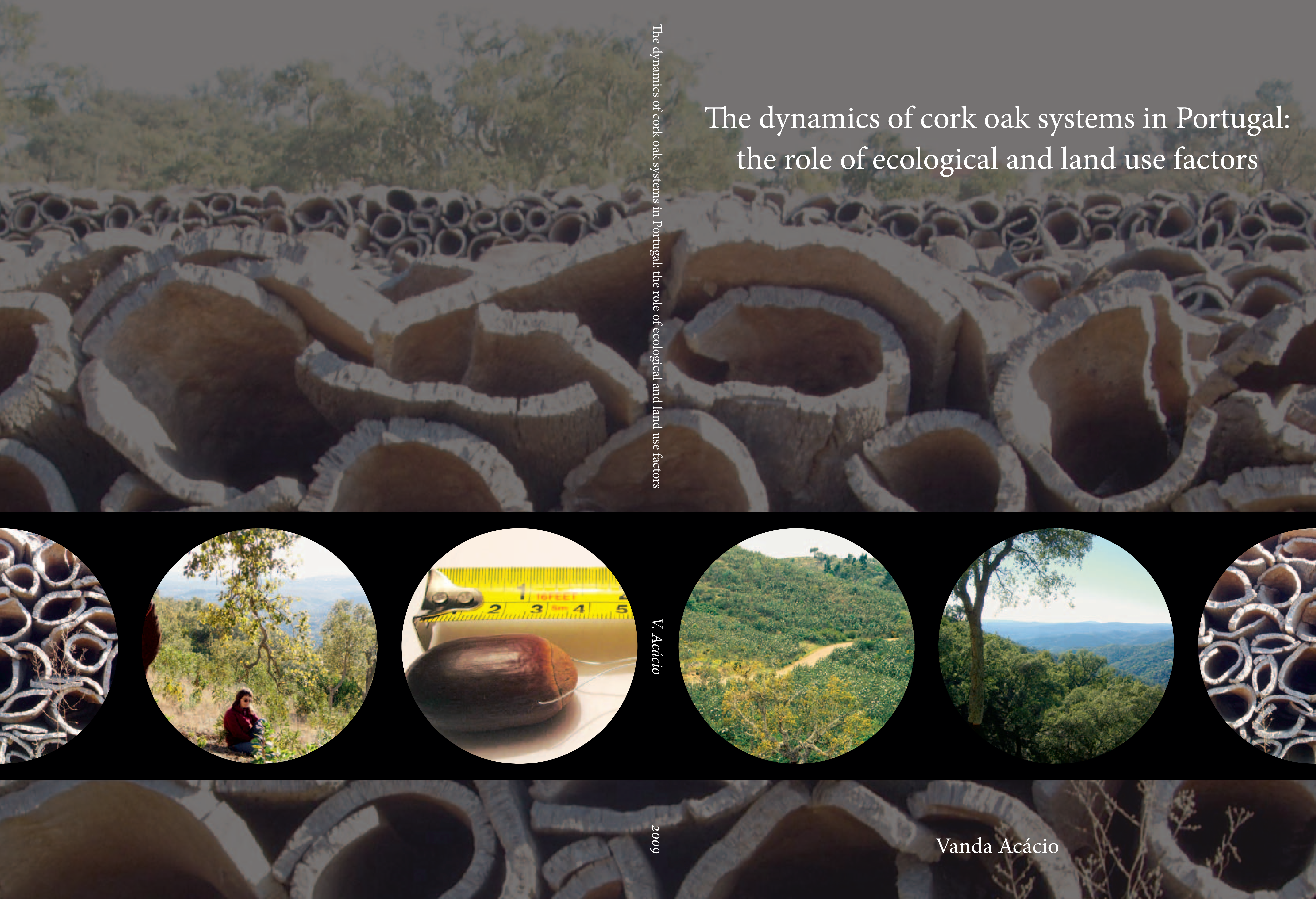

The dynamics of cork oak systems in Portugal: the role of ecological and land use factors

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Ao meu pai
To my father

Abstract

The landscape in southern Portugal is dominated by a distinctive Mediterranean land use system, in which cork oak (*Quercus suber* L.) is the main tree species. This area constitutes the largest cork oak habitat in the world. The cork oak land use system of today has a patchy appearance, which is the result of long-term combined ecological and land use dynamics that have shaped the landscape. In some cases, overexploitation of the land has led to soil degradation and erosion and a lack of natural regeneration of cork oak. Areas of degraded soil are commonly invaded and dominated by rockrose (*Cistus* spp.) shrubs; the resulting shrubby vegetation is very persistent and can be interpreted as a stage of regressive succession of the original forest. Succession has traditionally been thought to be a relatively linear process, but evidence from a variety of ecosystems indicates that persistent alternative vegetation states may occur, particularly after disturbances. The overall objective of this thesis was to evaluate if cork oak forests and *Cistus* shrublands represent alternative stable states in southern Portugal, and to ascertain the ecological and land use mechanisms underlying their resilience and persistence. All the data analysed for this thesis were collected at a study site in southern Portugal.

It is shown that *Cistus* shrublands have been the most persistent patch-type in the study area for 45 years (1958-2002) and have been expanding. Cork oak forests were also persistent but, contrary to shrublands, have been decreasing since 1985. Wildfires triggered transitions from forests to shrublands after 1995 and contributed to maintain shrubland patches, particularly on south-facing slopes. Persistence of *Cistus* shrublands is also explained by multiple mechanisms that severely constrain cork oak recruitment in shrubland patches (namely, limitation of seed source, dispersal, germination and establishment). On the other hand, cork oak persistence was more likely in areas with a combination of certain factors: where the understorey had not been managed before 1975, no cork oak had been planted since the 1980s, wildfires were absent and slopes were steeper. It was also found that fire resistance in cork oak is essentially determined by management decisions. Cork oak survival after a wildfire was lower in stripped trees, trees with thinner bark and trees with larger diameter (correlated with the number of stripping operations). Survival was also lower with increasing fire damage and on south to east oriented slopes in the study area, which are more xerophitic. The results also show that over half of the landowners interviewed hold traditional beliefs that run contrary to current scientific knowledge.

It is concluded that the future of the cork oak land use system in the study area is severely threatened by loss of resilience and that shrubland is an alternative stable state of lower vegetation biomass on the most degraded soils and dry areas, where conditions for forest recovery are extremely hostile. The findings suggest that cork oak land use systems in the study area are not sustainable if adequate management actions and restoration programmes are not enforced in the short term.

Key-words: *Quercus suber*, cork oak, *Cistus*, alternative stable states, wildfire, shrub encroachment, agroforestry, Mediterranean, landscape changes, tree recruitment, arrested succession, forest transitions, Portugal

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Chapter 1

General Introduction

Today's Mediterranean-type ecosystems have evolved through the major geological and climatic changes that took place during the Pleistocene period. Their vegetation, which has adapted successfully to natural disturbances throughout millennia, is considered highly resilient. The disturbance has been significantly increased by human activity such as tree and shrub clearing, livestock grazing, and ploughing for cultivation, especially in the Mediterranean Basin (Joffre *et al.*, 1999; Pulido *et al.*, 2001); this has contributed greatly to the present condition of the vegetation, sometimes jeopardizing its resilience.

Vegetation degradation and loss of woodlands has been observed in Mediterranean-type ecosystems worldwide, particularly in the Western Mediterranean Basin (Pignatti, 1978; Puigdefábregas, 1995; Puigdefábregas and Mendizabal, 1998). It is considered to be mainly caused by a combination of human management and climatic disturbances (Puigdefábregas and Mendizabal, 1998; Scarascia-Mugnozza *et al.*, 2000). Fire has also played a major role in shaping the landscape, having contributed to the present dominance of fire-resistant species, which have been able to survive due to their morphological traits, such as thick fire-resistant bark, resprouting and seed germination stimulated by fire.

The landscape in southern Portugal is dominated by a distinctive Mediterranean land use system. This area, where cork oak (*Quercus suber* L.) is the main tree species, is the largest cork oak habitat in the world. The cork oak is a sclerophyllous evergreen tree that develops a special bark: the cork. The cork oak land use system of today is the result of long-term combined ecological and land use dynamics that have shaped the landscape. In some cases, overexploitation of the land led to soil degradation and erosion and a lack of natural regeneration of cork oak (Natividade, 1950; Gonçalves, 1991; Montero *et al.*, 1994a). Areas of degraded soil where cork oak natural regeneration becomes difficult are commonly invaded and dominated by rockrose (*Cistus* spp. shrubs); the resulting shrubby vegetation is very persistent and can be interpreted as a stage of regressive succession of the original forest.

Succession has traditionally been thought to be a relatively linear process, but evidence from a variety of ecosystems indicates that persistent alternative vegetation or ecosystem states may occur, particularly after disturbances (Friedel, 1991; Laycock, 1991; Scheffer *et al.*, 2001). The existence of alternative stable states causes discontinuous responses to increasing disturbances; such responses are often difficult to reverse (Noy-Meir, 1973; Westoby *et al.*, 1989; Laycock, 1991; Rietkerk and Van de Koppel, 1997; Rietkerk *et al.*, 1997; Scheffer *et al.*, 2001). Beyond a certain critical threshold, the response changes and the ecosystem suddenly collapses to another state. Alternative stable states separated by critical thresholds have been observed for different semi-arid Mediterranean vegetation types around the world, for example in Chile (Fuentes *et al.*, 1984; Holmgren, 2002), California (Laycock, 1991), Australia (Friedel, 1991; Standish *et al.*, 2007; Standish *et al.*, 2009), South Africa (Friedel, 1987), and the Mediterranean Basin (Pignatti, 1995; Puigdefábregas and Mendizabal, 1998).

The persistence of shrubland (i.e. scrub) in cork oak areas in southern Portugal implies that forest resilience has been lost and a threshold has been exceeded beyond which former vegetation can no longer be restored and is replaced by a different vegetation of lower biomass. Shrubland may represent an alternative persistent state of lower vegetation biomass on the most degraded soils and drier areas, possibly jeopardizing the long-term viability of cork oak ecosystems. To date, there have been no studies identifying alternative stable states for cork oak ecosystems or analysing the underlying mechanisms of alternative states for these ecosystems. The research reported in this thesis aimed to evaluate if cork oak forests and *Cistus* shrublands represent alternative stable states in southern Portugal and to elucidate the ecological and land use mechanisms underlying their resilience and persistence. Sustainable management, conservation and restoration of the cork oak land use system depend on better knowledge of likely vegetation states, the transitions between states, the mechanisms that drive these transitions and their irreversibility.

Ecology of Mediterranean cork oak forests

MEDITERRANEAN-TYPE ECOSYSTEMS

The Mediterranean climatic regime is characterized by dry summers and mild winters. It occurs in five main regions of the world, located between latitudes 32° and 40° north and south of the equator, on the western side of the continents, namely in the Mediterranean Basin, California, central Chile, southwestern Australia and the southwestern tip of South Africa (Naveh, 1974). The Mediterranean climate developed during the Pleistocene (2 million years ago) when summer rainfall decreased greatly (Raven, 1973). At present, Mediterranean climate regions occupy only about 1% of the Earth's surface (Perez, 1990), but more than half of this area is in the Mediterranean Basin (Aschmann, 1973). However, despite their small area, Mediterranean ecosystems are recognized as biodiversity hotspots (Myers *et al.*, 2000; Olson and Dinerstein, 2002).

The original Mediterranean vegetation is considered to be evergreen forest (Walter, 1973; Pignatti, 1978). Fossil evidence suggests that sclerophylly evolved in response to a low-nutrient status regime during the Paleogene (Paleocene-Oligocene – 65 to 24 million years ago), before the development of Mediterranean climate, and proved to be an advantage when summer drought became the predominant climatic feature (Clark, 1996). These evergreen forests were characterized by great stability over time, whereas deciduous forests seem to be younger: they did not appear until the Pleistocene (1.8 million years ago), mostly at higher altitudes (Pignatti, 1978).

THE EVOLUTION OF VEGETATION IN THE IBERIAN PENINSULA AND THE CORK OAK SPECIES

The Iberian Peninsula had assumed its current form by the Pliocene Epoch (3 million years ago) (Pignatti, 1978). Recent results from pollen analysis clearly show that the forest cover of the Iberian Peninsula after the Pliocene was predominantly composed of species from the *Fagaceae* family, such as *Quercus*, including cork oak (*Quercus suber*), and conifers (*Juniperus* and *Pinus*) (Castro *et al.*, 1997). It has been argued that during the last glacial period (18 000 years ago, the Würm period), cork oak would have survived in the southern and coastal areas of the Iberian Peninsula and North Africa (Carrión *et al.*, 2000). After the glacial period (10 000 years ago, Holocene) the cork oak spread from such refuges that functioned as the recolonization nuclei, and there was an increase of the area under cork oak and other evergreen forests (Capelo and Catry, 2007).

There is still debate about the exact origin of the cork oak species (Magri *et al.*, 2007; Lumaret *et al.*, 2009). The higher genetic diversity in the Iberian populations (Toumi and Lumaret, 1998), the findings of geobotanical studies (Sauvage, 1961), and the current absence of the species from the eastern Mediterranean area, suggest that Iberia was either the local origin of the cork oak or was a secondary centre for its evolution, after the beginning of the Quaternary glaciations (Natividade, 1948). However, based on fossil records, several authors also contend that cork oak probably first appeared in the Balkan Peninsula or the Caucasus region (Bellarosa *et al.*, 2005 and references therein), and genetic studies indicate an eastern Mediterranean origin for the cork oak (Lumaret *et al.*, 2009).

Present-day Mediterranean climatic conditions have existed for less than 10 000 years (Paskoff, 1973). Many authors agree that since then the forest cover of the Iberian Peninsula has predominantly consisted of woods of evergreen *Quercus* species, mainly cork oak (*Quercus suber*) and Holm oak (*Quercus ilex* L.) (Castro *et al.*, 1997). The cork oak seems to be an older and more persistent species than the Holm oak (Castro *et al.*, 1997). It is likely that cork oak and Holm oak made up different combinations of mixed forests, together with other *Quercus* species (*Quercus coccifera* L., *Quercus faginea* Lam. and *Quercus canariensis* Willd.), *Pinus* species (*Pinus pinaster* Sol. in Aiton and *Pinus pinea* L.), and a diverse shrubby understorey (species of *Erica*, *Pistacia*, *Myrtus*, *Viburnum*, *Sambucus*, *Phillyrea*, *Cistus*, *Buxus*, *Rhamnus*) (Carrión *et al*., 2000; Aguiar and Pinto, 2007). Some of these shrubs are common today in cork oak forests whose understorey is less disturbed.

At present, southern Iberian Peninsula forests dominated by cork oak form the climax community named *Quercetum suberis*, which may be accompanied by other oaks (*Quercus ilex*, *Quercus faginea*, *Quercus robur* L. or *Quercus pyrenaica* Willd.) and shrubs such as *Phillyrea angustifolia* L., *Lonicera implexa* Aiton, *Viburnum tinus* L., *Rhamnus alaternus* L., *Pistacia lentiscus* L., *Arbutus unedo* L., *Asparagus acutifolius* L., *Ruscus aculeatus* L. and *Rubia peregrina* L. (Natividade, 1950). In degraded climax cork oak forests, understorey shrub species are replaced by more ruderal and sclerophyll species (*Cistus*, *Lavandula* and *Ulex*).

THE CORK OAK TREE

Cork oak is a sclerophyllous evergreen tree, today limited to the Western Mediterranean region (Natividade, 1950), its largest extent being in Portugal, approximately 737 000 ha, about 30% of the species area worldwide (DGRF, 2007). Its optimum climate is a Mediterranean climate tempered by Atlantic influence, with annual precipitation between 600 and 800 mm and temperature ranging from 15 to19ºC, but thanks to their extensive and deep root systems, trees can survive in drought years with less than 500 mm of annual precipitation. The cork oak is almost entirely restricted to soils derived from siliceous rocks, being commonly considered acidophilus and calcifugous or lime intolerant (Natividade, 1950; Montero, 1988).

Cork oak begins fructifying at an age of 15-20 years. Florescence occurs during a prolonged period from March to June. The vector for pollination is wind and the development of male and female flowers is asynchronous in each tree. Acorns can mature the same year as the flowers that produced them (annual acorns), or in the autumn of the next year (biennial acorns). The proportion of annual and biennial acorns varies in response to environmental factors and meteorological conditions (Díaz-Fernandez *et al.*, 2004). The biennial cycle seems to be related to short plant growth periods, limited by cold or drought (Pausas *et al.*, 2009b). Cork oak is a mast-seeding tree: in each ten-year period there are two or three more abundant acorn harvests. Usually, abundant harvests coincide with rainy springs (Natividade, 1950). In addition, acorn production can vary greatly between individual trees within a population in any given year, depending on whether male or female flowers dominate in the tree, on tree density or aspect (Pausas *et al.*, 2009b).

Acorns fall to the ground from mature trees between October and January. They can be dispersed by animals or predated. The main seed dispersers are wood mouse (*Apodemus sylvaticus*) and European jay (*Garrulus glandarius*). Jays promote long-distance dispersal, whereas mice promote short-distance dispersal (Pausas *et al.*, 2009a). Animals such as jays and mice, which cache the seeds, are often effective dispersal agents of oak species, with recruitment originating from unrecovered seeds (Herrera, 1995). The acorn predators are mainly insects, such as the acorn weevil (*Curculio* spp., Coleoptera) and the acorn moth (*Cydia* spp., Lepidoptera), and wood mice. In open areas, the predators can also be deer, wild boar, birds and rabbits; under a shrub canopy the main predators are small rodents, since neither large mammals nor birds will penetrate the dense vegetation (Herrera, 1995). Livestock (pigs, cows, goats and sheep) also eat the acorns.

When temperature, canopy and soil moisture conditions are favourable, fallen acorns germinate during December-January and emerge from February until June. Although oaks are shade species during their first years of life (Callaway, 1992; Pulido *et al.*, 2001), cork oak seedling survival and growth may be severely limited by light deficit under dense oak canopies, as well as by summer water deficits, and also by the interaction of both. The interaction between drought and shade on cork oak seedling performance has been the subject of debate (Pausas *et al.*, 2009a), but it has been shown that in the Mediterranean environment, shading may significantly alleviate drought stress in cork oak seedlings (Quero *et al.*, 2006). Seedlings growing under a shrub canopy may also compete with shrubs for water and nutrients (Montero *et al.*, 1994a). It is likely that facilitation by shrubs occurs simultaneously with competition for light, soil water and nutrients (Callaway, 1992; Holmgren *et al.*, 1997). Whether the interactions between oak seedlings and shrubs are positive or negative probably depends on the environmental context (Holmgren *et al.*, 1997; Rousseau and Lepart, 2000).

Cork oak is a slow-growing tree with a high longevity like other oaks, with a lifespan of 250-300 years. Tree growth is more active during spring and summer (February-July), especially May-July, and slows down or even stops due to summer high temperatures, resuming in October. In the winter (November-March), tree growth stops until temperatures rise again in spring; the replenishment of soil moisture by winter rainfall contributes to the next year's spring growth (Costa and Pereira, 2007a).

The cork cambium (also called phellogen) is a meristematic layer of cells found in many vascular plants, which is responsible for secondary growth and replaces the epidermis in roots and stems. It is normally only one or two cell layers thick: the inner layer produces phelloderm on the inside and the outer layer produces cork on the outside (similarly to the vascular cambium that produces xylem inwards and phloem outwards). The periderm thus consists of three different layers: the phelloderm, the cork cambium (or phellogen) and the cork (also termed phellem). Cork is a tissue of dead cells (without any physiological activity) that contains suberin, a waxy substance that protects the stem against water loss and the invasion of insects, and prevents infections by bacteria and fungal spores. The growth and development of cork cambium varies greatly between different species, and is also highly dependent on age, growth conditions, etc. In most tree species, the cork cambium lives for only a few years and new cork cambium is periodically formed inside, deeper in the phloem tissue. Thus, the outer bark of most trees is made of successively deposited thin layers of cork intercalated with a tissue called rithydome, which is dead phloem. In the cork oak, however, the same cork cambium remains active, throughout the tree's life, and the outer bark is therefore formed of continuous layers of suberized cells (Graça and Pereira, 2000). The cork increases in thickness by about 2-5 mm per year, up to 20 centimetres; the thickness depends on various factors, such as tree genetics, tree age, climatic conditions and soil type (Pereira, 2007a). When cork is removed by cork stripping, the cork cambium cell layer dies and a new cork cambium forms in the non-active part of the underlying phloem tissue. The new cork cambium immediately starts cell division, and a new cork layer is formed. Because it is impermeable, cork functions as a protective barrier between the living tissues inside the tree and the exterior environmental conditions, for example preventing water loss and protecting against high temperatures.

