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Chapter 1

The Tree

Juli G. Pausas, João S. Pereira, and James Aronson

To understand and appreciate it properly, we should first recognize that cork oak is in many ways a typical Mediterranean tree. It can survive adverse conditions of both human and nonhuman origin. It resists cutting, grazing, prolonged drought, and fire but not extreme cold. On suitable, deep soils and with adequate rainfall, the tree may reach up to 20 meters tall and live for several centuries. However, it has one feature that is extremely rare throughout the plant kingdom: an outer coat of insulation consisting of corky bark of continuous layers of *suberized* cells (see Chapter 5), up to 20 centimeters thick, that may have evolved as an adaptation to fire (see Color Plates 1a, 1b). What is more, the tree survives and grows new bark when the original bark on its trunk has been removed.

Like other evergreen Mediterranean oaks, cork oaks survive drought, thanks in part to their extensive and deep root systems. During a drought, the tree may protect crucial organs and tissues from dehydration by closing stomata on leaves, restricting water loss, and the tree's deep roots may tap water from the deeper soil or subsoil (Pereira et al. 2006). The deep root system of cork oak helps the tree maintain water status and xylem conductance above lethal levels throughout the summer drought period (see Chapter 6). In some cases, under severe drought, the tree may shed its leaves and resprout when the drought is over (in spring). During the early stages of plant life, there is a clear priority for root growth (Maroco et al. 2002). This early investment in roots, rather than in stems and foliage, may contribute to survival in the first years in drought-prone environments because seedling survival cannot be guaranteed before roots reach a soil depth that holds available water in summer. Symbiosis with *mycorrhizae* that live in or on the roots is also an important aid to cork oak seedlings in resisting drought, as described in Chapter 7.

Once aboveground parts begin to develop, cork oak has a unique leafing *phenology*. For an evergreen tree, it has short-lived foliage and a late flushing pattern (Pereira et al. 1987; Escudero et al. 1992). In fact, the average leaf life expectancy is only about 1 year, much shorter than in other evergreen oaks, such as Iberian holm oak (*Quercus rotundifolia* = *Q. ilex* subsp. *ballota*), whose leaves last 1–3 years, or the kermes oak (*Q. coccifera*), whose leaves can last 5–6 years. Leaf phenology is under strong genetic control, and the beginning of shoot flushing of populations belonging to different provenances but cultivated together can vary by as much as 4 weeks, from late March to late April.

Cork oak leaves themselves are also well designed to cope with an unpredictable climate. They are *sclerophyllous*, which means they are stiff, thick, and waxy (see Color Plate 1d). This is typical of many trees and shrubs that grow in regions with strong seasonal water deficits, such as the Mediterranean. They are also small, which allows efficient heat dissipation, thus partly avoiding overheating in the hot summer. In cork oak, as in many kinds of trees whose roots tap water from deep in the soil, supplementary cooling is often achieved through transpiration, as stomata open for some time on long summer days. Harmful leaf tissue dehydration is prevented by the highly efficient gradual closure of stomata (see Chapter 6, where other adaptations to drought are discussed in more detail).

Sclerophylly is often considered an adaptive trait of woody plants in seasonally dry climates, but it does not automatically confer greater tolerance to drought, and it may have evolved because it provides protection from many different types of stress (Read and Stokes 2006), such as poor mineral nutrition or attacks by defoliators (Salleo and Nardini 2000). In fact, sclerophylly implies a long leaf development time and fairly high ratio of carbon to nitrogen, both of which traits make the foliage undesirable to herbivores. Thus, most defoliators attacking cork oak feed on the young, tender leaves, before sclerophylly fully develops. This, in turn, conditions the nature of the web of organisms dependent on cork oak leaves.

