Spatiotemporal variation in acorn production and damage in a Spanish holm oak (*Quercus ilex*) dehesa

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Abstract

**Aim of study:** There is a lack of knowledge about spatio-temporal patterns of acorn production in dehesas, especially regarding the influence of different agents causing acorn damage. We examined the spatial and temporal variability on acorn production and damage in four stands within a dehesa farm in 1997, 1998 and 1999.

**Area of study:** The study was carried out in a 1800 ha dehesa farm of Cáceres province, western Spain.

**Material and methods:** Acorns were sampled by means of seed traps placed in the canopy of six holm oak trees per stand. Acorns collected were counted and assessed for damage by *Curculio* weevils, *Cydia* moths and the bacterial pathogen *Brenneria quercina*.

**Main results:** Mean acorn production for the whole study period was 44.60 acorns m⁻², which did not vary significantly either among stands or among years. The variability among individual trees was very high (0-300 acorns m⁻²). The rate of infestation by *Curculio* was 7.64 ± 10.72%, by *Cydia* was 1.76 ± 3.33%, whereas 10.29 ± 16.12% of acorns were infested by *Brenneria*. We found no significant spatial differences, but the rates of acorn loss by insects varied among years. These rates were independent of annual acorn production and there was no correlation among damages by different pests, except between *Curculio* and *Cydia* in two crop years.

**Research highlights:** It can be concluded that acorn crops are synchronized at the within-farm level and that the temporal variation in acorn damages can be independent of crop size.

**Key words:** acorn production; *Brenneria; Curculio; Cydia; dehesa; Quercus ilex; spatio-temporal variation.*

Introduction

Dehesas are ecosystems consisting of low-density oak woodland with an understory composed of grasslands, shrublands, and croplands where livestock is extensively raised (San Miguel, 1994). The dehesa is the most widespread agroforestry land-use system in Europe (Moreno and Pulido, 2009) where it covers 3.1 million hectares in Spain and Portugal. Holm-oak (*Quercus ilex*) is the dominant tree species in this ecosystem, and it can be considered as an "ecosystem engineer" influencing many ecological processes (Jones et al., 1994).

Holm oaks are small- to medium-sized trees that grow in poor substrates. Because of low stand density and tree pruning, dehesa trees greatly exceed forest trees in height and canopy area (Montero et al., 2002). Holm oak is monoecious. Wind pollination occurs in late April to early May, though fertilization and fruit set is delayed until late June. Fruit development proceeds until final size is reached in late September. Fruits may fall before maturity because of abortion, abnormal fruit development with sap exudation ("drippy" fruits) caused by *Brenneria quercina*, or insect infestation by borer larvae of moths (*Cydia spp.: Tortricidae*) and weevils (*Curculio elephas* Gyll.: Curculionidae).

In dehesas and other temperate oak-dominated systems acorns play a basic role in livestock and wild-life feeding. As a result of acorn predation by these animals, most forests and woodlands are threatened by lack of sexual regeneration (Gea-Izquierdo et al., 2006). Despite this, our knowledge of acorn production patterns in space and time is still very limited, especially regarding the influence of different agents causing acorn damage in dehesas (Alejano et al., 2012). Previous reports showed that production is highly variable, both between and within years and individuals (Álvarez et al., 2002; Torres et al., 2004; García-Mozo et al., 2007).
but there is a lack of studies analyzing spatial effects
at local or regional scales.

The relationship between acorn production and site
characteristics (climate and soil) has been widely re-
ported in other oak species, showing that different sites
can show great differences in acorn production at large
geographical scales (Kelly and Sork, 2002; Abraham-
son and Layne, 2003; Fearer et al., 2008; Peter and
Harrington, 2009). At regional scales Koenig et al.
(1999) in North America reported synchrony of acorn
production between individual trees. At lower scale,
Díaz et al. (2009) in dehesas noted that holm-oak pro-
duction was apparently not synchronized between po-
pulations separated by only a few tens of kilometers.

It has been reported that a strong inter-annual varia-
bility in seed production (e.g. masting) may reduce
seed predation by insects by the combined effect of
satiating and starving seed consumers (Crawley and
Long, 1995; Espelta et al., 2008). Thus, annual fluctua-
tion in acorn production can alter the dynamics of in-
sect predators (Fukumoto and Kajimura, 2011). How-
ever, there is very little information on the variation
of acorn damage between stands and years, which ham-
pers decision making in relation to pest management.