The only other oak known to develop cork is the Chinese cork oak (*Quercus variabilis* Blume); however, its cork yield is lower. Natividade (1948) contends that cork did not evolve as a response to drought, but as a genetic modification of some kind. He points out that oaks with greater affinity to the cork oak (such as the Holm oak) can withstand more severe drought conditions but have not developed such a feature.

Human management

LONG-TERM HUMAN IMPACT

The Mediterranean Basin has been populated for about 20 000 years (Pignatti, 1978). Humans' need for wood for heating, construction and shipbuilding, combined with the spread of agricultural practices and grazing in deforested lands for several millennia caused the destruction of the original Mediterranean forest (Pignatti, 1978; Scarascia-Mugnozza *et al.*, 2000).

Evergreen oak forests used to be widespread in the Mediterranean Basin (Walter 1973; Pignatti 1978). The existence of scattered small cork oak woods all over the Iberian Peninsula suggests that the area of distribution in the past used to be larger and more continuous (Castro *et al.*, 1997, Carrión *et al.*, 2000). It is thought that only about 10% of the former Iberian cork oak forests remain (Castro *et al.*, 1997). Cork oak areas were gradually transformed into open woodlands as a result of overgrazing, clearing and ploughing for agriculture. In some cases, degraded woodlands were substituted by other vegetation types, such as shrublands like the Mediterranean "macchia" and the "garrigue" (Pignatti, 1978; Scarascia-Mugnozza *et al.*, 2000). Human demography and human needs affected the frequency and intensity of the disturbance through the ages, and hence the expansion or contraction of the area occupied by forest (Quézel and Barbero, 1990).

THE ROLE OF FIRE

In all Mediterranean climate regions worldwide, many plant species have evolved strategies to survive the natural fires, which can occur periodically during the dry summers. However, the influence of fire on shaping Mediterranean vegetation and landscape increased greatly after humans started using fire as a management tool. Fire has been used as a management tool for about 10 000 years in the Mediterranean Basin (Thirgood, 1981; Trabaud, 1981) to prevent the regeneration of the forest, and for hunting, cooking, heating, pasturage, fertilizing, weed and pest control (Naveh, 1990).

The fires started by humans were generally regular and frequent: they led to a loss of biodiversity and of stratification, and to the vegetation becoming dominated by species that are fire-adapted (Barbero *et al.*, 1990; Trabaud, 2003). The overall fire adaptation of Mediterranean plants can be divided into two opposite strategies: plants that are fire-resistant (withstand fire passively), and plants that are dependent on fire to germinate (active pyrophytes) (Naveh, 1974). The development of specialized features such as thick fire-resistant bark, resprouting, seed germination stimulated by fire, and flammability, allowed for these responses. Today, most species that dominate Mediterranean-type ecosystems show adaptive strategies for post-fire recovery. Less resistant species have been eliminated.

Cork oak is fire-resistant, being partially protected against fires by bark insulation (the cork) and being able to resprout after fire. Resprouting is an efficient mechanism through which the tree is able to recover aboveground biomass. Sprouting shoots originate from dormant buds located aboveground or from the base of the plant (collar, roots or underground stems) (Bond and van Wilgen, 1996; Del Tredici, 2001; Keeley, 2006). The cork oak is the only European tree able to resprout from epicormic buds located high on the tree (Pausas *et al.*, 2009b). Thus, most trees will survive after a fire. However, the rate of tree recovery may decrease with increasing wildfire frequency because of lower resprouting success and higher oak seedling mortality (Díaz-Delgado *et al.*, 2002). Intense wildfires may also kill mature trees, especially if the cork has recently been harvested and hence the remaining cork layer is too thin to protect the tree against the heat from the fire (Moreira *et al.*, 2007; Pausas *et al.*, 2009b).

HISTORICAL HUMAN USE OF CORK OAK FORESTS IN PORTUGAL

Before the 15th century, cork oak woods were used by kings and nobility to hunt large game, for firewood and for extensive grazing. Between the 15th and the 17th centuries the area covered by cork oak in Portugal diminished substantially because wood was increasingly needed for shipbuilding, and the land was need for growing crops and for pastures.

Cork began to be used for wine bottle stoppers after the 17th century, and acquired an increasing commercial value. From the 18th century onwards, a land use system that included cork extraction, crop cultivation and livestock grazing at the farm unit level became common, and constituted what is called an agro-silvopastoral production system or agroforestry system (Joffre *et al.*, 1999; Pulido *et al.*, 2001; Mendes, 2007; Pinto-Correia and Fonseca, 2009). Cork oak agro-silvopastoral systems in the Iberian Peninsula have a specific name: "montados" in Portugal and "dehesas" in Spain. They generally have a low tree density (40 to 80 trees/ha), with trees exploited for cork and the understorey cleared of shrubs for grazing, crops (mainly wheat, barley and oats) or both.

When the canopy structure of Iberian cork oak agro-silvopastoral systems has a low tree density, the vegetation closely resembles natural savannas. This is probably why these systems have been compared to savanna ecosystems, although there is no real ecological similarity. Mediterranean climatic and soil conditions favour woody rather than herbaceous species, which is why savannas have always had an anthropogenic origin in the Mediterranean Basin (Tomaselli, 1981). Such systems must be continually maintained through human management by thinning and understorey use through grazing, ploughing and shrub clearing (Marañón, 1988; Huntsinger and Bartolome, 1992; Díaz *et al.*, 2003).

It is likely that the management of such agro-silvopastoral systems throughout the centuries also included promoting natural regeneration of oak and artificially seeding or planting, in order to maintain cork production. In fact, during the first half of the twentieth century, the area under cork oak in Portugal doubled (from 410 000 ha to 824 000 ha), although these figures are estimates since they are based on completely different sources and methods of calculation (Capelo and Catry, 2007).

From 1929 until the early 1960s, most of the land in southern Portugal was cultivated for wheat, following a government policy known as the Wheat Campaign that strongly subsidized wheat production (Baptista, 1993), which resulted in depleted soil fertility and increased erosion (Puigdefábregas and Mendizabal, 1998; Pinto-Correia and Vos, 2004). Only the forest areas on steep slopes were not put under wheat, because here the gradient made understorey management for crops difficult or impossible.

Between the 1960s and 1970s the agricultural workforce in Portugal decreased by about one third (Baptista, 1993) as a result of wide-ranging national and international socio-economic changes (industrialization, agricultural mechanization, the exodus to cities and emigration) and there was massive rural depopulation. The land use system followed a dual process: 1) abandonment of understorey use in the least productive land and smaller properties, with cork maintained as the single production component; 2) maintenance of the agro-silvopastoral system in flat areas and on larger properties, sometimes with intensified production within more fertile regions (Pinto-Correia and Mascarenhas, 1999).

Between 1975 and 1995, the area occupied by cork oak in Portugal increased by approximately 10% (from 657 000 ha to 713 000 ha) (DGF, 2001) because new plantations were subsidized by Common Agriculture Policy (CAP) (Pereira *et al.*, 1999). From 1995 to 2006 there was a further rise – of over 3% – in the area under cork oak in Portugal, to 737 000 ha in 2006 (DGRF, 2007). But the area of pure stands of cork oak in Portugal fell from 592 300 ha in 1995 to 591 700 ha in 2006 (DGRF, 2007). There were regional differences: the area under cork oak increased in the provinces around Lisbon and Alentejo (south of Lisbon) between 1995 and 2006 (DGRF, 2007), probably due to new plantations (Vallejo *et al.*, 2009), but it decreased in the north, centre and Algarve provinces (of about 53%, 46%, and 29%, respectively) (DGRF, 2007).

CURRENT USE OF CORK OAK FORESTS IN PORTUGAL

At present there are two main types of cork oak management systems in Portugal: 1) cork oak forests, which are managed solely for cork without understorey cultivation; 2) agro-silvopastoral systems (the montados or dehesas), which are managed for cork, with the understorey used for pasture, crops, or both.

Cork oak forests have higher tree density than agro-silvopastoral systems (more than 100 trees/ha) and when not regularly cleared for fire prevention the understorey contains diverse shrub species (e.g. *Arbutus unedo*, *Pistacia lentiscus, Phillyrea angustifolia*, *Lonicera implexa*, *Ruscus aculeatus*). Cork oak forests today cover a small percentage (about 30%) of the total cork oak area in Portugal and are located mainly in the mountain regions of Algarve, hilly areas of Alentejo and the north of the country, where the soils have low fertility and are shallow (Diniz, 1994). The forests in Algarve and Alentejo result from understorey use being abandoned after the rural exodus in the 1960s, which allowed the forests to recover, but also include areas where understorey management was rarely practised because of the difficult terrain. The cork oak forests in northern Portugal constitute only 1% of the total cork oak area and are the closest approximation to pristine forests.

Agro-silvopastoral systems currently cover 70% of the total cork oak area in Portugal (Costa and Pereira, 2007a) and are found mainly in the province of Alentejo, on flat terrain. Tree density is determined by the need for space for pasture or cereal cultivation in the understorey; the density is lower in the areas preferred for cereal cultivation (Gómez-Gutiérrez and Pérez-Fernández, 1996). Land use intensity (grazing and crop production) depends on soil fertility and landholding size: on smaller properties and where soils are less fertile, grazing is more extensive; on larger properties and very fertile soils, land use is intensified.

The recent changes to the CAP in which grants paid to farmers for growing cereals and keeping grazing livestock have been replaced by single payments to farmers (decoupled from production) have contributed to the decay of the traditional agro-silvopastoral system and to a fall in cereal and livestock prices (Bugalho *et al.*, 2009). Cork is currently the most valuable product from the cork oak land use system (Pereira, 2007b; Mendes and Graça, 2009). This being the case, the agro-silvopastoral land use systems are gradually being transformed into cork oak forests managed for cork production. Additionally, new cork oak plantations are being planted with high tree densities for cork production (Costa and Pereira, 2007a). Since 1985, particularly on large private estates (100 ha or more) in southern Portugal, these plantations have increasingly included mixed stands of cork oak and stone pine (*Pinus pinea*), which are exploited for cork and pine nuts (Coelho and Campos, 2009).

FOREST MANAGEMENT FOR CORK PRODUCTION

Cork is removed for the first time ("virgin cork") when trees have a perimeter at breast height of 70 cm (around 20-25 years of age) and every nine years thereafter, within a rotation of 150-200 years, which corresponds to 16-20 consecutive cork extractions (every 9 years) during the life of a tree. The first and second extracted corks have low economic value. Only the third debarking allows obtaining cork with adequate characteristics for industrial processing, which means that the tree only becomes profitable when it is about 40 years old.

Cork is stripped in late spring and early summer, when the phellogen is active, which facilitates the extraction of cork and avoids killing the stem (Pausas *et al.*, 2009b). Cork is removed manually by using a special axe to cut along vertical and horizontal lines on the stem and thicker branches, stripping off large planks of cork. The procedure must be done very carefully, to avoid wounding the tree; the axe is disinfected between every tree debarking. Recent experiments using machinery to extract cork have not yielded successful results. The harvested cork is stacked in big piles on flat areas in the open air and left to dry. The cork planks lose water very rapidly and in about 9 days their water content is less than 14% and they may be considered as commercially dry cork (Pereira, 2007b).

Next, the cork is stored for a few months and boiled to remove any toxins or other harmful agents, before being graded and cut. After a final cleaning and drying, the cork is sorted and ready for use.

One of the main consequences of cork extraction for the tree is the loss of water through evaporation (Correia *et al.*, 1992), but the tree recovers quickly. Other consequences of cork stripping that can have very negative impacts on the trees are the susceptibility of the exposed bark to the invasion of pathogens, and the temporary reduction of protection from fire damage. Portuguese legislation prescribes that a minimum period of 9 years must elapse between any two consecutive cork extractions from the same tree. Reducing that period may have a negative impact on future yields from the tree, or even lead to mortality (Natividade, 1950). However, it seems that it was the need to obtain cork planks of a certain thickness for industrial use that dictated the duration of the cycle (Pereira, 2007b). Portuguese legislation also prescribes that a tree for cork extraction must have a minimum perimeter of 70 cm at breast height (1.30 m). Additionally, cork oaks are legally protected and cannot be felled without government authorization.

Other technical interventions that are usually carried out in cork oak stands managed for cork extraction include pruning, thinning and shrub clearing. Pruning is necessary to select and form the main trunk in young trees and to gradually clear the trunk of lower branches. The first pruning is done when the tree is 4-8 years old; the next is 4-8 years later. The third pruning is done after the first debarking, and the fourth after the second debarking (Soares *et al.*, 1998). There are strict legal requirements regarding pruning. Pruning can only be done between November and March, when the tree is not actively growing.

Thinning is done to reduce tree density, select the best trees, and also to eliminate sick or dead trees in mature stands. It is done every 6-9 years in young stands and every 15-20 years in mature stands. Because cork oak is legally protected, thinning has to be authorized by the forest services. A density of 120 trees per hectare is the optimum figure quoted for an uneven-aged mature cork oak stand for cork production (Costa and Pereira, 2007b). However, average tree density in Portugal is low: about 67 trees per hectare (Costa and Pereira, 2007b).

Shrub clearing is usually done regularly (every 4-5 years), to minimize the risk of fire, and before every cork extraction. Clearing can be done more frequently when stands are young, to prevent competition between the roots of the saplings and shrubs.

One important distinction between the cork oak silvicultural system and general silvicultural systems for wood production is that cork is obtained without felling the trees and therefore it is important to have an uneven age structure so that stands can be renewed and young trees can replace older ones. Stands can be renewed through natural regeneration, or by sowing or planting. However, artificial reforestation does not create uneven-aged stands with a diverse tree age structure, and the soil preparation necessary during the first few years of reforestations reduces the diversity of flora and fauna. Furthermore, mature stands with an even-aged structure create a smaller number of habitats for fauna species than stands with a diverse age structure (Zavala *et al.*, 2004).

In recent decades, planted cork oaks have had low survival rates (Almeida *et al.*, 2009). Natural regeneration is thus the best method for the perpetuation of stands and therefore the survival of seedlings is essential. In stands with high grazing intensity, it is necessary to protect existing natural regeneration from livestock, particularly cattle, as they can be very harmful to young trees. Restricting livestock to certain areas is a common practice (Zavala *et al.*, 2004), but this is only possible if the landholding is large enough (Bugalho *et al.*, 2009). Another common practice is to use individual tree shelters to protect young saplings from grazing, especially in cork oak reforestations. And when removing shrubs, care should be taken not to damage existing seedlings. Shrubs should not be cleared from large areas, because shrubs are the natural habitats of animals like the wood mouse that promote seed dispersal, and shrubs may also provide some protection when oak seedlings are establishing (Zavala *et al.*, 2004).

In summary, to manage and perpetuate cork oak forests and agro--silvopastoral systems without sowing or planting, it is necessary to ensure that adequate silvicultural practices are applied and to carefully consider the season and the number and type of grazing animals, in order to optimize economic production while having the minimum impact on natural regeneration, biodiversity and ecosystem functioning.

Forest resilience and sustainability

Disturbances

Centuries of farming practices (shrub clearing, grazing and ploughing) have affected the understorey vegetation, whereas forestry practices (thinning and pruning) have affected tree density and cover. The heavier machinery (wide ploughs, disk harrows and scarifiers) used in the second half of the 20th century had disastrous results on natural regeneration and young trees, and damaged tree roots, especially in drier sites or during drought periods when trees become more dependent on their extensive superficial root system for survival (Aronson *et al.*, 2009; Bugalho *et al.*, 2009).

Lack of cork oak natural regeneration is currently considered one of the main threats to the sustainability of cork oak landscapes in the Iberian Peninsula, despite successful regeneration in some places (Montero *et al.*, 1994a; Montero *et al.*, 2000; Pulido and Díaz, 2002; Costa and Pereira, 2007a, Pausas *et al.*, 2009a). Most cork oak agro-silvopastoral systems in the Iberian Peninsula are almost devoid of juvenile age classes (Plieninger *et al.*, 2003), which may lead to a lack of tree replacement. Tree density in Portugal has fallen over the last decade: stands with less than forty trees per hectare increased from 10% of the cork oak area in 1995 to 30% in 2005 (Vallejo *et al.*, 2009).

Regeneration and stand structure might be also influenced by past grazing regimes acting over decades (Plieninger and Pulido, 2009). In Portuguese agro-silvopastoral systems, which account for more than half of the cork oak area in Portugal, the trees are aging, natural regeneration is almost non-existent and tree recruitment is not sufficient to compensate for natural or induced mortality (DGF, 1990; Oliveira and Costa, 1992; CESE, 1996; Costa and Pereira, 2007a). If not protected, established seedlings are eaten by livestock; when the livestock density is high, major disturbance to the soil and to tree roots is caused through trampling (Diniz, 1994; Pinto-Correia and Mascarenhas, 1999). Overgrazing and the lack of acorn dispersal agents have been pointed out as the two key factors limiting oak regeneration in agro-silvopastoral oak systems (Pausas *et al.*, 2009a). In moderately grazed stands, recruitment occurs in most years (Pons and Pausas, 2006; Pausas *et al.*, 2006).

In cork oak forests, where tree density is higher, natural regeneration is more likely to succeed thanks to the shade from the canopy; the microclimate is benign, with moister soil and less thermal stress. Furthermore, here the understorey is not cultivated, livestock is absent or rare, and dispersal agents are present (both jays and mice, which promote long and short distance acorn dispersal, respectively) (Pausas *et al.*, 2009a). However, shrubs are regularly cleared from cork oak forests to prevent combustible material accumulating and thus to reduce the risk of fire, and also to facilitate cork extraction; if heavy machinery is used, the clearing can disturb the soil and damage natural regeneration of oak. Nowadays, lighter machines are used more often, which results in less impact on the physical and chemical soil properties. In any case, bare soil in hilly areas on rocky and low fertile soil types where cork oak forests frequently grow is very prone to erosion, especially given the common heavy rainfall events.

Abnormal cork oak mortality has been reported in the Mediterranean region since the end of the 19th century, but has become a matter of great concern more recently. Indeed, a dramatic increase in cork oak vulnerability to pests and diseases has been confirmed throughout the Western Mediterranean in the last few decades, including in Portugal (Branco and Ramos, 2009). Thousands of trees have died in recent years from disease, which seems to be part of the general decline in oak throughout Europe. Cork oak mortality has been attributed to several causes. Among the factors quoted are pathogen attack (particularly a fungus - *Phytophthora cinnamomi*), drought stress, intensive cereal cultivation, deep furrowing, the use of heavy modern machinery that has weakened the root systems, and ecological regression of the cork oak forest associations (Ferreira, 2000). Many researchers claim that plagues and diseases are a consequence of the trees' weakness, and not the major cause of the problem, since a healthy tree has good resistance, and such diseases have been around for some time. In short, a com<bination of natural and anthropogenic factors predisposes, or leads to, or else unleashes the decline (Ferreira, 2000). Decline is more evident in the southern part of Portugal, especially in Algarve, perhaps reflecting the influence of environmental factors: poor soils and south-facing sites seem to favour the occurrence of *P. cinnamomi* (Moreira and Martins, 2005). Scientists have been researching for decades to solve this problem, but have not found unequivocal answers, so the precise causes of generalized cork oak decline remain unclear (Branco and Ramos, 2009). Furthermore, there are no sound statistics on the real area affected by the disease.

Another recent threat to cork oak systems is the great increase in fire frequency in the last few decades in the Mediterranean Basin, particularly in Portugal (Perez-Trejo, 1994; Moreno *et al.*, 1998, Silva and Catry, 2006). Portugal is the country with the highest incidence of forest fires in the whole of Europe (relative to the forest area) (FAO, 2001a). This is due to rural desertification since the 1970s, the very fragmented landholdings, and the absence of forest management techniques (Gomes, 2006; Mendes and Fernandes, 2007), probably in combination with increasing temperatures and drought periods in recent decades (Pereira and Santos, 2003).

Although cork oak is able to withstand fire due to its protective bark (cork), frequent or intense wildfires may kill mature trees, especially if wildfires occur immediately after cork extraction (Cabezudo *et al.*, 1995; Pausas, 1997; Moreira *et al.*, 2007), which takes place in the summer, when the wildfire season begins in Mediterranean Europe. Furthermore, the capacity of cork oaks to resprout after fire may decrease (Díaz-Delgado *et al.*, 2002).

Additionally, present climate change models predict more frequent droughts and intense rain events for Mediterranean climate regions (Cubash *et al.*, 1996; McCarthy *et al.*, 2001). Under this scenario, wildfire frequency and soil erosion are expected to intensify. Climatic conditions might also interact with diseases: drought and changes in rainfall regimes may contribute to the development of new forest plagues and diseases and increasing pest attack (Moreira and Martins 2005; Pereira, 2007a). Recent climate simulation models in particular predict that climate change will have a very severe impact on the cork oak forests in Portugal, due to difficulties in regeneration and an increase of tree mortality, especially in the south of the country, while shrublands are expected to expand at the expense of cork oak areas (Pereira *et al.*, 2002). Future climate scenarios seem to favour cork oak migration to higher latitudes and altitudes. However, the climate change may be too rapid to allow the species to migrate, so it may become extinct locally (Pereira *et al.*, 2009a).

