

Natural Regeneration

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In plants, the colonization of forest gaps and new habitats and the maintenance of genetic diversity and evolutionary potential are achieved mostly through sexual *regeneration*. It is therefore surprising that despite more than a century of interest by foresters, very little detailed information is available on the regeneration cycle of the cork oak and the dynamics between its different regeneration stages. Yet understanding natural regeneration is critical for any efficient conservation and restoration plan. By regeneration we mean the complex processes occurring from the time a seed is produced to the time offspring reach maturity (i.e., seed to seed). Thus, for cork oak, the cycle includes production, predation, dispersal, and germination of acorns, establishment of new individuals (recruitment), and growth to mature (reproductive) trees.

In this chapter we review what is known about cork oak regeneration, based on our own research in Spain and Portugal over the past decade. We first review the different stages of the regeneration process in cork oak populations and the performance (survival and growth) of the seedling. Then, we discuss recruitment and regeneration patterns in three Iberian areas. Finally, we discuss the relevance of our findings for the conservation, restoration, and holistic management of cork oak woodlands. The process of postfire vegetative regeneration was discussed in detail in Chapter 1 (see also Pausas 1997).

From Seed to Seedling

The seed regeneration mechanism of cork oak is similar to that of many oaks in that they share dispersal vectors, acorn predators, and seedling establishment problems (i.e., first summer drought mortality under Mediterranean

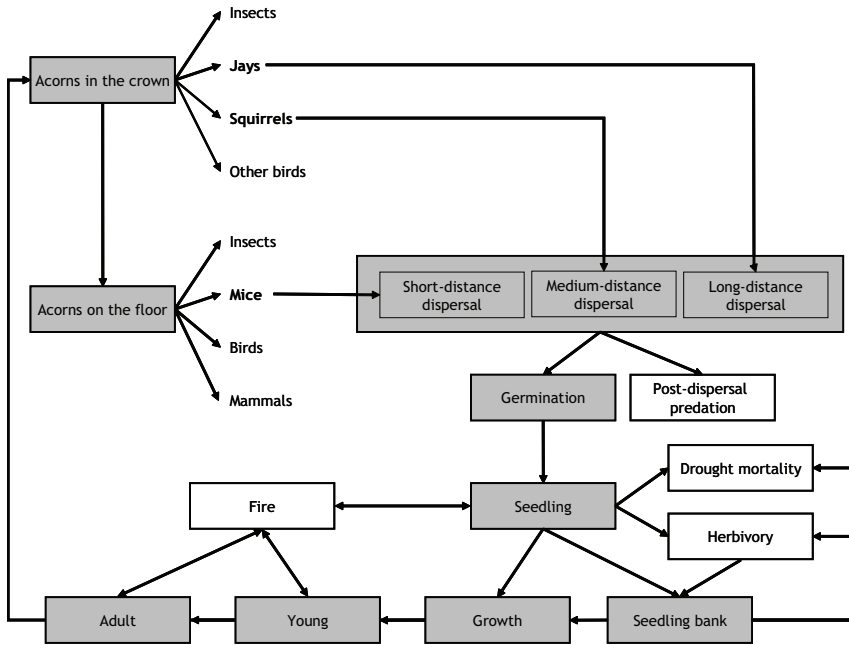


FIGURE 10.1. Conceptual model of the cork oak regeneration process (simplified). Gray boxes indicate the pathway of successful regeneration.

climate conditions). The outcome of each regeneration process determines the success or failure of the regeneration. In other words, the collapse or failure of any one of them will impede or halt the overall regeneration of the population (Figure 10.1).

Acorns are large, single-seeded fruits (1.5 to 3 centimeters long) that constitute highly digestible, high-energy (lipids), low-protein food for many animal species. They ripen either in the autumn of the flowering year (annual acorns) or in the autumn of the next year (biennial acorns) (Elena-Roselló et al. 1993). The main dispersal agent of most European oaks, including cork oak, is the European jay (*Garrulus glandarius*), which is a forest bird occurring not only in Europe (as the name suggests) but also in North Africa and Asia. The strong evolutionary relationship between this corvid and oaks has led to acorns becoming a very important food source for the former, and jays have become a very important dispersal agent for oaks (Bossema 1979; Pons and Pausas 2007a, 2007b, 2008). It is worth noting that both squirrels and mice also move and sometimes disperse acorns, though over shorter distances than jays (Figure 10.1; Pons and Pausas 2007a, 2007b, 2007c); however, mice may also play a crucial role in oak woodlands that lack jays.