Biogeography

Cork oak occurs in regions with average annual precipitation above 600 millimeters and average temperature near 15°C (Blanco et al. 1997). In Europe, it is low winter temperatures that appear to set the geographic distribution limits and most cork oak stands are located in areas below 800 meters in altitude. Cork oak leaves are less tolerant to frost (Larcher 2000; Garcia-Mozo et al. 2001) and to drought than those of the more widespread holm oak. In addition, whereas holm oak is indifferent to soil types, cork oak usually grows in acidic soils on granite, schist, or sandy substrates or, more rarely, in limestone-derived soils or in neutral soils overlying dolomitic bedrocks (Chapter 8).

Today cork oak occurs only in the western Mediterranean (Figure 1.1), from Morocco and the Iberian Peninsula to the western rim of the Italian peninsula. It also flourishes on all the large islands between the Iberian and Italian peninsulas, and in scattered parts of southern France and some coastal plains and hilly regions of Morocco, Algeria, and Tunisia. Total area today adds up more than 1.5 million hectares in Europe and about 1 million hectares in North Africa (Figure 1.2).

Figure 1.1 shows clearly that cork oak's current distribution is very patchy and disjunct, which suggests that much of what we see today is relictual. It is also possible that, over past centuries, humans intentionally introduced the tree to some islands and disjunct continental areas where it did not naturally occur. However, in Europe and especially in North Africa, cork oak areas have diminished in size and vitality because of overgrazing, which limits regeneration, and the expansion of plow agriculture in managed woodlands (see Chapter 3), the replacement of cork oak by pine and eucalyptus, imprudent cork stripping, and the extraction of tannins, which kills the tree. Wildfires may also be an important source of cork oak mortality, but mainly after cork extraction, when the lack of protection makes the tree susceptible to fire. In southwestern Spain and Portugal, however, the area of cork oak stands has increased in the last 200 years (Figure 1.2), despite some episodes of decline, such as that in the mid-twentieth century (see Chapter 20).

Phylogenetically, cork oak is considered to be closely related to three Asian species of oak, all of which are deciduous. These are the turkey oak (*Q. cerris*) of southwestern Asia, sawtooth oak (*Q. acutissima*) of eastern Asia, and Chinese cork oak (*Q. variabilis*) (Manos and Stanford 2001). Moreover, recent genetic studies suggest that the evolutionary origin of cork oak was quite a bit east of its current distribution area (Lumaret et al. 2005; see Chapter 2). Indeed, fossils of the ancestors of cork oak, in the *Q. sosnowsky* group, have been found in France, Poland, Romania, Bulgaria, Turkey, and Georgia (Bellarosa 2000). However, the origin of cork oak is still under debate (Magri et al. 2007).

In the last century, cork oak was artificially introduced in several countries outside the Mediterranean region, as an ornamental shade tree and botanical oddity or in hopes of generating local cork production. Reasonably good acclimatization has been attained in Bulgaria (Petrov and Genov 2004), New Zealand (Macarthur 1994), southern Australia, Chile, and California. However, none of these places has successfully developed a cork industry, even