ECOLOGICAL RESILIENCE

When the understorey of agro-silvopastoral cork oak systems stops being managed for crop cultivation or grazing, natural succession is expected to develop through the gradual colonization by different shrub species (pioneer *Cistus* shrubs, followed by late-successional shrub communities like *Arbutus* and *Erica*), mixed with oak natural regeneration, which will lead to forest establishment in the medium term (Natividade 1950; Gonçalves 1991). However, on very disturbed soils with loss of moisture and nutrients, and dry conditions (e.g. southern aspects, or drought periods), cork oak seedling survival and tree recruitment can be severely limited (Retana *et al.*, 1999; Bugalho *et al.*, 2006) and the understorey becomes dominated by pioneer heathland species such as *Cistus* sp. mixed with *Erica* and *Genista* species (Nuñez *et al.*, 1986; Diniz, 1994; Seng and Deil, 1999). Furthermore, it is likely that competition between oak seedlings and *Cistus* for water will predominate over facilitative factors such as shrub shade and protection from herbivory. Well-developed *Cistus* shrubs may have a competitive advantage over cork oak seedlings, as *Cistus* shrubs are well adapted to very poor and dry soils. Additionally, *Cistus* are unpalatable to livestock (Natividade, 1950), which improves their chance of survival. It would also appear that *Cistus* shrubs have allelopathic effects, inhibiting seedling germination and survival. Such effects are aggravated by high temperatures and long photoperiods (Lobón *et al.*, 2002; Chaves and Escudero, 2001). *Cistus* shrubs can also act as reservoirs for diseases in infested areas (Moreira and Martins 2005).

Fire may also contribute to the expansion of shrublands. *Cistus* shrubs and other heathland species such as *Erica* sp., *Ulex* sp., *Genista* sp. and *Lavandula* sp. are highly inflammable and highly resilient to fires (Natividade, 1950). In particular, *Cistus* species are typical active pyrophytes, propagated solely by seeds (Trabaud, 1981; Trabaud and Oustric, 1989; Alonso *et al.*, 1992), and are able to disseminate numerous seeds that colonize extensive areas after fire (Trabaud, 1981; Corral *et al.*, 1989). The seed bank persists in the soil for a long period because the seeds have hard coats and are impermeable to water, which prevents them from germinating (Baskin and Baskin, 1989).

In such ecological conditions, shrublands can be very persistent, and the vegetation succession becomes “arrested” under a pioneer phase

(Zavala, 2003). Cork oak forest recovery can become very difficult, be it through natural regeneration or even artificial reforestation (Natividade, 1950, Gonçalves, 1991). Shrublands persistence implies that forest resilience has been lost and a threshold beyond which former vegetation can no longer be restored and is replaced by a different vegetation of lower biomass has been exceeded. Signs that the threshold has been crossed are poor natural regeneration of cork oak, decreasing forest cover, and expansion of *Cistus*-dominated shrubland. Shrublands may represent an alternative persistent state of lower vegetation biomass on the most degraded soils and drier areas, possibly jeo-pardizing the long-term viability of cork oak ecosystems (for more information on resilience and alternative stable states see Holling, 1973; Holmgren and Scheffer, 2001; Scheffer *et al.*, 2001; and Hobbs and Suding, 2009).

SOCIOECONOMIC PERSPECTIVES

Portugal is the greatest cork producer (54% of the world production, about 157 000 tons in 2007), the greatest processor (about 60% of the world cork processing), and the largest exporter (60% of total cork exports in 2005) mainly to EU countries and the USA (Cork Information Bureau, 2008). Cork is mostly processed for wine bottle stoppers (69% of total national production in 2007) (Cork Information Bureau, 2008), but it can also be used in civil construction, bulletin boards, automobiles, flotation devices, floor tiles, rocket technology, musical instruments and shoes. Cork is responsible for 3% of total Portuguese exports (cork exports reached 854 million € in 2007) (Cork Information Bureau, 2008; Branco and Parejo, 2008), and represents approximately 10% of total employment in the Portuguese forest sector (Mendes, 2002).

Cork prices have been rising significantly in the last few decades because of worldwide demand for cork, primarily due to increasing wine consumption. However, in the last seven years, estimated cork prices in

Portugal have fallen by about 28% (from 2.89 € /kg of cork in 2000 to 2.07 € /kg in 2008; prices include extraction costs), with a more significant decrease after 2003 (Cork Information Bureau, 2008). Moreover, total world sales of cork stoppers decreased by 3 billion units between 2000 and 2005, representing a decrease of more than 18% in 5 years (ICMC, 2005). Portugal in particular experienced a major loss in cork stopper exports to the USA between 2000 and 2004 (a decrease of more than 30 million €) and also to Australia between 2002 and 2004 (a decrease of 24 million €) despite the fact that during the same period wine production increased in these countries (WWF, 2006). The major reason for these trends is the increasing use of synthetic wine bottle closures (Bugalho *et al.*, 2009).

A further factor is the parlous state of the cork industry: the industry is suffering from lack of investment and limited labour productivity, most factories are not economically efficient due to their small size, and there has been a contraction of the product diversification that originated from agglomerate cork (Zapata *et al.*, 2009). Cork stopper specialization merely increases the vulnerability of the industry, particularly because of the increased use of plastic stoppers and screw caps. Recently, the cork industry has been commissioning research and improving management quality in order to mitigate cork tainting of wine; it has implemented certification schemes and is publicizing cork and cork oak landscapes as biodiversity hotspots and sustainable land uses.

Despite the falling prices of recent years, cork is still today the major economic asset in the cork oak areas in Portugal (Pereira, 2007b). The cork oak forest area in Portugal is almost completely (about 99.6%) privately owned (Mendes *et al.* 2004). Assuming an average cork productivity of about 150 kg per hectare in southern Portugal (Costa and Pereira, 2007a), and present cork sales value of 2.07 € /kg (Cork Information Bureau, 2008), one can calculate a rough estimate of a profit of 310 € /ha (price refers to sale price of cork on the tree and includes extraction costs). In large estates with uneven-aged stands and good land management, production can be fairly uniform from year to year, as cork can be extracted from trees of different ages (remembering that cork can only be extracted every 9 years from each tree). However, when the property is small, which is common in Portugal, sales may not generate a profit, and therefore landowners will avoid investing, or in the worse scenario, will cease management. Furthermore, investments such as facilitating natural regeneration through silvicultural practices, or planting cork oak, generate cash losses (assuming benefits and costs at current market prices) during the long period before the time of first commercial cork stripping, after the cork oak has been planted (Ovando *et al.*, 2009).

Cash losses make the renewal of cork oak woodlands economically unattractive to private landowners and they will not undertake such practices without subsidies. Cork oak afforestation therefore requires strong government subsidies, which provide sufficient incentives to encourage private investments from landowners. On the other hand, there are no public subsidies for the restoration of aging and degraded cork oak forests; this may represent a policy failure, since recent studies show that compared with the artificial creation of new stands, the restoration and sanitary treatments of established woodlands might be better in terms of biodiversity preservation and carbon mitigation (Campos *et al.*, 2006; Ovando *et al.*, 2009).

Cork oak landscapes are a fascinating ecosystem and are European Union protected habitats (Habitats Directive 92/43/EEC). The mixture of forest-type habitats, savanna-like forests and open spaces at both regional and local scales allows for the existence of high biodiversity, including many endemic species (Díaz *et al.*, 2003; Zavala *et al.*, 2004; Costa and Pereira, 2007a; Berrahmouni *et al.*, 2009). Cork oak ecosystems also allow for the protection of soils in dry environments like the southern Iberian Peninsula, and provide important ecosystem services in all categories established by the Millennium Ecosystem Assessment (2005). In 2002, the environmental organization World Wildlife Fund (WWF) started an international campaign for consumers to buy wine bottled with cork stoppers, as the best way to conserve the biodiversity of Mediterranean cork oak ecosystems (Petersen, 2002). If cork loses its market value, these unique landscapes of southern Europe will become endangered. Seeking and developing alternative activities, which generate additional income, such as ecotourism, the production of edible mushrooms, fruits and natural oils, beekeeping or hunting, and the use of both carbon credits and biodiversity credits, may provide incentives to conserve these systems. The development of entrepreneurial skills is indeed a new challenge facing landowners in order to develop businesses based on a new multipurpose use of cork oak ecosystems.

This thesis

STUDY SITE

The fieldwork presented in this thesis was conducted in a site in Serra do Caldeirão (37° 14´ N, 7° 56´ W; 11 000 ha), a mountain range in the north-eastern part of the Algarve province, southern Portugal (Figure 1). The climate is Mediterranean, with most rainfall concentrated in the winter months (December to February) and only 2.5% of the annual total falling in the summer (June to August). Mean annual precipitation is 900 mm and mean annual temperature is 16.6°C. It is a hilly area, with altitude ranging from 146 to 588 m. The soils are homogeneous, consisting mainly of schist lithosols (soils with bedrock occurring at less than 10 cm depth, in this case schist rock).

The landscape is a mosaic formed by various densities of trees (the dominant tree species being cork oak), large patches of shrublands, and cleared areas with scattered grasslands, occasionally with scattered shrubs. A massive rural exodus during the 1960s led to land abandonment and desertification, and the only agriculture at present is subsistence farming around the few scattered settlements. Livestock is today reduced to only few flocks of goats and sheep and is mainly based on the grazing of fallow land or shrubland. The population density in the area and surrounding region is low (35.46 persons per square km: INE, 2001). The landholdings within the area are very fragmented and all owned privately. The study site constitutes one of the main cork-producing areas in Portugal and cork extraction represents the main economic activity for the local people. This area is one of the most continuous remnants of cork oak forests of southern Portugal and is included as a classified area under the Natura 2000 Network (the site Caldeirão – PTCON0057). All the data analysed for this thesis (both ecological and land use data) were collected at this site.

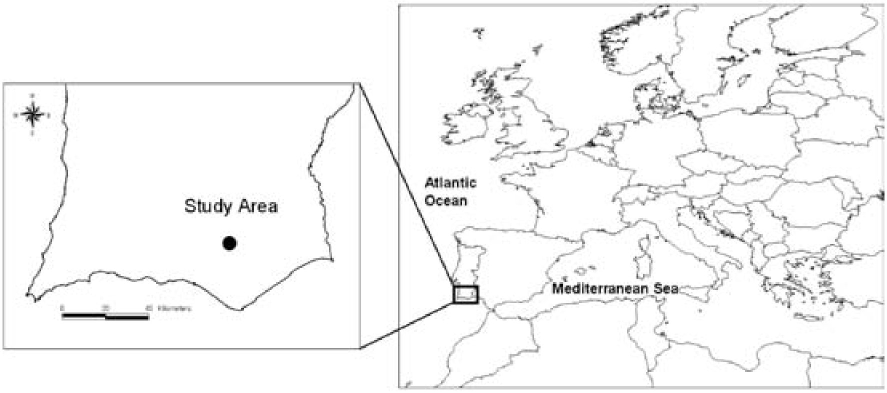

Figure 1 – Location of the study area

HYPOTHESES AND OBJECTIVE

The traditional succession model predicts degraded vegetation states as a retrogressive succession from a single stable state (climax) and that vegetation responses (degradation and improvement) will occur continuously and reversibly along a continuum (Westoby *et al.*, 1989). However, in semiarid ecosystems, vegetation changes in response to disturbances have often been found to be discontinuous and irreversible (Westoby *et al.*, 1989). These concepts are closely related to the concept of ecological resilience and alternative stable states presented by Holling (1973). In this thesis, alternative stable states are described and analysed by means of state and transition models (*sensu* Westoby *et al.*, 1989). These models were devised to provide a framework for describing the dynamics of arid ecosystems, in response to the shortcomings of classical gradual continuum models (Westoby *et al.*, 1989; Friedel, 1991). They focus on mechanisms that cause transitions between successional stages and provide explicit goals for restoration (Walker and Del Moral, 2009). State and transition models have been used to describe the dynamics of Iberian cork oak ecosystems by only few authors (Huntsinger and Bartolome, 1992; Alés, 1999; Cortina *et al.*, 2006) but to date no one has identified or quantified the underlying mechanisms of alternative stable states with experimental research. The research described in this thesis set out to do exactly that. In this research, the cork oak landscape in southern Portugal is conceived of as a mosaic of four main types of vegetation patches:

1) cork oak forests, with higher tree density (more than 100 trees/ha) where the understorey is usually not managed and may contain several layers of diverse shrub species;
2) cork oak agro-silvopastoral systems (savanna-like forests), with lower tree density (40 to 100 trees/ha) where the understorey is managed for pastures or crops; there may also be shrubs in the understorey, with low diversity and low abundance;
3) shrubland (i.e. scrub) dominated by *Cistus* (pure or mixed with *Erica* and *Genista* species);
4) grassland dominated by annual herbaceous species (native or improved pastures).

Each patch type is conceived of as a vegetation state that is achieved and maintained in different ways (*sensu* Westoby *et al.*, 1989). In this thesis, hypothetical transitions between patch types in southern Portugal are shown in Figure 2. Cork oak forests have been transformed into agro-silvopastoral systems (cork oak savannas) by long-term human management. In cork oak savannas, pastures and crops are maintained in the understorey through grazing and ploughing. In the absence of human management, the understorey of cork oak savannas quickly becomes dominated by shrubs and gradually by cork oak seedlings. In the long term, seedlings are recruited into the mature population and cork oak savannas shift to cork oak forests. Given that a cork oak tree takes about twenty years to become a mature tree, it is assumed that restoration takes forty years. Grasslands also have to be maintained by human intervention (ploughing and grazing). In the absence of human intervention, they become dominated by shrub species quickly (two to five years, assuming typical time intervals used by land managers between each shrub clearing) and shift to shrublands (Nuñez *et al.*, 1986; Oliveira, 1998; Seng and Deil, 1999; Díaz *et al.*, 2003). However, in this thesis it is hypothesized that in very dry conditions, land over-exploitation (intensive grazing, intensive crop cultivation, clearing and intensive cork extraction) and failure to protect naturally regenerating cork oak can hamper or prevent the recruitment of cork oak seedlings, thus encouraging a shift from the cork oak savannas and forests to shrublands. Decades of overgrazing and intensive land use without protecting cork oak natural regeneration could have triggered feedback mechanisms that led to decreasing cork oak natural regeneration and in the long-term to a persistent shrub-dominated vegetation, where the establishment of cork oak seedlings became very difficult. Shrublands could therefore represent an irreversible tree loss; the reason they remain stable is because of severe limitations to cork oak seedling recruitment (Figure 2).

In this thesis, the cork oak forests and shrublands in southern Portugal are hypothesized to be alternative stable states, which change slowly or not at all in the absence of human intervention. It is hypothesized that failures in natural regeneration of cork oak trees triggered by land overexploitation may be the reason for a shift to the alternative stable state of shrublands, especially in very dry conditions (Figure 2).

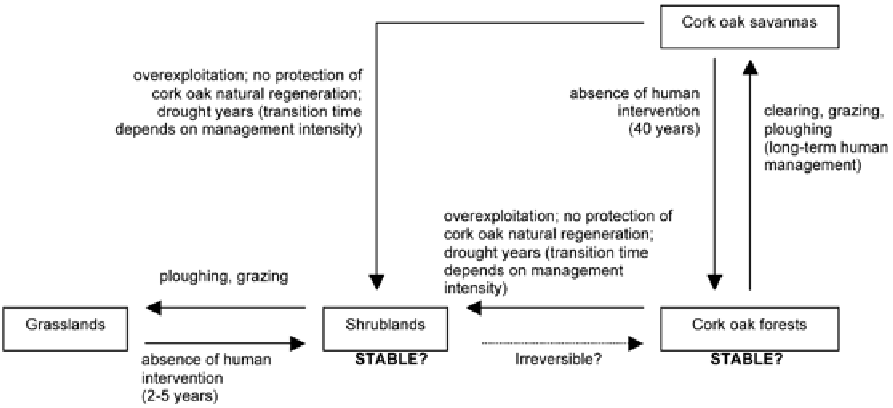

Figure 2 – A hypothetical state and transition model for the cork oak landscape in southern Portugal

The overall objective of the research described in this thesis was thus twofold: to evaluate if cork oak forests and shrublands represent alternative stable states in southern Portugal, and to ascertain the ecological and land use mechanisms underlying their resilience and persistence.

THESIS OUTLINE

The thesis consists of six chapters, including this general introduction (Chapter 1), two chapters presenting an analysis at landscape scale (Chapters 2 and 5), two chapters presenting an analysis at local scale (Chapters 3 and 4), and the synthesis (Chapter 6). The landscape analysis in Chapter

2 uses ecological variables only, whereas in Chapter 5 a multidisciplinary approach is applied, in which the ecological variables used in Chapter 2 are augmented by land use variables. Chapter 3 describes a field experiment done on plots, in which ecological variables are quantified, whereas Chapter 4 describes an experimental study on plots and trees, using both management and ecological variables. The plots are not the same as those used in Chapter 3.

Chapter 2 analyses and explains vegetation changes at a landscape scale, based on aerial photographs and a geographical information system. Cork oak ecosystems are structured as a mosaic landscape with four main types of patches (cork oak forests, cork oak savannas, *Cistus* shrublands and grasslands), and patch-type transitions and persistence for the last 45 years (1958-2002) are quantified and described. The correlations between patch-type transitions and ecological factors (topography and wildfire) are investigated in order to understand landscape changes and the dynamics of two-phase states of cork oak forests and shrublands.

Chapter 3 analyses and explains vegetation changes at a local scale in terms of ecological mechanisms that limit cork oak recruitment, drawing on a field experiment implemented in three types of patch: cork oak forests, cork oak savannas and *Cistus* shrublands. Data were collected in each patch type and for each phase of the early recruitment cycle: seed production, seed removal and dispersal, seed germination, and seedling survival. In this chapter it is shown how cork oak seedling establishment is differently constrained in each patch type, and how establishment influences and explains the constraints to cork oak forest regeneration and the persistence of shrublands.

Chapter 4 analyses variables that affect cork oak survival 18 months after a large wildfire that occurred in the study area. Data were collected on individual trees and on plots. Management data (on cork exploitation of individual trees) and ecological data are combined in an analysis to ascertain the likelihood of tree survival after a wildfire, and the importance of fire as an ecological factor influencing cork oak tree loss is demonstrated. Chapter 4 enables areas where fire prevention is crucial to be identified, plus management strategies for increasing tree survival in case of wildfire.

In Chapter 5 the cork oak landscape is viewed as a social–ecological system in which patch-type changes are explained by both human management and by ecological factors. The ecological variables quantified in Chapter 2 are combined with land use variables collected from landowner interviews to explain patch-type transitions and the persistence of cork oak forests.

Chapter 6 summarizes the main results of the thesis, discusses the findings in a wider perspective, considering both their theoretical and practical relevance and focusing on the resilience and sustainability of cork oak land use systems.

The cork oak landscape at the study site (Serra do Caldeirão, Algarve)

Chapter 2

Are drought and wildfires turning Mediterranean cork oak forests into persistent shrublands?

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Abstract

In the Iberian Peninsula Mediterranean oak forests have been transformed into a mosaic landscape of four main patch-types: forests, savannas, shrublands and grasslands. We used aerial photographs over a period of 45 years (1958–2002) to quantify the persistence and rates of transitions between vegetation patch-types in southern Portugal, where cork oak is the dominant tree species. We used logistic regression to relate vegetation changes with topographical features and wildfire history. Over the 45 years, shrublands have been the most persistent patch-type (59%), and have been expanding; forests are also persistent (55%) but have been decreasing since 1985; savannas and grasslands were less persistent (33% and 15%, respectively). Shrublands persistence was significantly correlated with wildfire occurrence, particularly on southern exposures after 1995. In contrast, forest persistence decreased with wildfire occurrence, and forests were more likely to change into shrublands where wildfire had occurred after 1995.

Key-words: Alternative stable states, *Cistus*, Semiarid, Shrub encroachment, Vegetation shifts, *Quercus suber*

Introduction

Mediterranean forests are one of the biodiversity “hotspots” on earth (Myers et al. 2000; Olson and Dinerstein 2002). Due to a long history of human disturbance, approximately 70% of the original Mediterranean forests and shrublands were already destroyed by 1990 (Millennium Ecosystem Assessment 2005). The remaining cover is considered to be in critical or endangered conditions (Olson and Dinerstein 2002; Mooney et al. 2005). Despite this long history of degradation, forest cover has expanded in some areas of Mediterranean Europe since the 1960s after agricultural abandonment and rural exodus (Mazzoleni et al. 2004). In contrast, the opposite trend has apparently taken place in the drier evergreen oak forests of the southern Iberian Peninsula. Here, canopy trees have decayed reducing tree density (Gonçalves 1991; Ferreira 2000; Vicente and Alés 2006), tree seedling mortality is high (Anon 1990; Montero et al. 1994a) and xerophytic *Cistus* shrublands have expanded in areas formerly covered by oak forests and savannas (Calvão and Palmeirim 2004).

