Chapter 7
Acorn Production Patterns

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Frontispiece Chapter 7. Forest–dehesa transition in central Spain (Photograph by M. Díaz)

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Abstract  Acorns—the fruits of oaks—are a key resource for wildlife in temperate forests throughout the Northern Hemisphere. Acorns are also economically important for extensive livestock rearing, and as a staple food have supported indigenous human populations. Consequently, differences in how individual trees and populations of oaks invest in acorn production, both in terms of the size of the acorn crop and of the size of individual acorns, are of interest both ecologically and economically. Acorn production by oaks in both California and Spain tends to be highly variable and spatially synchronous. We summarize studies conducted in the two regions that investigate the factors influencing acorn production. One hypothesis explored is that, as a consequence of management, acorn production tends to be affected by different environmental factors in the two regions; another hypothesis is that acorn production in oaks in Spanish dehesas produce larger and more predictable acorn crops than trees in less managed Spanish forests or in California woodlands. Other factors potentially influencing acorn production are summarized, including biotic factors, trade-offs with growth, trade-offs with acorn size, and pollen limitation. We conclude with a discussion of spatial synchrony and acorn production at the community level. There remain many questions concerning the mating systems of oaks, trade-offs between different oak life-history characters, and the patterns and drivers of spatial synchrony. Environmental conditions in the two regions are similar, but understanding how their subtle differences influence acorn production is likely to yield important insights about the proximate and ultimate factors affecting acorn production and masting behavior.

Keywords  Acorns · Acorn production · Acorn size · Dehesa · Masting · Oak savanna · Spatial synchrony

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7.1 Introduction

Acorns—primarily the fruits of oaks (genus *Quercus*)—are a key resource for wildlife in temperate forests throughout the Northern Hemisphere. Acorns are also economically important for extensive livestock rearing, as well as for a staple food for some indigenous human populations, at least historically. Consequently, differences in how individual trees and populations of oaks invest in acorn production, both in terms of numbers—the size of the acorn crop—and of the size of individual acorns themselves, are of interest both ecologically and economically.

What makes oaks particularly exciting scientifically is the propensity of many, if not all, populations to engage in the phenomenon of “masting” or “masting-fruition”; that is, they produce acorn crops that vary markedly from year to year and do so more or less synchronously over what, in at least some cases, can be tens or hundreds of millions of individuals across large geographic areas. How and why they accomplish this feat, at both the proximate and ultimate levels, are questions of considerable evolutionary interest (Kelly and Sork 2002).

Spain and California are comparable in size (Spain: 505,000 km\(^2\); California: 411,000 km\(^2\)) and both have oak-dominated, foothill landscapes with scattered trees over a grassland matrix (savannas in California and dehesas in Spain) that cover nearly 10% of their land area (Chapter opening photograph and Figs. 7.1, and 7.2). The fact that a Mediterranean climate, with cool wet winters and hot, dry summers (Hobbs et al. 1995) characterizes oak habitats in both regions renders comparisons of oaks and acorn production in the two regions particularly appealing and scientifically valuable (Huntsinger and Bartolome 1992). Making a comparison even more intriguing is the fact that the scattered spatial configuration of oak tree populations is man–made in Spanish dehesas but apparently natural in Californian savannas. Given that the spatial distribution of trees is likely to affect reproductive effort because spacing limits competition (Chap. 6), intercontinental comparisons linked to comparisons between dehesas and nearby oak forests in Spain could help determine management practices and environmental factors that have the capacity to change patterns of acorn production by oak trees, as well as the likely mechanism causing these changes.

In this chapter, we summarize what is known and not known about acorn production—including both acorn crop size and acorn size—in Spain and California. Our ultimate goals are to use similarities and differences between the two regions to help understand the evolution of this poorly understood phenomenon and to improve our understanding of the ecological effects of variability in this important natural resource.
7.2 Acorn Crop Size

There are three major classes of factors potentially affecting acorn crop size that are particularly relevant for a comparison of California and Spain. First are environmental factors, including rainfall and temperature. Second are biotic factors, including birds and mammals that eat or collect acorns and herbivores that live in them prior to acorn fall. Third involves differences in habitat and management such as whether trees are in forests or open habitats and the effects of pruning, soil treatments, and other landscape management practices that are virtually universal in dehesa. After briefly summarizing work on these three sets of factors, we consider the evidence for there being differences in one or more of the components of acorn production between California and Spain. Next we discuss several issues related to acorn production currently being investigated in both regions, including trade-offs between acorn production and acorn size, trade-offs between acorn production and growth, and pollen limitation. We end with a discussion of spatial synchrony and acorn production at the community level, questions currently being investigated in both regions.
7.2.1 Environmental Factors

A summary of some of the environmental factors that have been found to correlate with acorn production in Californian and Spanish oaks (Table 7.1) suggests some intriguing differences. In California, conditions during the spring appear to be particularly important for valley oak (*Q. lobata*) and blue oak (*Q. douglasii*), two deciduous species that mature acorns in a single year, and, when lagged appropriately, for California black oak (*Q. kelloggii*), a deciduous species that requires two years to mature acorns. Rainfall in a prior year is important to two of the evergreen species, coast live oak (*Q. agrifolia*) and canyon live oak (*Q. chrysolepis*), as well as for California black oak. In Spain, three species have been studied in this regard including holm oak (*Q. ilex*), cork oak (*Q. suber*) and downy oak (*Q. humilis*). A reoccurring factor affecting both the size of the acorn crop and, in a few cases, other variables including acorn mass and synchrony, is water stress during the summer and early fall as acorns mature, as indicated by xylem water potential, measures of summer drought, and even canopy foliage (NDVI or the “normalized difference vegetation index”; Camarero et al. 2010). Although some evidence for a similar effect of summer drought on acorn production in Missouri oaks, including red oak (*Q. rubra*) and black oak (*Q. velutina*) has been reported (Sork et al. 1993), summer conditions do not appear to play an important role in acorn crop size of any of the species of California oaks for which there are currently data, a result we confirmed for the same five populations studied by Fig. 7.2 Forest-dehesa transition in the National Park of Cabañeros in Spain, where long-term studies of acorn production in paired holm oak populations in forest and dehesa are being conducted. (Photograph by M. Díaz)
Table 7.1 A summary of the environmental variables correlating with acorn production in California and Spanish oak populations.

