

Acorn production in Spanish holm oak woodlands

G. Gea-Izquierdo*, I. Cañellas and G. Montero

*Departamento de Sistemas y Recursos Forestales. CIFOR-INIA.
Ctra. La Coruña, km 7. 28040 Madrid. Spain*

Abstract

We present a review on the state-of-the-art of fruit production in Western Iberia woodlands («dehesas»), and particularly in *Q. ilex* (holm oak) «dehesas». This threatened ecosystem is of very high ecological and economical importance. *Quercus* sp. fruits (acorns) are essential for wildlife, and for pig fattening in «dehesas». In the first part of this review we briefly describe the phenology of the holm oak and the factors affecting acorn morphology and chemical composition. In the second half we analyze the main known factors reported in the literature that determine acorn production: pruning, stand characteristics, and site (weather and soil). We make several suggestions to improve future research and detect the existing gaps in the understanding of acorn production.

Fruit production is highly variable, both between and within years and individuals. The mean production in «dehesas» (mean density circa 50 trees/ha) is around 250-600 kg/ha (≈ 100 g/canopy-m², CV > 100%). Acorn morphology is also very variable, with mean sound acorn size around 3.5 × 1.6 cm, CV $\approx$ 10% (3.5 g/acorn, CV > 50%). Silviculture plays an essential role in acorn production. Acorn production per tree seems to be negatively related to density. The effect of pruning is less clear: production seems to be reduced in the first and second years after pruning. After the third year it is not possible to discern from the literature whether there is any response to pruning or not. Weather and soil (site) also impact production and their effects should be explored in future management. The influence of genetics is unknown and should also be addressed. Longer data series are necessary. The dasometric features of the stands need to be characterized, in order to better understand production and compare results from different locations. Much research is still required to understand the functioning of fruiting in these woodlands.

Key words: *Quercus ilex*, holm oak, acorn, fruit production, dehesa, agrosilvopastoral systems.

Resumen

Producción de bellota en las dehesas españolas de encina

El alto interés ecológico y económico de la producción de fruto en las dehesas ibéricas, concretamente las de encina (*Quercus ilex*), nos ha movido a realizar una revisión del estado actual de conocimientos. Los frutos (bellotas) de *Quercus* sp. resultan esenciales para la fauna salvaje y el engorde de ganado porcino en las dehesas. En la primera parte de este trabajo se describen brevemente las características fenológicas de la especie, así como los factores que influyen en la variabilidad morfológica y la composición bromatológica del fruto. En la segunda parte se analizan los factores fundamentales estudiados en la bibliografía que determinan la producción: la poda, las características dasométricas (densidad y distribución diamétrica) y la influencia del sitio (suelo y clima). Se realizan sugerencias para mejorar futuras líneas de trabajo, así como se subrayan áreas de conocimiento deficitarias.

La producción es muy variable tanto intra- como interanualmente. La producción media en las dehesas ibéricas (densidades medias alrededor de 50 pies/ha) es de unos 250-600 kg/ha (100 g/m² de copa, CV > 100%), presentando las bellotas una morfología muy variable, con valores medios en bellotas sanas alrededor de 3,5 × 1,6 cm (CV $\approx$ 10%), correspondientes a 3,5 g/bellota (CV > 50%). Los tratamientos selvícolas juegan un papel fundamental, estando posiblemente la producción de bellota por árbol negativamente relacionada con la densidad de la masa arbórea. El efecto de la poda sobre la producción presenta cierta controversia. Parece que se reduce los primeros uno o dos años, no siendo concluyentes los resultados a partir del tercer año. El clima y el suelo (sitio) también influyen en la producción, aunque sus efectos deben ser estudiados con mayor detalle en futuros trabajos. De igual modo, la influencia del factor genético se desconoce y debería ser estudiada. El nivel de conocimiento alcanzado hasta ahora es del todo insuficiente, siendo necesarias series temporales más largas para caracterizar la producción de fruto. Es estrictamente necesario multiplicar el esfuerzo realizado si queremos llegar a comprender las razones que determinan la producción

* Corresponding author: guigeiz@inia.es

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de fruto en este ecosistema y así ser capaces de optimizar de un modo sostenible un recurso tan valioso. La sistematización del modo en que se ofrecen los resultados y el uso de métodos de estimación validados y fiables, resulta fundamental para poder comparar posteriormente diferentes estudios y responder a cuestiones específicas.

Palabras clave: *Quercus ilex*, encina; bellota, producción de fruto, sistema agrosilvopastoral.

Introduction

Acorn production in *Quercus* sp.

Supra-annual variability is the rule among many polycarpic woody plants. Traditionally, this pattern of reproduction, in which there is an intermittent synchronous production of large seed crops by plant populations, has been termed «mast» or «mast-seeding». Mast seeding of woody species is a complex phenomenon that has not yet been perfectly understood (e.g. Herrera *et al.*, 1988; Kelly and Sork, 2002; Rees *et al.*, 2002; Koenig *et al.*, 2003). Two main explanations have been proposed: i) mast seeding is a direct response to environmental variability («resource matching»); ii) it is an evolved reproductive strategy, related to some economy of scale such as wind pollination or predator satiation. These two hypotheses are compatible; masting might be a result of their interaction (Herrera *et al.*, 1998; Kelly and Sork, 2002; Abrahamson and Layne, 2003). Masting seems to be more patent in dominant wind pollinated species and higher in mid-latitudes, paired to the variability of rainfall (Kelly and Sork, 2002; Koenig and Knops, 2000). According to recently published theoretical models, the availability of out-cross pollen (pollen coupling) might also be another determining factor in masting (Iwasa and Satake, 2004).

The *Quercus* genus, hereafter oak, is one of the most widespread in the Northern Hemisphere, and is dominant in many forests and woodlands. There is a vast literature in acorn production, the majority from North America. In Europe fewer studies exist despite the great importance of this genus. Particularly in the Mediterranean Region acorns play a basic role in domestic and wildlife feeding and most forests and woodlands are threatened by lack of regeneration. It has been demonstrated for some oak species that climatic conditions during the reproductive stages, from bud initiation to acorn maturation, account for some of the variability in acorn production (Sork *et al.*, 1993; Masaka and Sato, 2002; Abrahamson and Layne, 2003). Some oak species' fruiting patterns can be approached to species specific cycles, meaning either positive or negative

annual autocorrelations (synchrony) in annual acorn production. The cycles are partly explained by the acorn maturation pattern, either 1-year or 2-year (Koenig and Knops, 2000; Kelly and Sork, 2002; Liebhold *et al.*, 2004), and are influenced by resource limitations, either light, nutrients or rainfall. So, like mast seeding patterns in other genera, oak acorn production is likely to result from resources interacting with plant endogenous reproductive patterns (Sork *et al.*, 1993; Koenig and Knops, 2000; Kelly and Sork, 2002; Abrahamson and Layne 2003).