Since in semi-arid Mediterranean ecosystems, tree seedlings often establish under the shade of adult nurse shrubs and trees (Holmgren et al. 2000; Pulido and Díaz 2003; Castro et al. 2004; Gómez-Aparicio et al. 2004), removal of the original vegetation makes conditions for seedling establishment difficult, resulting in a positive feedback of increasing vegetation loss that can be difficult to reverse (Mulligan et al. 2004). Persistent loss of original vegetation has been described for the five Mediterranean-type regions around the world (e.g. Friedel 1987 for South Africa; Westoby et al. 1989 for Australia; Laycock 1991 for California; Puigdefábregas and Mendizabal 1998 for the Mediterranean Basin; and Holmgren 2002 for Chile).

Succession has traditionally been conceived as a relatively linear process, but evidence from a variety of ecosystems indicates that persistent alternative vegetation or ecosystem states may occur, particularly after disturbances (Friedel 1991; Laycock 1991; Scheffer et al. 2001). In these cases, succession is strongly delayed or practically stopped in a condition called arrested succession (Putz and Canham 1992; Sarmiento 1997).

In the southern Iberian Peninsula, original forests dominated by cork oaks (*Quercus suber*) and Holm oaks (*Quercus ilex*) have been transformed into an agroforestry system. Long-term human management has included combinations of clearing, livestock grazing, and ploughing for agriculture cultivation (Joffre et al. 1999; Pulido et al. 2001). During the

1960s socio-economic changes (industrialization, immigration to cities, emigration, and opening of international markets) led to rural exodus and a gradual abandonment of crops and pastures (Joffre et al. 1991; Pinto-Correia 2000).

At present, oak systems in southern Portugal are a mosaic of four types of patches: forests, oak savannas (traditionally known as montados in Portugal and dehesas in Spain), shrublands and grasslands. Oak savannas and grasslands are maintained through grazing and ploughing in the traditional agroforestry system (Marañón 1988; Huntsinger and Bartolome 1992; Díaz et al. 2003). In the absence of human management, the usual pathway of natural succession is through the gradual colonization by different shrub species (pioneer *Cistus* shrubs, followed by other shrub species like *Arbutus* and *Erica*), followed by oak natural regeneration leading eventually to forest recovery (Natividade 1950; Gonçalves 1991). However, under a combination of dry conditions (either drought periods or south facing slopes) and wildfires, forest recovery may be impeded and a transition to *Cistus* shrublands more likely. The last decades have been characterized by drier conditions (Cabrinha and Santo 2000; Esteban-Parra et al. 2003; Pausas 2004) and a higher wildfire incidence (Pausas 2004; Anon 2006) whereas ploughing and livestock grazing have tended to decrease in Portugal (Alves et al. 2003; Pinto-Correia and Vos 2004).

In this paper, we quantify the rate of change between vegetation patch-types (cork oak forests, cork oak savannas, shrublands and grasslands) in the Mediterranean oak forests of southern Portugal during 45 years (1958–2002) and assess the role of drought and wildfire to explain these transitions. We use aerial photographs and a Geographic Information System (GIS) to quantify the persistence of vegetation patch-types and the rates of transitions between them. We project our results for the coming decades and discuss the forest changes in southern Portugal in relation to the trends described for other European Mediterranean regions.

Materials and methods

STUDY AREA

The study area is located in Serra do Caldeirão, a mountain ridge in the northeastern part of the Algarve province, southern Portugal, with an approximate area of 11,000 ha. Climate is Mediterranean, with an average annual temperature of 16.6°C and average annual precipitation of 900 mm (45-year period: 1958–2002, Barranco do Velho station). Altitude ranges from 146 to 588 m. Soil type is homogeneous, consisting mainly of schist lithosols (soils with hard rock at less than 10 cm depth). These soils are shallow, with low fertility and prone to erosion. Cork oak is the dominant tree species and cork extraction represents the main economic activity for local people. Our study area is one of the most continuous remnants of cork oak forests of southern Portugal.

IMAGE PROCESSING

We used hardcopy aerial photographs and digital orthophotos (rectified copy of an original aerial photograph) from five different years covering a 45-year period: 1958 (scale 1:26,000), 1972 (scale 1:8,000), 1985 (scale 1:5,000), 1995 (scale 1:40,000) and 2002 (scale 1:5,000). Aerial photographs (1958, 1972 and 1985) were previously scanned and then orthorectified and georeferenced with ENVI 3.4 (Anon 2001a) in order to produce geometrically correct images and project them to the same coordinates reference as the digital orthophotos (1995 and 2002) (Transverse Mercator projection, datum WGS84). Digital elevation models with a spatial resolution of 8 m were used for altitude coordinates (orthorectification process), and ground control points (between 10 and 15 per photo) were taken from the 2002-orthophoto for map coordinates (georeferentiation process). We obtained a RMS Error of about 10 m.

PHOTO INTERPRETATION AND LAND COVER CLASSIFICATION

We used a regular 0.5 x 0.5 km grid of 441 points covering the entire study area, and photo interpreted on screen a 50 m-radius circle (sampling unit) around each photographic point. Photo interpretation was performed on a photo-by-photo basis. The grid was created with Arcview GIS 3.2 (Anon 1999) and laid over the aerial photographs and orthophotos (imported into the GIS as scanned images). Our grid has a resolution higher than the usual 4 x 4 km grids used for monitoring forest conditions in Europe and allows detecting changes in vegetation types (Köhl et al. 1994). Systematic point sampling is commonly used in forest inventory and gives better estimates than simple random sampling for large areas. Each of the 441 sampling units was classified into one of the following five vegetation patch-types for each image year:

1) cork oak forests with high cork oak density (more than 100–150 trees/ha) and a diverse shrubby layer (e.g. *Arbutus unedo*, *Viburnum tinus*, *Erica arborea*, *Pistacia lentiscus*, *Rhamnus alaternus*, *Phillyrea latifolia*); this class corresponds to a tree cover higher than 30%;
2) cork oak savannas where cork oak density is lower than in forest patches (usually less than 100 trees/ha) with sparse shrubs in the understory; this class corresponds to a tree cover between 10% and 30%;
3) shrublands dominated by *Cistus* ladanifer shrubs, pure or mixed with *Ulex argenteus*, *Genista hirsuta* and *Lavandula stoechas* shrubs; in this class, less than 10% of the sampling unit is covered by trees;
4) grassland patches dominated by cultivated croplands, semi-natural pastures, or fallow land; in this class, less than 10% of the sampling unit is covered by trees;
5) others (e.g. plantations, pine forests, eucalyptus forests, riparian forests, and urban).

When more than one vegetation patch-type occurred in a sampling unit, it was classified based on the predominant type. Sampling units with only one type of patch-type were predominant (more than 50% of the total units) and when not, we could usually clearly assign one dominant class to each unit. We used tree cover percent rather than tree density since in many cases it was not possible to count the number of trees on the images. Boundaries for forest density (10% and 30% of ground cover) follow the National Forest Inventory norms (Anon 2001b).

Before photo classification (2003), we visited the study area several times to recognize the different vegetation types and compare them with the patterns on the aerial photos of 2002. Photo interpretation was carried out by a group of four persons and results were cross-validated within the group. Approximately 10% of the sampling units were validated in the field.

ACCURACY ASSESSMENT OF LAND COVER CLASSIFICATION

Accuracy assessment was evaluated with the calculation of the error matrix (Walsh and Burk 1993). The error matrix allows us to quantify the overall accuracy of the land cover classification procedure, dividing the number of units in the diagonal cells of the matrix by the total number of field-validated units. It allows us also to estimate the probabilities of classification of a unit of class i in class j, as nij/nj (where i represents the observed class, j the predicted class, and nj the sum of all training observations predicted as class j). Overall accuracy was about 82%. The highest omission error occurred in savannas (0.4) due to confusion with cork oak forests and pines, followed by forests (0.24) and shrublands (0.14), due to confusion with pine forests. On the other hand, pine forests and shrublands showed the highest commission errors (0.36 and 0.33, respectively), confused mainly with cork oak forests.

QUANTIFICATION OF VEGETATION CHANGES

The information for each sampling unit was stored as a five-layer Arcview GIS database, where each layer represented the landscape at a single point in time. Five transition matrices (Usher 1981; Rego et al. 1993) were built for the five-year set (1958–1972, 1972–1985, 1985–1995, 1995–2002), and for 1958–2002 (overall period). We estimated the (1) percentage of land covered by each type of vegetation patch (expressed as the % of total number of points); (2) transitions between vegetation patch-types by counting the number of sampling units of any vegetation patch-type that changed into any other between two discrete time periods (expressed as percentages); (3) rates of change (percentage of change/year) between vegetation patch-types, dividing the percentage of transitions from one patch-type to another by the total number of years during which the transitions occurred; (4) projection of changes for the coming decades, multiplying the observed rates of transitions for a given period by the number of hectares of each vegetation patch-type registered in 2002, and estimating its area for 2003; multiplying again the estimated area by the transition rates and estimating a new area for the following year; calculations were started in 2002 and were successively repeated until 2050. We projected two scenarios: a conservative one based on the average of the four rates of transition observed for the overall period (1958–1972; 1972–1985; 1985– 1995; 1995–2002), and a second one based on the most recent trends (1995–2002). To project such changes we assumed that the probabilities of transitions between vegetation patch-types were constant throughout the whole period of projection, following a Markovian process (Rego et al. 1993).

CORRELATES OF VEGETATION CHANGES

Topographical variables (slope and exposure) were derived from digital elevation models (Portuguese Military Geographic Institute) and stored as two Arcview GIS layers. We assigned one class of slope and exposure to each sampling unit based on the most common type. The slope categories were: low to medium (0–20%); steep (20–30%); very steep (>30%). The exposure categories were: north facing slopes (including NW, N and NE), south facing slopes (including SW, S and SE) and others (E and W).

Wildfire occurrence was available as spatially referenced and digitized data for every year between 1984 and 2002 (General Directorate of Forests). The limits of the burned area per year were stored as an Arcview GIS layer and overlaid with the sampling units in order to identify the sampling units that burned between 1984 and 2002. The maximum number of times a unit was burned in the period 1984–2002 was two.

STATISTICAL ANALYSIS

We overlayed the Arcview GIS layers containing the information on slope, exposure and wildfire occurrence with the layer containing the vegetation transition types (e.g. forest to shrubland) for each time period (1958–1972, 1972–1985, 1985–1995, 1995–2002). We used logistic regression to explore the relative importance of slope steepness, exposure and wildfire occurrence on the observed vegetation changes. We analysed (1) transitions from each vegetation patch-type (except “others”) to shrublands and (2) vegetation type persistence (except “others”) for each of the 4 periods, yielding a total of 28 models (4 persistences plus 3 transitions, times 4 time periods). For each model, the predictor variable took the value 1 if a transition (or persistence) occurred for each sampling unit during the specified period, or 0 if not. Slope categories were ranked from 1 to 3, respectively for 0–20%, 20–30%, and >30%. Exposure and wildfire (presence/absence) were assumed as categorical variables. Forward stepwise selection was used, and variables entering the model selected based on the likelihood-ratio test (Hosmer and Lemeshow

1989). To check whether the models could be improved, some variables were square-transformed and interactions between all variables explored, using the procedures suggested by Hosmer and Lemeshow (1989). Consequently, we created the simplified dummy variables Exposure_South and Expo-sure_North, which took the value 1 for the specified exposure and 0 for the others categories. Model goodness of fit was assessed through the likelihood ratio statistic and the χ^2 test. Due to a low number of "occurrences" in some transition types, statistical analyses could not be undertaken.

Results

LAND COVER CHANGES

During the 45-year study period there were significant changes in land cover. Between 1958 and 1972, shrublands expanded rapidly (54% increase) while grassland cover registered a decline of 481% (Table 1). In those 15 years, shrublands became the patch-type with the highest cover (33.8%). By 1972, only 4.8% of the total area was covered by grassland patches which remained as such onwards (Table 1). During the following two decades, shrublands slightly decreased (around 28% of the total area) to became again the predominant patch-type in 2002 (32.4%). Cork oak forests, the most abundant patch-type in 1958 (about 30%), decreased during the next 45 years to cover around 24.5% of the area in 2002 (Table 1). Savannas initially expanded but have decreased since 1972 onwards. During the whole period, only shrublands and the category "others" registered net increases (51.9% and 62.4%, respectively, Table 1). The high net increase of "others" is mainly due to plantations and pine regeneration and expansion (both sum up about 80% of the category "others" in 1958 and 90% in 2002).

Table 1 – Temporal changes of vegetation patch-types (% of total number of sampling units) and net changes from 1958 to 2002

	1958	1972	1985	1995	2002	Net changes 1958-2002
Forests	29.9	26.8	31.1	29.3	24.5	–22
Savannas	19.7	24.9	21.5	21.1	18.6	–5.9
Shrublands	15.6	33.8	28.1	27.9	32.4	+51.9
Grasslands	27.9	4.8	3.9	3.6	6.3	–342.9
Others	6.8	9.8	15.4	18.1	18.1	+62.4

PATCH-DYNAMICS: PERSISTENCE AND TRANSITION RATES BETWEEN VEGETATION PATCH-TYPES

The dynamism of this landscape can be better appreciated in Fig. 1 showing the percentage of transitions between vegetation patch-types from 1958 to 2002 in a conceptual state-and-transition model. Forests and shrublands were the most persistent patch-types, contrasting with savannas and grasslands. The largest changes occurred in grasslands, switching mostly to shrublands (40%), but also to savannas (25%) and others (20%). Other important transitions occurred in savannas, as they changed to shrublands (28%) or forests (23%). Despite the high persistence of cork oak forests (55%), an important fraction became shrublands (20%).

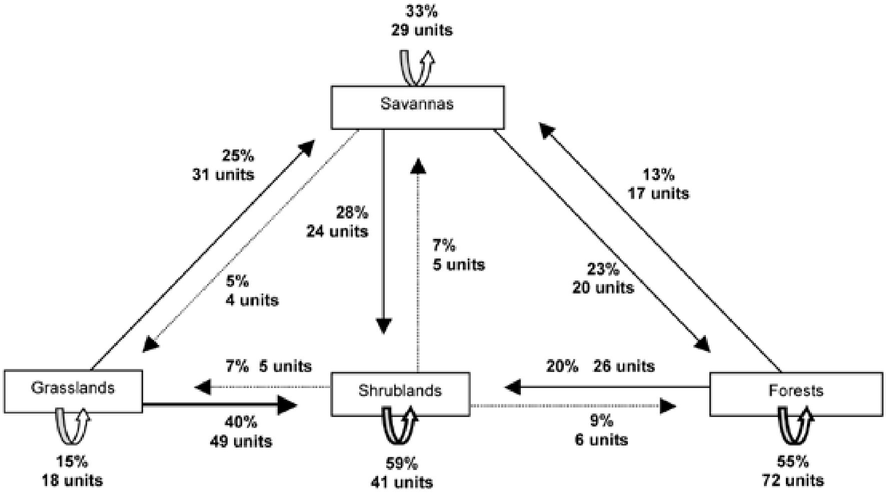

Figure 1 – State-and-transition model with observed transitions (%) between vegetation patch-types in southern Portugal (1958-2002). Changes (% and number of units) for each patch-type are based on the number of sampling units classified as that patch-type in 1958 that changed (or remained) in 2002. Dotted lines indicate frequency of transitions < 10%. The % of transitions from each patch-type to "others" are not shown in the Figure; such % is the difference between 100% and the total % of transitions shown from each patch-type

Forests changed faster into savannas than into shrublands (Fig. 2), but more forest patches changed into shrublands (20%) than into savannas (13%) during the overall period (Fig. 1), which indicates that most of these changes are not direct transitions, implying a gradual loss of the tree canopy: forest patches change first into savannas and then these savannas change into shrublands. In any case, forests are changing at an increasing rate since 1985.

Oak savannas have become shrublands at increasing rates, while less savannas have returned to forests (Fig. 2). Between 1972 and 1984, forests recovered when savannas switched into forests at the highest rate, but since then there has been a clear decreasing trend. At present, savannas change six times faster into shrublands than into forests.

Shrublands have been the most persistent patchtype (59%) changing very little into something else (around 7% into forests, grasslands or savannas) (Fig. 1). The vegetation transition rates indicate that cork oak recruitment seems to be particularly difficult in shrublands. Only 7% of shrublands changed into savannas and forests compared to 25% of grasslands changing into savannas, and 23% of savannas becoming forests (Fig. 1). Grasslands have been transformed mainly into shrublands and in a smaller extent, into savannas (Fig. 1), both at a decreasing rate since 1958 (Fig. 2).

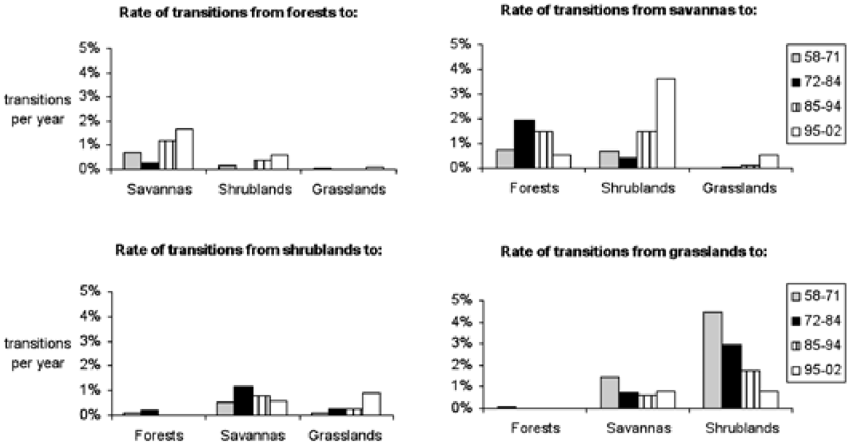
Rate of transitions from forests to:
Rate of transitions from savannas to:
Rate of transitions from shrublands to:
Rate of transitions from grasslands to:

Figure 2 – Rate of transitions (% of transitions per year) from each vegetation patchtype to the others (1958–2002)

PROJECTION OF CHANGES FOR THE COMING DECADES

Projection of our results for the coming decades shows an increase of shrublands and a decrease of forests and savannas (Fig. 3). Obviously, the conservative approach based on the transition rates for the 45 years (1958–2002) suggests smoother changes than the one projected using the most recent rates (1995–2002). It is interesting to notice that present rates of transition suggest a future increase in grassland patches, which have increased in the last years (see Fig. 2).

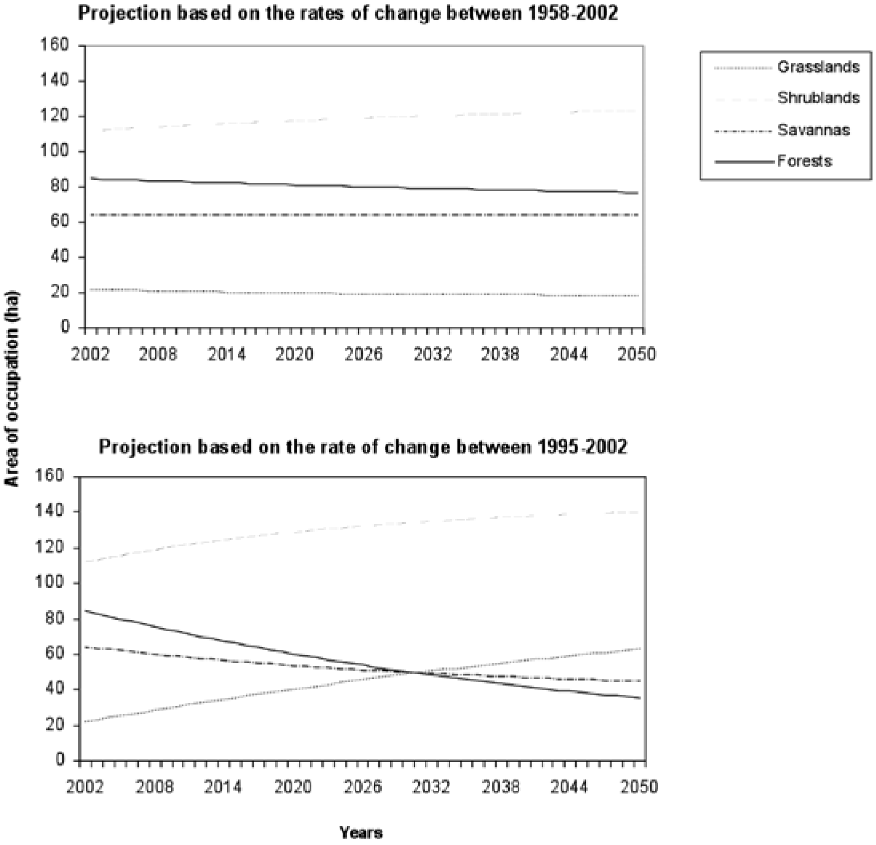

Figure 3 – Projection of the area (ha) of occupation of vegetation patch-types for 2002–2050, based on the rates of change observed in 1958–2002 (average) and 1995–2002

THE ROLE OF TOPOGRAPHIC VARIABLES AND WILDFIRE HISTORY ON VEGETATION CHANGES

Forest persistence increased with slope steepness during each time period and decreased with wildfire occurrence since 1985 (Table 2). In contrast, shrubland persistence was significantly correlated with wildfire, particularly on southern exposures after 1995 (Table 2). Grassland persistence was higher on lower slopes and particularly when they were located on southern exposures. Savanna persistence was not influenced by any studied variable except during the period 1958–1972, when they were more likely to persist on steeper and no north-facing slopes (Table 2). Of the three potential patch transitions to shrublands, wildfire increased the probability of transition from forests to shrublands in the period 1995–2002, and grasslands were more likely to change into shrublands if located on lower slopes (until 1985). None of the studied variables influenced the transitions from savannas to shrublands (Table 2).