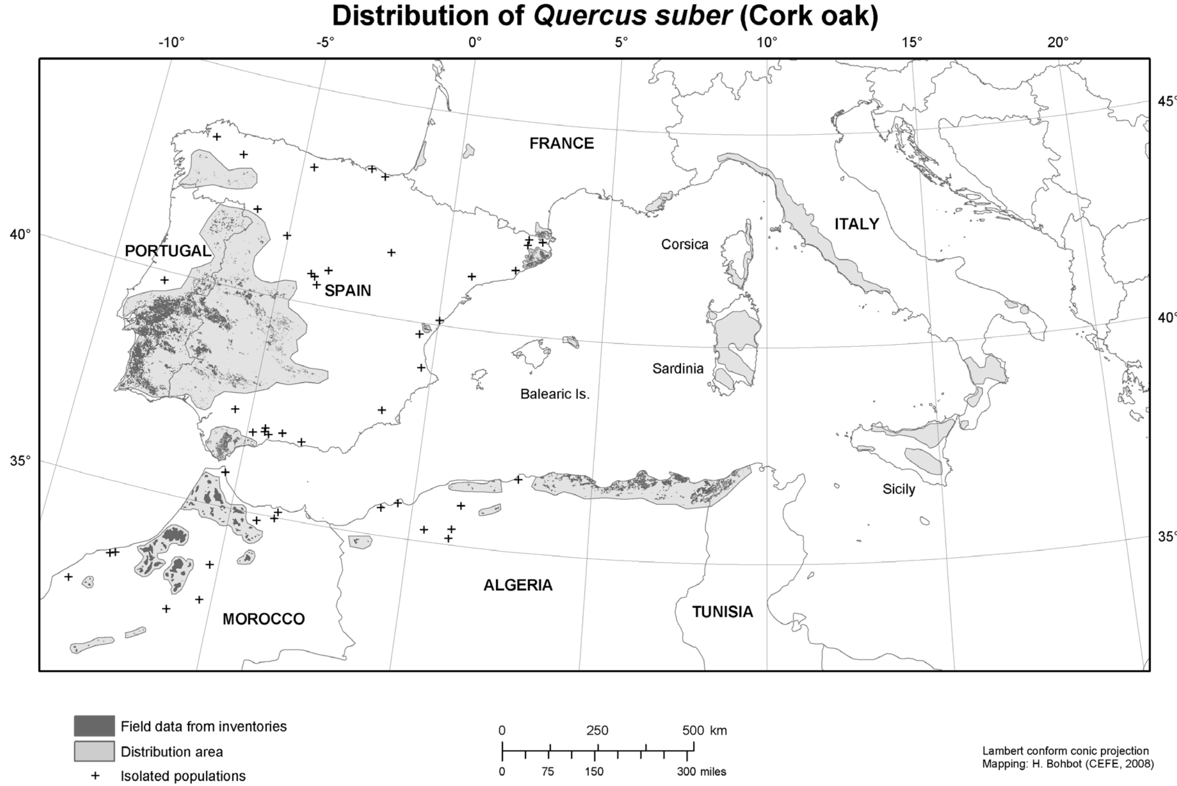


FIGURE 1.1. Current distribution of cork oak. (Algeria: Gaussen and Vernet 1958; Barry et al. 1974; Alcaraz 1977; Italy: modified from Bellarosa et al. 2003b; Morocco: Sbay et al. 2004; Portugal: DGF 2001; Spain: after www.inia.es, 2006; Tunisia: Khaldi 2004, after IFPN-DGF 1995)

though the tree grows reasonably well on appropriate soils. At present, despite ongoing tree decline, Portugal remains by far the largest producer of cork and has the largest industry, followed by Morocco, Italy (especially Sardinia), and Spain (see Chapter 5).