In this paper we compared acorn production and da-
mage in four stands within a dehesa farm in three con-
secutive years. Thus, we hypothesized that (i) as a con-
sequence of edaphoclimatic and management variation,
acorn production differs among stands within a farm;
(ii) for a mast fruiting species, the spatial variation
depends on the mast cycle, that is, the spatial pattern
is not consistent among years; (iii) there are spatio-
temporal differences in acorn infestation levels by
different pre-dispersal agents; and (iv) the interaction
of seeds and their predators is density-dependent as
found in previous studies, probably fitting to an ex-
ponential function.

Material and methods

Study site

The study was carried out in a 1800 ha dehesa farm
of Cáceres province, western Spain (San Blas, 39° 42’
9” N, 5° 55’ 18” W). The site is located on a flat area
at about 350 m asl. Holm-oaks grow scattered over a
grassland matrix at an average density of 36 trees ha–1
on oligotrophic, acid soils (pH 5.2). The climate is Me-
diterranean with dry and hot summers and cool and
rainy winters. Annual precipitation was 1180, 590 and
605 mm, and mean annual temperature was 18.9°C,
18.8°C and 18.6°C for 1997, 1998, and 1999, respectively.
Based on our own records for the period 1965-2000, 1998
and 1999 were dry years whereas 1997 was the wettest
year. All years sampled showed mean temperatures
above the average value of the whole series (17.2°C).

Experimental design and collected data

Within the studied dehesa farm we established one
study plot divided in four paddocks for management
purposes. We randomly selected and marked a point
inside each paddock and selected the six nearest adult
trees (acorn-bearing individuals of at least 10 cm in
stem diameter) from each site (24 trees in total) in
October 1997. Tree density in these paddocks ranged
from 22 to 66 trees ha–1. The distance between plots
ranged from 709 m to 3,200 m. Average size of trees
was 7.48 ± 1.50 m (mean ± 1 SD) in height whereas the
mean canopy radius was 3.97 ± 0.72, 4.73 ± 0.76,
3.56 ± 0.64 and 4.08 ± 0.57 m in the stands A, B, C and
D, respectively. The pre-dispersal predation and
cumulative production of mature acorns was monitored
for these trees in October-January 1997-1998, 1998-
acorn seasons).

Four seed traps were installed in each of the 24 trees.
They consisted of 0.12 m² plastic buckets 25 cm in
depth that were attached with wire to the lower canopy
of trees in random positions. Traps operated from Oc-
tober 1997 to January 2000. Every January acorns
accumulated into the traps in the previous autumn were
collected and assigned in situ to one of the following
categories: (1) sound acorns; (2) acorns infested by
Cydia moths; (3) acorns infested by Curculio weevils,
and (4) drippy fruits infested by Brenneria.

Tree fecundity or acorn production was estimated
as the mean number of acorns m–2. The incidence of
each source of pre-dispersal damage was calculated as
the number of acorns in a given category divided by
the total number of acorns fallen in the traps.

Statistical analysis

The effects of year and stand on acorn production,
sound acorns and damage were analyzed by means of
General Linear Models (GLM) on a repeated-measured
ANOVA-type design with year as within-subject factor and trees as replicates (the same individual trees were sampled each year). Means were compared using Fisher’s protected least significant difference (LSD) test at \( p \leq 0.05 \). Rates of pre-dispersal damage were arcsine-transformed. Relationships between different types of damages and their relationship with acorn crop size were evaluated by means of Pearson correlation analyses. We used STATISTICA 7.0 for all statistical analyses. Throughout the paper means are reported ± 1 SD.

**Results**

Mean acorn production was 36.81 ± 34.14, 51.64 ± 52.18, 47.63 ± 69.43 acorns m\(^{-2}\) in 1997, 1998 and 1999, respectively. Production ranged from 0 to 300 acorns m\(^{-2}\). Fig. 1 shows acorn production for each individual tree as an average over the three study years in each stand. Stand A showed the highest average acorn production and stand D the lowest. Coefficients of variation (CV) were 1.26, 0.93, 1.00 and 0.95 for stands A, B, C and D, respectively. Despite this, acorn production was homogeneous among different sites and years (Table 1).

