived from crown-regeneration pruning (96.7% higher than with other pruning treatments) can be ascribed to this treatment improving the hydraulic structure of trees by shortening water transport distances. Because pruning alters the hydraulic architecture of trees [17], based on Zimmermann's *segmentation hypothesis* their water status may be altered as xylem embolism can occur throughout trees and decrease xylem conductivity over long distances [37]. Also, xylem embolism in *Quercus ilex* in mid-summer has been found to be much lower in trunks than in minor branches and twigs [34]; thus, leaves, twigs and minor branches experience higher strain under water stress conditions than do major branches and trunks. In addition, the more compact and closed crown provided by this treatment may reduce wind speed and light exposure of leaves inside the crown, all of which facilitates retention of water within the plant [28,38]. Accordingly, it is unadvisable to alter (open) the natural structure of the crown, at least at such low densities.

The conclusions drawn from our results allow us to make some recommendations as regards management of dehesa systems. As shown above, traditional pruning at different intensities fails to substantially increase acorn production – so much so that heavy pruning tends to decrease it. Pruning treatments can provide other products such as firewood, but their demand – and hence their value – has almost disappeared as alternative sources of energy have become available [27]. Therefore, the most immediate general recommendation for land owners and managers is to re-approach their exploitation of dehesas by applying the principle of minimum intervention in accomplishing their pursued aims. Regarding maintenance pruning, the authors recommend suppressing it in particularly vulnerable zones and reducing it in others (by decreasing its frequency and, especially, its intensity).

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