In autumn, jays harvest healthy acorns from the tree crowns. They bury these acorns for later consumption, preferentially in open spaces, such as open grasslands, clear shrublands, recently abandoned old fields, and pine woodlands with low shrub cover (Bossema 1979; Pons and Pausas 2006; Pausas et al. 2006). A pair of jays may scatter and hoard several thousand acorns in a single season (Cramp 1994). As a result, cork oak dispersal ranges from a few meters to a few kilometers (Pons and Pausas 2007a). A few months later, when the acorn season has passed, and especially during the breeding season, when they need extra food to feed their progeny, jays collect the acorns they have stored in advance. By that time (April and thereafter), most of the acorns have already germinated, but the resulting seedlings do not necessarily die when the acorn, which is still attached to the seedling, is removed by the jay (Sonesson 1994). Two additional birds that feed heavily on cork oak acorns are the woodpigeon (*Columba palumbus*) and the common crane (*Grus grus*), which overwinter in many Iberian and North African oak woodlands. However, there is no published evidence that they contribute to acorn dispersal.

Mice (*Apodemus* and *Mus* species) are also major acorn predators, especially of acorns that fall from the tree to the ground (Pons and Pausas 2007c). Acorns buried by jays are usually safer from mice because jays tend to hoard in open spaces, where high rodent exposure to predation (e.g., raptors) results in low rodent activity. However, mice may also contribute to dispersal, especially in *mast years*, when high acorn availability satiates rodents. Although mice may disperse acorns at short distances (a few meters; Pons and Pausas 2007c), they may promote the persistence of oak populations through within-stand replacement dynamics and in systems lacking jays, such as some open oak forests (*dehesas*). Similarly, squirrels (*Sciurus vulgaris*) also scatter-hoard acorns, although no studies have yet quantified their role in oak recruitment. They probably play a minor role because squirrels inhabit dense forests, where tree seedlings have few opportunities to grow; indeed, most of the germinated acorns remain as a seedling bank on the forest floor, waiting for the occurrence of a major disturbance that would allow them to grow up to fill the new gap created in the forest canopy.

Acorns are also a food source for insects, and it is very common to find small exit holes, made by larvae of the acorn moth (*Cydia* spp., Lepidoptera) or the acorn weevil (*Curculio* spp., Coleoptera), in both cork oak and holm oak trees. The proportion of acorns predated by these insect larvae is highly variable; values from 17 to 68 percent have been reported (Branco et al. 2002; Pérez-Ramos 2007). Although many damaged acorns maintain their germination ability, the resulting seedlings show reduced

vigor and a lower probability of surviving drought stress. A striking case of oak–insect interaction involves the dung beetle (*Thorectes lusitanicus*), which buries cork oak and Algerian oak acorns and eats them over a period of a few weeks. Sometimes buried acorns are abandoned after being partially consumed and can still germinate and establish themselves as rooted seedlings, but the distances the acorns are moved are very short (centimeters; Pérez-Ramos et al. 2007).

Finally, large vertebrates, such as red deer and especially wild boar, consume large amounts of acorns under cork oak trees. Similarly, in *dehesas* and related cork oak woodland agrosystems, livestock (pigs, cows, sheep, goats) are also acorn consumers; in fact, in Spain and Portugal, domesticated pigs are encouraged to eat acorns freely because the quality of their meat is closely related to the amount of acorns they eat (see Chapter 4). By the end of winter, in open *dehesa* woodlands, most of the annual acorn crop below the parent trees is usually eaten by the various seed predators of all shapes and sizes (Pulido and Díaz 2005b).

Seedling Performance

After germination, acorns quickly develop a strong taproot. This facilitates access to water and permits the seedling to allocate reserves and have protected buds in the root collar. The aerial part usually appears at the beginning of spring, although under certain conditions, such as extreme drought, some acorns—generally less than 10 percent—will delay aerial shoot appearance until the first rains of September. In cases of severe summer drought or strong competition occurring in the understory (Figure 10.1), many seedlings lose their aerial parts but resprout again in autumn. In understory conditions, saplings may remain as a resprouting sapling bank and complete the final regeneration process only when there is an opening in the canopy that allows the sapling to grow and reach maturity (Pons and Pausas 2006). Browsers, such as deer, sheep, and cows, can also heavily defoliate seedling shoots. Although seedlings are generally able to resprout, repeated browsing and soil compaction can kill most oak seedlings and impede natural regeneration. In such situations, seedlings growing under spiny shrubs may benefit from the nurse shrub effect (Castro et al. 2004b), which allows them to grow safely above the browsing line. However, the balance between the positive and the negative (increased competition) effects, induced by the nurse plant, may depend on the environmental conditions (Callaway 1995; Maestre et al. 2005).