The proportion of sound acorns for the whole study period was 67.00%, which differed among years (Table 1). The mean percentage of acorns infested by insect and pathogens was 19.69% for all individuals and study years pooled. On average, Curculio infested 7.64% of acorns, Cydia 1.76% and Brenneria 10.29%. These rates did not vary significantly among different stands. However, we found a significant annual variation for the Cydia damage, which was consistent across stands in view of the non-significant Year × Stand interaction (Table 1). The rate of predation by Cydia only differed among the years 1997 and 1998, with values of 0.79% and 3.08%, respectively (Fig. 2). Other significant annual variation was found for the damage by Curculio, which varied across the stands since a significant effect was observed when we analyzed year and stand jointly (Table 1). Predation of acorns by Curculio ranged from 4.5% in the year 1999 to 13.8% in 1998 (Fig. 2). The rate of Brenneria damage did not change either among stands or years.

Regarding the relationship between these different pre-dispersal agents, Curculio was related linearly and positively to Cydia in 1997 and 1999 (Table 2). The remaining pests were independent from each other in every year (Pearson’s correlation, \( p > 0.05 \); all stands pooled; Table 2).

The percentage of acorns infested by the different agents did not fit any of the hypothesized linear (Pearson’s correlation, 0.110 < \( p < 0.927 \)) or non-linear functions (exponential function, 0.018 < \( R^2 < 0.315 \); 0.927 < \( p < 0.110 \)). Therefore, damage was independent of tree acorn production (Fig. 3). Only the rate of acorns infested by Cydia in 1999 showed a significant exponential relationship (\( R^2 = 0.476, p = 0.009 \)) (Fig. 3).

**Discussion**

**Crop size of acorns in dehesas**

Mean values of holm oak acorn production obtained in this study by means of seed traps (44.60 acorns m\(^{-2}\))
Acorn production and damage in holm oak

Table 1. Results from GLM analyses on a repeated-measured ANOVA-type design testing for the effects of year, stand and year×stand on acorn production, sound acorn and acorn damages

<table>
<thead>
<tr>
<th></th>
<th>Year</th>
<th>Stand</th>
<th>Year×Stand</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F_{2,68}</td>
<td>p</td>
<td>F_{3,67}</td>
</tr>
<tr>
<td>Production</td>
<td>0.725</td>
<td>0.491</td>
<td>1.044</td>
</tr>
<tr>
<td>% Sound acorns</td>
<td>7.931</td>
<td>0.001</td>
<td>0.064</td>
</tr>
<tr>
<td>% Infested Cydia</td>
<td>4.930</td>
<td>0.012</td>
<td>1.064</td>
</tr>
<tr>
<td>% Infested Curculio</td>
<td>11.493</td>
<td>0.000</td>
<td>0.986</td>
</tr>
<tr>
<td>% Infested Brenneria</td>
<td>2.162</td>
<td>0.129</td>
<td>1.639</td>
</tr>
</tbody>
</table>

Figure 2. Annual variations of acorn production (acorn m⁻²) and insect and pathogen damage in the three study years. Vertical bars show standard deviation. Different letters indicate significant differences between years (LSD test at p ≤ 0.05).

Table 2. Pearson correlation coefficients for the relationships between different kind of insect and pathogen damage in the three study years

<table>
<thead>
<tr>
<th></th>
<th>1997</th>
<th>1998</th>
<th>1999</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>r</td>
<td>p</td>
<td>r</td>
</tr>
<tr>
<td>Cydia (%) - Curculio (%)</td>
<td>0.476</td>
<td>0.022</td>
<td>0.299</td>
</tr>
<tr>
<td>Cydia (%) - Brenneria (%)</td>
<td>0.339</td>
<td>0.114</td>
<td>-0.032</td>
</tr>
<tr>
<td>Curculio (%) - Brenneria (%)</td>
<td>0.284</td>
<td>0.188</td>
<td>0.157</td>
</tr>
</tbody>
</table>

were lower than those found in dehesas using the same method by Rivest et al. (2011) and it was very similar to those found by Díaz et al. (2009) and Alejano et al. (2011) (Table 3). Since most studies in dehesas have reported acorn production values as acorn mass per area unit, to compare our results with those obtained elsewhere we transformed our data by multiplying acorn number per the mean fresh acorn mass in the study area (6.5 g ± 1.39 SD; Pulido, 1999). As shown in Table 3, acorn production, expressed as mass per unit area (289.9 g m⁻²) was within the range of values reported by other authors in dehesas (119.7-357.5 g m⁻²), and above values given for forest and dehesas with pollarded trees (Table 3). All these studies (included ours) report a huge variability between trees.