Table 2 –Results of multivariate logistic regression to predict persistence and transitions between vegetation patch-types

	1958–1972	1972–1985	1985–1995	1995–2002
Fo→Sr	n=3 (*)	n=0 (*)	_ n=5	Fire (+) *P*=0.057 n=5
Sa→Sr	_ n=8	_ n=6	_ n=13	_ n=26
Gr→Sr	Slo (–) *P*=0.049 n=77	Slo (–) *P*=0.003 n=8	n=3 (*)	n=1 (*)
Sr→Sr	_ n=57	_ n=108	Fire (+) *P*=0.007 n=97	Fire x Asp_S (+) *P*=0.004 n=105
Fo→Fo	Slo (+) *P*=0.002 n=106	Slo (+) *P*<0.001 n=105	Slo (+) *P*=0.002 Fire (–) *P*=0.026 n=115	Slo (+) *P*<0.001 Fire (–) *P*=0.027 n=103
Sa→Sa	Slo x Asp *P*=0.026 Slo x Asp_O (+) Slo x Asp_S (+) n=67	_ n=66	_ n=66	_ n=58
Gr→Gr	Slo (–) *P*<0.001 n=19	Slo (–) *P*=0.001 Slo x Asp_S (–) *P*=0.002 n=11	Slo (–) *P*=0.002 Slo x Asp_S (–) *P*=0.001 n=12	Slo (–) *P*=0.003 Slo x Asp_S (–) *P*=0.002 n=14

For each combination of transition/persistence type and time period, variables entering the model are shown, as well as their direction of association (+/–) with the response variable, and significance (Likelihood ratio test). Vegetation types include shrublands (Sr), forests (Fo), savannas (Sa) and grasslands (Gr). Variables include slope (Slo), exposure (Asp), exposure south (Asp_S), exposure "others"—east or west (Asp_O) and Wildfire (Fire). n = number of occurrences. The asterisk (*) signals low frequency-transitions that were not considered for analysis. For all analyses, sample size was 441 sample units

Discussion

OVERALL VEGETATION CHANGES

Shrubland encroachment has been the most conspicuous landscape change in this part of the southern Iberian Peninsula since 1958 when forest understory use for agriculture and pastures was abandoned in many areas (Alves et al. 2003; Pinto-Correia and Vos 2004). Shrublands increased during the last 45 years at the expense of the other vegetation patch-types. Persistent shrub encroachment has also been found in other Mediterranean ecosystems like the Italian ‘macchia’ (Pignatti 1978; Scarascia-Mugnozza et al. 2000), the cork oak forests of southern France (Trabaud and Galtié 1996), as well as in the Spanish dehesas, an oak savanna system comparable to the Portuguese montados (Huntsinger and Bartolome 1992). In contrast, forest expansion has been described as the dominant landscape change throughout Mediterranean Europe since the 60s (Mazzoleni et al. 2004). There, shrublands are usually reported as intermediate phases prior to forest recovery (Mazzoleni et al. 2004).

Shrublands and forests are more persistent vegetation types (59 and 55% respectively) than savannas (33%) and grasslands (15%). The main vegetation changes along the study period (above 20% in Fig. 1) were the (a) replacement of grasslands by shrublands, savannas and others, (b) replacement of savannas by shrublands and forests, and (c) replacement of forests by shrublands. Grasslands decreased in more than 300% and since 1972 only 4.8% of the total area has remained covered by grassland patches, probably maintained for family subsistence close to human settlements.

PATCH-TYPE DYNAMICS

Shrubland persistence was positively correlated with wildfire occurrence, particularly on southern exposures since 1995. Shrublands usually grow in very dry and degraded soil conditions and are commonly dominated by *Cistus* spp., especially on south-facing slopes (Nuñez et al. 1986; Diniz 1994; Seng and Deil 1999). In addition, *Cistus* shrublands are active pyrophites, thus their persistence can be supported by a positive feedback mechanism triggered by frequent wildfires. Particularly, *Cistus ladanifer* is a highly flammable species due to its external resins (Trabaud 1981). Our results point towards the same pattern with a tendency of *Cistus ladanifer* shrublands to be maintained by wildfire occurrence and on south-facing slopes, where conditions are drier and more limiting for seedling recruitment and cork oak survival. *Cistus* shrubs will survive wildfires and maintain themselves as long as the interval between successive fires is higher than the time that is needed for seed bank restoration. *Cistus* seed banks seem to be restored every 3 years for *Cistus ladanifer* in Spain (Ferrandis et al. 1999) or only 2 years for *Cistus* sp. in California (Montgomery and Strid 1976), which is much less than the time interval between successive fires in the region.

Shrublands expanded initially at grassland patches. The rate of this transition has been decreasing across time, and was particularly evident on flatter areas until 1985, perhaps because deeper soils contribute to faster shrub encroachment, after the abandonment of agriculture and pastures. In contrast, cork oak forests have been decreasing since 1985. Although cork oak forests can be highly persistent, a significant proportion (20%) has turned into shrublands. Our results showed that forests persisted longer on steeper slopes, likely because they were less accessible to human interventions. After 1995, we observe a clear effect of wildfire occurrence on tree density: when no wildfire occurs forests persist at steeper slopes, whereas occurrence of wildfire causes tree loss and conversion of forests into shrublands. Although the cork oak is partially protected against fires by bark insulation and is able to resprout after fire, frequent or intense wildfires may kill adult trees, especially if wildfires occur immediately after cork extraction (Cabezudo et al. 1995; Pausas 1997; Moreira et al. 2007), which takes place in the summer, when the wildfire season begins in Mediterranean Europe. In addition, the rate of tree recovery might decrease with increasing wildfire frequency because of lower resprouting success and higher oak seedling mortality (Díaz-Delgado et al. 2002).

After an initial recovery following agriculture abandonment (1958–1984), savannas have also been changing into shrublands since 1985. Initial cork oak recruitment in old fields at the beginning of abandonment was also found in Eastern Spain, followed by shrub encroachment (Pons and Pausas 2006). Shrub encroachment could be limiting tree recruitment onwards, especially on drier conditions. Our results suggest that savannas were more likely to persist in steeper slopes and drier exposures that did not face north.

Forests and savannas have been converted into shrublands at an increasing rate. Forest replacement by shrublands has been positively associated with wildfire incidence since 1995, but the transition of savannas to shrublands was not associated with any studied variable. Drought has probably played an important role on the replacement of savannas by shrublands: savannas have lower tree density and therefore seedlings and saplings are exposed to higher irradiance and water stress than in forests. Patches converted into shrublands have been highly persistent and rarely switched into a different vegetation type. Experimental evidence indicates that shrubland persistence can be explained by oak seedling recruitment limitation in multiple phases (Acacio et al. 2007).

Grassland persistence has been higher on lower slopes, probably because these are the areas where farming activities are maintained. Grasslands tend to persist on southern slopes likely due to soil and climatic conditions slowing successional changes.

MECHANISMS LIMITING FOREST RECOVERY

Limited cork oak recruitment in shrublands might be more related to seedling recruitment than to seed availability. Indeed our transition rates from grasslands to savannas and from savannas to cork oak forests suggest similar probabilities of cork oak recruitment in grasslands and savannas patches despite the likely difference in seed availability between these two types of patches (Pulido and Díaz 2003). Dense *Cistus* stands may preclude cork oak regeneration in different ways. It is known that *Cistus* shrubs have allelopathic effects, inhibiting seedling germination and survival (Chaves and Escudero 2001; Lobón et al. 2002). There could be also limitations in acorn dispersal, increased acorn predation (Herrera 1995; Leiva and Fernández-Alés 2003), or limitations in seedling germination and or survival under the dense and dry shrub cover (Retana et al. 1999).

Experimental work at the study area showed that different mechanisms of oak recruitment limitation (namely, seed source limitation, dispersal limitation, germination limitation, and establishment limitation) were significantly more severe in *Cistus* shrublands than in oak forests and savannas, hence cork oak seedling recruitment in shrubland was impeded in multiple ways (Acacio et al. 2007). Cork oak recruitment is also rare in the shrublands of eastern Spain (Pons and Pausas 2006) where very low oak seedling survival rates have been found under *Cistus* shrubs (Gómez-Aparicio et al. 2004; Pulido and Díaz 2005).

CORK OAK FORESTS UNDER CLIMATE CHANGE

Mean annual temperatures and rainfall intensity with erosive potential (number of days with rainfall >13 mm) have clearly increased in southern Portugal since 1972 (Water Institute, National Meteorological Institute and Regional Coordination Commission of Algarve).

The increase of mean annual temperature and rainfall extremes during the last decades follows the trends predicted by present climate change models projecting a higher frequency of droughts and intense rain events for Mediterranean-climate regions (Cubash et al. 1996; Mc-

Carthy et al. 2001). Under this scenario, wildfire frequency and soil erosion are expected to intensify. This will undoubtedly reduce forest cover and limit regeneration, while facilitating shrubland persistence and expansion. Comparable results have been found in Spanish and French cork oak forests where higher wildfire frequency was also related to a decrease in forest resilience and their switch into shrublands (Díaz-Delgado et al. 2002; Trabaud and Galtié 1996, respectively). Also modelling results show that increasing wildfire frequency promotes shrublands dominated by *Cistus* and limits *Quercus* growth (Pausas and Vallejo 1999). Moreover, *Cistus* species are well adapted to drought through physiological responses (Werner et al. 1998). In addition to drought and wildfires, cork oak mortality has been correlated to pathogens whose incidence might interact with climatic conditions (Moreira and Martins 2005).

Recent climate simulation models also predict a very severe impact of climate change on cork oak forests and savannas in Portugal due to difficulties in regeneration and increase of tree mortality, especially in the south of the country, while shrublands are expected to expand at the expense of cork oak areas (Pereira et al. 2002). Such future trends are shown in our projections, especially the one based on the most recent rates. Predictions based on the most recent trends are more reliable than the ones based on the average rate (1958–2002), since transitions are more likely to change over time. Nevertheless, we probably underestimate the changes by assuming that the probabilities of transitions follow a Markovian process, which is clearly unlikely given the varying transition rates from 1958 to 2002.

Our findings indicate a serious threat to the cork oak production system in southern Portugal, which is the basis of the local economy and has high conservation value, protected by European Union (Habitats Directive 92/43/EEC). The combination of increasing temperatures and increasing wildfire frequency has contributed to the expansion of shrublands in previous cork oak dominated areas. Shrublands may represent an alternative persistent state of lower vegetation biomass on the most degraded soils and dry areas, where conditions for forest recovery become extremely difficult. If observed trends continue, the sustainability of this unique landscape of the Western Mediterranean area will be in jeopardy.

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Cork oak forests (top) and Cistus shrublands (bottom) at the study site
(Serra do Caldeirão, Algarve)

Chapter 3

Multiple Recruitment Limitation Causes Arrested Succession in Mediterranean Cork Oak Systems

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Abstract

Lack of tree regeneration and persistency of species-poor shrublands represents a growing problem across Mediterranean evergreen oak forests. What constrains forest regeneration is poorly understood, and restoration attempts have been largely unsuccessful. We assessed the contribution of four different mechanisms of tree recruitment limitation (that is, source, dispersal, germination, and establishment) in a cork oak (*Quercus suber*) system in southern Portugal. Using a combination of field studies and experiments, we quantified seed production, seed removal and dispersal, seed survival and germination, seedling establishment and survival, as well as cork oak natural regeneration for the three dominant vegetation types in this system (*Cistus ladanifer* shrubland, oak forest, and oak savanna). We found that all four forms of cork oak recruitment limitation were significantly more severe in shrublands than in oak forests and savannas, so that oak seedling recruitment in shrubland was impeded in multiple ways. Our results explain why transitions from shrublands to oak savannas and forests are extremely difficult, and that the release from arrested succession in this system requires the simultaneous relief of multiple constraints on recruitment limitation in early life history of oaks. These results have important implications for the restoration and conservation of Mediterranean oak systems.

Key-words: alternative states; *Cistus ladanifer*; facilitation; forest regeneration; seed dispersal; seed predation; seedling establishment; shrub encroachment; *Quercus suber*.

Introduction

Succession has traditionally been conceived as a relatively linear process, but evidence from a variety of ecosystems indicates that persistent alternative vegetation or ecosystem states may occur, particularly after disturbances (Friedel 1991; Laycock 1991; Scheffer and others 2001). In these cases, succession is strongly delayed or practically stopped in a condition called arrested succession (Putz and Canham 1992; Sarmiento 1997). Clearly, understanding the mechanisms responsible for arrested succession and their relative importance across ecosystems will not only contribute to ecological theory but will also be of key importance to the development of conservation and restoration strategies.

Mediterranean ecosystems have been the subject of a long tradition of ecological studies. More recently, the recognition of Mediterranean ecosystems as one of the Earth‘s biodiversity hotspots (Myers and others 2000; Olson and Dinerstein 2002) has boosted the search for a clear understanding of the mechanisms of natural regeneration and the role of arrested succession. Mediterranean ecosystems have a long history of alteration by human disturbances such as grazing, clearing, and fire (Aschmann 1973; Trabaud 1981; Conacher and Sala 1998). Regeneration of original vegetation types after disturbance seems to be halted under certain circumstances, and some successional stages become notoriously persistent (Fuentes and others 1984; Westoby and others 1989; Puigdefábregas and Mendizabal 1998; Holmgren 2002).

Evergreen oak forests used to be widespread in the Mediterranean Basin (Walter 1973; Pignatti 1978). Today, small remnants persist in a very patchy landscape. In the Iberian Peninsula, original evergreen oak forests have been transformed by human management into a mosaic landscape of forest patches, oak savannas, shrublands, and grasslands. In the absence of human management, the usual pathway of natural succession in oak savannas is through the gradual colonization of the understorey by different shrub species (pioneer *Cistus* shrubs, followed by other shrub communities like *Arbutus* and *Erica*), mixed with oak natural regeneration, which leads to forest recovery in the medium-term (Natividade 1950; Gonçalves 1991). Although some natural forest regeneration has indeed occurred in some areas after agricultural land was abandoned during the 1960s (Mazzoleni and others 2004), the transition from shrublands to oak savannas and forests is rare (Natividade 1950; Rivas-Martínez and others 1990; Gonçalves 1991; Montero and others 1994a). Recent estimations for southern Portugal indicate that 60% of the shrubland patches remain as such after 45 years (1958– 2002) and less than 10% progress to oak savannas or forests (Acacio and others, unpublished results). The switch to shrublands may occur from the combination of different types of disturbances (grazing, large clearing for agriculture, or fire) with dry conditions (either south facing slopes, or several dry years). Furthermore, several studies have reported a lack of tree regeneration across the Iberian Peninsula both in oak-dominated patches (Montero and others 1994a; Campos and others 1998; Montero and others 2000; Pulido and Díaz 2005), and in shrubland patches (Pons and Pausas 2006; Pausas and others 2006). Tree recruitment limitation in Mediterranean oak systems has been attributed to a variety of causes, including (1) low seed input due to scarcity of viable seeds and poor seed dispersal (Pulido and Díaz 2005), (2) high levels of seed predation by wild and domestic animals (Herrera 1995; Pulido and Díaz 2002; Gómez and others 2003; Leiva and Fernández-Alés 2003); and (3) low seedling survival due to thermal and water stress (Borchert and others 1989; Pulido 1999; Retana and others 1999; Gómez-Aparicio and others 2004).

In this paper, we assess the contribution of four mechanisms of recruitment limitation (sensu Nathan and Muller-Landau 2000; Schupp and others 2002) – source limitation, dispersal limitation, germination limitation, and establishment limitation – to the persistence and dynamics of the three dominant vegetation types in the cork oak landscapes of southern Portugal: forests, oak savannas, and shrublands. We expect seedling recruitment to be more constrained by each form of recruitment limitation in shrubland than in the other two vegetation types. Specifically, we tested the following hypotheses: (1) source limitation (that is, low seed availability) is greater in shrublands than in savannas and forests, due to a lack of adult trees and lower seed production per tree; (2) dispersal limitation (that is, failure of viable seeds to disperse to potential recruitment sites) is greater in shrublands than in savannas and forests, due to a higher pre-dispersal seed predation by mice and weevils (below adult trees) and lower dispersal by mice and jays in shrublands; (3) germination limitation (that is, failure of viable seeds to survive and germinate) is greater in shrublands than in savannas and forests, due to higher post-dispersal seed predation in shrublands and lower rates of germination; (4) establishment limitation (that is, failure of germinating seeds to establish into seedlings and survive) is greater in shrublands than in savannas and forests, due to higher seedling water stress in shrublands as a result of lower soil water availability and higher temperatures (Diniz 1994). We also tested whether these four types of limitation differed between forests and oak savannas.

Identification of the mechanisms that limit cork oak recruitment and contribute to their decreasing resilience is of vital importance for the management and restoration strategies of Mediterranean cork oak forests, which are classified as a protected nature conservancy area of Europe (Habitats Directive 92/43/EEC), and represent high economical value from cork production.

Methods

STUDY AREA

The study area was located in Serra do Caldeirão (37º 14´ N, 7º 56´ W; 11,000 ha), a mountain ridge in the northeastern part of the Algarve province, southern Portugal. The climate is Mediterranean with most rainfall concentrated in the winter months (December to February) and only 2.5% of the rainfall falling in the summer (June to August). Mean annual precipitation is 900 mm and mean annual temperature is 16.6ºC (45-year period: 1958–2002, Barranco do Velho station). Altitude ranges from 146 to 588 m. Soils are homogeneous, consisting mainly of schist lithosols (soils with hard rock occurring at less than 10 cm depth, in this case schist rock) (National Center for Soil Survey and Land Planning).

The landscape is a mosaic of three vegetation types, where each patch-type represents a different stage in the natural succession: (1) cork oak forests, (2) cork oak savannas, and (3) *Cistus ladanifer* shrublands. Cork oak forests have a closed canopy with high tree density (over 200 trees ha^{-1}) and a diverse shrub layer (for example, *Arbutus unedo*, *Viburnum tinus*, *Erica arborea*, *Pistacia lentiscus*, *Rhamnus alaternus*, *Phillyrea latifolia*, *Calluna vulgaris*, *Smilax aspera*). Cork oak savannas (human--made savannas, traditionally named montados in Portugal and dehesas in Spain) are open canopy patches with lower tree density (less than 200 trees ha^{-1}) and an herbaceous layer, which have been exploited as agroforestry systems for cork extraction, grazing, and crop production. *Cistus* shrublands are patches dominated by *C. ladanifer* shrubs with some *Ulex argenteus*, *Genista hirsuta* and *Lavandula stoechas*, and scattered cork oak trees (less than 100 trees ha^{-1}). They are pioneer heathland species which usually invade cleared understorey patches that were exposed to long--term intensive land use and that have low soil water and nutrient conditions (Gonçalves 1991; Diniz 1994; Latorre 1996; Blanco and others 1997; Seng and Deil 1999).

Cork oak (*Quercus suber*) is a mast-seeding evergreen tree that dominates the late successional stages of this system. Seed predation is mainly caused by insects such as *Curculio elephas* (Coleoptera: Curculionidae) and *Cydia splendana* (Lepidoptera: Tortricidae), and wood mouse (*Apodemus sylvaticus*). The main seed dispersers are wood mouse and European jay (*Garrulus glandarius*), which tend to differ in abundance among vegetation successional stages; rodents are more abundant in shrublands, as jays are in forests.