<table>
<thead>
<tr>
<th>Environmental variables</th>
<th>Effect</th>
<th>Species</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Spanish oaks</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer water stress (drought)</td>
<td>–</td>
<td><em>Q. ilex</em></td>
<td>Pérez-Ramos et al. (2010)</td>
</tr>
<tr>
<td>Torrential rain in spring</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Min temp, rel. humidity, rainfall (January)</td>
<td>+</td>
<td><em>Q. ilex</em></td>
<td>García-Mozo et al. (2001)</td>
</tr>
<tr>
<td>Rainfall (March)</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Relative humidity (April)</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean temp (June)</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rainfall (September)</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring rainfall</td>
<td>+</td>
<td><em>Q. ilex</em></td>
<td>Alejano et al. (2008)</td>
</tr>
<tr>
<td>Autumn rainfall</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Xylem water potential (mid-summer)</td>
<td>+</td>
<td><em>Q. ilex</em></td>
<td>Carevic et al. (2010)</td>
</tr>
<tr>
<td>Xylem water potential (mid-summer)</td>
<td>+</td>
<td><em>Q. ilex</em></td>
<td>Camarero et al. (2010)</td>
</tr>
<tr>
<td>Maximum canopy foliage</td>
<td>+</td>
<td><em>Q. suber</em></td>
<td>Pons and Pausas (2012)</td>
</tr>
<tr>
<td>Spring temp</td>
<td>+</td>
<td><em>Q. ilex</em></td>
<td></td>
</tr>
<tr>
<td>Summer water stress (drought)</td>
<td>–</td>
<td><em>Q. suber</em></td>
<td>García-Mozo et al. (2001)</td>
</tr>
<tr>
<td>Spring frost</td>
<td>–</td>
<td>(acorn mass)</td>
<td>Alejano et al. (2011)</td>
</tr>
<tr>
<td>Mean temp (September)</td>
<td>–</td>
<td><em>Q. ilex</em> and <em>Q. humilis</em></td>
<td>Espelta et al. (2008)</td>
</tr>
<tr>
<td>Summer water stress (drought)</td>
<td>+ (synchrony)</td>
<td><em>Q. ilex</em> and <em>Q. humilis</em></td>
<td>Espelta et al. (2008)</td>
</tr>
</tbody>
</table>

**California oaks**

<table>
<thead>
<tr>
<th>Environmental variables</th>
<th>Effect</th>
<th>Species</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean temp (April)</td>
<td>+</td>
<td><em>Q. lobata</em></td>
<td>Koenig et al. (1996)</td>
</tr>
<tr>
<td>Mean fall temp (year –1)</td>
<td>–</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean temp (April)</td>
<td>+</td>
<td><em>Q. douglasii</em></td>
<td>Koenig et al. (1996)</td>
</tr>
<tr>
<td>Rainfall (year –1)</td>
<td>+</td>
<td><em>Q. agrifolia</em></td>
<td>Koenig et al. (1996)</td>
</tr>
<tr>
<td>Rainfall (year –2)</td>
<td>+</td>
<td><em>Q. chrysolepis</em></td>
<td>Koenig et al. (1996)</td>
</tr>
<tr>
<td>Mean temp (winter, year –1)</td>
<td>–</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rainfall (year –1)</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rainfall (spring, year –1)</td>
<td>–</td>
<td><em>Q. kelloggii</em></td>
<td>Garrison et al. (2008)</td>
</tr>
<tr>
<td>Mean temp (spring, year –1)</td>
<td>+</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Correlations are with the size of the annual acorn crop except where noted. Data for *Q. suber* is for trees maturing acorns in one year.

Koenig et al. (1996) using the summer drought index of Espelta et al. (2008) and 32 years of data through 2011 (correlation between the drought index and subsequent acorn production ranged from −0.18 to 0.13, all P > 0.3).

At this stage, the cause of this apparent difference remains speculative. However, one possibility is that it is related to climatological differences between the two regions. Although both are unambiguously Mediterranean in that winters are relatively cool and wet while summers are warm and dry, there is a notable difference in terms of the length and relative dryness of the summers, which are apparently shorter in Spain (Jackson 1985), where summer precipitation occurs as
summer storms that are unpredictable from year to year (Fig. 7.3). One way to quantify this difference is to compare the percent of total annual precipitation falling in the four months from June through September, the main months during the summer when acorns are maturing. For the four arbitrary Spanish sites depicted in Fig. 7.3, this value is $11.9 \pm 5.0\%$, whereas in the California sites, only $3.7 \pm 0.8\%$ of rain occurs during this period. This suggests that the summer dry season is longer and drier in California than in Spain. To the extent that this is true, one might predict that summer water stress would be even more important in California than Spain, but this does not appear to be the case for oaks. The more cogent difference, however, may be that there is very little variation in the environmental conditions during the period of acorn maturation in California compared to Spain. For example, from daily weather records going back to 1939 data at Hastings Reservation in central coastal

Fig. 7.3 Representative climate graphs for Mediterranean regions in California (left) and Spain (right). Broken lines and circles are mean monthly precipitation; solid lines are mean monthly temperatures. The summer dry season is more compressed in Spain.
California, where W. Koenig and J. Knops have studied acorn production since 1980, the mean (±SD) precipitation falling between 1 June and 30 September was only 1.2 ± 1.4 cm with 62 of 72 years (86%) having <2 cm of rain during this 4-month period. Given this lack of variability, it is not surprising that summer conditions appear to have little effect on the acorn crop in California. It would be of interest to make additional such comparisons in order to better understand the relationship between environmental variability and the ecological factors affecting acorn crop size in specific populations.

Despite this difference, it is notable that some of the most common environmental factors correlating with acorn production in both California and Spain take place while trees are flowering in the spring or during acorn development (summer drought). This indicates that factors other than resources available to trees at the start of the season are important to acorn production, including pollen limitation, fertilization success, and resources that become available during acorn development itself (Espelta et al. 2008; Pérez-Ramos et al. 2010).

### 7.2.2 Biotic Factors

Although not studied as intensively as abiotic factors, biotic (herbivory-related) factors can have important effects on acorn production. Working with holm oak, Pulido and Díaz (2005) found biotic factors caused 29% of predispersal losses to acorns in forests and 10% in dehesas. In a comparative analysis of holm oak recruitment in grazed, cropped, and encroached dehesas, Pulido et al. (2010) showed that resource-mediated effects overrode the effects of insect predation and pathogens on tree fecundity in all habitats, primarily by causing acorn abortion. These results suggest that in holm oak, production of sound acorns is environmentally rather than biotically determined, in the absence of population peaks of its natural enemies.

In some cases, however, herbivores and pathogens can clearly affect fecundity in oaks. In both California and Spain, elongating shoots bearing male catkins and pistillate flowers are potentially defoliated by insects, mainly moth caterpillars in the families Noctuidae, Tortricidae, and Lymantridae (Fig. 7.4). By feeding upon leaf tissues, caterpillars not only reduce carbon assimilation in the growing shoots, they also interfere in shoot elongation and development of the pistillate flowers in the distal portion of the shoots.