Brief review of acorn production estimation methods

Estimating acorn production is a laborious activity as large samples are required and collecting acorns demands a great effort. Different estimation techniques driving to different estimates and indexes of distinct accuracy have been developed, and could be summarized as follows:

Visual surveys

a) Partial or total counts: acorn counts are performed directly from standing acorns on the crown, with the aid of binoculars if necessary. The counts are made during a fixed time period, in sectors of the crown, or in quadrats (Koenig *et al.*, 1994; Garrison *et al.*, 1998; Perry and Thill, 1999). A variation of this method has been extensively applied in [dehesas] (Vázquez *et al.*, 1999), and the traditional way of estimating acorn crops are subjective estimations called «aforos».

b) Score methods: subjective visual estimations are made from standing crops according to ranked categories based on the amount and distribution of acorns in the crown. Several kinds and numbers of scores (generally between 4 and 10 categories) have been used in the literature (Perry and Thill, 1999, 2003; Peter and Harrington, 2002). However, only surveys using fewer than six categories have yielded statistical differences among categories (Perry and Thill, 1999).

Acorn collection

a) Partial acorn collection: acorns are collected in seed traps or quadrats (ground plots) evenly distributed beneath the crown. The number of traps or quadrats is preferably proportional to the crown area (Gysel, 1956; De Zulueta and Cañellas, 1989; Perry and Thill, 1999).

b) Total acorn collection: all acorns reaching the ground, either naturally or man induced by using sticks, are collected in canvases placed beneath the crown (Gysel, 1956).

The election of the estimation method should be based on economy, time, availability of workers, and scientific accuracy required. The visual methods are biased if the procedures are not standardised and the observers well trained before the survey. In traps, only acorns reaching the ground are collected. Therefore the estimation is of acorns available for regeneration and terrestrial animals, rather than total production, since acorn collections are biased from arboreal acorn consumption. If we aim at estimating the total production, every method except the total counts requires a previous estimate to relate either the total acorn production or the production per surface area to the estimative method (scores, counts, traps or quadrats) selected, what adds an extra source of error. As a rule, quantitative methods rather than qualitative should be preferably selected, as more statistical inferences can be applied (Perry and Thill, 1999). Counting methods are more appropriate for wildlife, whereas traps are more appropriate for regeneration (Perry and Thill, 1999) and domestic animals, such as the Iberian pig.

The total collection method is, hence, the most accurate one. Nevertheless, it requires the highest effort and, like all collection methods, does not permit estimating acorn yields in advance. Estimating yields in advance, i.e. counting green acorns in the middle of summer, would be useful e.g. for calculating pig stocking rates in Iberian woodlands, but the actual yield is susceptible to large errors related to irregular weather conditions prior to ripening (e.g., storms, drought, and temperature) and insect infestation. Visual surveys permit estimations in advance of acorn crops. They are more efficient, although they do not detect small differences among individuals and areas. Larger sample sizes can be attained with visual surveys, and can be appropriate to detect from moderate to big differences between individuals and areas (Perry and Thill, 1999). With collection methods, other variables such as incidence of disease, acorn size and weight, and acorn

quality can also be analyzed. Although acorn size and weight are frequently neglected in studies of acorn production, we believe that they should be measured in tree subsamples when estimating yields, particularly when using scores. As acorn size and morphology are likely to vary between years and among trees within the same year, the same score can be applied to trees with different acorn features. When using scores, the inclusion of crown size as covariate increases accuracy, as in the way scores are defined, a high ranked tree with a small crown might produce less than the same score in other tree with a bigger crown. Other factors likely to influence acorn estimation are sampling date, whether we consider acorns after or previous ripening, and whether we consider all acorns or just the sound ones.

The holm oak and Iberian dehesas: a Mediterranean anthropic ecosystem

The Mediterranean climate is characterized by large fluctuations in rainfall both within and between years, and by a long summer drought. One of the most abundant *Quercus* tree species in the Mediterranean region is the holm oak (*Quercus ilex* L.). Two main morphotypes have been described, and are variably considered as either two species (*Q. ilex* and *Q. rotundifolia* Lam.), or two subspecies [*Q. ilex* ssp. *ilex* and *Q. ilex* ssp. *ballota* (Desf.) Samp. in Bol.] (Do Amaral, 1990; Barbero *et al.*, 1992; Lumaret *et al.*, 2002). *Q. ilex* ssp. *ballota* (= *Q. rotundifolia*) occurs in Southern France, throughout Iberia, on many islands in the Mediterranean, and in Northern Africa. This evergreen species has broad ecological amplitude, growing in a wide variety of soils within the Mediterranean bioclimate (Afzal-Rafii *et al.*, 1992; Barbero *et al.*, 1992; Lumaret *et al.*, 2002). Throughout the Mediterranean holm oak forests have suffered severe degradation as a consequence of human impacts in history (Lossaint and Rapp, 1978).

In Western Iberia, holm oak occupies large extensions growing either in pure stands or mixed stands, commonly with *Quercus suber* L. (cork oak), *Quercus faginea* Lam., *Quercus pyrenaica* Willd. and *Fraxinus angustifolia* Vahl., as the most conspicuous species. This vegetation community transformed along history by human interaction forms the traditional agrosilvo-pastoral system called «dehesa» in Spain (Joffre *et al.*, 1988; San Miguel, 1994) and «montado» in Portugal



Figure 1. Broad distribution of «dehesas» (dashed line) and «montados» in the Iberian Peninsula.

(Pinto-Correia, 1993) (Fig. 1). This ecosystem consists of an open-woodland with an understory composed of a mosaic of croplands, grasslands and shrublands, where cattle, sheep, pigs and goats are extensively raised. The dehesas occupy specific geographic and topographic locations that are marginal for agriculture (see Fig. 1 for a broad area of distribution). They are characterized by poor shallow soils (acidic and sandy) with granites and slates as parent materials.