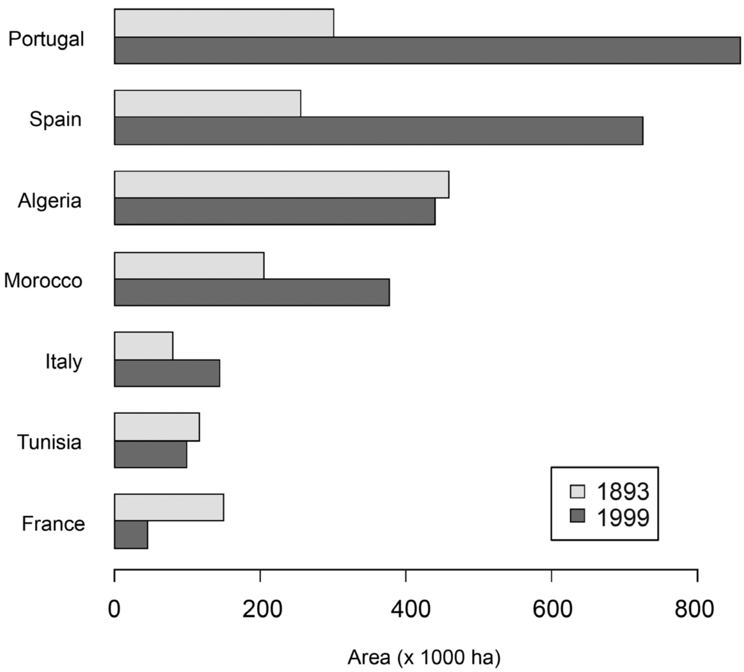


FIGURE 1.2. Areas covered by cork oak in different periods and countries. Light bars refer to areas covered in 1893 (Lamey 1893), except for that of Morocco, which refers to 1917 (Boissière 2005); dark bars indicate the area covered in 1999 (Instituto del Corcho, la Madera y el Carbón, Mérida, Spain).

Flowers and Fruits: The Ecological Role of Acorns

Like all other oaks, cork oak produces male and female (unisexual) flowers in different inflorescences on the same individual (monoecy). Staminate (male) flowers are born in catkins (see Color Plate 1e), whereas pistillate (female) flowers grow in small groups, generally no more than eight. Most trees have flowers of both sexes, with a high degree of self-incompatibility. The development of male and female flowers is asynchronous in each tree. The vector for pollination is wind, and the ovaries of fertilized flowers mature into acorns (i.e., dry fruits with a single seed).

Cork oaks produce both annual and biennial acorns. Annual acorns mature the same year as the flowers that produced them, whereas biennial acorns grow and mature in the autumn of the next year. The proportion of annual and biennial acorns varies spatially and temporally in response to environmental factors and meteorological conditions (Elena-Roselló et al. 1993; Díaz-Fernandez et al. 2004). This pattern contrasts with those of other closely related species, such as the turkey oak and the sawtooth oak, which exhibit consistently biennial fruit maturation (Schwarz 1964; Borgard and Nixon 2003), or the co-occurring holm oak, which offers annual acorns only. A biennial cycle appears to be related to short plant growth periods, limited by cold or drought.

Overall, cork oak acorn production is also quite variable in space and time. There is interannual variation in population-level reproduction, with occasional years of exceptional production followed by years with little or no production. In addition, within a population, in any given year, there can be very high variability of acorn production between individual trees for no obvious reason. In some cases, variations result from the different dominance of male or female flowers among trees. Other partial explanation can be found in tree density and relative aspect: Trees in high-density stands or on north-facing slopes tend to produce fewer acorns than isolated trees or trees located on south-facing slopes. Indeed, fruit production usually is favored in well-lit crowns because of the warmer temperatures and abundance of photosynthetic assimilates. Spring frosts also reduce acorn production.

Cork oak acorns are large (1.5 to 3 centimeters long; see Color Plates 1c, 1d), and dispersal is mediated mainly by birds, although squirrels and other animals may also play an important role (Pons and Pausas 2007a, 2007b, 2007c; see Chapter 10). Mice are major acorn predators, although they may also contribute to short-distance dispersal. Some insects, mainly weevils and moths, are also very important predispersal predators of acorn. In fact, acorns are important components of food webs in oak landscapes because they are a highly digestible, high-energy (lipids), low-protein food for many wildlife species, although secondary metabolites, such as tannins and phenolic compounds, may deter consumption by some animals.

Cork Harvest: Nature's Gift and Weakened Trees?

Each year, cork oak trees produce a new layer of suberized cells. This corky bark is not shed naturally, forming annual rings, as happens in wood. When enough cork has accumulated (e.g., up to 3 centimeters of cork in 9–12 years) harvesting may take place, as people learned thousands of years ago (see

Color Plate 2a). Cork stripping must be done when the *phellogen*, or cork cambium, is active, in late spring and early summer. If performed when the cork cambium is inactive (i.e., winter or autumn), stripping may kill the stem because the inner bark is removed through the vascular (woody) cambium. Unlike the phellogen, the vascular cambium does not regenerate once exposed.