Thus far, few studies have tested for the effects of shoot defoliation on oak fecundity, and those that have been performed report differing results. Insecticide spraying suppressing herbivory increased fecundity in pedunculate or English oak (Q. robur) in England (Crawley 1985) but not in holm oak in Spain (Díaz et al. 2004). The latter study showed that holm oak overcompensated for the tissue lost at the shoot level, thus stressing the importance of carbohydrate stores and the timing of resource allocation for growing acorns to predict the impact of folivores.
A more realistic way to look at the effects of shoot defoliation is to compare acorn crops among control sites and sites where large-scale spraying for pest control has been carried out. A preliminary study comparing 12 paired dehesa sites with and without spraying showed a non-significant 1.2-fold increase in the acorn crop index in treated sites (F. Pulido, unpublished data). Since acorn production partly depends on resources stored in previous years, however, spraying in a given year might still be expected to result in increased acorn production the year following treatment.

After fertilization, growing acorns can be infested by bacterial pathogens (mostly in the genus *Brenneria* [= *Erwinia]*) causing the so-called “drippy nut” disease (Fig. 7.4; Hildebrand and Schroth 1967; Biosca et al. 2003). Bacteria enter acorns through holes or crevices, so that borer insects, especially acorn weevils (*Curculio* spp.), are potential vectors of this poorly known disease. As a result of bacterial activity inside the acorn, a sugar-rich exudation is produced that leads to cessation of acorn growth. In holm oak dehesa local losses of developing acorns due to this disease range from 16 to 24 % in one study (Pulido and Díaz 2005) and from 4 to 16 % in another site (Pulido et al. 2010). In a large-scale survey including 89 sites in 14 counties in southwestern Spain, the mean occurrence of the disease ranged from 0 to 60 % of infested trees (Vázquez et al. 2000). Although it is believed that the prevalence of bacterial infection is triggered by summer storms, further studies are needed to clarify the origin and economic impact of this important disease.

The third cause of predispersal acorn damage in savannas and dehesas is infestation by borer insects. This is a conspicuous phenomenon resulting in potentially important economic losses in Spain due to rejection of infested acorns by livestock (Rodríguez-Estévez et al. 2009). Briefly, acorns can be infested by moth larvae (mostly *Cydia* spp.) that reach the cotyledons after boring by themselves through the acorn cap or, alternatively, they can be occupied by weevil larvae that emerge from eggs previously deposited by the adult female by perforating the pericarp (Bonal et al. 2010; Díaz et al. 2011). Infestation rates of acorns

**Fig. 7.4** Images of the three main biotic agents causing predispersal losses in acorn production. a The leaf rolling tortricid moth *Tortrix viridana* feeding on new shoots of holm oak (photograph by F. Pulido). b Sugar-rich exudation dropping from a holm oak acorn infested by bacterial pathogens (photograph by M. Díaz). c Cross section of a holm oak acorn showing consumption of cotyledons by larvae of *Curculio* weevils (photograph by F. Pulido)
are variable but they are reasonably well predicted by the size of acorn crops, both across individual trees (Bonal et al. 2007) and between years (Díaz et al. 2011). In holm oak dehesas infestation rates remain below 20% in good acorn years, while more than 60% of the acorns can be attacked in poor acorn years (Leiva and Fernández-Alés 2005; Pulido and Díaz 2005; Pulido et al. 2010).

In California, Koenig et al. (2002) estimated that a mean of 39–100% of acorns from individual valley oak were removed by arboreal predators—primarily birds and squirrels—prior to acorn fall, with the proportion removed being inversely correlated to the overall mean acorn crop. Similarly, the proportion of remaining acorns damaged by insects decreased with focal tree productivity in two of three species (valley oak and blue oak, but not coast live oak), with the mean annual proportion of acorns infested with insects varying from 0 to 63%. In neither case were neighborhood effects detected; that is, trees outproducing local conspecifics did not appear to attract a disproportionate number of arboreal seed removers (predators but also potential seed dispersers) or insect predators.

Reviewing studies of the same three Californian oaks, Tyler et al. (2006) found mean infestation rates of canopy-collected acorns ranged from 0 to 31%. Acorns parasitized by weevils tend to occur with higher frequency than moth-infested acorns, especially when there were late summer rains, which favored the emergence of adult weevils from the ground underneath oak trees. The fraction of cotyledon tissue eaten by these larvae before exiting acorns determines the chance for germination and seedling establishment. As a result, the effect of such parasitism on seedling recruitment from large acorns produced in dehesas is less pronounced than the effect on recruitment from small acorns produced in dense stands (Siscart et al. 1999; Leiva and Fernández-Alés 2005).

In California, Dunning et al. (2002) found that the majority of ground-collected acorns had some insect damage in *Quercus agrifolia* and *Q. engelmannii* (Engelmann oak). The level of insect damage was less than 20% of the entire acorn, and the portions of the acorn most likely to be damaged were the cotyledons rather than the embryo, again suggesting that infested acorns should be taken into account when analyzing oak recruitment prospects.

### 7.2.3 Management and Habitat

A third class of factors potentially influencing acorn crop size is management, habitat, and site differences, including whether trees are growing in forests where competition may be considerable or in more open habitats, and whether trees are pruned or otherwise managed. Such factors have been examined in some detail in Spain, where dehesas are intensively managed both for acorn production as a food source for livestock (Parsons 1962) and, in the case of cork oak, for their unique bark (i.e., cork production). Acorn production measured in Spanish sites are highly variable, with productivity ranging from 0.5 to 147.0 kg acorns/tree for holm oak forests and dehesas, and 0.5–135.0 kg/tree for cork forests, scaling up to an
estimated 79.3–469.6 kg acorns/ha for holm and 256.9–448.5 kg/ha for cork oak (Carbonero 2008; Díaz and Pulido 2009). To what extent is such variability due to differences in management, habitat, or sites?

In a study of regeneration of holm oak, Pulido et al. (2010) found that trees in “cropped” habitats—that is, plots that are fenced and used for cereal production—produced more female flowers and larger acorn crops in each of two years compared to trees in grazed and shrub-encroached plots, indicating an important role for management. Habitat and/or sites can also be important, as indicated by studies of the differences in acorn crop size of holm oak in forest and nearby dehesa sites in Cabañeros National Park where acorn production, but not acorn size, were significantly greater in the dehesas (87.0 ± 49.1 vs 34.7 ± 27.9 acorns m$^{-2}$; $P = 0.03$; means for acorn crops between 2003 and 2009; Beamonte 2009). Such differences are most likely due to differences in resources available in the two different habitat types (Díaz et al. 2011).