The tree mean density is generally between 30-50 trees/ha, but can vary from isolated trees to complete density (over 100 trees/ha). Pruning to obtain firewood is a traditional activity. In spite of having lost almost all its value, pruning is still quite common because it is traditionally performed and there is a general belief that it increases acorn production (San Miguel, 1994; Gómez and Pérez, 1996). Coppice originated from firewood exploitation is common in the steepest slopes and shallowest soils, and now plays an essential role for wildlife and game species. The ecosystem is in great danger as a result of the changing social and economic structure (Pinto-Correia, 1993; San Miguel, 1994; Gómez-Limón and de Lucío, 1999) and the almost absolute lack of tree regeneration in most stands (Pulido *et al.*, 2001; Leiva and Fernández-Alés, 2003; Pulido *et al.*, 2005). Lack of regeneration is one of the greatest problems of the ecosystem and is likely to become more problematic in the climate change scenarios expected for Mediterranean regions.

Acorns are one of the most profitable products in the dehesa system today, because during the oak fruiting period Iberian pigs are raised extensively feeding on acorns. One animal, fed only on acorns and grass, can consume 7-13 kg of acorns per day while they are in the dehesa, coinciding with the end of their fattening period, when they grow from 100 to 160 kg (López-Bote, 1998; Nieto *et al.*, 2002; Rueda, 2004). Holm oak acorns are preferably consumed than other oak species present. Traditionally, people have selected sweet-acorned trees, as in poor areas even until several decades ago, acorns were still an important food resource for humans in times of scarcity (García-Gómez *et al.*, 2002).

Understanding fruit production in these oak woodlands is crucial in order to achieve a sustainable management assuring regeneration and enhance pig and wildlife feeding. This review is motivated from the extremely high economical and ecological importance of this ecosystem and, particularly, fruit production within the ecosystem. Additionally, we have been encouraged from the many lacks in knowledge we encountered when starting to work in the topic. Although several studies have been conducted in Mediterranean woodlands that explore acorn production, this complex process is still not well understood. In Spain, most studies are at a small scale, sparse and unlinked. In this study, we review the existing literature to determine the current knowledge on oak fruit production, and make recommendations for future research directions. We focus on the holm oak, making comparisons with other ecosystems and, when available, with other species within the same ecosystem. We had to simply discuss qualitatively the bibliography without making any statistical inferences or other quantitative analyses as the data series currently available are too limited. We will first briefly introduce holm oak flowering and fruiting patterns, then analyze the biotic and abiotic factors affecting oak acorn size and acorn chemical composition. Finally we discuss relationships between holm oak acorn production and management and environmental factors.

Flowering and fruiting

Oaks are monoecious species, with separate male and female flowers. Commonly, in some oak species including the holm oak, there are trees that produce almost exclusively female flowers whereas other trees

produce male flowers (Sork *et al.*, 1993; Greenberg, 2000). Within the genus *Quercus* two general patterns of acorn development have been described: annual and biennial. *Q. ilex* is traditionally included in the Subgenus *Quercus*, Section *Quercus* (= *Lepidobalanus*). The species included in this group, the white oaks, exhibit an annual pattern of maturation, with acorns maturing around 6 months after pollination (Do Amaral, 1990; Cecich, 1997; Castro-Díez and Montserrat-Martí, 1998). Therefore, the full fruit cycle spans two years: from the spring prior to flowering, when the staminate and pistillate floral buds are initiated, to the autumn of the year when flowers bloom (Abrahamson and Layne, 2003). The time required for the acorn to develop is important because whether flowers mature in 1 or more years influences the acorn production pattern and its relationship to climate (Sork *et al.*, 1993; Koenig *et al.*, 2003). Detailed information on the reproductive morphology of the genus can be found in Kaul (1985).

Weather, especially in spring, affects both flowering and fruiting (Sork *et al.*, 1993; Cecich and Sullivan, 1999). High irradiance is associated with increased flowering in many plants (Peter and Harrington, 2002), which in fruit trees results in differences in flowering and flower morphology depending on the canopy position (Nuzzo *et al.*, 1999). In several oak species there is a positive correlation between acorn crop and total flower crop, which is inversely correlated with colder temperatures in the flowering period (Sork *et al.*, 1993; Masaka and Sato, 2002). Conditions favorable for pollination and fertilization (warm weather, absence of hail and freeze, higher rainfall) are likely to enhance mean annual acorn production (Cecich and Sullivan, 1999). However, the high number of flowers produced many years does not guarantee high acorn crops. Overproduction of flowers and subsequent abortion is a widespread phenomenon (Obeso, 2004). Production of female flowers does not seem to be affected by a certain level of herbivory (Díaz *et al.*, 2004), and according to the same authors herbivory might enhance production of female flowers at the branch level. Stressed trees selectively abort low viable acorns (Díaz *et al.*, 2003), and leaf asymmetry as a reflection of biotic or abiotic stress is related to flower and fruit production (Díaz *et al.*, 2003, 2004). Extreme climatic factors in the acorn growing period, such as drought, or insects can diminish acorn yields.

The holm oak is a wind pollinated dyszoochorous species (Kaul, 1985). The species adapts its phenology to the different environments where it thrives, partly

as a response to temperature and water availability. Low air temperature and water stress are limiting factors for bud opening and vegetative activity (Gratani and Crescente, 1993; Gratani, 1996; La Mantia *et al.*, 2003). Holm oaks produce flowers beginning at 8 years old, and start producing acorns when 15-20 years old (Corti, 1959; La Mantia *et al.*, 2003). The flowering flush happens in spring (April-May), and in some years a small secondary flowering occurs in autumn (La Mantia *et al.*, 2003). Acorn growth occurs in summer. Ripening and dispersion occurs from October to February of the same year, varying slightly among locations and years (Castro-Díez and Montserrat-Martí, 1998; Siscart *et al.*, 1999; Nieto *et al.*, 2002; Olea *et al.*, 2004). The establishment of young seedlings occurs during the first spring after acorn dispersion (Siscart *et al.*, 1999; Gómez, 2004; Pulido and Díaz, 2005). In these Mediterranean ecosystems, provisional shade (from shrubs or mature trees) is crucial for the survival of young seedlings (Pulido and Díaz, 2005).

Acorn size and morphology

Most oak studies are based on acorn number estimations (Sork *et al.*, 1993; Abrahamson and Layne, 2003), focused on estimating seed number production rather than fruit crops, *per se*. Consequently, these studies leave out acorn size and weight, which are important in calculating acorn yields. There is high variation in seed size both within and across oak species (Sork, 1993; Greenberg, 2000). Some authors have suggested the hypothesis that woody species with longer intermast interval are likely to produce larger seeds, likely as an adaptation to increase seedling survival (Aizen and Woodcock, 1992; García *et al.*, 2000; Sork, 1993). It has been shown in some oak species how acorn size correlates positively with the length of its development period and with rainfall (Sork, 1993; Díaz-Fernández *et al.*, 2004).