In December 2003, we randomly selected nine experimental sites in the study area, with three replicates for each vegetation type, namely three forests, three savannas, and three shrublands, which measured 2,500 m^2 each. In December 2004, we selected seven additional sites (three forests, two savannas, and two shrublands) to compensate for sites that were destroyed by a forest fire and shrub clearing practices and to rebalance the experimental design. The total number of sites used was 16. All sites were located less than 8 km apart, on north-northwest exposures. Adult cork tree density in our sites was 280 ± 14 trees ha^{-1} in forests, 165 ± 22 trees ha^{-1} in savannas, and 86 ± 17 trees ha^{-1} in shrublands (average ± SD). For all experiments we collected fresh acorns at the end of November–beginning of December (natural period of availability) from the ground below several trees scattered through the study area. At each of the experimental sites, we quantified for cork oak: (1) natural regeneration; (2) seed production; (3) seed removal and dispersal; and (4) seed germination and seedling survival.

NATURAL REGENERATION

To quantify seedling recruitment in the three vegetation types, we counted the naturally established seedlings (<50 cm tall) in three 4.5 x 1 m plots per each site, separated by a distance of 3 m between each other. Natural regeneration was assessed at six forest sites, five savanna sites, and five shrubland sites. We counted seedlings in 3 years (May 2004, February 2005 and March 2006). Natural regeneration at each moment in time was then averaged per site and per vegetation patch-type. Natural regeneration at all sites includes seedlings originated from seeds and root sprouts because both can establish as new trees. We used analysis of variance (ANOVA) to test for differences in natural regeneration (no. seedlings/4.5 m^2) among forests, savannas, and shrublands and the post-hoc Tukey‘s pairwise test to test for differences. Values were log-transformed before analyses to meet the normality assumption.

SEED PRODUCTION

To test whether seed source limitation was greatest in shrublands (hypothesis 1), we compared seed densities among the three vegetation types. We quantified seed availability by counting the number of acorns on a ground area of 0.5 m^2 below five randomly selected adult cork oak trees at each site, located more than 15 m apart from each other. We sampled four sites for each vegetation type (including sites selected in both 2003 and 2004) in December 2005.

To estimate the crown area of each selected tree, we measured maximum and minimum diameters of the crown (visually selected under the crown) and calculated the crown projection area (using the formula for an ellipse). Crown surface was then averaged per site. To estimate the crop size, we multiplied the average crown surface by the geometric mean of the number of acorns per site. We finally multiplied the crop size by the number of trees ha^{-1} for each site, and obtained the number of acorns ha^{-1}.

We used ANOVA to test for differences in seed production among vegetation types and the posthoc Tukey‘s pairwise test to test for differences. Values were log-transformed before analyses to meet the normality assumption.

SEED REMOVAL AND DISPERSAL

To test whether dispersal limitation was greatest in shrublands (hypothesis 2), we compared rates of seed removal and dispersal by scatter-hoarding rodents among the three vegetation types. Seed removal was measured by following the fate of tagged acorns placed at the experimental sites. We randomly selected three trees at each of 12 sites (four of each vegetation type). Trees were more than 15 m apart. We released 25 tin-tagged acorns on a 1 x 1 m area at the base of each tree at the end of December during the natural period of acorn availability. These seeds had a thin 8-cm-long metal thread with a numbered metal tag in the end (following Li and Zhang 2003; Xiao and others 2006). To make sure that the tagging did not affect seed removal, we released 25 extra acorns (numbered with a wax pen) at two trees in each experimental site. We found no differences in acorn removal between tagged and untagged seeds. A total of 38 trees and 1,510 acorns were used (520 acorns at shrublands and savannas sites; 470 acorns at forests).

We recorded the number of seeds that remained at 3, 30, 60, and 90 days after placement. At each census, we searched a 20-m radius circular area around each release tree for tags of acorns that had been removed. For each retrieved tag (with or without acorn attached to it), we recorded whether the acorn was buried or eaten, and we measured the distance to the release point. Non-retrieved acorns were recorded as missing and were not included in the seed fate analysis. We also recorded infestation by insects of acorns that were not removed, because this factor is likely to affect the attractiveness of acorns for rodents; insect-infested acorns have a lower nutritional value and are more perishable (Den Ouden and others 2005). All tagged-buried acorns that we retrieved were monitored for germination for 90 days.

We used survival analysis (Klein and Moeschberger 1997) to test for differences in seed removal with R 2.3.0 (R Development Core Team 2006). Seed removal time was calculated as the time between release of the seed at the experimental tree and the first census in which the seed was recorded missing. We used Cox proportional hazards models (Cox 1972) to test for differences in seed removal between vegetation types. The cluster option was used to obtain robust coefficient-variance estimates, accounting for dependence of seed fate within stations (trees). Thus, stations (trees), rather than seeds, were treated as replicates. Additionally, we used ANOVA to test for differences among vegetation types in the proportion of seeds ultimately removed and the post-hoc Tukey‘s pairwise test to test for differences. Proportions were arc-sin(square root)-transformed before analysis to meet the normality assumption.

GERMINATION AND SEEDLING SURVIVAL

To test whether germination limitation (hypothesis 3) and establishment limitation (hypothesis 4) were greatest in shrublands, we compared rates of seed germination and seedling survival among the three vegetation types. We sowed 50 seeds in each of our 16 study plots (six plots located in forests, five in savannas, and five in shrublands). We sowed 10 acorns with 50 cm interspacing along five parallel transects 2 m apart. Planting was done twice, at the beginning of December in 2003 (first cohort) and 2004 (second cohort at new sites). Three plots of the first cohort were destroyed by fire, and three plots (two of the first cohort and one of the second) were destroyed by shrub clearing before the end of our experiment.

We monitored acorn germination and seedling survival once a month at all plots during 2 years for the first cohort (March 2004–March 2006) and 1 year for the second (March 2005–March 2006). A seedling was considered dead if it was missing or if it was dry and did not resprout during the next 4 months. To relate seedling performance to the light microenvironment, we recorded whether each emergent seedling was in each of these four conditions: full-sun, half shaded by a tree, completely shaded by a tree, or shaded by a shrub. Most seedlings were shaded by trees in forests and were in full-sun in savannas. In shrublands, most seedlings were under the shade of *Cistus* shrubs, whereas shrub-shade in forests and savannas resulted from other shrub species.

We used survival analyses (see above) to test for differences in seed germination and seedling survival. Germination time was calculated as the time between sowing and germination (that is, aboveground appearance of the radicle). Seedling survival time was calculated as the time between germination and the natural death of the seedling. Seeds/seedlings that were not removed by animals or had not germinated/died at the end of the study (or at the time of plot destruction) were included as censored observations (observations with incomplete information).

We used Cox proportional hazards models to test for differences in seed germination and seedling survival between vegetation types, taking into account differences in observation time among seeds and seedlings, and using the cluster option to obtain robust coefficient-variance estimates, accounting for dependence of seed and seedling fates within plots. Thus, plots (rather than seeds and seedlings) were treated as replicates. Additionally, we used one-way ANOVA to test for differences among vegetation types in the proportion of seeds ultimately germinating and the proportion of seedlings ultimately surviving. Proportions were arcsin(square root)-transformed before analyses to meet the normality assumption.

RECRUITMENT CYCLE

We used the data on the four mechanisms of recruitment limitation to calculate the proportion of seedlings from the total seed production that could successfully establish in each vegetation type, as in Wang and Smith (2002). From the total estimated seed production (seed rain) we subtracted the proportion of seeds eaten by mice before dispersal (pre--dispersal predation, which we define as the proportion of acorns eaten below the parent tree) and after dispersal (post-dispersal predation, based on the proportion of acorns removed and eaten). We then calculated the proportion of seeds that were able to germinate, multiplying estimated germination rates by the total number of non-predated seeds. Some of the removed seeds were scatter-hoarded and buried by mice (secondary dispersal), and were able to germinate. This proportion was added to the germinating proportion. Finally, from the total estimated number of germinated seedlings, we subtracted the proportion of seedlings that died (using estimated rates for seedling survival for each vegetation type) to calculate the proportion of seedlings that was able to establish successfully after 2 years, in each vegetation type.

Results

NATURAL REGENERATION

Natural seedling recruitment (averaged for the 3 years) was more abundant in forests (3.6 seedlings m^{-2}) than in savannas (1.1 seedlings m^{-2}), and very low in shrublands (0.1 seedlings m^{-2}). Differences among the three vegetation types were significant ($F_{2, 26} = 35.2$, $P < 0.001$, and Tukey test).

SEED PRODUCTION

Acorn crop size (that is, number of acorns per tree) was highest in savannas and lowest in shrublands (Figure 1A), but the difference among vegetation types was not significant (ANOVA: $F_{2, 9} = 1.01$, $P = 0.4$). On the other hand, acorn production per ha differed significantly among vegetation types (Figure 1B, ANOVA: $F_{2, 9} = 11.9$, $P = 0.003$). The overall seed production per ha was markedly higher in forests because of the larger tree density. However, differences between forests and savannas were not significant (Tukey test, $P = 0.54$). Shrublands had the lowest seed production per ha (Figure 1B), significantly different from the other two vegetation types (Tukey test, $P = 0.003$ for forests, and $P = 0.02$ for savannas), which agrees with hypothesis 1 (source limitation).

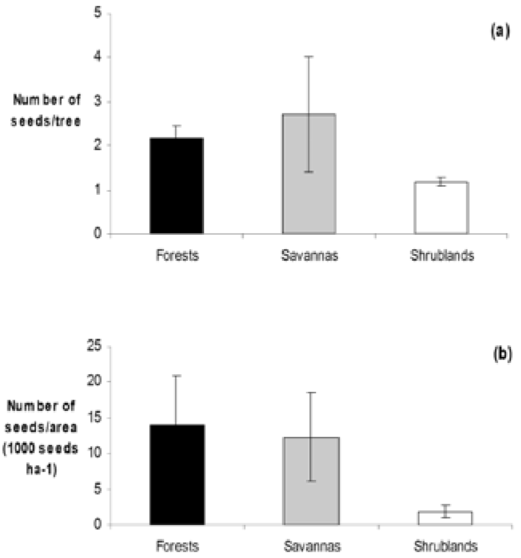

Figure 1. Seed production per tree (a) and per area (b) per vegetation type. Data are geometric means ± 1 SE.

SEED REMOVAL AND DISPERSAL

Predispersal seed predation by mice was lowest in savannas (2%) and similar between forests (10%), and shrublands (8%). Weevil-attack on intact acorns was higher in shrublands (42%) than in savannas (12%) and forests (9%). Therefore, the overall proportion of pre-dispersal predation (both mice and weevils) was highest in shrublands.

Seed removal was faster in shrublands than in savannas and forests (Figure 2). The difference among vegetation types was significant, even when accounting for dependence of removal rates within trees (Robust Cox regression: $U_2 = 9.43$, $P = 0.009$). The estimated removal rate was 3.9 to 4.5 times higher in shrublands than in savannas and forests, but not significantly different between forests and savannas. After 3 months, the proportion of intact seeds remaining was lower in shrublands (17%) than in savannas (53%) and forests (64%) (Figure 2), but this difference was not significant (ANOVA: $F_{2,9} = 3.2$, $P = 0.09$).

Among the retrieved acorns, the highest proportion was eaten in shrublands (91%). Buried (that is, scatter-hoarded) acorns were more common in savannas (33%) and forests (24%) than in shrublands (9%) (Figure 3). However, buried acorns only germinated in forests (16%). Dispersal distances ranged from 0.7 to 23 m and in average were greatest in shrublands (4 m). Although most caches (that is, locations of buried acorns) contained a single acorn, we found three caches with more than one acorn at one of the forest sites. Evidence (footprints, dental marks on acorns, fur, burrows, and trapped individuals) indicated that the wood mouse (*Apodemus sylvaticus*) was the main agent responsible for acorn removal.

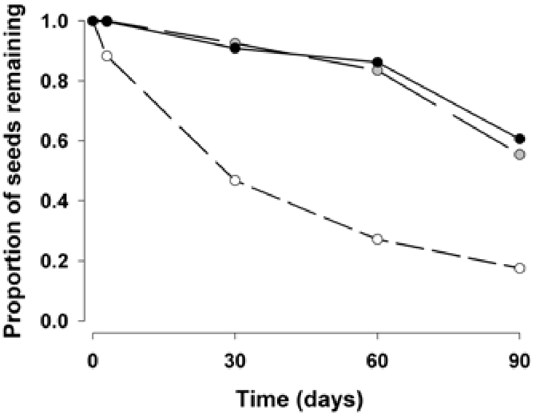

Figure 2. Seed removal per vegetation type. Proportion of seeds remaining over time in forests (black dots, solid line), savannas (grey dots, broken line), and shrublands (white dots, dashed line).

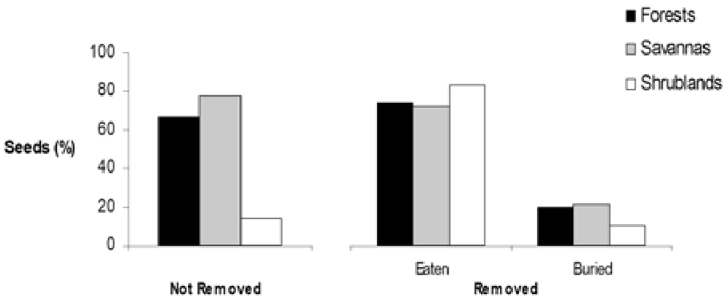

Figure 3. Seed fate per vegetation type (3 months after releasing). Eaten and buried seeds sum up to 100% of retrieved seeds; data are in percentages ±1SE, n = 1,510.

GERMINATION AND SEEDLING SURVIVAL

Shoots started emerging in February and continued until June; the median germination time was 4 months in all vegetation types. The proportion of seeds ultimately germinating (Kaplan Meier estimates ± SE) was lower in shrublands (56 ± 3%) than in forests (76 ± 2%) and savannas (84 ± 2%) (Figure 4A), which agrees with hypothesis 3 (germination limitation). However, the difference among vegetation types was not statistically significant when accounting for dependence of germination rates within plots (Robust Cox regression: $U_2 = 3.4$, $P = 0.19$). The ultimate proportion germinating was also not significantly different among vegetation types considering: all cohorts (ANOVA: $F_{2, 11} = 2.41$, $P = 0.14$), cohort 1 ($F_{2, 6} = 1.4$, $P = 0.32$), and cohort 2 ($F_{2, 2} = 7.31$, $P = 0.12$).

Survival among the 575 emergent seedlings (Kaplan–Meier estimates) was much lower in shrublands (18%) than in savannas (60%) and forests (69%) (Figure 4B). Seedling mortality was estimated to be three times higher in shrublands than in forests (Robust Cox regression: $z = 2.4$, $P = 0.015$) and savannas (Robust Cox regression: $z = 2.4$, $P = 0.017$). The proportion of acorns that had died by the end of the survey was also significantly different among vegetation types (ANOVA: $F_{2, 7} = 5.4$, $P = 0.038$): more acorns died in shrublands than in the other two vegetation types ($P = 0.05$, Tukey test).

Within each vegetation type, there were no significant effects of shading categories (full-sun, half-shade, tree-shade, and shrub-shade) on seedling mortality (Robust Cox regression: $U_3 = 1.9$, $P = 0.59$ for forests; $U_3 = 3.9$, $P = 0.27$ for savannas; $U_3 = 1.5$, $P = 0.69$ for shrublands). Among vegetation types, mortality was lowest among seedlings shaded by trees (32 ± 4%), higher among seedlings in full-sun (47 ± 4%) or in half-shade (49 ± 6%), and highest for seedlings shaded by shrubs (79 ± 6%) (Figure 4C). Among vegetation types, mortality below shrubs was significantly higher than mortality below trees (Robust Cox regression: $z = 3.0$, $P = 0.003$), whereas the difference in mortality with half-shade and full-sun was marginally significant. Overall, shading by shrubs and trees explained seedling mortality better ($R^2 = 0.10$) than did vegetation type ($R^2 = 0.05$). The main (97%) natural cause of death for the 214 experimental seedlings was drought (seedlings were dried without being eaten); other causes were (in decreasing frequency) shrub-clearing practices and fire.

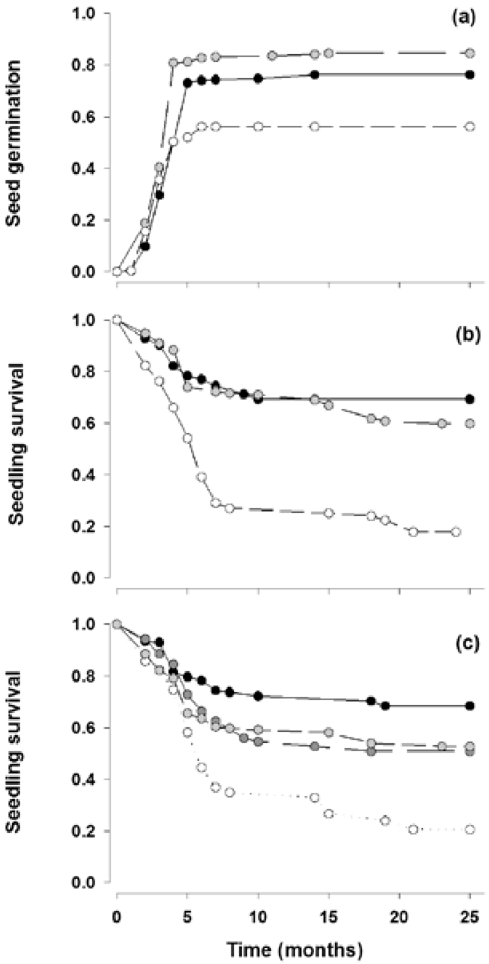

Figure 4. Performance of seeds (germination and survival) per vegetation type. A Proportion of seeds germinated (emergent seedlings); **B** and **C** proportion of seedlings surviving during the study period (Kaplan– Meier estimates). Lines in **A** and **B** represent forests (black dots, solid line), savannas (grey dots, broken line), and shrublands (white dots, dashed line). Lines in **C** represent seedlings shaded by trees (black dots, solid line), half-shaded by trees (dark-grey dots, broken line), in full-sun (light-grey dots, broken line), and shaded by shrubs (white dots, dashed line).

RECRUITMENT CYCLE

Overall, all four forms of recruitment limitation were more severe in shrublands than in forests and savannas (Figure 5). The strength of all types of recruitment limitation was similar between forests and savannas. Higher seed rain in forests compared to savannas was offset by higher pre-dispersal seed predation in forests; therefore source limitation was similar between these two vegetation types. In total, 33% of the seed rain was depredated in savannas and 37% in forests. In shrublands, seed-source scarcity and establishment failure seemed to be the strongest limitations for tree recruitment, whereas germination failure seemed to be less important and approached the values of savannas and forests.

As a consequence, the densities of established seedlings were similar between forests and savannas (although higher in forests) but very low in shrublands. Our estimate of seedling density is lower than the quantified natural regeneration, probably because natural regeneration included not only seed-originated seedlings, but also root sprouts (root sprouting is common among evergreen oaks).

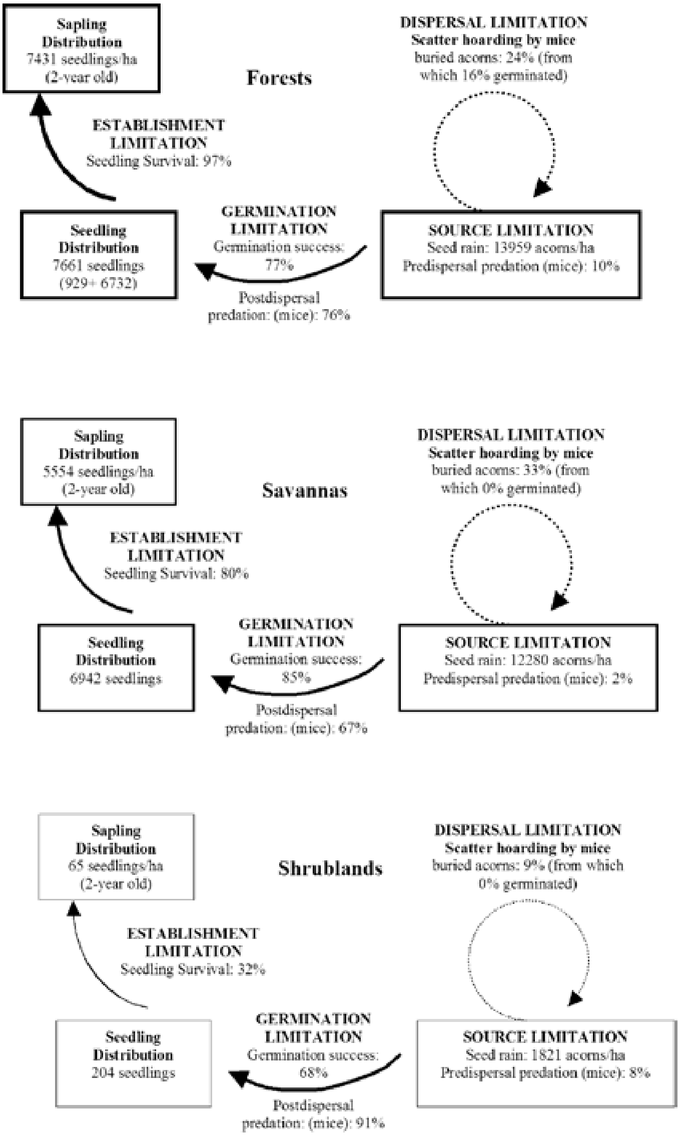

Figure 5. Estimated rate for some phases within the tree recruitment cycle. Final number of established seedlings/ha for each vegetation type, based on observed seed rain, mice predation and scatter hoarding, and rates of seed germination and seedling survival. Germination rates include both cohorts; survival rates include the 2003-cohort (2-year old seedlings); arrow and box thickness is proportional to the probability of seeds/seedlings shifting to the next phase.

