Acorn predation and seedling production in a low-density population of cork oak (*Quercus suber* L.)

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Abstract

Prospects for cork oak recruitment were examined in a scrub-dominated area with low tree density in southern Spain by sowing acorns experimentally in a variety of sites. Seeds placed on the ground surface were invariably eaten within a few months by a variety of vertebrate herbivores (cattle, red deer, fallow deer, wild boar and rabbits). Predation reached 100% whether acorns were placed beneath trees or more than 100 m away from trees. Seeds placed under dense heath scrub were also rapidly removed, although their final fates could not be ascertained. Single acorns buried under open or dense scrub experienced the lowest predation (52% and 0%, respectively) and had relatively high emergence rates (38% and 60%, respectively). Heavy shoot browsing occurred in both scrub types, and out of the 49 buried acorns which produced a shoot, only two seedlings were alive 1 year after germination. None survived 2 years after sowing.

Keywords: Herbivory; Predation; *Quercus suber*; Seedling production

1. Introduction

Plant species with large seeds, including oaks, beeches, dipterocarps and bamboos, show synchronized production of large fruit crops, which is termed mast seeding. In these species dispersal often results because predation on the large number of seeds is limited by the number of potential consumers (i.e. there is predator satiation: Janzen, 1971, 1976; Silvertown, 1980). Vertebrates which cache seeds such as birds (Vander Wall and Balda, 1977; Bossema, 1979) and mammals (Stapanian and Smith, 1978; Vander Wall, 1993) are often effective dispersal agents of these species, since recruitment originates from unrecovered seeds.

Mast-seeding trees in the genus *Quercus* are major constituents of the sclerophyllous forests that once dominated vast areas of the Mediterranean region. After millennia of human disturbance, both the range and the structure of these once dense forests have been extensively modified (Pignatti, 1978). Clearing has often resulted in open, savanna-like woodlands and sparse populations of isolated trees surrounded by scrub (Pons and Quezel, 1985). The extent to which such structural changes may have altered natural patterns of recruitment of forest species is not known.

The present study investigated some consequences of low tree density on the dispersal and regeneration of *Quercus suber* L., an evergreen, mast-seeding Mediterranean oak. Because individual cork oak trees are long-lived, a short-term study cannot realistically depict significant demographic trends. The aim here is simply to document the
short-term consequences of low tree density on seed predation and recruitment rates.

2. Study area and methods

The Donana Biological Reserve (Donana National Park, southern Spain) is a coastal area of about 6700 ha near the Gulf of Cadiz (37° 1' N, 6° 33’ W). The climate is typically Mediterranean. Rainfall occurs predominantly from October through May, and averages 537 mm year⁻¹. January is the coldest month and July is the hottest month (mean temperatures 9.8°C and 24.6°C, respectively).

A large area of the Reserve is covered by scrub growing on old, stabilized sand dunes. The rest of the Reserve floods during winter and completely lacks woody plant cover (see Rivas-Martinez et al., 1980, for a description of the vegetation). *Quercus suber* trees are distributed either in the marsh-scrub ecotone or are scattered over the stabilized dunes, usually near ephemeral ponds (Allier et al., 1974). A detailed demographic analysis of this species is lacking, but it seems that old individuals predominate throughout the Reserve. Preliminary estimations indicate that *Q. suber* density ranges from 0.1 trees ha⁻¹ in the non-flooding area to 3 trees ha⁻¹ in the marsh-scrub border (unpublished data). The study zone epitomizes the historical and regional trend towards trees becoming rare and scrub spreading throughout the area.

An isolated (nearest conspecific > 500 m) group of four adult *Q. suber* trees growing at the transition from heath to xerophytic scrub was selected for study in October 1991. One of these trees (labelled 339 in the Reserve’s catalogue) was consistently used as a seed source because its acorns were abundant (the year’s crop was estimated at 10⁴ acorns) and similar in size (mean fresh mass 4.3 ± 0.3 g, cup not included, n = 10) to those of other cork oak populations in southern Spain (personal observation).