It is not clear whether seedling establishment is positively related to seed size (Sork, 1993; Díaz *et al.*, 2003; Gómez, 2004). The role of acorn size is controversial: bigger acorns are preferably consumed by predators (Gómez, 2004) including pigs (García *et al.*, 2003), which might hamper regeneration (Leiva and Fernández-Alés, 2003). Seedlings from bigger acorns average higher number of leaves and higher leaf area (Díaz *et al.*, 2003), which might be an advantage for young seedlings. Variability among holm oak individuals

in acorn size and weight is high. Holm oak acorn size can vary strongly between years in the same location and between locations (Carbonero *et al.*, 2003; Porras, 1998). The variability of holm oak acorn weight found in the bibliography ranges from 1.2 to more than 6.5 g, and is likely to be explained by tree individual characteristics (genetics), climate, soil properties, and stand structure (Afzal-Rafii, 1992; Porras, 1998). Acorn size seems to be negatively correlated with continentality. Afzal-Rafii *et al.* (1992) report significantly higher mean holm oak acorn weights (around 3.5 g vs. 1.6 g) in non-continental calcareous sites as compared to a continental siliceous Mediterranean climate in Central Spain, although data come from a single year. In Porras (1998), mean acorn diameter (1.60 cm) ranges from 0.69 to 2.07 cm in different locations, which might be related to climate and soil. Gómez (2004) fits acorn weight to a log-normal distribution, with mean varying in two years from 2.25 ± 0.02 g to 2.64 ± 0.03 g, also under a continental Mediterranean climate, however 200 mm more humid in average than Afzal-Rafii *et al.*'s continental site. The reduction of acorn size as a response of the shorter, cooler growing season has been reported elsewhere for other oak species (Aizen and Woodcock, 1992; Díaz-Fernández *et al.*, 2004).

Acorn size and morphology are also likely to be affected by soil properties and stand characteristics. In Álvarez *et al.* (2002) the richest site (foothills) produced heavier acorns during most of the season. Acorn mass in their study ranged from 2.78 to 4.71 g (mean 3.81 g) in the foothills, and from 1.94 to 4.94 g (mean 3.12 g) in the slopes (lower fertility), with acorn weight from holm oaks located in the plains occupying an intermediate position. Additionally, they found heavier acorns in the higher diameter class (DC) trees, with acorn diameter ranging from 2.98 to 4.90 g in $DC > 55$ cm, and from 1.85 to 3.71 g in $DC < 35$ cm. However on slopes both the higher tree densities and lower diameter distribution coincided, masking the real influence of each isolated factor. Additionally this study lacks replication. In results from North Eastern Spain, acorn weight in coppice stands (mean around 0.8 g/acorn) is significantly lower compared to isolated holm oaks (mean around 2.9 g/acorn) in a single year (Milla *et al.*, 2002). The studies discussed are only preliminary; the effect of site should be addressed more thoroughly.

Pruning is an additional source of variability in these woodlands. The influence of pruning on acorn size and morphology seems to be minimal (Porras, 1998; Car-

bonero *et al.*, 2002, 2003; Álvarez *et al.*, 2004), but results are currently inconclusive. The difference between acorn size in pruned and un-pruned trees oscillates between years and stands. Most studies reflect a slight increase in acorn size the first year after pruning, with no effect the following years. In Porras (1998), in some locations the pruned stands produced significant but slightly larger acorns (around 3% in acorn diameter) than the un-pruned stands, whereas other locations show the opposite behaviour. Other authors found similar results. The first year after pruning, Carbonero *et al.* (2003) found an increase in acorn size (trees one year after pruning vs. more than one year after pruning: acorn length 3.8 cm vs. 3.2-3.4 cm; acorn diameter 1.6 vs. 1.4 cm) coinciding with a significant decrease in acorn production in the pruned stands. The second year after pruning acorn production was not different between pruned and un-pruned stands; the difference in acorn length decreases (3.4 vs. 3.2 cm) and acorn width is similar in both stands (around 1.6 cm). A similar effect has been observed in some scrub oaks in North America, where the species with the smallest acorns has the highest number of acorns per bearing ramet (Abrahamson and Layne, 2003). No authors analyzed acorn size and morphology before pruning, so it is not possible to determine whether the differences reported might be partly explained by site and stand characteristics.

Other factors also influence acorn size and morphology. In fruit trees, it is accepted that high light level availability is required for good production. Light availability affects bud quality, by increasing carbohydrate reserves, which positively affects fruit developmental potential (Nuzzo *et al.*, 1999). Following this hypothesis, a difference in acorn size would be expected between crown positions and maybe aspects. Carbonero *et al.* (2002, 2003) did not detect size differences in crown position, although their results were not conclusive and acorns from the south part of the crown were bigger. Throughout the fruiting period, acorn size and acorn dry pulp weight remain constant according to most authors (Carbonero *et al.*, 2003; García *et al.*, 2003; López-Carrasco *et al.*, 2004). Conversely, Álvarez *et al.* (2002) suggest an increase in acorn weight during the fruiting season (total average = 3.32 g), which could be related to insect-infested acorns falling in the first weeks (Soria *et al.*, 2005), or to late ripening. Insects, and to a lesser extent freezing temperatures, have a considerable effect on fallen acorn size. Insect infestation, particularly by *Curculio*