Discussion

SHRUBLANDS AS AN ARRESTED SUCCESSIONAL STAGE

Vegetation changes in semiarid Mediterranean ecosystems worldwide have proved to be remarkably persistent (Fuentes and others 1984; Westoby and others 1989; Puigdefábregas and Mendizabal 1998; Holmgren 2002). Several studies indicate that replacement of original oak forests by *Cistus* shrublands remains in a condition of arrested succession for at least several decades (Natividade 1950; Rivas-Martínez and others 1990; Gonçalves 1991; Montero and others 1994a). We have demonstrated that shrubland persistence results from multiple constraints on early oak life history phases including limitations on seed availability (that is, low seed production and high rates of infestation by weevils), dispersal (that is, lower rates of scatter-hoarding), germination (that is, high rates of post-dispersal seed predation and low rates of germination), and establishment (that is, high seedling mortality).

We found that seed sources were scarce supporting our first hypothesis of higher source limitation in shrubland patches. From the few acorns that were available for dispersal, almost half suffered weevil-attack. Insect attack is at the cost of seed viability and seedling growth (Branco and others 2002). Seed removal (that is, potential dispersal) rates were about four times higher in shrublands than in savannas and forests, probably because mice populations are higher in shrubland patches (Pausas and others 2004; Torre and Díaz 2004) and because there is less food available. Comparable results have been found in other Mediterranean oak forests (Pons and Pausas 2007).

However, most of the seeds removed in shrublands were eaten rather than dispersed. The proportion that was scatter-hoarded was lowest in shrublands. Thus, our hypotheses 2 (dispersal limitation) and 3 (germination limitation) were supported. Furthermore, seed dispersal in shrublands is likely to be distance-restricted (sensu Schupp and others 2002) because the main agent responsible for long-distance dispersal - the European jay (*Garrulus glandarius*) -tends to avoid closed shrublands (Bossema 1979; Herrera 1995; Gómez 2003; Den Ouden and others 2005).

None of the acorns that mice cached in shrublands germinated. On the other hand, our experimental results indicate that if acorns are buried deep enough, germination in shrublands is comparable to that in oak savannas and forests. This discrepancy in germination success between the naturally buried acorns and our experimental ones may be explained by soil depth. In our experiments, seeds were fully buried (about 3 cm deep), whereas mice are probably not able to bury acorns that deep on the hard-rock schist soils of the study area.

Oak seedlings faced markedly higher mortality in shrublands than did seedlings in savannas and forests. Mortality was especially high under *Cistus* shrubs, higher even than under full-sun conditions. In summary, this means that the seeds that are produced and effectively dispersed in shrubland patches are not only fewer but also have lower probabilities of producing new recruits from which tree cover might increase. Also, in Spain seedling survival rates under *Cistus* shrubs are much lower than under other shrub species (Gómez-Aparicio and others 2004; Pulido and Díaz 2005) suggesting that in contrast to the facilitative effect of nurse shrubs on seedlings in forests and savannas, competition with seedlings seems to prevail in *Cistus* shrublands. Moreover, *Cistus* shrubs seem to have potential allelopathic effects able to inhibit seedling germination and growth (Chaves and others 2001; Lobón and others 2002).

TREE RECRUITMENT IN FORESTS AND SAVANNAS

Our results show that the four potential mechanisms of recruitment limitation, (namely seed availability, seed dispersal, seed survival and germination, and seedling survival) are comparable between forests and savannas, and contribute to a rather similar final density of established seedlings after 2 years of experimental planting. Nevertheless, natural regeneration was about three times higher in forests than savannas, implying higher difficulties for tree recruitment in savannas. Therefore, there might be other mechanisms limiting tree recruitment in savannas. Other studies have pointed to seed dispersal as the key process limiting tree recruitment in savannas, due to the difficulty of dispersing acorns to shaded sites (Pulido and Díaz 2005 for Spain). Among the mice-buried acorns, none were able to germinate in savannas, whereas 16% of buried acorns germinated in forests. Our experiment clearly shows that seeds can germinate and establish into seedlings in savannas (at least when buried at 3 cm depth). Finally, it is likely that our 2-year-old experimental seedlings will face increasing mortality by drought in the more open savannas than under the forest canopy in the coming years. In fact, we found seedling survival to be significantly lower in full-sun conditions than under tree shade, suggesting that forests provide better establishment conditions than savannas. In summary, our results demonstrate that tree recruitment in savannas does not seem to be strongly limited and that savannas represent an unstable vegetation type that could shift to forests.

IMPLICATIONS FOR RESTORATION

Our results show that oak seedling recruitment is severely limited in shrublands, which may explain the persistence of *Cistus* shrubland patches. Succession in these patches appears arrested, and unable to progress towards savannas and forests. Cork oak recruitment is also rare in the shrublands of eastern Spain, despite shrubland patches being close to oak forests (Pons and Pausas 2006; Pausas and others 2006). We found that all four forms of cork oak recruitment limitation were significantly more severe in shrublands than in oak forests and savannas, hence that oak seedling recruitment in shrubland was impeded in multiple ways. These results have significant implications for the restoration and conservation of Mediterranean oak systems. Management actions would need to simultaneously relieve low seed availability, high rates of seed predation, low rates of seed germination and low rates of seedling survival found in shrublands as compared to other vegetation states. Some concrete actions could include a combination of *Cistus* removal, acorn addition, planting of nurse shrubs (for example, *Genista*) to facilitate oak seedling germination and survival (Gómez-Aparicio and others 2004; Padilla and Pugnaire 2006; Smit and others 2008), as well as facilitating predators of rodents. Note that, also competition after tree establishment can additionally affect the ability of oaks to maintain a viable population in shrublands.

CORK OAK FOREST REGENERATION UNDER CLIMATE CHANGE

Previous studies have indicated that the interaction between disturbance and overall climatic conditions is the key to understanding arrested successions (Holmgren and Scheffer 2001). In our system we found that multiple mechanisms inhibit cork oak recruitment at shrubland patches. It is likely that such mechanisms become reinforced by drier climate conditions especially on the already most degraded and xeric sites. Climate change models predict an increasing frequency of extreme drought and fire events for Mediterranean climate-regions (Cubash and others 1996; McCarthy and others 2001). Since 1972 mean annual temperature has clearly increased in the study region (Water Institute, National Meteorological Institute and Regional Coordination Commission of Algarve), a trend also observed in the rest of the country with the six hottest recorded years occurring in the last 12 years (for the period 1931–2000) (Cabrinha and Santo 2000; Miranda and others 2002). Because mean annual rainfall has not significantly changed in the study region, this increase in temperature implies higher evapotranspiration and plant water stress. Drier conditions will impose stronger constraints to seedling germination and survival especially on the drier southern exposures and open sites, but can potentially reduce seed production as well. Under the current and forecasted climatic trends, shrublands are likely to expand because *Cistus* shrubs are physiologically well adapted to dry conditions and recurrent fires (Werner and others 1998). More extensive shrublands will not only have lower oak seed availability, but also higher densities of mice predating on the oak seeds. All these conditions may further limit oak recruitment and favor the persistence of *Cistus* shrublands making conservation and restoration of diverse Mediterranean forests increasingly challenging.

Acknowledgments

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2-year old cork oak seedling at one of the experimental plots

Chapter 4

Cork extraction as a key factor determining post-fire cork oak survival in a mountain region of southern Portugal

Francisco Moreira, Inês Duarte, Filipe Catry and Vanda Acácio

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Abstract

Bark thickness, a key variable determining post-fire tree survival, usually increases with tree diameter. The cork oak (*Quercus suber*) is an exception to this, as it is the only European tree where the commercial exploitation of bark (cork) occurs. Human management thus becomes the most influential factor determining bark thickness. In this paper, we describe the survival rates and variables affecting cork oak survival 1.5 years after a large wildfire in southern Portugal, with a focus on the management of bark exploitation. The status of 1151 cork oaks was assessed in 40 sampling plots, and logistic regression used to explore the variables affecting survival likelihood, collected at the tree and plot levels. Survival rate was 84%. The most important factors affecting survival were those related to the management of cork extraction: stripped trees, trees with thinner bark and trees with larger diameter, correlated to the number of stripping operations, showed lower survival. Survival also decreased with increasing charring height, an indicator of fire damage. Stripped trees in unfavourable aspects (South to East) also showed lower survival. A survival model was built that can be used to identify areas vulnerable to future fires, if spatially explicit data on stand structure and cork management status are available.

Keywords: Post-fire survival; *Quercus suber*; Portugal; Tree mortality; Tree management; Stand management

Introduction

Post-fire tree survival is determined by factors related to both individual tree and fire characteristics. Important tree features include tree height, tree health and bark thickness (e.g. Ryan, 1990; Pausas, 1997;

Miller, 2000; McHugh and Kolb, 2003). In terms of fire characteristics, intensity is a key factor (e.g. Miller, 2000; Schwilk et al., 2006), and it depends on wind, topography (in particular slope and aspect), fuel moisture and fuel load (determined by the nature and amount of understory vegetation) (e.g. Rothermel, 1983; Whelan, 1995; Schwilk et al., 2006). Other stand characteristics such as average crown base height and tree density, may determine the potential for crown fires (e.g. Van Wagner, 1977; Whelan, 1995; Cruz et al., 2006; Schwilk et al., 2006). Fire intensity will strongly influence fire damage, which can be indirectly evaluated through, e.g. bark char height or the percentage of the crown scorched or consumed (e.g. Stephens and Finney, 2002; Pausas et al., 2003; Rigolot, 2004).

Several studies carried out in coniferous species that do not have resprouting capacity have shown that percent crown volume damaged and bark thickness are key variables influencing post-fire tree survival (e.g. Ryan and Reinhardt, 1988; Dikinson and Johnson, 2001; Stephens and Finney, 2002; Rigolot, 2004). Necrosis of canopy components (foliage, buds, etc.) depends on plume temperatures created by convection heat and their impact on living tissues, and the higher the level of canopy damage the lower the carbon fixation rates and the survival probability (Dikinson and Johnson, 2001). Heat from the flames is conducted through the bark into the underlying cambium, so the thicker the bark, the less cambium damage will occur for a given flame temperature and residence time, increasing survival probability (Miller, 2000; Dikinson and Johnson, 2001).

The cork oak (*Quercus suber* L.) is an evergreen oak occurring in an area of ca. 2 million hectares around the Western Mediterranean basin, mostly the Iberian Peninsula (Portugal and Spain), holding more than 50% of the world distribution area, but also Algeria, Morocco, France, Tunisia and Italy (Pereira and Tomé, 2004; Silva and Catry, 2006). This species has two unique features related to post-fire crown regeneration and to bark that make it different from every other European tree. Firstly, it is able to resprout from stem (epicormic shoots), so the crown volume damage is not a key aspect influencing post-fire tree survival, as trees with 100% crown scorch may easily recover their canopy (e.g. Pausas, 1997). Thus, cambium damage seems the key variable for this species, as previous studies showed the importance of a thick bark for post-fire cork oak survival (e.g. Pausas, 1997; Amo and Chacón, 2003). Secondly, the cork oak has the unique ability, among other evergreen oaks, of having a phellogen, active across all the tree life, producing an increasingly thick layer of cork tissue in the outside. Cork is a valuable raw material for industry and during the cork oak exploitation it is periodically removed, by manually cutting with an axe along vertical and horizontal lines on the stem and thicker branches, and subsequent stripping-off of large cork planks (Pereira and Tomé, 2004). After each cork stripping, the tree has the capacity of producing a new cork bark by adding new layers of cork every year (Pereira and Tomé, 2004). After the first cork debarking (the first cork taken is called virgin cork), the minimum period between successive extractions is 9 years (Pereira and Tomé, 2004). Usually there is a legal size restriction for the first bark extraction (only trees above a given diameter at breast height can be debarked). So, because of cork extraction, the observed bark thickness is not only a function of tree size (or age) in cork oaks, in contrast with other species where bark thickness usually increases with tree age and diameter (e.g. Dikinson and Johnson, 2001).

Cork oak forests are acknowledged for their economical importance (e.g. Barberis et al., 2003; Silva and Catry, 2006). This is particularly so for Portugal, as it holds one third of the world's cork oak surface, from which more than half of the world's cork production is originated (Pereira and Tomé, 2004; Silva and Catry, 2006). Additionally, cork oak forests represent a valuable wildlife habitat, and cork oak stands are classified as protected habitats in the framework of the European Union Directive 92/43/CEE since 1993 (Silva and Catry, 2006).

The previous few studies on post-fire cork oak survival showed a reasonable discrepancy in the obtained results, although a positive relationship between cork oak survival and bark age was always present. For example, Lamey (1893) presents data on cork oak mortality as a function of bark age in Algeria, showing only 10% survival for trees with 2-year cork age when fire occurred, but Barberis et al. (2003) found a much more variable survival rate (up to 95%) for trees with the same cork age in Sardinia. Cabezudo et al. (1995) described only 46% survival in cork oak trees with 6 years of cork age, in Southern Spain, but Pausas (1997) found 99% tree survival rate in North-eastern Spain, with stem death inversely related to tree diameter and canopy height recovery also dependent on bark thickness. More recently, Catry et al. (2006) found 98% survival in adult cork oaks not stripped in the last 30 years, in central Portugal. Clearly, more research is needed to unveil the factors behind cork oak survival after fire, and including other factors besides tree size and cork age, that may influence fire intensity and tree survival.

Cork oak stands occur in a wide range of structures and densities; they can be managed as forest stands, mainly for the production of cork, or alternatively as agro-forestry systems (named “montados” or “dehesas”) with lower tree density and the understory used for crops or pasture (Natividade, 1950; Pereira and Tomé, 2004). The former usually occur in more mountainous regions and are particularly fire-prone. During the summer of 2004 a large wildfire burned more than 20.000 ha in a mountain region of southern Portugal, including vast areas of cork oak stands. We carried out a study of post-fire oak survival in this region, with the objectives of: (i) evaluating cork oak survival 1.5 years after fire; (ii) exploring the tree and site factors affecting individual tree survival; (iii) building a survival model that can be used to identify areas particularly vulnerable to fire where fire prevention should be a priority.

Methods

STUDY AREA AND PLOT DEFINITION

The study area is located in "Serra do Caldeirão", a mountain ridge in the northeastern part of the Algarve province, southern Portugal (Fig. 1). The climate is Mediterranean, with average annual temperature of 16.6 ºC and average annual rainfall of 900 mm. Altitude ranges from 150 to 580 m. Soil type consists mainly of shallow schist lithosols with low fertility and prone to erosion. The landscape is characterized by vast expanses of cork oak forests with varying tree density, ranging from areas with high tree cover to "montados" with scattered trees and the understory usually cleared for crops or pastures. Other land cover types include shrublands dominated by *Cistus ladanifer*, as well as a few pastures or cultivated crops. There are also scattered stands of maritime pine (*Pinus pinaster*) and eucalyptus (*Eucalyptus* spp.). Land property is fragmented and private. Cork extraction is the main economic activity for local communities.

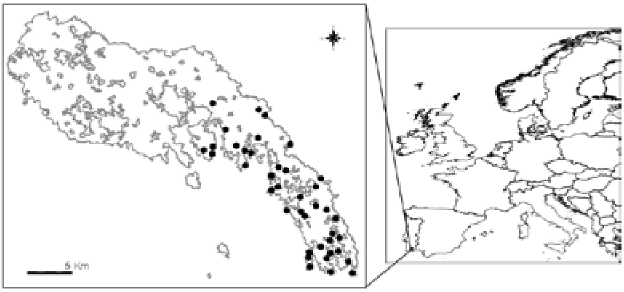

Fig. 1. Study area in the Serra do Caldeirão, showing the fire perimeter and the location of the 40 study plots.

In the summer of 2004 (between 26 July and 4 August), a large wildfire burned 28,620 ha in this region (DGRF APIF, 2005). We used a regular 1 km x 1 km grid of points covering part of the burned area (ca. 15,000 ha; Fig. 1) and defined a 50 m-radius circle (sampling plot) around each point. Plots were checked in the field for accessibility, to confirm if they had burned, and to confirm if they were dominated by cork oak trees. Plots were discarded if these three conditions were not simultaneously met. In the end, a total of 40 plots were selected and assessed. Large within-plot variability in tree size and cork age (and, consequently, bark thickness) was common, as cork debarking was not carried out simultaneously in all individuals (uneven-aged cork).

PLOT VARIABLES

For each 50-m circular plot, tree (variable Tree cover) and shrub (variable Shrub cover) cover prior to fire were visually estimated (to the nearest 5%) with aerial photographs (taken in 2002) and the help of a reference scheme (DGRF, 1999). Up to 4 strip transects were defined in each plot (see Section 2.3), and the dominant aspect (N, S, E,W, NE, NW, SE or SW) (variable Aspect) and slope (in percentage, measured with a hypsometer) (variable Slope) were registered for each one. Additionally, the understory vegetation cover prior to fire was visually estimated for each transect, and classified as sparse/nil, medium or dense, based on the amount of burned shrub remains (branches) (variable Understory cover). The modal vegetation height of this pre-fire situation was also estimated (to the nearest 10 cm) from the height of burned branches (variable Estimated understory height). In some transects not all variables were measured because post-fire management actions (such as ploughing or shrub clearing) had occurred, and so sample sizes were not the same for all variables. The values for these plot and transect variables (Table 1) were assigned to every tree in a given plot and transect.

Table 1 Descriptive statistics the variables considered in this study Level of measurement relates to whether the variable was measured at the plot, transect or tree level. *n* = sample size (number of trees); S.D. = standard deviation.

Variable	Level of measurement	n	Minimum	Maximum	Mean	S.D.
Slope (%)	Transect	1151	12.3	32.4	21.2	4.25
Aspect (8 categories)	Transect	1151	–	–	–	–
Understory cover (3 categories)	Transect	992	Sparse	Dense	–	–
Estimated understory height (cm)	Transect	1052	80	350	155.2	56.21
Tree cover (proportion)	Plot	1151	0.20	0.80	0.34	0.161
Shrub cover (proportion)	Plot	1151	0.05	0.90	0.40	0.264
Tree height (m)	Tree	1151	1.8	14.7	7.1	2.17
Diameter at breast height (cm)	Tree	1151	9.0	91.0	27.1	12.18
Minimum charring height	Tree	1151	0	1.00	0.31	0.339
Mean bark thickness (cm)	Tree	1151	0	6.65	2.53	1.21
Stripping (presence/absence)	Tree	1151	0	1	0.75	0.435

TREE VARIABLES

Individual tree appraisal in the plots took place between December 2005 and April 2006, so roughly 1.5 years after the fire. Trees were assessed along 50-m strip transects (20-m wide) departing from the plot centre at right angles. Given the very high young-tree density in many plots, we only measured trees larger than 9 cm diameter at breast height (DBH). Trees along each transect were measured to obtain a sample of 30 trees per plot. In plots with higher tree density, one transect was enough to attain this sample size. In other plots, up to 4 transects had to be sampled. In a few plots this maximum was not achieved, thus the range was 14–30 trees per plot and the median was 30 trees. A total of

1151 individuals were measured, and five variables were measured for each (Table 1), related to: (a) tree size (tree height (m), measured with a hypsometer (variable *Tree height*), and DBH (cm), taken as the average of two perpendicular measurements (variable *Diameter at breast height*)); (b) fire damage (minimum height of charring, usually measured on the windward side of the tree, Dikinson and Johnson, 2001, expressed as proportion of tree height (variable *Minimum charring height*)); and (c) cork bark thickness (average thickness (cm) at breast height, taken from 4 measurements made with a bark gauge around the trunk (variable *Mean bark thickness*)). The latter is obviously related with time since the last stripping (cork age) in stripped trees, and we confirmed this by registering the stripping year, frequently painted on the bark for management purposes. Thus, for a sample of 259 stripped trees where the number corresponding to the stripping year was still visible in the bark, there was a significant linear relationship between bark thickness (in cm) and cork age when the fire occurred (ranging from 0, corresponding to trees stripped in the year of the fire, to 13 years) ($r = 0.78$, $P < 0.001$). Maximum height of charring is commonly used to characterize fire severity and was also estimated, but we found that in many trees this was difficult to measure due to the time passed since the fire (and the fading of charred color) and the subsequent canopy regeneration. However, there was a significant correlation between minimum and maximum charring height (both measured as a proportion of tree height) (Spearman $r = 0.55$, $P < 0.001$), so we used the former as a surrogate of the latter. The presence/absence of cork stripping was also registered for every tree (variable *Stripping*), in order to separate trees which had never been stripped, thus with virgin cork (unstripped), from trees in which cork exploitation had started and taken place at least once (hereafter named stripped or debarked). Finally, for each tree we registered the presence/ absence of sprouting from canopy and trunk base.