Sound acorns with no external signs of invertebrate infestation were collected and sown experimentally in an area covering about 4 ha around the study trees. Seed locations were selected to assess the relative suitability of each vegetation type (open xerophytic scrub dominated by *Halimium halimi-
Table 1
The fate of *Quercus suber* acorns following experimental sowing into a variety of microsites in an area in southern Spain

<table>
<thead>
<tr>
<th>Sowing position</th>
<th>Number of acorns</th>
<th>Eaten (^{a})</th>
<th>Taken away</th>
<th>Failed to germinate</th>
<th>Produced a shoot alive in autumn</th>
</tr>
</thead>
<tbody>
<tr>
<td>Placed on the ground surface</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Under tree canopy</td>
<td>170</td>
<td>170</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Open scrub, &gt; 100 m from mature trees</td>
<td>124</td>
<td>120</td>
<td>0</td>
<td>4 (^{b})</td>
<td>0</td>
</tr>
<tr>
<td>Closed scrub, &gt; 100 m from mature trees</td>
<td>121</td>
<td>0</td>
<td>121 (^{c})</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Buried at 8 cm near another surface acorn</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open scrub</td>
<td>60</td>
<td>60</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Closed scrub</td>
<td>60</td>
<td>0</td>
<td>59 (^{c})</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Singly</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open scrub</td>
<td>31</td>
<td>16</td>
<td>0</td>
<td>3</td>
<td>12</td>
</tr>
<tr>
<td>Closed scrub</td>
<td>60</td>
<td>0</td>
<td>0</td>
<td>24 (^{d})</td>
<td>36</td>
</tr>
</tbody>
</table>

\(^{a}\) See text for the identity of animals.
\(^{b}\) Desiccated.
\(^{c}\) Presumably by rodents.
\(^{d}\) Rotten.

neither large mammals nor birds penetrate this dense vegetation (personal observation).

3. Results

All acorns that were placed on the ground surface below the trees were consumed by large vertebrates before they could germinate (Table 1). In 1 week, animals removed over 90% of these acorns (Fig. 1), and in fact 40% of the 170 acorns disappeared within 5 h of placement. From dawn to dusk, ungulates (up to two red deer, one wild boar, and one cow at a time) were observed foraging around the tree, so that the ground was devoid of acorns in spite of the constant ‘rain’ of seeds. The only birds observed foraging on acorns were woodpigeons. Dispersers such as jays were never seen.

Surface-sown acorns placed more than 100 m from trees in open xerophytic scrub were invariably consumed by ungulates (Table 1), primarily wild boars. A few acorns remained undetected for 2 months (Fig. 1), but eventually they became desiccated and failed to germinate. Buried acorns were more likely to be consumed when planted close to a surface acorn (Fig. 2a). After finding the seed on the ground, boars searched and rooted around, which resulted in the discovery of the buried acorn. Only one seed escaped predation in this sample and one seedling was produced. Most acorns were removed during the first half of November (Fig. 2a), but a few remained undetected until February.

Acorns placed on the soil surface below dense heath scrub disappeared rapidly. This was also the case for buried acorns near surface acorns (Table 1). No sign of large mammal activity was found in these cases, and rodents were assumed to have taken the seeds away.
Acorns buried alone under open xerophytic scrub were preyed on less by vertebrates (52%) than those placed on top of the soil (100%; Table 1). Acorns buried alone under dense heath scrub, on the other hand, experienced zero vertebrate predation. Final emergence of buried acorns placed under low-cover and high-cover scrub was 38% and 60%, respectively ($X^2 = 3.72, p = 0.05$).