Variation in acorn production

Our data showed no significant differences between stands within the dehesa farm studied, contradicting the hypothesis 1. At first glance this could be due to the huge variability in acorn production shown by individual trees within stands. Thus, individual acorn production ranged from 0 to 300 in stand A, 0 to 142 in stand B, 0 to 162 in stand C, and 0 to 60 acorns m⁻² in stand D. Under these conditions, significant differences were unlikely to be found even with greater sample sizes within stands. This extreme individual variability has been already reported in previous studies (e.g., Torres et al., 2004; García-Mozo et al., 2007). Therefore, it can be concluded that differences among paddocks, either due to edaphoclimatic conditions or management, did not translate into noticeable differences in acorn crops.

At a spatial scale similar to that used in our study, Martín-Vicente et al. (1998) found differences of acorn production between mixed stands of Q. ilex, Q. suber and Q. canariensis, but in this case acorn production
could be compensated between different species. In North American oak species Peter and Harrington (2009) observed differences at the level of local populations in Q. garryana, whereas Liebhold et al. (2004) reported synchrony between trees over distances less than 10 km in different Quercus species. In other oak species a trend of acorn production to synchronize over large geographic areas has been established (Sork et al., 1993; Healy et al., 1999; Koening and Knops, 2000). Due to the limited number of years in our annual series we did not evaluate any synchrony coefficient. Nevertheless, the lack of spatial variability detected, and its consistency over time, would imply spatial synchrony at least at the farm level. This result implies that spatial differences would be detected at a larger (regional or geographical) scale. This is in agreement with most long-term studies on spatial synchrony. Thus, Peter and Harrington (2009) reported synchrony up to a radius of 33 km. In holm-oak, studies from local to geographical scales are clearly needed to clarify the extent of spatial synchrony and its implication for tree and livestock management.

**Variation in acorn damage**

Though many studies have estimated the pre-dispersal losses of acorns caused by Curculio weevils, Cydia moths and Brenneria disease (Soria et al., 1999; Vázquez et al., 1999; Pulido and Díaz., 2005), few studies have addressed to what extent these losses fit any spatial pattern. Concerning acorn losses, it must be noted that studies based on acorns collected on the ground tend to overestimate acorn damage, as sound acorns are selected by post-dispersal predators (Bonal and Muñoz, 2007). In our study, based on acorns collected from the canopy, the mean attack rate by both insects was 9.40%, that is well below figures reported in comparable studies in holm-oak in dehesas: 18% (Pulido and Díaz, 2005), 58% (Bonal et al., 2007), and 20% in Pulido et al. (2010). On the other hand, Brenneria infested 10.29% of acorns, a figure lower than the 16.30% found by Pulido and Díaz (2005) and 25.60% reported by Vázquez et al. (1999). As previous studies have found (Bonal et al., 2007; Díaz et al., 2009), our analysis show extreme individual variation in the impact of all these damages, which could be related to individual variation in the defensive mechanisms elicited by holm oaks facing damage (Díaz and Pulido, 1995; Díaz et al., 2004).

The levels of infestation did not vary between different stands, a result contradicting previous studies and the hypothesis 3. Thus, Jiménez et al. (2008), analyzing the spatial distribution of Curculio populations in a dehesa of southern Spain, concluded that the spatial distribution was heterogeneous in space but stable over time. Leiva and Fernández-Alés (2005) in a nearby area found differences among stands in dehesas and shrublands. In forests from northern China significant spatial and temporal heterogeneity of acorn damage by insects in Q. liaotungensis was established in relation to topography (Yu et al., 2003). Therefore, spatial hete-
rrogeneity seems to be the rule in acorn-insect interactions, a point that deserves further research in dehesa systems. In our case, as there is a positive effect in the stand and year interaction in Curculio damage, it could be possible that in some stand the Curculio damage varies along the time.