Cork oak seedling survival and growth may be severely limited by summer water deficits. The longer the seasonal drought, the lower the survival rate

(see Chapter 6). Moreover, cork oak seedling recruitment may occur in the forest understory, where light levels can be as low as 5 percent of the incident radiation. Light and water deficits often interact as limiting resources for young seedlings. However, in areas where dispersers are abundant, seeds can also reach open spaces, and therefore seedlings need to cope with high solar irradiance and potential evapotranspiration in summer. Although mature cork oak is considered to be shade intolerant, seedlings can tolerate some degree of shade. For example, Cardillo and Bernal (2006) found that well-watered seedlings had similar relative growth rates at 20 percent of full light and full sunlight and that etiolation symptoms and growth stoppage were apparent at 5 percent of full light. Light is essential for seedling growth, but shade and canopy protection can also be important for seedling survival during the summer drought. In fact, in Mediterranean woody species, the impact of drought on survival and growth is often higher in exposed conditions than under shade (Sánchez-Gómez et al. 2006; Quero et al. 2006).

The interaction between shade and drought on cork oak performance has been subject to some debate (e.g., Sack 2004; Quero et al. 2006). Recent studies of cork oak seedlings (Aranda et al. 2005b; Pardos et al. 2005) showed no significant interaction between shade and drought, although seedlings growing in shade were less efficient at developing physiological mechanisms of water stress tolerance, such as osmotic adjustment. However, in a greenhouse experiment, cork oak seedlings grown in deep shade under drought conditions were able to achieve higher photosynthetic rates, stomata conductance, and leaf N concentrations than those grown in full light, indicating an apparent alleviation of the impact of drought under shade (Quero et al. 2006). Indeed, the integrated response of tree seedlings to shade and drought involves several physiological and structural mechanisms. In a recent field study in Portugal (unpublished), cork oak seedling survival was higher under the canopy of mature oak trees than in the open, and the difference in survival increased by about 30 percent in a dry year, confirming that facilitation by canopy cover can be crucial in stressful conditions.

Thus, these experiments, carried out under controlled conditions, suggest that shading may alleviate drought stress in cork oak seedlings. However, we need to consider the complex ecosystem interactions (e.g., predators and grazers, often excluded from field experiments) to fully understand the limiting factors for regeneration. This is because environmental conditions that may be optimal for one aspect of regeneration may be limiting for others. This is the case for the higher seedling survival but also higher acorn predation and lower seedling growth observed in shaded sites as compared to open sites.

Recruitment Patterns: Three Case Studies

We now summarize the information available on recruitment patterns in three case studies carried out in different parts of the Iberian Peninsula that encompass a large range of the known variability in cork oak regeneration processes. Very little is known about the regeneration of cork oak stands outside the Iberian Peninsula, but regeneration patterns there probably are comparable to those presented here.

Case Study 1: Eastern Iberian Woodlands

In the Iberian Peninsula, the core area of cork oak is the center-west and the south; however, farther east, fragmented cork oak woodlands also occur (Pausas et al. 2004c, 2006; Pons and Pausas 2006, 2007a, 2007b, 2007c, 2008), occupying about 80,000 hectares in the Valencia region (see Site Profile 8.1). One of the main characteristics differentiating these eastern Iberian woodlands is the absence of large herbivores. The observed patterns of seedling recruitment and regeneration in this area are summarized in Figure 10.2.

There is a clear dynamic process in the colonization of old fields (Figure 10.2, left): Recruitment is observed at the beginning of abandonment. Then, as the vegetation cover increases, the rate of new seedling arrival decreases,