elephas Gyll., and *Cydia* sp., frequently provokes the early falling of acorns from growth stops as a result of the infestation (Villagrán *et al.*, 2002; Bonal, 2005). It is not clear whether infestation affects size, however it reduces acorn weight. While Soria *et al.* (1996) report a reduction of 4% in mean acorn width (mean 1.54 ± 0.03 cm) and acorn length remains constant (mean 3.42 ± 0.36 cm) in infested acorns, Soria *et al.* (2005) reported bigger infested acorns (2 years: 35.1 ± 0.2 cm $\times$ 13.1 ± 0.1 cm; 32.6 ± 0.2 cm $\times$ 13.2 ± 0.1 cm), both in length and width, than sound acorns (2 years: 34.6 ± 0.1 cm $\times$ 12.4 ± 0.1 cm; 30.4 ± 0.4 cm $\times$ 12.3 ± 0.2 cm). Sound acorns are always heavier than acorns injured by insects, sound acorns averaging 3.73 ± 2.10 g and insect infested acorns averaging 2.99 ± 1.79 g (Soria *et al.*, 1996). López-Carrasco *et al.* (2004) report a mean pulp dry weight of 2.55 g for sound acorns with a significant reduction in insect-infested acorns (1.59 g) and frozen acorns (2.25 g). No significant differences have been observed in the effect of the different insect species studied (Soria *et al.*, 1996; López-Carrasco *et al.*, 2004). The average germination rate is reduced in infested acorns, from an average of 2.6% non germinated sound acorns to a mean of 25% non germinated infested acorns (Soria *et al.*, 1996). Pigs selectively consume the biggest acorn sizes according to García *et al.* (2003). These authors report a decrease in acorn size collected on the ground during the fruiting period in plots with pigs (from average 2.75 g to average 1.78 g), whereas they did not detect any differences in plots where pigs were excluded. This reduction in acorn size from pigs feeding coincides with the hypothesis that predator select bigger acorns (Gómez, 2004), and bigger acorns are more likely to be sound. However,

we can not exclude from García *et al.*'s study that pigs could be selecting non-infested acorns.

The percentage of kernel/shell ranges from 65 to 79% in the bibliography (Olea *et al.*, 2004; Espárrago *et al.*, 1993). However they only provide preliminary results, Olea *et al.* (2004) observed that, in two years, the kernel/shell ratio was smaller (67.8 against 75.3%) when mean temperatures were warmer (18.0°C against 16.8°C) and both annual (888.2 mm against 704.4 mm) and fall (484.8 against 165.2) rainfall were higher. The relation kernel/shell has much interest for pigs and wildlife feeding, as pigs just consume the kernel, rejecting shells. Finally, it should be noticed that not all authors specify whether they report dry matter results when studying either acorn size or production. We will not discuss this point, but it should be kept in mind that it is a potential source of error as the acorn water content varies.

Acorn chemical composition

The nutrient content of holm oak acorns has been widely studied, mostly as a result of the high economic importance of Iberian pigs. Acorn nutrient content values are quite variable in the literature (Table 1), especially when samples are small (Nieto *et al.*, 2002). Acorns have high fat (4-12%) and starch content (more than 50%), but low protein content (4-6%) (López-Bote, 1998. Table 1). However a high fat content seems to be a characteristic of holm oak, the two morphotypes exhibit differences in some nutritional elements: *Q. ilex* ssp. *ballota* has a higher fat content (7.3-11.3%) than *Q. ilex* ssp. *ilex* (3.4-4.2%) (Afzal-Rafii *et al.*,

Table 1. Holm oak dry pulp acorn chemical composition in dehesas according to several authors. Between brackets standard deviations are shown when the authors provided them. Data from Afzal-Rafii *et al.* (1992) are means from location «El Pardo», the one included in the dehesa range (Northern limit)

Source	Afzal-Rafii <i>et al.</i> (1992)	Nieto <i>et al.</i> (2002)	Cañellas <i>et al.</i> (2003)	López-Carrasco <i>et al.</i> (2004)	Olea <i>et al.</i> (2004)
Pulp (%)	—	80.8 (0.4)	—	—	71.5 (4.5)
Dry matter (%)	—	59.3 (0.05)	—	63.5	—
Crude Protein (%)	4.9 (0.1)	4.8 (0.1)	5.0	5.6 (0.7)	4.7
Lipid (%)	6.3 (1.4)	12.1 (0.2)	7.0	11.3 (2.8)	—
Crude fiber (%)	—	—	3.2	0.9 (0.7)	—
Ash (%)	2.2 (0.2)	1.6 (0.1)	2.0	1.8 (0.2)	—
P (%)	0.15 (0.01)	—	0.08	—	0.22
Ca (%)	0.02 (0.01)	—	0.24	—	0.09
Mg (%)	0.04 (0.02)	—	0.07	—	—

1992). Acorns have a high content of oleic acid (> 63% of total fatty acids), and palmitic and linoleic acids concentrations (12-20%). Acorns have a considerable amount of antioxidants such as α -(19-31 mg/kg dry matter) and γ -tocopherol (113-66 mg/kg DM). The latter is in higher concentration in acorns than in grass (63-66 mg/kg DM). These compounds are very important in the pig diet because they affect the Iberian dry ham aging process (Cantos *et al.*, 2003).

The acorn chemical composition can vary depending on several factors. Acorn protein, fiber, fat, C, and P content collected in the ground does not change along the fruiting period (López-Carrasco *et al.*, 2004; Olea *et al.*, 2004). The effect of freezing does not seem to affect the acorn chemical composition. There is a decrease in the acorn fat content in insect infested acorns, while the protein content is not affected by insect infestation. Insects can consume a high proportion of the annual yield (farther discussed below), which would have a negative impact on Iberian pigs as fat is essential in their diet (López-Carrasco *et al.*, 2004). However the effect of acorn position within the canopy which might significantly affect its chemical composition has not been studied. It has been observed in fruit trees that the carbohydrate content of fruits varies according to the position within the crown, responding to light availability (Nuzzo *et al.*, 1999).

The relationship of site and acorn chemical composition has not been studied in much detail. Afzal-Rafii *et al.* (1992) did not find any apparent relationship between soil and acorn chemistry. However, they studied an overall relationship for each location, lacking more specific relationships within site or plot. They detected significant differences in acorn chemical composition between populations within the same morphotype (*ballota* and *ilex*) and among trees within a population, what could be related either or both to individual genetic variability or site. These effects should be addressed in future studies.

Acorn production

Oak acorn production has not been yet well described in any of the species thriving on dehesas. The time series studied are far too short to provide any solid explanation to acorn production. The great variability reported by all authors (Martín *et al.*, 1998; Álvarez *et al.*, 2002; Carbonero *et al.*, 2002; Torres *et al.*, 2004), both between individuals and within individuals

between years, is common to most other woody species (Herrera *et al.*, 1998; Koenig and Knops, 2000). From the previously discussed, we might expect the holm oak (as a wind pollinated species) to exhibit a high individual variability, with high population seed production synchrony, that would result in masting (Kelly and Sork, 2002; Koenig *et al.*, 2003). We might also expect an effect of weather and soil nutrient availability, with more pronounced masting in less productive habitats (Kelly and Sork, 2002). However, these trends are still to be demonstrated in *Quercus ilex*.