Carevic et al. (2010) failed to find significant effects of two soil treatments (ploughing; ploughing and sowing of European yellow lupine ($Lupinus luteus$)) on acorn production patterns in holm oak dehesa. Xylem water potential in ploughed soils was higher than in control areas, but the unusually wet summer in both years of the study may have reduced the importance of water for acorn development (Alejano et al. 2008).

Pruning—a widespread procedure conducted mainly to produce firewood and increase browse production that varies from modest thinning of small branches to more drastic opening up of the canopy (Huntsinger et al. 1991)—has also been shown to affect acorn production, although the effect appears to be variable. Cañellas et al. (2007) found no effect of moderate pruning (removing 30% of crown biomass) in a mixed holm and cork oak dehesa when acorn production was poor, but pruning at this level apparently decreased acorn production when it was good.

Studies by Alejano et al. (2008) investigated the effects of pruning on holm oak in more detail, comparing oaks that had been subjected to light, moderate, and heavy traditional pruning along with a non-traditional method of “crown-regeneration pruning” in which the outermost branches of the tree crown were removed, thereby shortening water transport distances and resulting in a more compact crown that was hypothesized to improve water balance. Results over five years failed to indicate any significant overall effect of the traditional pruning method on acorn production. Similar results were obtained by Carbonero (2011) studying the influence of moderate pruning on acorn production in holm oak dehesas in Córdoba, Spain. There was, however, evidence that the non-traditional pruning method tested by Alejano et al. (2008) significantly enhanced acorn production, indicating that although traditional methods of pruning have questionable effects, new methods conducted taking into consideration the architecture of the trees may increase productivity. Parallel work by Alejano et al. (2011) investigating the factors influencing acorn mass in holm oak has found significant effects of location and year but not pruning, tree size, topography, or crowding (interspecific competition).
7.2.4 Components of Acorn Production

Most species of oaks that have been studied thus far, including all those for which there are data in either California or Spain, exhibit both considerable variation in seed production from year to year and a great deal of individual variation within and often between populations. One approach to understanding the causes of this variation is to quantify variability in a way that can be compared across populations.

Herrera (1998) was possibly the first to use a series of metrics to quantify the components of masting behavior in a comparative way, including variables measuring annual and individual variability, between-individual synchrony, and the endogenous cycles of temporal autocorrelation—that is, the degree to which acorn production by individuals and populations is correlated with production in a prior year. In general, oaks conform to the pattern predicted by “normal masting” (Kelly 1994; Koenig and Knops 2002) in which there is significant, but not complete, bimodality in seed production across years and for which there is evidence for resource switching. The latter is important because it demonstrates that reproductive effort is not simply being driven by variation in annual resource abundance (the “resource tracking” hypothesis), but rather is an evolutionary strategy that involves diverting resources from acorn production to other functions in some years and overinvesting in reproduction in others (Sork et al. 1993; Koenig et al. 1994b). Are similar patterns exhibited by Spanish and California oaks, and if not, what is driving the differences?

Although the data available to make such a comparison are limited, we are able to summarize data from 49 populations of eight species of California oaks studied at various sites around the state for up to 32 years (a total of 1,065 individuals) by W. Koenig and J. Knops and 42 populations of three species of Spanish oaks (primarily the ballota subspecies of holm oak (Q. ilex subsp. ballota) but also two populations of cork oak, one of downy oak and one of the ilex subspecies of holm oak (Q. ilex subsp. ilex), studied over 4–12 years (2,112 individual trees). For each study, masting metrics were calculated for each subpopulation and then averaged for all populations of the same species surveyed in the same study. This yielded data for a total of 16 studies, including nine for Spanish oaks (7 for holm oak and 1 each for cork and downy oak), and eight for California oaks (1 each for valley, blue, canyon live, coast live, California black, interior live (Q. wislizeni), Engelmann (Q. engelmannii), and Oregon (Q. garryana) oaks). Methods for quantifying the acorn crop (see Box 1) involved visual surveys in California and for three of the Spanish studies (Koenig et al. 1994a) and crown or branch sampling for the other Spanish studies (Carbonero 2008; Espelta et al. 2008; Díaz et al. 2011). Analyses were conducted using untransformed data and are summarized in Table 7.2.

Five metrics were compared, including mean population coefficient of variation ($CV_p$), which provides an index of the mean annual variability of acorn production in the population, and the mean individual coefficient of variation ($CV_i$), which
Table 7.2  Mean (±SD) population and individual characteristics of acorn production by Californian and Spanish oaks

<table>
<thead>
<tr>
<th>Variable</th>
<th>(1) California</th>
<th>(2) Spain</th>
<th>(2a) Spain (dehesas)</th>
<th>(2b) Spain (forests)</th>
<th>P value (1 vs. 2)</th>
<th>P value (1 vs. 2a)</th>
<th>P value (1 vs. 2b)</th>
<th>P value (2a vs. 2b)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean population CV (CV_p)</td>
<td>96.4 ± 14.2</td>
<td>84.4 ± 58.0</td>
<td>52.4 ± 27.3</td>
<td>124.4 ± 64.3</td>
<td>0.58</td>
<td>0.01</td>
<td>0.25</td>
<td>0.06</td>
</tr>
<tr>
<td>Mean individual CV (CV_i)</td>
<td>158.1 ± 24.2</td>
<td>117.9 ± 59.6</td>
<td>79.4 ± 15.3</td>
<td>165.9 ± 60.3</td>
<td>0.10</td>
<td>0.00</td>
<td>0.75</td>
<td>0.02</td>
</tr>
<tr>
<td>Mean pairwise synchrony (T_p)</td>
<td>0.45 ± 0.09</td>
<td>0.45 ± 0.18</td>
<td>0.36 ± 0.16</td>
<td>0.54 ± 0.19</td>
<td>0.94</td>
<td>0.21</td>
<td>0.31</td>
<td>0.20</td>
</tr>
<tr>
<td>Mean population temporal autocorrelation (1-yr lag) (ACF1_p)</td>
<td>-0.28 ± 0.20</td>
<td>-0.14 ± 0.18</td>
<td>-0.12 ± 0.22</td>
<td>-0.19 ± 0.14</td>
<td>0.20</td>
<td>0.23</td>
<td>0.54</td>
<td>0.73</td>
</tr>
<tr>
<td>Mean individual temporal autocorrelation (1-yr lag) (ACF1_i)</td>
<td>-0.18 ± 0.10</td>
<td>-0.17 ± 0.09</td>
<td>-0.21 ± 0.05</td>
<td>-0.09 ± 0.10</td>
<td>0.87</td>
<td>0.56</td>
<td>0.29</td>
<td>0.10</td>
</tr>
</tbody>
</table>