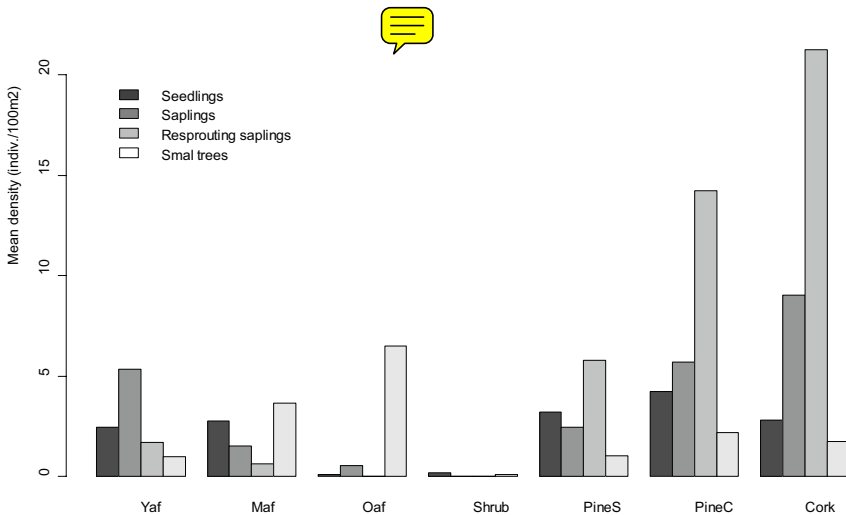


FIGURE 10.2. Cork oak recruitment density in different vegetation types in the eastern Iberian Peninsula. Recruits were classified as seedlings (with acorn attached and thus 1 or 2 years old), saplings (juveniles with no acorn attached), resprouting saplings (with symptoms of topkilling and resprouting), and small trees (<3 m). Lines and arrows indicate the main trends. (Modified from Pons and Pausas 2006)

and the seedlings present develop into saplings and then into full-sized trees. Finally, when shrubs and herbs achieve nearly full soil cover, no new seedlings appear (as in the shrublands), suggesting that the recruitment window is closed, and the initial saplings develop into young trees. Thus, in these conditions regeneration occurs thanks to the arrival of seeds soon after abandonment. The low proportion of saplings that have suffered top dieback (resprouting saplings in Figure 10.2) suggests very low stress conditions in old fields.

In contrast, there is very limited recruitment of cork oak in shrublands (Figure 10.2). Although we cannot yet pinpoint the causes, possible hypotheses include limited seed arrival, high seed predation, germination failure, and competitive exclusion. Because all of these are sequentially connected, the first seems to be the most limiting one because the jay's habit of directing dispersal to open soil and actively avoiding closed shrublands has been widely reported (Bossera 1979; Frost and Rydin 2000; Gómez 2003; Pons and Pausas 2007a). Furthermore, the highest acorn predator densities (mice in particular) are often found under shrublands (Hulme 1997). Indeed, there is evidence from other parts of the cork oak area of distribution suggesting that shrublands block cork oak colonization by limiting different regeneration processes (Acácio et al. 2007).

Finally, in mixed oak–pine forests, there is a high recruitment of new cork oak individuals; however, seedling desiccation and topkilling are very important processes in these habitats, with the result that many sprouted seedlings accumulate in a “sapling bank” without developing into trees (Figure 10.2, right).

Case Study 2: Dense Forest in Southern Spain

Cork oak dominates a dense and continuous forest of about 90,000 hectares in southern Spain, currently preserved as Los Alcornocales Natural Park (see Site Profile 17.1). In this area, rainfall is quite high (ranging between 700 and 1,300 millimeters annually) in comparison with other Mediterranean regions, but there is still a prolonged drought period in summer. The strong grazing pressure from free-range cattle and the increased deer population in the area has led to very poor cork oak regeneration and a general decline in the oak population. Currently, managers are striving to stimulate cork oak regeneration by regulating the deer population (e.g., building fences and hunting) and by planting oak seedlings.

Recent studies in these protected forests suggest high interyear variability in acorn production, including some years with very poor production

(Pérez-Ramos 2007). During the period 2003–2005, approximately 70 percent of the acorns on the trees aborted and fell, and fully half of the well-developed fruits were infested by insect larvae. Thus, only 17 percent of the seeds collected in seed traps placed under cork oak trees proved to be viable. After acorns fell to the ground, they were heavily predated, particularly those falling in deep-shade microsites, where rodents tend to forage. When the viable acorns collected in the seed traps were artificially dispersed in the field, about 70 percent germinated, and of these about 82 percent emerged as seedlings. Soil water content generated a double environmental stress consisting of high water content (waterlogging) in winter and very dry conditions (water deficit) in summer. Open microsites showed very different conditions compared with shaded sites (under trees) because waterlogging in winter and water stress in summer were more common on open sites than on shaded sites. Thus, both germination and emergence diminished exponentially as winter soil moisture increased, and seedling survival was higher under oaks (49 percent) than on open microsites (33 percent) (Pérez-Ramos 2007). In fact, the best predictor for seedling survival was emergence time, as winter waterlogging delayed seedling emergence and thus reduced summer survival. However, the surviving seedlings showed higher growth rates in the open than in the shaded microsites, under both field (Pérez-Ramos 2007) and greenhouse conditions (Quero et al. 2006). Thus, environmental conditions that are optimal for one aspect of the recruitment process may be suboptimal for others (Schupp 1995; Marañón et al. 2004).