Synchrony within a species and section (1-year vs. 2-year) and asynchrony among species is common in American mixed oak formations (Sork *et al.*, 1993; Abrahamson and Layne, 2003; Liebhold *et al.*, 2004). This same pattern has been observed in Southern Spain in mixed oak forests and dehesas in seven year data sets. Stands of the same *Quercus* species at close locations exhibited synchrony, whereas asynchrony was found when distinct species (*Q. ilex*, *Q. suber*, *Q. canariensis*) were compared (Martín *et al.*, 1998). This phenomenon would smooth the variability of acorn production within mixed stands as each year there is more probability that at least one species is producing (Sork *et al.*, 1993; Martín *et al.*, 1998; Abrahamson and Layne, 2003).

Production per crown unit area is the most objective way to measure productivity and to compare between different stands and locations. Holm oak acorn annual mean values in the literature in dehesas are between 80 and 300 g/m² (Table 2). These figures are higher than productions in forests of NW Spain and SW France reported by Siscart *et al.* (1999). These results (which varied between 15 and 60 g/m²) were estimated from litter traps. The authors do not specify, but it is likely that the litter traps were not displaced to estimate production per crown unit area, which would explain at least part of the great difference encountered with Table 2. Coefficients of variation over 100% are fairly common in the bibliography. Within the same location it is possible to find individuals with null annual production and trees producing up to 155 kg/tree (Carbonero *et al.*, 2003) or even 300 kg/tree (López-Carrasco, unpublished data). In the northwest foothills of the Sistema Central Range (northernmost range of dehesas, Salamanca province) Álvarez *et al.* (2002) report ranges from 0.1 to 87.9 kg/tree, corresponding to an average of 19.0 kg/tree. These results are similar to some studies, with a tree annual production in 6 years of 20.7 kg/tree (Medina-Blanco, 1963), from the Central West Range of dehesas (Extremadura), but higher than

Table 2. Acorn production of Western Iberian holm oak woodlands according to different authors. Data are averages of several years and different stands. Pruning is not taken into account. Means of annual standard deviations (SD) as naïve estimates of dispersion are between brackets; they were weighted by number of years estimating production when possible. *This work is just an example of a list of studies carried out by the same authors along the last years. See text for farther discussion about these studies

References	Procedence	Estimation method	Sample size (trees)	Sampling design	N.º of years	Stand density (trees/ha)	Mean production		
							(g/crown m ²)	(kg/tree)	(kg/ha)
Porras (1998)	Huelva	Total acorn collection	140	3 sites × 2 pruning treatments/site	From 8 to 2	—	—	22.9 (10.8)	—
Álvarez <i>et al.</i> (2002)	Salamanca	Total acorn collection	—	3 × 2,500 m ² plots	1	25	—	19.0	475
Gómez <i>et al.</i> (1980)	Salamanca	Traps	3	—	2	—	86.6	—	—
Escudero <i>et al.</i> (1985)	Salamanca	Traps	—	—	3	—	120.1	—	—
Martín <i>et al.</i> (1998)	Sevilla	Traps	—	2 × 1 ha plots	7	23	285.8 (194.5)	25.3 (6.5)	—
						60	115.8 (83.2)	7.1 (1.9)	
						—	—	—	
Carbonero <i>et al.</i> (2003)	Córdoba	Traps	50	10 trees × 5 pruning years	2	60-78	—	26.7 (5.1)	—
Torrent (1963)	Spain	—	2,000	—	10	—	—	—	587
Medina (1963)	Extremadura	—	—	—	6	—	—	20.8	—
Olea <i>et al.</i> (2004)	Badajoz	Traps	20	4 trees × 5 sites	2	20-45	—	—	674.3 (120.4)
García <i>et al.</i> (2005)	Extremadura	Visual surveys	2,851	—	1	40	—	12.86 (6.54)	—

other results in that same area (15 kg/tree; Espárrago *et al.*, 1963). In [dehesas] within 8 provinces of Spain, in 10 years, Torrent (1963) visually estimated a mean annual average of 586.4 ± 131.6 kg/ha (this study will be farther discussed later) and similar average values around 550 kg/ha have been reported by other authors (San Miguel, 1994; Martín *et al.*, 1998. Table 2).

The influence of pruning

Assessing the effect of pruning on acorn production is complex; long data series would be required both prior to, and after pruning. Additionally, several types of pruning with different pruning frequencies are applied. Thus, any comparison between two studies will include possible uncontrolled biases coming from the pruning history of the stands. As we previously stated, it is not clear whether pruning enhances acorn production as has traditionally been believed (San Miguel, 1994). It is difficult to obtain any conclusions from the existing studies, as most of them lack many necessary details,

e.g. production previous to pruning and stand characterization (especially tree diameter distribution and crown sizes). They also do not study a whole pruning period (between 10 and 20 years) (Gómez and Pérez, 1996; Álvarez *et al.*, 2004). The great variability of acorn production and short datasets mask the influence of pruning. Most authors find a decrease of production the first year after pruning (Porras, 1998; Carbonero *et al.*, 2003; Álvarez *et al.*, 2004; Cañellas *et al.*, in press) that might be related to tree reallocation of resources to rebuild the aboveground biomass. Acorn production results two years after pruning are not conclusive, although it seems that the reduction in acorn production also affects the second year (Porras, 1998). Porras (1998) studied 180 trees divided in three sites in a period of 2 and 6-7 years after pruning. The difference between pruned and un-pruned plots fluctuates between years and stands, although it looks that after the third year the production in the pruned stands increases. In his results the differences were not significant in all years. The differences were clear only when the year production was above the average. In the two

sites studied up to seven years, the pruned plots averaged 24.1 ± 15.0 kg/tree-year vs. 18.9 ± 10.8 the unpruned plots. The authors did not characterize the stands, and since they report acorn production per tree, it is not possible to discern whether these differences are related to other factors such as crown size. Additionally, in one of these sites the production was estimated one year before pruning, and acorn production was higher in the plot to be pruned. In the third stand, studied only up to two years after pruning, the pruned trees averaged significantly lower production than the unpruned stands (27.8 ± 1.0 kg/tree-year in the pruned; 36.8 ± 8.1 in the unpruned). Also in dehesas, but in *Q. suber*, Cañellas *et al.* (in press) report a decrease in production per crown unit area up to 5 years after moderate pruning. Acorn production ranged from 0.74 dry matter g/crown-m² to 332.85 g/crown-m² (average 155.6 g/crown-m² in the unpruned trees vs. 81.2 g/crown-m² in the pruned) and was significantly higher in unpruned trees just the years production was above the average. *Q. suber* flowering and fruiting phenology is more complex than in holm oak (Díaz-Fernández *et al.*, 2004), and this could influence any comparisons between the species.