Number of populations included was nine for Spain (five in dehesas and four in forests) and eight for California, each population representing the averaged results of 1–18 subpopulations of the same species studied in different parts of the region. California data from W. Koenig and J. Knops (unpublished). Spanish dehesa data from R. Alejano (unpublished data), Carbonero et al. (2008) and Díaz et al. (2011); Spanish forest data from Espelta et al. (2008), M. Díaz and F. Pulido (unpublished data) and Díaz et al. (2011). Data from pairwise synchrony was not available for the dehesa study by Carbonero et al. (2008) and temporal autocorrelation data was not available from the Espelta et al. (2008) forest study.
measures the mean individual annual variation and provides an upper limit to $CV_p$. The third measure, mean pairwise synchrony between all individuals in the population ($rp$), is an index of how synchronous acorn production is among the trees sampled in the population. Also calculated when possible are $ACF1_p$ and $ACF1_i$, measures of temporal autocorrelation, or the extent to which acorn production of the population ($ACF1_p$) and of individual trees ($ACF1_i$) correlates with acorn production the prior (or the next) year. These provide an index of the degree to which acorn production is driven by endogenous factors such as stored resources, since they are indicative of the extent to which trees “switch” resources to or away from reproduction from one year to the next (Sork et al. 1993; Koenig et al. 1994b).

Results indicate no significant differences between measures of masting in the two regions as a whole (Table 7.2). However, standard deviations were quite large for the Spanish data due to an apparent difference between values for populations from the dehesas compared to those from a higher-density forest. Dividing the Spanish data into these two groups revealed significantly lower $CV_p$ and $CV_i$ for trees in Spanish dehesas compared to either California or Spanish forests. There were no significant differences, however, in either pairwise synchronies ($rp$) or temporal autocorrelations, although these comparisons were based on smaller sample sizes.

These results, although preliminary, at least suggest that management practices may significantly influence acorn production patterns in Spain. Specifically, oaks in managed dehesas appear to exhibit reduced masting behavior, yielding acorn crops that are more predictable at the stand level and subject to greater external (environmental) influence (Koenig et al. 2003).

More data are clearly needed, however. For example, analyses of four nearby forest and dehesa stands in the National Park of Cabañeros (Díaz et al. 2011) suggests that dehesas exhibit $CV_p$ values at least as large as those from forest stands ($99.3 \pm 27.5\%$ vs. $79.6 \pm 89.7\%$, respectively); trees in the dehesa sites also exhibited higher synchrony than those in the forest sites. Such findings suggest that differences between dehesas and forests may be due less to differences in management and more to areas managed as dehesas being located in higher-quality sites than remnant forest stands (see Sect. 7.2.3).

It has also been suggested that larger and more predictable acorn crops by trees in dehesas are due to an active selection of individual trees, either by retaining only the best trees during dehesa formation or by planting acorns of better-producing trees in open land (Montero et al. 2000). Whether such artificial selection has taken place or not is unknown, although it seems unlikely given what is known about the history of dehesas and the normal practices of land managers (Díaz et al. 1997; Moreno and Pulido 2009).

Regardless of whether or not the acorn production patterns of trees in dehesas are altered by management, endogenous influences are apparently still important, as seen in the strong negative individual temporal autocorrelations ($ACF1_i$ values) found in all populations including those in Spanish dehesas and forests and in
California (Table 7.2). Ongoing studies are designed to clarify the ways management has or has not altered the inherent acorn production patterns of oaks in dehesas.

7.2.5 Trade-Offs with Acorn Size

Although not studied as intensively as acorn crop size, a second key aspect of acorn production is size of the acorns themselves. Three studies are relevant, including two on holm oak in Spain and a third on valley oak in California. The first was particularly detailed, examining the effects of tree size, topographic position, crowding and interspecific competition, climatic factors, pruning, and size of the acorn crop over six years in trees growing in a dehesa (Alejano et al. 2011). As with crop size, there was considerable variation among trees. Drought during September, the key month for acorn growth, was particularly important, whereas no factor related to tree size or position was significant. They also found that the size of the acorn crop correlated negatively with acorn size and concluded that there appeared to be a trade-off between acorn size and number, as expected from life-history theory (Smith and Fretwell 1974; Wilbur 1977).

An eight-year study carried out in forests and dehesas of Cabañeros (Beamonte 2009; Beamonte and Díaz, unpublished data) showed quite different results. As in the above study, there were significant between-habitat differences in crop size but not in seed size, with crops being larger in dehesa than forest stands. However, no correlation was detected between seed size and crop size in the dehesa, while there was a positive, rather than a negative, correlation between these variables in the forest ($r = 0.30$, $P = 0.02$). Apparently forest trees are able to invest simultaneously in large seeds and large seed crops, an unexpected finding given that positive covariations between life-history characters are expected to be found when resources are not limiting (Venable 1992), whereas environmental conditions are relatively poor in forest stands due to competition for light and nutrients (Díaz et al. 2011).

This study also estimated the repeatability over a four-year period of seed and seed crop size, a measure of consistency that provides an upper limit to its heritability (Falconer and Mackay 1996). Repeatability ($R$) of both mean seed size and crop size was significant but moderate, especially for the dehesa (seed size: $R = 0.339 \pm 0.002$; crop size $R = 0.382 \pm 0.002$), but also for forest trees (seed size: $R = 0.227 \pm 0.007$; crop size $R = 0.010 \pm 0.005$), indicating moderate heritability of these traits. The hierarchical partitioning of seed size variation between habitats, among-trees within habitats, among branches within trees, and within branches (seed traps) indicates that majority of variance in seed size occurs within trees—particularly within branches—and among trees within habitats. Variation between habitats was small and not significant. Moderate repeatability of seed size between years and low variance related to environmental (among-habitat) factors suggest that neither seed size nor crop size are controlled by
environmental factors, and that processes affecting variability in seed size operate primarily among plants by promoting variable rather than optimal seed sizes (Herrera 2009).

Lack of consistent selective pressure for optimal seed size undermines the theoretical basis for size-number trade-offs (Smith and Fretwell 1974). This trade-off was the focus of a study by Koenig et al. (2009a), who examined acorn mass in valley oak over a four-year period. They found that trees produced larger acorns when they had larger acorn crops, again failing to confirm a trade-off between seed size and number.