Case Study 3: Open Woodlands (Dehesas and Montados)

The *dehesa* and *montado* agroforestry systems described in Chapter 3 (see also Site Profiles 4.1 and 13.1 and Color Plates 4–6 and 7a) have scattered oak trees, mostly evergreen, over low vegetation, often used for raising livestock (cows, sheep, and pigs). The land is sometimes plowed for cultivation of cereal crops (see Chapters 3 and 4 and Color Plate 5). Most of these open cork oak woodlands have an even-sized class distribution, almost devoid of younger trees. This is a worrisome pattern, indicating a lack of regeneration to counteract current mortality, stressing, and overall lack of sustainability of the land use system as it is currently practiced.

In these managed woodlands, many or most oak trees receive high solar radiation, and they have access to enough soil water to survive the dry summer and produce many more acorns than oak trees in a dense forest. Livestock, birds, and rodents consume most of the acorn crop, and the surviving seeds germinate and grow mainly under the mother trees. The lack of seed

dispersal appears to be the key factor limiting tree recruitment in clearings (Pulido and Díaz 2005b). Jays and squirrels are absent from these open woodlands because they need a forest habitat (Pons and Pausas 2008). Mice are present only in shrubby microsites, where they can hide from predators. Given the high density of domestic animals in open, grazed pastures, the few surviving oak seedlings are almost completely defoliated. They can resprout several times, but overgrazing often drives them to death. Thus, the lack of acorn dispersal agents and overgrazing are the two key factors limiting oak regeneration in *dehesa* and *montado* woodlands.

Conclusions

There is a general decline and an alarming lack of regeneration in many Iberian cork oak populations throughout the western Mediterranean, despite successful regeneration in some places. Our results suggest that in the eastern Iberian Peninsula, cork oak colonizes abandoned croplands, and recruitment in shrublands is very limited. It also colonizes pine forests, but seedling growth is very low there, forming an understory sapling bank. In this region, acorns are abundantly dispersed by jays, but there is much seed predation by rodents, particularly in shrublands, and a very low predation of seedlings and saplings by herbivores (Table 10.1). In the dense woodlands of southern Spain, the patterns are similar with respect to seed dispersal and predation, with one very important difference: the high browsing pressure by the overly abundant red deer (Table 10.1). In the *dehesas* and *montados* of central and western Iberian Peninsula, acorn production is very high, but there is a lack of both dispersal and safe sites for recruitment. In addition, the very high grazing pressure limits the growth of the few surviving seedlings. In conclusion, to understand cork oak regeneration, it is important not only to consider the different socioeconomic and ecological conditions but also to adopt a landscape perspective, because different processes may occur in different landscape units. Our point is that it is important to understand the sequential demographic stages involved in the regeneration cycle and then to quantify each transition in order to detect the main factors limiting regeneration in the different patches and regions (Table 10.1).

Our findings on oak regeneration patterns and mechanisms can be transferred to woodland managers to help design practices and recommendations aimed at the conservation and sustainable management of cork oak stands and ecosystems. These practices may include management of both vegetation and fauna, with the objective of increasing acorn dispersal and establishment (passive restoration). Different woodlands with different socioeconomic

TABLE 10.1.

Comparison of the three systems studied (eastern, alcornoques, and dehesas), and with the theoretical equilibrium (natural, currently nonexistent).

	Dispersal agents	Herbivores	Herbivore predators	Regeneration
Natural	=	=	=	Yes
Eastern	=	-	-	Yes
<i>Alcornocales</i>	=	+	-	Low
<i>Dehesas</i>	-	+	-	No

Symbols: =, in equilibrium; -, too low (e.g., undergrazing); +, too high (e.g., overgrazing).

and ecological conditions, such as the three case studies presented here, will require different management approaches. For instance, sustainable management of the aged *dehesa*-type woodlands seems to call for landscape mosaics that include both shrubland patches, where mice can disperse acorns, and dense tree canopy patches to provide the habitat for jays. Shrubs can also facilitate oak seedling survival and growth by alleviating drought stress and protecting seedlings from grazers (the nurse effect from spiny shrubs). Temporary reductions or even exclusion of grazers from certain patches, in both *dehesa*-type woodlands (see Case Study 3) and forests with high grazing pressure (see Case Study 2), would allow saplings to reach sufficient height above the browsing line to become reproductive oak trees. In contrast, to conserve and increase population size in eastern Iberian cork oak patches, shrub clearing may be necessary to open the regeneration window. In the chapters that follow we will learn about specific techniques that may help to restore cork oak woodlands, especially when managing natural regeneration is not sufficient.

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