It is not straightforward to make comparisons between pruning methods, because pruning descriptions are always qualitative. There seems to be an increase when pruning is light (i.e. removing dead and «unproductive» branches) although not significant in Torres *et al.* (2004), which might be a result of the small sample size used. These authors studied acorn production up to three years after different pruning methods. They found the lowest annual mean values in the untreated plot (177.2 ± 293.4 g/crown m²), and the heavy pruning plot (average 180.6 ± 168.2 g/crown m²), whereas the most productive were two light pruning plots (269.9 ± 245.5 g/crown m²). However, these light pruning are seldom applied in practice. Álvarez *et al.* (2004) did not find any difference between two heavy pruning types in holm oaks pruned up to 18 years ago. They do not compare with any plot where pruning was not applied. The effect of pruning on acorn production should be studied in more detail in the future with multi-year data series in stands where acorn production could be estimated several years before pruning (depending on the sample, differences between trees and stands could already exist previous to pruning). We acknowledge the difficulty of performing these experiments, because most stands as they are found today were pruned some time. Pruning provides jobs in rural depressed areas and pruned branches are used as fodder

for livestock. However, as the existence of a positive effect of pruning on acorn production has not been observed, and charcoal and firewood are depreciated nowadays, pruning might be unprofitable from an economic point of view.

Tree and stand production

The effect of tree density and stand characteristics

However it has not been studied in depth in «dehesas», acorn production is likely to vary with stand density. Martín *et al.* (1998) estimated a holm oak annual production per crown unit area ranging from 0.5 to 577.2 g dry matter /m² (Table 2). Holm oaks in stands of low density (23 trees/ha) averaged higher productions per tree (285.8 g/m²; 25.3 kg/tree). However, these trees produced less per ha (291.5 kg/ha) than stands with higher densities (59.5 trees/ha), which exhibited the opposite trend (115.8 g/m²; 7.1 kg/tree; 296.0 kg/ha). The same negative relationship was observed for cork oak stands in the same area: stands with lower density (20 trees/ha) averaged higher production per tree but lower per ha (171.7 g/m²; 16.9 kg/tree; 250.9 kg/ha) than stands with higher densities from 94 to 253 trees/ha (Martín *et al.*, 1998). The highest mean production per ha (58.5 g/m²; 399.2 kg/ha) was obtained in the stand with 160 trees/ha, which was located in the more humid and warmer area (Martín *et al.*, 1998). Hence, lower densities seem to account for higher tree production, as a result of increased light availability (Abrahamson and Layne, 2003), and decreased intraspecific competition. Vázquez *et al.* (1996) studied three stands with densities 19, 56 and 133 trees/ha. The stand of middle density averaged the highest acorn production per ha (21.3 ± 32.8 kg/tree), and the stand with lower density the highest acorn production per tree (31.5 ± 3.4 kg/tree). The third plot produced 2.3 ± 0.6 kg/tree. In North America (Healy *et al.*, 1999; Perry and Thill, 2003) and Central America (Guariguata and Sáenz, 2002) several oak species average higher productions after thinning, and also it has been shown in two North American *Quercus* species how acorn production decreases with increasing stand basal area (Perry and Thill, 2004). In calcareous holm oak ecosystems in North East Spain, Bellot *et al.* (1992) found mean annual productions of 14.3 ± 11.0 g/m² for dense coppice stands. In holm oak closed forests with 1,400 trees/ha, mean dbh (diameter at 1.3 m) 18.0 cm and

average height 10–12 m in France, the average reported is 512.3 ± 365.5 kg/ha-year (Lossaint and Rapp, 1978). It is noticeable that the high density forest yields are comparable to the achieved in dehesas with lower density. This indicates the success achieved by this traditional system, in which acorn production seems to be kept at its highest compatible with additional uses such as livestock and cropping.

The stand diameter distribution is also likely to affect acorn production (Abrahamson and Layne, 2003). Tree diameter is directly related to crown volume and age. In other oak species it has been shown that the larger the dbh, the higher the total tree production (Greenberg, 2000), although this is partly related to the greater crown volume. The effect of dbh, crown size, and tree age into production per crown m^2 is not clear. Some authors have stated that trees with dbh under 25 cm are significantly less productive per crown unit area (Greenberg, 2000; Carbonero *et al.*, 2002). This fact could be related to the first age of flowering of trees and maturing of individuals, and should be studied in more detail.

The effect of site

The relationship of acorn production to site characteristics (climate and soil) has been widely reported in other species, meaning that different sites within a taxon can show great differences in acorn production (Kelly and Sork, 2002; Abrahamson and Layne, 2003). In «dehesas» there is also a lack of studies analyzing the effect of site. Álvarez *et al.* (2002) observed differences in acorn production between stands thriving on slopes, plains and foothills. Foothill soils have higher clay and loam content (Puerto and Rico, 1992), and slopes tend to be poorer and more acidic. These plots are very different in density and diameter distribution, which would account for part of the variability. Similarly, Carbonero *et al.* (2004) reported higher production in heavy soils (loamy-clay soils or clay), than in sandy or sandy-loam soils. Siscart *et al.* (1999), in holm oak forests of NW Spain, report an increase in acorn number and biomass in nitrogen fertilized plots. In the same study, irrigation was found to be closely related to fertilization and affected positively annual acorn production just in years with high summer drought. In America, Abrahamson and Layne (2003) also explained part of the variability they found by the occurrence of sandy soils. According to the previously discussed,

masting would be likely to be more pronounced in the highest elevations, as lower productivity increases the time required to accumulate resources between high seed crops (Kelly and Sork, 2002; Abrahamson and Layne, 2003). In «dehesas», two authors have studied the relationship between fertility and acorn production (Martín *et al.*, 1998; Carbonero *et al.*, 2004) but neither of them found any significant effect. This can probably be explained by their sampling methodology, e.g., Martín *et al.*, 1998 collected samples just from shallow horizons (10 cm).