### 7.2.6 Trade-Offs with Growth

A second commonly studied trade-off is that between growth and reproduction. Although the intensity of a growth-reproduction trade-off is again expected to be more apparent in habitats with low nutrient availability or other environmental stresses (Reznick 1985), these costs can be difficult to detect among long-lived organisms such as oaks in poor environments because reproductive failure is likely to be relatively frequent.

Analysis of 70 holm oak trees over a period of nine years in Cabañeros, Spain, revealed no correlation between radial growth and acorn production during the same year (Díaz et al. 2011; Beamonte and Díaz, unpublished data). Growth was negatively correlated with reproduction the prior year and positively correlated with reproduction the following year, while reproduction was negatively correlated with reproduction the following year (a negative lag-1 autocorrelation). These results suggest the existence of stronger trade-offs in life-history characters acting across years rather than within years, as also found in California oaks (Knops et al. 2007).

Much more work needs to be done before we achieve a full understanding of how long-lived organisms partition their resources between the classic trade-offs of seed size and number, growth and reproduction, and male and female effort. Ongoing long-term studies of oaks in both California and Spain are making considerable headway on these evolutionarily important issues, yielding results that continue to challenge traditional life-history theory.

### 7.2.7 Pollen Limitation

All oaks are wind-pollinated, but determining how this key feature of their reproductive biology affects patterns of acorn production has proved difficult. One of the main problems has been to determine how far pollen travels. It has sometimes been assumed that pollen in such species was abundant and capable of traveling long distances, thus resulting in extensive gene flow (Koenig and Ashley 2003; Davis et al. 2004; Friedman and Barrett 2009), but a growing body of
empirical and theoretical work has indicated that pollen limitation may play a key role in masting (Kelly et al. 2001; Satake and Iwasa 2002). Recent studies employing modern molecular methods capable of determining paternity of acorns have begun to address this issue, which is important due to the potential for pollen abundance to be limiting acorn production both within and among years.

In Spain, Garcia-Mozo et al. (2007) addressed this issue by measuring pollen emissions and environmental correlates of acorn production. They found rates of pollen emission were the most important factor determining mature acorn yields, indicating that pollen limitation is a key factor influencing acorn production in this species. Although pollen emissions have yet to be quantified in California, studies on blue and valley oaks have indicated that pollen dispersal may be far more restricted than previously thought in a way that could have an important influence on acorn production (Knapp et al. 2001; Sork et al. 2002). The latter study, based on results of molecular analyses of \( Q. \) lobata acorns in combination with a statistical model of paternity and genetic structure, is particularly notable as it found that the effective number of pollen donors per tree was strikingly small (\( N_{ep} = 3.68 \)) and the average pollen dispersal distance was extremely short (64.8 m). Based on these results, these authors concluded that ongoing demographic attrition could reduce neighborhood size in this species to the extent that there could be a risk of reproductive failure and genetic isolation.

An alternative approach, taken by Abraham et al. (2011) on a different population of valley oak in California, is to directly determine paternity of acorns. Based on their analyses, \( N_{ep} \) was determined to be 219 and only 30% of acorns were apparently fertilized by pollen coming from trees within 200 m, indicating significantly farther gene flow than estimated by the Sork et al. (2002) study. It would clearly be of interest to obtain comparable data from dehesas where trees are regularly spaced and intensively managed.

Regardless of how this controversy plays out, it would appear that pollen limitation plays a key role in acorn production. For example, recent work by Koenig et al. (2012) examining the relationship between phenology and acorn production in valley oak has found evidence that trees flowering in the middle of the season, when the majority of other trees are flowering and producing pollen, produce more acorns than trees flowering early or late in the season. The potential for differences in phenology playing a role in driving annual differences in the acorn crop has yet to be investigated, however.

### 7.2.8 Spatial Synchrony

Masting is a population-level phenomenon: a single tree may produce a variable acorn crop, but masting occurs by virtue of the fact that trees throughout the population do so more or less synchronously. Only recently, however, have researchers begun to investigate exactly how large that population is through the study of what is known as spatial synchrony (Liebhold et al. 2004).
Spatial synchrony is currently being investigated in California oaks by means of a statewide survey conducted since 1994 by W. Koenig and J. Knops. Preliminary results indicate relatively high spatial synchrony in at least some cases extending throughout the state. As an example, results for blue oak measured at 10 sites (Fig. 7.5) demonstrate (1) a decline in synchrony with distance, a pattern expected under most circumstances, and (2) significant spatial synchrony between sites across the entire geographic range of the species. These results indicate that acorn production in blue oak, perhaps the most abundant oak in California dominant across an area of over 50,000 km$^2$, is highly synchronous, providing wildlife with vast quantities of food in a mast year and leaving large areas with few acorns in a poor year. Comparable results have been found for holm oak by R. Alejano (unpublished) based on data acquired over six years at 18 sites up to nearly 500 km distant in Spain.

What drives such geographically widespread synchrony? One possibility is the “Moran effect,” the hypothesis that environmental factors drive spatial synchrony (Ranta et al. 1997; Koenig 2002). In the case of oaks, ongoing analyses suggest that spatial synchrony in the variables correlating with acorn production within populations—in the case of blue oak, mean April temperature (Table 7.2)—may drive spatial synchrony among populations as well (Koenig and Knops, unpublished data).

The primary alternative to the Moran effect is the hypothesis that trees are synchronized by their mutual dependence on pollen produced by surrounding trees for fertilizing their flowers, a phenomenon known as “pollen coupling” (Satake...
and Iwasa 2000). Thus far, the evidence for pollen coupling as a driver of spatial synchrony in oaks is mostly indirect, but theoretical considerations have shown that even if pollen does not usually travel large distances, pollen coupling is capable of synchronizing reproduction over relatively large areas (Satake and Iwasa 2002). Resolving this issue will require not only more data on acorn production gathered over large geographic areas—the acquisition of which may in the future be facilitated by remote sensing (Yao et al. 2008)—but also by a greater understanding of the pattern and process of pollen dispersal itself.

Evidence thus far suggests that variability in flowering effort in oaks is relatively small compared to the high annual variation in the acorn crop (Pérez-Ramos et al. 2010). To the extent this is true, this further emphasizes the importance of pollen flow and successful fertilization—factors likely to be influenced by environmental factors during flowering and seed development—in determining the size of the acorn crop.

### 7.2.9 Acorn Production at the Community Level

Although the above analyses suggest the possibility of key differences in patterns of acorn production within populations, many communities of predators—particularly of vertebrates—tend to be generalists eager to depredate acorns of any species. Consequently, for some questions the relevant variable is overall acorn production by all species of oaks in the community rather than production by any individual species.