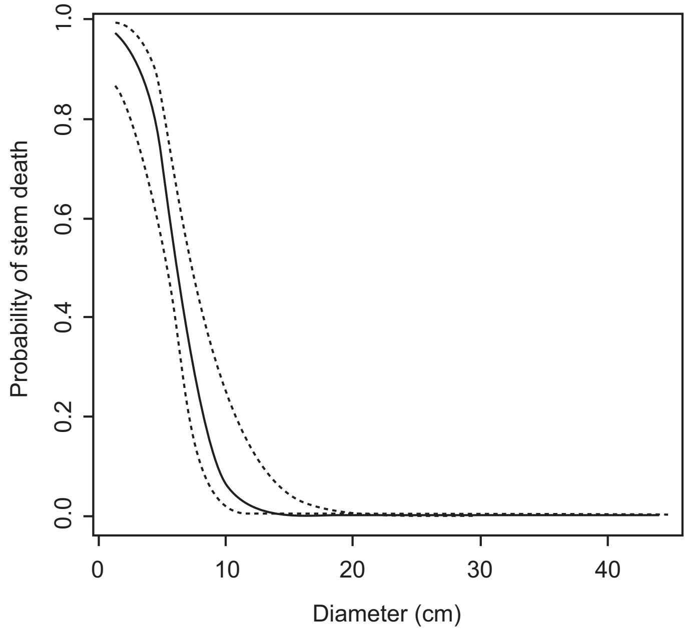
Cork harvesting has attracted a lot of interest and inspired much admiration and curiosity. It is commonly believed that cork harvesting weakens the trees. However, this is not the result of the loss of the plant tissue per se; the trees can and do cope with such a loss of biomass, which usually amounts to only a few percent of the total biomass production by the tree on a yearly basis. In the short term, cork stripping may cause the tree water stress (Correia et al. 1992; Werner and Correia 1996), but it recovers rapidly. A major negative consequence of cork stripping may be the exposure of the unprotected surface area of the trunk to invasion by pathogens (e.g., *Hypoxylon mediterraneum*; see Chapter 9) and the temporary reduction of protection from fire damage.

Surviving Fire: The Ecological Role of Cork

Fire has exerted a selective evolutionary pressure on flora and vegetation in all Mediterranean climate regions worldwide, and many species have evolved strategies to survive periodic fires (Pausas et al. 2004b; Pausas and Verdú 2005). Indeed, cork oak is an excellent example. If not harvested, the cork layer on the tree becomes very thick and constitutes a protective barrier against fire, as cork is a good insulating material protecting stem tissues from scorching and burning (Pausas 1997).

Most oak species have the capacity to resprout after severe disturbances, including fire, and most of them resprout from basal buds. However, the thick and insulating bark of cork oak protects almost all the *epicormic* or stem-borne buds, permitting them to resprout quickly and effectively from stem and crown buds (Pausas 1997; see Color Plates 12a–12d). Therefore, after a fire has burned a cork oak forest, most trees will survive. Some young trees may suffer stem death from fire because the bark is still too thin to provide thermal protection for stem buds (Figure 1.3a), although individuals may survive because they resprout from basal buds. Trees with trunk diameters larger than about 12 centimeters often survive a fire and resprout from crown epicormic buds. In these cases, the larger the cork oak tree, the quicker it will regenerate, and for a given trunk diameter, the thicker the bark, the quicker the tree will recover (Figure 1.3b). However, old trees may fail to resprout and thus die after

(*a*)



(*b*)