The effect of weather on acorn production should also be considered, since its influence has been widely reported for other oak species (e.g., Sork *et al.*, 1993; Koenig and Knops, 2000; Abrahamson and Layne, 2003). We have detected a lack of studies analyzing the relationship between weather and production in Mediterranean oaks. In Southern Spain, Martín *et al.* (1998) did not find any correlation between annual rainfall and acorn production. The lowest annual production in the oak stands he studied coincided with the end of a five-four years dry period, with the minimum annual yield in a site coinciding with the driest and the highest mean temperature year. Maybe the trees are able to reallocate nutrients and resources in bad years, after which they are depleted and need good years to recover and start storing again (Sork *et al.*, 1993; Isagi *et al.*, 1997). This behavior would be particularly important in regions with Mediterranean climates. Intense drought can lead to losing of female flowers (Díaz-Fernández *et al.*, 2004), which would negatively influence both acorn production, and most probably also acorn size for the surviving flowers.

Other factors affecting acorn production

The position within the canopy affects holm oak phenology and flowering (Innes, 1994; Nuzzo *et al.*, 1997; La Mantia *et al.*, 2003). Peter and Harrington (2002) found higher acorn production in the top half of the canopy in *Quercus alba* stands. Carbonero *et al.* (2002) report a non-significant increase in both the outer part and the south facing part of the crown (29.6 g/m² in the South-outer; 26.4 g/m² in the North-outer; 21.2 g/m² in the South-interior; 20.4 g/m² in the North-interior) in holm oak trees in dehesas. These differences could be a result of higher light availability (Guariguata and Sáenz, 2002) as acorns in the more shaded branches receive less light for maturation, in a similar way

to subcanopy tree species (Kato and Hiura, 1999). Additionally, branches located in different orientations receive different quantities of sap (Infante *et al.*, 2001). Therefore, it might be thought that South and South West aspects would be more productive. This effect has been observed in some North American oaks sites, whereas other stands did not show differences among orientations (Liebhold *et al.*, 2004).

Pre-dispersal and post-dispersal acorn losses owing to biotic and abiotic factors can deplete year acorn production (Pulido *et al.*, 2005). Insect attack provokes an early fall of acorns (Soria *et al.*, 2005). The negative effect of insects can be very intense some years, with reductions in acorn yield up to 50% (Espárrago *et al.*, 1993; Soria *et al.*, 1996, Cañellas *et al.*, submitted), however these figures are likely to increase some years attending to results in other European oak species (Crawley and Long, 1992). Some authors report an adjustment of some insect life-cycles to two or more year patterns, suggesting that insects would synchronize their diapause to fruit masting (Maeto and Ozaki, 2003). The exudation of sap in acorns, a phenomenon called «drippy nut disease» («melazo») possibly caused transmission of pathogens by insects, is another common source of acorn losses. In García *et al.* (2005) 27.5 ± 10.7 % of trees produced acorns with «melazo», which generally fall earlier from the tree. Finally, Díaz *et al.* (2003) report a negative relationship between the number of acorns/shoot and average leaf asymmetry, a parameter directly related to herbivory. Other activities such as grazing and ploughing could influence acorn production. And tree selection through centuries in dehesas could have led to a genetic differentiation compared to the original forest. However, to our knowledge, no studies have been conducted analyzing the effect of genetic selection and genetic tree variability on acorn production in this ecosystem.

The importance of the estimation method and systematization of acorn results

Finally we would like to make emphasis on the importance of presenting clear complete results, estimated with appropriate, scientifically tested methods. In this study we could not make any inferences and extract clear conclusions from the existing literature, as the results reported in the bibliography are heterogeneous and generally incomplete. The most conspicuous acorn production studies discussed and their sampling main

characteristics can be seen in Table 2. We include Medina (1963) and Torrent (1963) studies as the first works found in the literature studying acorn production in this ecosystem. In these studies acorn production was estimated through traditional visual surveys and in this way some of the results reported are likely to include a big error and, hence, be just mere approximations. We include in Table 2 the study García *et al.* (2005), as an exponent of a list of studies from the same research group, some of them also included in this review (Vázquez *et al.*, 1998, 1999). These authors use visual surveys with a series of ratio corrections. They report production for different tree densities that they calculate proportionally to production estimated for a generic medium density, 40 trees/ha (they multiply by 0.60 and 0.90 to extrapolate to 20 trees/ha and 60-70 trees/ha). Along with Medina (1963) and Torrent (1963), these studies are useful as management plans or informal estimations, but they seem insufficient to be used as a reference to explain acorn production and give an explanation to the factors affecting production, in particular the effect of tree density. Visual surveys have been shown to be useful in some situations, but must be used carefully. It is very important to validate scientifically any method proposed, and in this sense we encourage authors to publish their results in scientific journals that will guarantee the echo of their results.

Other studies showed in Table 2 use more reliable estimation methods, mostly traps. However the method been reliable in most of them, the sampling design is usually insufficient. This makes their results preliminary, and in this way interesting, but it is impossible to compare them to obtain robust conclusions. For all these reasons and as it has been already discussed, most questions posed in this study about the influence of tree density, site, etc., are still to be answered. Acknowledging the difficulty of designing and performing complete and balanced experiments, we believe that more effort should be made to develop longer data series with more balanced, bigger samples.

Conclusions

The most important conclusion from this study should be the need of more detailed, longer studies to explain acorn production patterns in this Iberian ecosystem. The heterogeneity of methodologies and incomplete way in which results are reported in most studies makes impossible the extraction of clear con-

clusions of any of the factors analyzed. Acorn production is economically and ecologically important enough to deserve more attention than it has received so far. Specific, well designed studies are urgently needed if we want to approach the understanding of this phenomenon and all details involved.

Holm oak acorn production is an extremely variable phenomenon. A variety of factors including weather, soil, genetics, tree density, tree age, and pruning affect production in a way that is not yet well understood. The two first years after pruning, acorn production decreases, but it is not clear whether there is any trend thereafter. It is important to characterize stands in terms of density and diameter distributions; a lack of these stand variables may have masked the results of many studies. Tree production seems to be negatively related with density. However, the optimum density depending on the different objectives pursued in the ecosystem should be studied: the studies analyzing the relationship between density and production are preliminary. With current densities, mean productions around 20-25 kg/tree are common in the literature, corresponding to an average around 250-600 kg/ha. Acorn size and morphology also varies between years, sites, individuals and densities. Mean acorn width values are around 1.5 cm and 3 cm, while acorn weight ranges from 1.2 g to 6.5 g. More research with longer data series is needed, as the comprehension of all factors discussed has shown to be still deficient. Of special interest is to determine the characteristics of great producer individuals. If different sites produced differently, it would be important for management to arrange a fruit index similar to the site-index in traditional forestry.

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