We currently know little about patterns of overall community acorn production either in California or Spain. In California, different species of oaks generally do not produce acorns synchronously, and thus annual variability in acorn abundance decreases with oak species diversity, a phenomenon that facilitates persistence by at least two acorn-dependent species, the acorn woodpecker (Melanerpes formicivorus) and western scrub-jay (Aphelocoma californica) (Koenig and Haydock 1999; Koenig et al. 2009b). Whether similar dependences exist among Spanish species and oak diversity has not been explored, although acorn-eating species such as the Eurasian jay (Garrulus glandarius) and European magpie (Pica pica) would be likely candidates.

There are, however, reasons to suspect that there might be intriguing differences between the two regions. One of the major factors facilitating asynchrony in acorn production by different species of oaks is the length of time needed for acorns to mature. In species in the white oak subgenus *Quercus* (“1-year” species), flowers produced in the spring are generally fertilized and mature into acorns the following fall, 5–7 months later. In contrast, species in the intermediate and black oak subgenera *Protobalanus* and *Erythrobalanus* generally, although not always, require an additional year to mature acorns (“2-year” species); that is, flowers produced in the spring of year $x$ do not mature and produce acorns until the fall of year $x + 1$. As we have already seen, acorn production by many populations is
influenced by environmental conditions during the period that flowers are produced and/or fertilized. As a result, acorn production between 1-year species of oaks is often at least somewhat synchronous, where there tends to be little or no synchrony between 1-year and 2-year species. For example, based on the five species Koenig and Knops have studied in central coastal California since 1980, the mean (±SD) population synchrony between the four combinations of species that require the same number of years to mature acorns is 0.57 ± 0.22, whereas mean synchrony for the six combinations of species that require a different number of years to mature acorns is only −0.23 ± 0.11, a significant difference (Wilcoxon rank sum test, \( W = 0.24, P = 0.01 \)). Similarly, Espelta et al. (2008) reported high synchrony in acorn production between holm and downy oaks (both 1-year species) in Northeastern Spain.

This is potentially significant because California oaks are fairly evenly divided between 1-year and 2-year species, whereas Spanish oaks are not. Of the seven widespread species of California tree oaks (blue, Oregon white, valley, canyon live, coast live, California black, and interior live oaks), four are 1-year and three are 2-year species. In addition, there are at least 10 shrub species, of which seven are 1-year and three are 2-year species. In contrast, of the four widespread Mediterranean species of Spanish tree oaks (Pyrenean (\( Q. pyrenaica \)), Portuguese (\( Q. faginea \)), holm, and cork oaks), three are 1–year species while one, cork, is primarily a 1-year species but sometimes matures acorns in two years, with the frequency of the two types varying geographically (Díaz-Fernández et al. 2004). In addition, there is but a single shrub oak, the Kermes oak (\( Q. coccifera \)), which is the only consistent 2-year species in the region. This greater diversity in both oak species and time for acorns to mature is likely to reduce variability in annual acorn production at the community level in California compared to Spain, with considerable potential consequences on wildlife populations that have yet to be investigated.

### 7.3 Conclusions

There is clearly much more to be learned from comparisons of acorn production in California and Spain. The intensive management of oaks in dehesas provides an outstanding opportunity to learn more about the role of endogenous compared to abiotic factors such as temperature and rainfall in influencing acorn production at both the individual and population level. There also remain many questions concerning the mating systems of oaks, trade-offs between different oak life-history characters, and the patterns and drivers of spatial synchrony. Environmental conditions in the two regions are similar, but understanding how their subtle differences influence acorn production is likely to yield important insights about the proximate and ultimate factors affecting acorn production and masting behavior.
Box 1. Methods for Estimating Acorn Production

Despite decades of attention from wildlife managers and forest researchers, there is still no consensus as to the best way to quantify acorn production. As a result, researchers use many different techniques, not all of which yield data that are readily comparable. Here we provide a brief review of these methods, dividing them into “direct” and “indirect” methods.

**Direct Methods**

Direct methods involve sampling in the crown or harvesting from the ground. They are more accurate for calculating real (or absolute) acorn production than indirect methods, although they suffer from the disadvantage of potentially ignoring acorns removed by birds or other wildlife prior to maturing. These methods include the following.

1. **Knocking down the acorns and collecting them under the crown**—This traditional method is also used for harvesting olives and some other fruits. Its primary disadvantages are that it is labor intensive, time consuming, and, in the case of large trees or of dense tree stands where individual canopies grow entangled, logistically difficult. It also potentially underestimates the crop by missing immature acorns that are not yet ready to fall. This is generally not a viable option if assessing many trees is desired, which is often the case due to large within-population variation and among population differences.

2. **Containers or traps method**—This method consists of placing containers or traps under the crown of the trees where acorns are removed on a regular basis (Fig. 7.B1). Many different kinds of containers have been used, varying in shape and construction. Containers may be on or attached to the ground, or hung from branches with ropes or wire to avoid consumption of acorns by large herbivores (wild ungulates or livestock). Typically, several containers are placed either regularly at different orientations or under the crown in a randomized design. Total acorn production per tree is obtained by adding, at the end of the dissemination period, the fruits periodically counted or weighed and then multiplying by the estimated fraction of the crown cover sampled by the traps.

Livestock and wild ungulates can be a problem for using containers since cattle and deer can easily knock over most traps. When livestock are present it is therefore a good idea to plan on protecting traps with fencing or use a design such as hanging containers in the tree that will minimize their impact.

The container method is also labor-intensive requiring considerable setup and repeated maintenance. Only a small proportion of the canopy is sampled, and only acorns that fall into the containers are counted or weighed, so arboreal acorn removal by animals is not considered—something that can be a serious problem in
certain years (Koenig et al. 1994a). If the goal, however, is to determine the acorn crop available for livestock, ground predators such as deer, or ground dispersers such as mice, this method should be seriously considered.

Acorn production measured with containers was quite consistent with the total acorn yield (measured by knocking down all acorns in the tree) divided by the crown surface ($R^2 = 0.82$, $F_{1, 39} = 184$, $P < 0.001$; Alejano et al. 2008).

3. Visual surveys—This method, which may involve a timed or complete survey of acorns on individual trees, is a nondestructive method allowing the subsequent harvesting of fruits. Other advantages include:

(a) Counts are made just once during the dissemination period, so it is quicker and far less labor intensive than other direct methods.

(b) Depending on the species and area, it can be performed one to two months before acorns mature, and thus to some extent allows crop prediction. It is important not to delay counting until after acorns start falling, since the method will then underestimate the crop unless caps remain on the tree and can be included in the survey.