Our results showed that acorn infestation by each insect species varied among years. Many authors have explained temporal variation in relation with predator satiation in peak years of acorn production, while predators would starve in low year of the masting interval (Kelly, 1994; Crawley and Long, 1995; Kelly and Sork, 2002; Espelta et al., 2009). We found significant temporal variation in the attack rate of insects acorn predators despite non-significant variation in acorn production. It can be hypothesized that climatic conditions might underlie the differences in infestation found between years, pest population fluctuating due to temperature (Manel and Debouzie, 1997) and precipitation (Debouzie et al., 2002; Soula and Menu, 2003). These environmental factors could also explain the lack of relationship between the rate of infestation and the annual acorn crop size per tree found in this study (see also Pulido and Diaz, 2005, for Q. iley and Fukumuto and Kajimura, 2011, for Q. variabilis).

Concerning the relationship between different agents infesting acorns, only Cydia and Curculio were related to each other in the years with lower acorn production. Both species are very selective when ovipositing (Soria et al., 1999), in such a way that trees with better acorns could be attacked more severely by both insects. However, other authors did not found any relationship between them (Pulido, 1999; Soria et al., 1999); the effect of interference between these species can be weaker in years with high acorn production (Pulido, 1999). On the other hand, Curculio appears to be a vector of Brenneria (Pérez-Laorga et al., 2005) but we did not detect any relation. The general lack of interactions between acorn pests could be explained also by the low levels of infestation found in this study.

To end up, the results obtained in this study highlight several points related to holm oak management in dehesas. First, huge individual variation between trees does not necessarily translate into significant differences between stands or paddocks within a farm. Second, estimation of the rates of acorn damage should rely on acorns still attached to the canopy, as acorns collection in the ground tend to overestimate attack rates. Finally, since damages between Curculio and Cydia seem to be related, joint measures could be designed to reduce their impact.

**Acknowledgments**

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**Table 3. Acorn production of holm-oak collected in traps according to different authors. Data are averages of several years and sites. DM and FM are dry mass and fresh mass, respectively**

<table>
<thead>
<tr>
<th>Reference</th>
<th>Habitat</th>
<th>Acorn production</th>
<th>No./tree^1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Current study</td>
<td>Dehesa</td>
<td>44.60 g/m² (DM)</td>
<td>289.90</td>
</tr>
<tr>
<td>Gómez et al. (1980)</td>
<td>Dehesa</td>
<td>86.60 g/m² (DM)</td>
<td>145.03*</td>
</tr>
<tr>
<td>Martin-Vicente et al. (1998)</td>
<td>Dehesa</td>
<td>200.80 g/m² (DM)</td>
<td>338.62*</td>
</tr>
<tr>
<td>Torres et al. (2004)</td>
<td>Dehesa</td>
<td>177.20 g/m² (DM)</td>
<td>298.82*</td>
</tr>
<tr>
<td>Pulido (1999)</td>
<td>Dehesa</td>
<td>5,715.15 g/m² (FM)</td>
<td></td>
</tr>
<tr>
<td>Bonal et al. (2007)</td>
<td>Dehesa</td>
<td>8,831</td>
<td></td>
</tr>
<tr>
<td>Cañellas et al. (2007)</td>
<td>Dehesa</td>
<td>145.28 g/m² (FM)</td>
<td>245*</td>
</tr>
<tr>
<td></td>
<td>Dehesa¹</td>
<td>73.18 g/m² (FM)</td>
<td>123.41*</td>
</tr>
<tr>
<td>Díaz et al. (2009)</td>
<td>Forest</td>
<td>10</td>
<td>65</td>
</tr>
<tr>
<td></td>
<td>Dehesa</td>
<td>55</td>
<td>357.5</td>
</tr>
<tr>
<td>Carevic et al. (2010)</td>
<td>Dehesa</td>
<td>339.70</td>
<td></td>
</tr>
<tr>
<td>Pérez-Ramos et al. (2010)</td>
<td>Forest</td>
<td>0.3-180.6 g/m² (FM)</td>
<td>0.51-304.55*</td>
</tr>
<tr>
<td>Alejano et al. (2011)</td>
<td>Dehesa¹</td>
<td>43.98 g/m² (FM)</td>
<td>238.83</td>
</tr>
<tr>
<td>Rivest et al. (2011)</td>
<td>Dehesa</td>
<td>50-73</td>
<td>71-119</td>
</tr>
<tr>
<td></td>
<td></td>
<td>119.73-200.67*</td>
<td></td>
</tr>
</tbody>
</table>

^1 Pollarded trees. * Dry mass transformed in fresh mass according to dry matter percentage reported by Nieto et al. (2002).
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