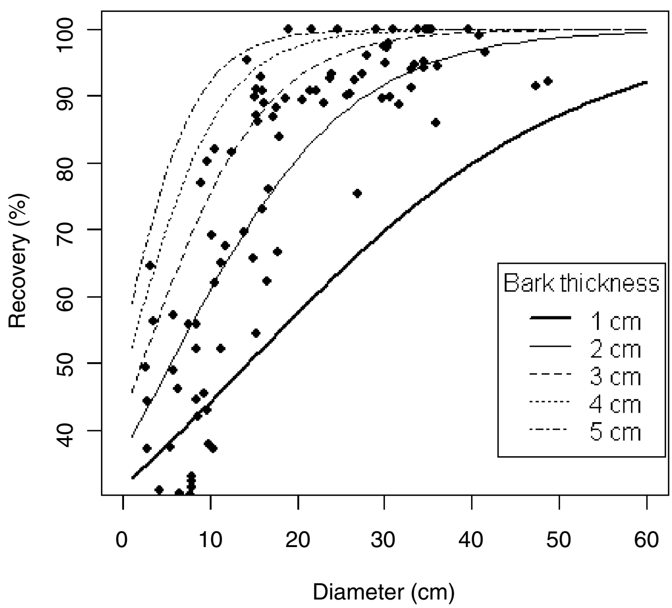


FIGURE 1.3. *(a)* Probability of postfire stem death mortality and *(b)* postfire height recovery from stem resprouts in cork oak. Height recovery is expressed as the percentage recovery from prefire height 1 year after the fire, in relation to stem diameter and bark thickness. (From Pausas 1997)

fire. Variations in bark thickness result not only from tree size or age but also from the number of years since the last bark stripping for cork production; indeed, when the bark has never been stripped (trees with virgin bark), the resprouting capacity tends to be higher (Moreira et al. 2007). Because bark thickness is a determining factor in postfire recovery, bark-stripping may reduce the ability of trees to recover from fires by reducing bud protection and thus increasing tree susceptibility to fire. Thus, recently harvested trees that have burnt resprout not from stem buds but rather from basal buds.

The evolution of an insulating corky bark is not exclusive to the cork oak; it also occurs in a few other trees growing in fire-prone ecosystems. For example, in southern Africa, the broad-leaved coral tree (*Erythrina latissima*, Fabaceae) and the spiked cabbage tree (*Cussonia spicata*, Araliaceae) both have thick, orange-colored corky barks. Also, the Australian forest she-oak (*Casuarina torulosa*, Casuarinaceae) has a vertically oriented corky bark. In these four unrelated species, as in the case of cork oak, the corky bark appears to be an adaptation for reducing fire damage. Thus, this unusual adaptation occurs in very different lineages and continents and could be considered a case of *convergent evolution*. Other trees living in fire-prone environments have also evolved thick barks composed of insulating structures different from cork, such as the thick bark of some *Pinus*, *Banksia*, or *Uapaca* species, or the thick peeling bark of some *Eucalyptus* and *Melaleuca* species from Australia. Nevertheless, there are some species with corky bark that do not occur in highly fire-prone ecosystems, at least currently, and their evolutionary history deserves further study. Examples of this group are found in the genus *Phellodendron* (from the Greek *phellos* = cork and *dendron* = tree; Rutaceae) and also include the so-called Chinese cork oak, both occurring in parts of Asia. The Chinese cork oak is related to the Mediterranean cork oak (Manos and Stanford 2001); its bark has been used for a variety of products (e.g., roofing), although the cork quality is much lower than that of cork oak.

Cork oak is undoubtedly one of the woody species best adapted to persist in recurrently burned ecosystems, and the postfire regeneration of cork oak–dominated landscapes is remarkably quick (Pausas 1997). It is the only European tree with the capacity to resprout from epicormic buds, high on the tree, a feature shared with many *Eucalyptus* species and the Canary Island pine (*Pinus canariensis*) but otherwise rare. The fact that cork oak can regenerate after fire from stem buds gives this species a competitive advantage over coexisting woody plants. For instance, a mixed cork oak and pine forest (see Chapter 13) may gradually be converted to cork oak woodland after repeated fires. Together with its socioeconomic importance and cultural significance (Chapters 13–16), this extraordinary resprouting capacity makes the cork oak a very good candidate for reforestation programs in fire-prone areas (Pausas et al. 2004a; Vallejo et al. 2006).