Shoots generally began to appear by the end of February (Fig. 2). In the open xerophytic scrub, shoots were soon browsed and very often the remains of the cotyledons were excavated and eaten by rabbits. As a result, a distinct drop in the number of acorns and seedlings occurred when shoots appeared (Fig. 2b). In contrast, browsing of seedlings under heath was delayed and none were excavated. However, by the end of May 37 out of a total of 49 seedlings (i.e. 75%) had been browsed at least once, and several were browsed on three separate occasions (Fig. 2c). Shoots of browsed seedlings were half as long as those of unbrowsed ones ($71 \pm 15$ mm, $n = 19$, and $138 \pm 12$ mm, $n = 12$, respectively; $t = 3.24$, $p = 0.003$). Only two unbrowsed seedlings growing in dense heath survived until autumn and resumed growth the next spring. The others dried up during the severe summer drought.

4. Discussion

Because $Q. suber$, and large trees in general, are rare in Donana, isolated oaks have become the favourite resting places for large herbivores. Moreover, because trampling largely eliminates plant cover beneath the oaks, fallen acorns are easily detected and eaten. In fact, red deer take advantage of the noise made when an acorn hits the soil to locate it (personal observation). Thus, the speed with which experimental acorns were removed was not surprising. Nevertheless, even exposed acorns placed well away from the trees were also eventually consumed by animals.

Placing acorns on soil below closed heath scrub was the best deterrent to ungulate predation. However, not a single seed remained in place after a few weeks, for which rodents were presumably responsible. Rodents eat a large proportion of the acorns they collect (Miyaki and Kikuzawa, 1988), although they are also known to perform dispersal (Jensen and Nielsen, 1986), so it is possible that some of the acorns experimentally placed under dense scrub may become established seedlings. Several studies have shown a positive correlation between plant cover and seed removal by rodents (Kikuzawa, 1988; Wada,

![Fig. 2. Removal of $Q. suber$ acorns: (a) planted close to a surface-sown acorn ($n = 120$); (b) buried alone in open scrub ($n = 31$); (c) buried alone in closed scrub ($n = 60$) in southern Spain. Bars represent seedlings with a shoot longer than 5 mm that were either browsed at least once (open) or never damaged by herbivores (closed).](image-url)
1993), but unfortunately trampling regularly eliminates shrubs from beneath tree canopies at the study site. This may also contribute to making rodent dispersal unlikely.

As reported in previous studies (Molinas and Verdaguer, 1993), experimental seedlings sprouted repeatedly either from the root or the stem. However, the need to form new shoots to replace browsed parts surely decreased root growth and, as a consequence, the ability of the seedlings to reach deep, summer-moist soil. Thus, herbivory would have lowered the chances of surviving the first drought for many seedlings.

At the study site, closed shrub canopies are ‘safe’ sites (Harper, 1977) for a number of bird-dispersed shrubs (personal observation), annuals (Herrera, 1991) and, as shown here, oak acorns and seedlings. Enhanced recruitment in such areas results from escape from vertebrate seed predators, decreased shoot herbivory and beneficial ‘nurse’ effects from shrubs (Callaway, 1992). The key question, however, is: what are the prospects that acorns will be buried naturally in such places? Known scatter-hoarders such as jays (Bossema, 1979) are common in the forests of Spain, where they collect and cache Quercus acorns (personal observation). Nevertheless, jays are usually absent from the scrub-dominated areas where this study was carried out (Valverde, 1960, and personal observation). Hoarding by rodents seems to be the only possible way for oaks to regenerate, but even this seems unlikely since ungulates rapidly remove most fallen acorns. Taken together, the evidence presented here suggests that prospects for natural establishment of cork oak seedlings are slim because of the low population density of trees, the lack of effective dispersers, and a superabundance of ungulates. Such conditions definitely have a harmful effect on the regeneration of this once abundant tree species.

References


Introduction
Study area and methods
Results
Discussion
Acknowledgements
References

Table 1: fate of Quercus suber acorns
Figure 1: removal rates of acorns
Fig. 2. Removal of Q. suber acorns