(c) Assuming the timing is right, counts will include most acorns that might later be removed from the crown by seed predators prior to acorn fall, and thus it potentially provides a more accurate measure of overall productivity than methods that quantify acorns that fall, such as the container method.

Fig. 7.B1 Containers for estimating acorn production under a flowering holm oak ($Q. ilex$) in Huelva, Spain. Note the dendrometers on the oaks for measuring radial growth. (Photograph by R. Alejano)
Visual surveys have been found to be consistent with the acorns harvested by using the container method (Koenig et al. 1994a), and has been widely used both in California and in Spain.

There are, however, disadvantages: counts are likely to be affected by factors influencing the ease with which acorns are seen such as light conditions, canopy cover, leaf density, and acorn coloration. The main disadvantage of timed visual surveys that do not completely sample the acorn crop, however, is that it only provides a measure of the relative, rather than the absolute, crop size. Counts are typically performed in an unknown area of the crown, so transforming this number into total number of acorns per tree or even total weight of acorns per tree is not an easy task.

Despite this caveat, however, tests of this method have generally been favorable. Perry and Thill (1999) tested five visual surveys methods and found the Koenig et al. (1994a) method to be the most efficient. Carevic et al. (2009; Fig. 7.B2) compared visual surveys and containers and obtained a regression that would be the starting point for estimating acorn weight from acorns counted for a particular species and geographical area. Residuals tended to deviate from expectations when many acorns were counted, and, to a lesser extent, when few acorns were seen. Counting for a longer period when acorns are rare or hard to see might improve the relationship between visual surveys and the “real” acorn crop when acorns are sparse; it is less clear how to distinguish between acorn crops at the upper end of the spectrum. To the extent that the acorn crop is good and such separation is desirable, an alternative method is probably needed.

The visual survey method proposed by Espárrago et al. (1992) and later modified by Vázquez (1998) has been used in Spanish dehesas as well. For its application, acorns within a 20 cm$^2$ wooden frame placed in front of different areas of the crown are counted. The average of at least 50 such counts per tree are done and used as an index of tree production. Several models have been proposed to translate the resulting acorn number into the total acorn crop assuming the crown to be a cylinder. Fernandez et al. (2008) checked the consistency of the method obtaining good results. A training period was desirable, however, since the experience of observers was found to influence the results.

Fig. 7.B2  Regression of acorn production estimated from visual surveys (APVS) on acorn production estimated from container traps (APC, measured in g m$^{-2}$ of crown area) for dehesas of holm oak in Huelva, Spain (from Carevic et al. 2009)
4. **Ranking methods**—Several methods have been used to evaluate acorn crops in dense oak forests in the USA. Sharp and Chisman (1961), studying white oak (*Q. alba*), proposed a qualitative method consisting of classifying a tree as a poor, good or extraordinary producer. Acorns in the end of the branches in the upper third of the crown were counted and averaged to yield acorn production per tree or per stand. A second method was proposed by Whitehead (1969) involving three qualitative parameters: the percentage of the crown containing seeds (0–3), the percentage of shoots within the crown producing seeds (also 0–3), and the average number of acorns per shoot (0–4). The Whitehead index is then obtained by adding the three values (thus 0–10), and was found by Perry and Thill (1999) to be highly correlated with the total number of acorns m$^{-2}$ of crown area.

In Spain, Pulido and Díaz have developed a ranking method for long-term monitoring of acorn and pollen production of holm oak populations (see [www.globimed.net/investigacion/Veceria01.htm](http://www.globimed.net/investigacion/Veceria01.htm), Díaz et al. 2011). Production is ranked into five categories: 0: no acorns or catkins; 1: <10% of the canopy covered by acorns/catkins; 2: 10–50%; 3: 50–90% and 4: >90%. Catkins are estimated in spring, when most trees are in full bloom, and acorns are estimated in early fall, after aborted seeds and those infested by insects have fallen. Several tests have demonstrated strong among-observers consistency in rank estimates after a short training period. Data taken in 2007–2010 from 145 trees provided with seed traps in Cabañeros National Park showed a strong correlation between this index and measures of the production of acorns in terms of the number of sound seeds m$^{-2}$ ($r = 0.55$, $P = < 0.001$, $N = 374$; Díaz et al. 2011). This method enables rapid estimates of the among-years and among-individuals variation in the production of acorns and catkins, and also of the production of new shoots and leaves in spring and of the proportion of the canopy with leaves dry or lost for large number of trees, either isolated or growing in dense stands.

**Indirect Methods**

Several indirect methods have been described or mentioned for estimating acorn crops. We mention them here for completeness.

1. **Pollen**—A positive correlation has been reported between the amount of airborne Mediterranean oak pollen released to the atmosphere and the size of the acorn harvest (García-Mozo et al. 2007). This finding supports the hypothesis that pollen may be limiting, at least under some conditions, and have an important effect on subsequent acorn production in these wind-pollinated species, similar to its effects in many anemophilous species (Galán et al. 2004). To the extent this is true, integration of aerobiological, phenological and meteorological data could represent an important step forward in forest fruit production research (García-Mozo et al. 2007).
2. **Remote sensing**—Several recent studies have employed remote sensing techniques, including hyperspectral imaging, to estimate acorn yields (Yao et al. 2008; Panda et al. 2010; Yao and Sakai 2010). Such methods can at least in theory allow the mapping of acorn production over large geographic areas so as to yield within-stand abundance and spatial synchrony of acorn production. Remote sensing methods have yet to be applied to studies in either California or Spain, although they may eventually offer a powerful and less labor-intensive tool for assessing acorn production in our Mediterranean oak forests.

3. **Dendrochronology**—Based on the assumption of a tradeoff between growth and reproduction, Speer (2001) proposed a technique for mast reconstruction using dendrochronology for non-Mediterranean oaks. Although his results provided some optimism for this approach, it has not been used or tested by later authors. One problem is that in some cases it is likely that a negative correlation between growth and acorn production may be due to correlated effects of environmental variables rather than a trade-off per se (Knops et al. 2007). Nonetheless, the strong negative correlation between growth and reproduction observed in many species (Drobyshshev et al. 2010) means that growth can potentially provide information useful for predicting subsequent acorn production in some species, regardless of the mechanism involved.

4. **Fattening of pigs** (for Spanish dehesas)—A traditional way to estimate acorn crops in Spanish dehesas is based on the degree to which pigs fatten during the dissemination period when they feed almost exclusively on acorns. Historical records with yearly controls would be required for this method to be practical.

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