Framework Tree of Natural Ecosystems and Cultural Derivatives

Although we assume that cork oak is often favored by fire, most contemporary, monospecific cork oak stands clearly owe their existence to land use history and management decisions made by people. It seems likely that people have transported not only cork but also the live acorns of cork oak around the Mediterranean since prehistoric times. In its current range—the western half of the Mediterranean—we know that cork oak has been artificially protected, favored, and conserved not only for cork production but also for the valuable framework it provides in different agro-silvopastoral systems. Perhaps the best known and most extensive of these systems is the *dehesa* or *montado*, also known by other local names in different parts of southern Europe and Africa (see Chapter 3). This is an anthropogenic open woodland, used for grazing, sometimes cropped (e.g., cereals), but also used to obtain cork and acorns, as will be discussed at length in Chapters 3 and 4 (see Color Plates 4–7). In English, the term *oakery* is also used, as is *savanna*. But we prefer the simpler *woodland* or *open woodland* in this book, intended for a wide international, multilingual audience. It should be clear that *dehesas* or *montados* are different from most oak woodlands and savannas in that the structure and, to a large extent, the composition are maintained by a strong human input. In other parts of the world, people (e.g., Aborigines in Australia, Native Indians in America) also maintained other kinds of open woodlands and savannas, especially by periodically burning the understory (Jones 1969). But the intensity of the human input in *dehesas* or *montados* is much stronger than in most other woodlands and savannas.

Seminatural woodlands that are gradually becoming forests dominated by cork oak (as opposed to the *dehesa* or *montado* open woodlands) also occur and are used for cork extraction and for recreation (see Color Plate 8). Good examples occur in the Los Alcornocales Natural Park (see Site Profile 17.1) and in smaller patches of cork oak–dominated woodlands along the northeastern coast of the Iberian Peninsula (Pausas et al. 2006; Site Profile 8.1).

In Chapter 10 we discuss the implications of these two systems (*dehesa*-type open woodlands and forests) for oak regeneration. Another traditional system is the combination of cork oak with pines, found in Portugal, providing cork, acorns, and wood (in the case of maritime pine, *Pinus pinaster*), or all of these plus edible pine nuts when stone pine (*Pinus pinea*) is used.

Chapter 13, in Part IV of the book, is devoted to a discussion of this system from an economic perspective.

As mentioned at the outset of this chapter, the unique features of cork oak are adaptive traits that evolved in the context of Mediterranean climate and have progressively been put to use by people. In that sense, cork oak can be considered not only an emblematic but also an archetypal Mediterranean plant. Along with the holm oak and the olive tree it is also an ecologically and economically emblematic tree for Mediterranean landscapes, where people and nature have interacted for millennia.

The contribution of cork oak to sciences extends far beyond the Mediterranean basin. For example, the term *cell* was coined by Robert Hooke (1665) as part of his anatomical investigations of cork. We argue that it, and the landscapes in which it forms an important part of the framework, can also contribute greatly to environmental science and the practice of adaptive ecosystem and landscape management in today's rapidly changing world.

Having presented a brief profile of the tree itself and the biophysical and socioeconomic matrix in which it lives, we shall explore the current state of knowledge and the art relevant to cork oak woodlands. Today, cork oak woodlands are threatened by multiple stresses, both anthropogenic and natural, and a study of its alternative future will help us understand—and perhaps influence—the future of the entire Mediterranean basin. That study should also provide food for thought for students throughout the world. As the next step in setting the scene, Chapter 2 presents an up-to-date overview of the origin and genetic variability of cork oak, resulting from nature and nurture.