DATA ANALYSIS

We considered that a tree presented post-fire survival if it resprouted from either or both the canopy (independently of the proportion of crown recovered) and base (i.e. it produced suckers). Binary logistic regression (Hosmer and Lemeshow, 1989) was used to find which variables had an influence on post-fire tree survival (coded as 1 if tree alive, and as 0 if tree was dead). The significance of each variable was first tested through a univariate model, by using the likelihood-ratio χ^2 statistic. Variables with $P < 0.1$ were retained for the multivariate logistic model, which was built using both forward and backward stepwise selection. To check whether the obtained models could be improved, some variables were square-transformed (to allow for curvilinear or unimodal trends) and interactions between variables explored, mainly the potential interaction between stripping status, bark thickness, exposure and tree size. Different models with several combinations of variables were compared using the Aikaike Information Criterion (AIC) (Burnham and Anderson, 2003), and the one with lowest AIC considered the more parsimonious. Model performance was assessed through the likelihood ratio statistic and by calculating the area under the receiver operating characteristics (ROC) curve (Saveland and Neueschwander, 1990; Pearce and Ferrier, 2000). Understory cover, aspect and stripping status were analysed as categorical variables.

Correlations between explanatory variables (Pearson correlation coefficient) were usually low. The highest values were observed for DBH and tree height ($r = 0.69$, $P < 0.001$), understory estimated height and tree cover ($r = 0.44$, $P < 0.001$), and slope and tree cover ($r = -0.32$, $P < 0.001$). All analyses were carried out using the SPSS software (SPSS, 2004). Unless otherwise stated, results are expressed as mean ± standard error.

Results

PLOT AND TREE VARIABLES

A summary of the descriptive statistics for the studied variables is shown in Table 1. The average cork oak tree was 7 m tall and measured 27 cm in DBH. Average bark thickness was 2.53 cm. Mean slope was ca. 20%, and most trees were located in NE aspect (20.2% of the trees) whereas the less common orientation was SW (2.6%), with no trees located in SE aspect. The most common understory cover prior to fire was medium (64.5% of the trees), followed by sparse (21.1%) and dense vegetation (14.3%). Of the 1151 sampled trees, 292 (25.4%) had never been stripped.

SURVIVAL RATES AND VARIABLES AFFECTING TREE SURVIVAL

The percentage of trees surviving 1.5 years after the fire was 84% (182 dead trees and 969 live trees). Using the univariate approach, the most important variable affecting survival was cork bark thickness, which had a positive contribution to survival (mean bark thickness of dead and alive trees, respectively, 1.86 ± 0.09 and 2.65 ± 0.04 cm) (Table 2). Aspect ranked second, and after checking survival probabilities associated with the different aspect categories, this variable was simplified and recoded into 2 classes: 1 for South or East, and 0 for the remaining categories (variable Aspect South or East). This recoded simpler variable was also significant ($\chi^2 = 21.27$, d.f. = 1, $P < 0.001$), showing a decreased survival probability in South to East-oriented slopes (76.8% survival against 87.7% survival in other aspect categories), and included in the multivariate analysis instead of the former (see below). The tree variables minimum charring height (mean value in dead and alive trees, respectively, 0.43 ± 0.03 and 0.28 ± 0.01), diameter at breast height (mean DBH of dead and alive trees, respectively, 31.4 ± 1.15 and 26.3 ± 0.36 cm) and stripping (proportion of stripped trees, respectively, 0.84 and 0.73 for dead and alive trees) were all negatively correlated to survival. Ranking last, shrub cover was inversely related to survival (proportional shrub cover for dead and alive trees, respectively, 0.44 ± 0.02 and 0.39 ± 0.07) whereas tree cover was positively related (proportional tree cover for dead and alive trees, respectively, 0.31 ± 0.01 and 0.35 ± 0.05). Tree height was marginally significant, with survival probability increasing in taller trees (mean height for dead and alive trees, respectively, 6.8 ± 0.17 and 7.2 ± 0.07 m).

Table 2 Results of univariate logistic regression to assess the effect of variables on post-fire cork oak survival For each variable, the coefficient (±standard error) and the value of the χ^2 test (equivalent to the change in −2 log Likelihood if the variable was removed from the model) are shown. Variables are ordered by decreasing importance. Significant variables ($P < 0.05$) are signalled in bold. cat = categorical variables.

Variable	Coefficient sign	χ2	d.f.	P
Mean bark thickness	0.584±0.075	67.37	1	<0.001
Aspect	cat	27.59	6	<0.001
Minimum charring height	−1.164±0.218	27.52	1	<0.001
Diameter at breast height	−0.029±0.006	23.47	1	<0.001
Stripping	−0.676±0.215	11.04	1	0.001
Slope	−0.060±0.019	10.11	1	0.001
Tree cover	1.661±0.566	9.44	1	0.002
Shrub cover	−0.881±0.320	7.49	1	0.006
Tree height	0.074±0.038	3.78	1	0.052
Understory cover	cat	3.44	2	0.179
Estimated understory height	−0.000±0.001	0.19	1	0.890

The more parsimonious multivariate model obtained (Table 3, Fig. 2) showed that the most important variables determining cork oak survival in the study area were mean bark thickness, stripping status and DBH. Tree height, minimum charring height and aspect were also important predictors. Stripped trees had lower survival probability than unstripped trees. Interactions between stripping status, bark thickness and aspect suggest that the effects of the two latter variables were only observed in the exploited trees, and not in unstripped ones. Thus, survival probability increased with bark thickness and decreased in unfavourable exposures, but only in stripped trees (Fig. 2a). Trees with larger DBH survived less, particularly if they had been debarked and were located in South to East exposures (Fig. 2b). Taller trees survived better, mainly if they were unstripped (Fig. 2c). The negative effect of minimum charring height was particularly visible in unfavourable exposures (Fig. 2d).

Table 3 Multivariate logistic model to predict post-fire cork oak survival For each variable, the coefficient (±standard error) and the value of the χ^2 test (equivalent to the change in-2 log Likelihood if the variable was removed from the model) are shown. Variables are ordered by decreasing importance. Full model $\chi^2 = 188.4$; d.f. = 8; $p < 0.001$. Area under ROC curve = 0.78 ± 0.02; $p < 0.001$. See also Fig. 2.

Variable	**Coefficient**	**χ2**	**d.f.**	***P***
Stripping x mean bark thickness	0.620±0.092	53.61	1	<0.001
Stripping	−1.759±0.363	24.81	1	<0.001
Diameter at breast height	−0.148±0.032	22.21	1	<0.001
Tree height	1.074±0.254	17.11	1	<0.001
Minimum charring height	−0.876±0.257	11.26	2	0.001
Diameter at breast height 2	0.001±0.000	7.43	1	0.006
Tree height 2	−0.043±0.016	7.08	1	0.008
Stripping x Aspect South or East	−0.526±0.210	6.18	1	0.013
Constant	0.613±0.840			

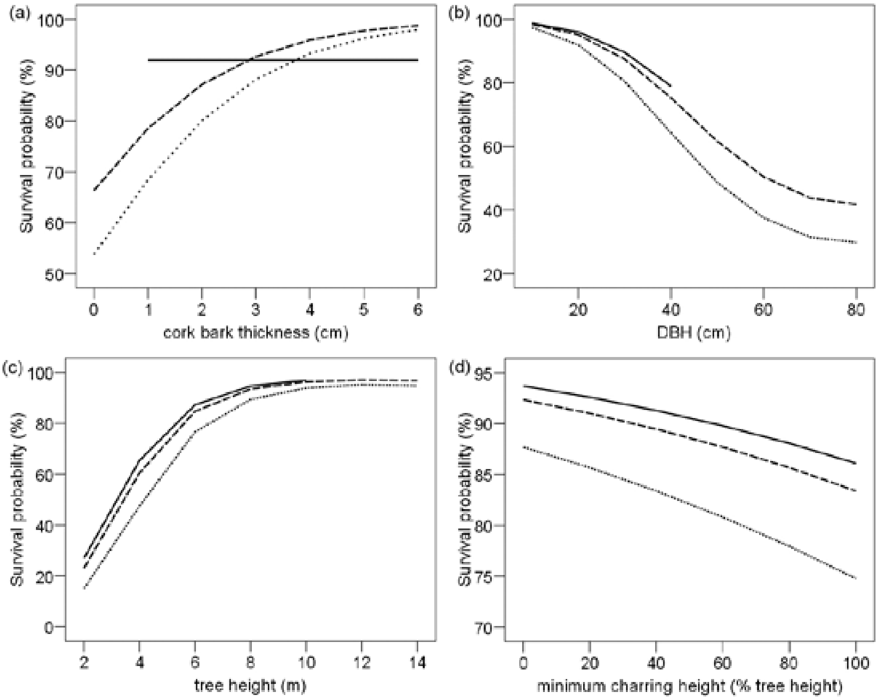

Fig. 2. Logistic model prediction of cork oak survival, based on the model in Table 3. Each figure shows survival probability in relation to (a) bark thickness; (b) DBH; (c) tree height; (d) minimum charring height. Each line represents trees with virgin cork (solid line), stripped trees in favourable exposures (dashed line) and stripped trees in unfavourable exposures (South or East) (dotted line). For each variable, the remaining variables in the model are held constant at their average values of: tree height: 7 m; DBH: 27 cm; bark thickness: 2.5 cm; minimum charring height: 30%. Only existing combinations of variables are shown.

Discussion

Average post-fire survival probability for cork oaks in this mountain region of southern Portugal, 1.5 years after a wildfire, was ca. 84%. Factors affecting survival could be divided into the ones related to individual tree resistance to fire and the amount of fire damage. Our results showed that part of the large variability in survival estimates obtained in previous studies (e.g. Lamey, 1893; Pampiro et al., 1992; Cabezudo et al., 1995; Pausas, 1997; Barberis et al., 2003; Catry et al., 2006) may be explained by the fact that bark thickness, although important, is not the only variable affecting survival. Thus, different studies on post-fire survival in trees having similar cork ages but widely variable tree size, understory composition, exposure, or fire intensity, may yield quite different survival rates. These latter variables were usually not taken into account previously.

Trees with virgin cork showed significantly higher survival rates (89.5%) than stripped ones (82.4%). In addition, their survival was not influenced by bark thickness or exposure, in contrast with trees being explored for bark extraction. This suggests that trees with virgin cork are more fire-resistant than stripped trees. One possible explanation for this is that the insulating properties of bark are particularly effective on unstripped cork oaks, due to a different bark structure. The cork of previously stripped trees has approximately twice the number of pores per unit of area than virgin cork, thus enabling easier heat penetration, particularly because these pores are often obstructed or surrounded by lignified walls (Calvão da Silva, 1996). It also has a higher bark density than virgin cork (Fonseca et al., 1994) and, consequently, a higher thermal conductivity that increases the rate of heat diffusion through the bark (e.g. Hengst and Dawson, 1994). A complementary explanation for the increased survival in unstripped oaks is that they do not suffer from wounding associated with cork stripping operations. Costa et al. (2004) showed that cork stripping damage (due to cuts penetrating down to the phellogen) has negative effects on tree health and growth, to which unstripped trees are not subjected.

Cork bark thickness was a key variable influencing the survival of debarked trees. In comparison with the average of 82% survival, stripped trees with bark thickness less than 1 cm (n = 140) had just 59% survival, and this proportion decreased to 35% for trees with bark thickness under 0.5 cm (n = 46). Previous studies (e.g. Lamey, 1893; Pausas, 1997;

Barberis et al., 2003) showed the crucial importance of this variable in conferring a higher resistance to fire, due to the insulating properties of cork oak bark. Slight increases in thickness will largely increase survival likelihood, as heat transfer models show that the time needed to kill the cambium of a tree increases with the square of bark thickness (Dikinson and Johnson, 2001). Our models suggest that above 3–4 cm bark thickness trees are well protected from fire (Fig. 2). To find out to which cork age this thickness interval could correspond, we sought to use available models of annual cork growth (Natividade, 1950; Tomé et al., 1998). However, annual cork growth is quite variable, with estimates ranging roughly from 2 to 9 mm, and being larger for younger aged cork (Tomé et al.,1998). Furthermore, as bark thickness was measured 1.5 years after fire, we would have to correct for the potential cork growth between fire occurrence and our field measurements. To overcome these drawbacks, we preferred to use the relationship between cork thickness (measured in 2005/2006) and cork age in 2004, obtained for the measured trees (see methods). Using this relationship, 3–4 cm of cork thickness corresponded to 6–8 years of cork age. Interestingly, the obtained model suggests that stripped trees do worst than trees with virgin cork if bark thickness is less than 3 cm, but do slightly better if they have thicker bark (Fig. 2a). However, a direct comparison of survival rates as a function of bark thickness yields significant differences for the former (if thickness <3 cm, 91.4% survival for trees with virgin cork versus 77.7% survival for stripped trees; $\chi^2 = 15.1$, $P < 0.0001$) but not for the latter (if thickness ≥ 3 cm, 88.5% survival for trees with virgin cork versus 92.1% survival for stripped; $\chi^2 = 1.4$, $P = 0.236$).

Trees with larger stem diameter usually have thicker bark (e.g. Ryan and Reinhardt, 1988; Miller, 2000; Dikinson and Johnson, 2001) and thus higher post-fire survival. But in cork oak, trees with larger DBH had lower survival probability. First of all, there was no correlation between DBH and cork thickness ($r = 0.02$, $P = 0.487$). Additionally, larger cork oak trees correspond to older trees which were more often subjected to stripping, and thus stripping damages, as well as likely poor management practices (e.g. deep ploughing or excessive canopy pruning). Thus, they may be more susceptible to stress or diseases affecting growth and vitality (Natividade, 1950; Costa et al., 2004; Silva and Catry, 2006). Even if older trees have a thick bark, wounds and scars may be present (Natividade, 1950; Costa et al., 2004), which represent weak points in terms of fire resistance (Miller, 2000). This could explain why bigger trees may be more susceptible to fire and have lower survival probability. In Sardinia, Barberis et al. (2003) also found that cork oaks stripped more often had higher mortality after fire (40%) than trees debarked only once (17%).

Survival probability increased with tree height, although the relationship seemed to have a ceiling above 8–9 meters (Fig. 2c). Taller trees will have their canopy further away from flames during the passing fire front, and consequently will suffer less crown scorch from a surface fire (e.g. Van Wagner, 1973; Gould et al., 1997; Miller, 2000; Rigolot, 2004), and will be less prone to crown fire (Van Wagner, 1977), which probably explains their higher likelihood of survival.

Trees with a higher proportion of the bole charred had lower survival (Fig. 2d). The height of bole charring is a measure of the potential direct impact of fire in the tree, i.e. an indicator of the heat received by a tree, which is determined by the temperature reached and the duration of exposure (Miller, 2000; Rigolot, 2004). Thus, trees with larger proportion of their total height charred probably had bigger damage.

Aspect was also an important variable influencing post-fire tree survival (Table 3). In other studies, variations in fire regime with aspect have been attributed to differences in fuel accumulation, structure and moisture (e.g. Whelan, 1995; Schwilk et al., 2006). In our study area, it is likely that South to East oriented aspects, where survival was lower, have a more xerophitic character that may have caused higher tree physiological stress and thus more vulnerability to fire. In addition, South and

Southeast aspects are the most exposed to the predominant hot summer winds in the region (Ribeiro et al.,1987).

Less important (only significant in univariate models) predictors of cork oak survival were slope and proportional shrub and tree cover (Table 2). Cork oak survival decreased with slope, probably because in steeper slopes water retention is lower, soils are thinner, and fire spreads faster and with higher intensity (e.g. Rothermel, 1983; Viegas, 2004), and therefore trees are more susceptible to fire. Trees located in plots with higher shrub cover experienced lower survival. Again, fire intensity is expected to be higher in these conditions of higher biomass accumulation (Rothermel, 1983). In contrast, higher tree cover in the plot increased survival probability, possibly because wind speed and fuel moisture, respectively, decrease and increase in denser stands, which mitigates fire intensity (FAO, 2001b). Alternatively, this result is due to the correlation between tree density and slope (higher tree density occurred in lower slopes).

IMPLICATIONS FOR MANAGEMENT

The present study showed that cork extraction is a key factor determining post-fire cork oak survival. Firstly, the more fire resistant trees are the unstripped ones, and the management decision of stripping virgin cork will increase tree susceptibility throughout life. Secondly, bark extraction creates a time window of several years during which the tree is particularly fire-prone (until bark regrows to the thickness conferring higher fire protection). Thirdly, throughout a tree's life, the more stripping operations are carried out, presumably the more fire susceptible it will become. Lastly, stripping increases tree susceptibility in unfavourable exposures. Thus, in contrast to most other trees, fire resistance in cork oak is essentially determined by management decisions, namely when to start debarking and the timing of successive cork extractions, rather than by natural biological processes such as tree and bark growth. The impact of debarking has been described to be so detrimental to the extreme that trees can die just because of the occurrence of hot and dry winds immediately after cork extraction (Lamey, 1893; Natividade, 1950).

The Portuguese law establishes a minimum cycle of 9 years between successive cork extractions (Pereira and Tomé, 2004), but in some regions it is common to wait 10–12 years between two successive strippings. Longer cycles will improve tree health, resistance to fires, and in many cases cork quality (Natividade, 1950). This author suggested that in mountainous areas like in Southern Portugal, it would be possible to obtain an appreciable improvement of cork quality by increasing the debarking cycle to 12–15 years. This could be particularly important as our data suggest that trees start to be well protected from fire at a cork age of 6–8 years, almost coinciding with the 9-year debarking cycle. In addition, the cork extraction of a stand may be carried out simultaneously in all trees (even-aged cork) or only in a selection of trees, resulting in differential cork age distribution in the stand (uneven-aged cork) (Pereira and Tomé, 2004). In the former situation, the probability that all trees in the stand will die if a fire occurs after debarking is much higher in comparison with the latter, so uneven-aged cork exploitation is preferable to minimise stand-level ecological damage and economic losses from wildfires.

To minimise tree mortality in plots with higher shrub cover, understory management to reduce cover, if carried out some time before the cork striping, will reduce fire severity in case a wildfire occurs in the first years after debarking (CELIÈGE, 2005). Whenever possible, understory reduction should be done without soil mobilization to minimize erosion. Furthermore, when trees growth on thin soils, the roots are more superficial, so it is convenient to not increase tree damage by ploughing or compacting the soil (Amo and Chacón, 2003).

The obtained survival model can be used in management, as it allows the mapping of areas more vulnerable to fire (where higher post-fire mortality will be expected) based on individual tree height and diameter (or average characteristics at the stand level), cork data (presence of virgin cork, cork thickness or cork age), and exposure. These areas should be given priority in terms of fire prevention. This vulnerability map should be updated as cork exploitation changes cork age stand-structure through time.

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Cork oaks recently debarked. Note the darker colour of the trunk from where cork was extracted; the number is for the last digit of the year of extraction (in this case, 2002) and the letters are for the landowner´s initials

Chapter 5

Interactive effects of human and ecological factors determine persistence of cork oak forests in southern Portugal

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SUBMITTED

Abstract

Mediterranean ecosystems have long been shaped by a history of human and ecological disturbances. Understanding the dynamics of these ecosystems requires understanding how human and ecological factors interact. In this paper, we assess the combined role of management practices and biophysical variables (wildfire, slope and exposure) to explain patterns of persistence in cork oak forests in southern Portugal. We use face-to-face interviews with landowners to collect information on management practices and social variables. Additionally, we use aerial photographs and a Geographic Information System (GIS) to classify forest transitions during 45 years (1958-2002) and logistic regression to explain such changes based on collected management and biophysical variables. The best model for tree persistence includes both biophysical and management variables and shows that cork oak persistence was more likely in the absence of wildfires, in steeper slopes, in areas where no understory management was carried out before 1975, and in areas where no tree plantings were carried out after the 1980s. We have found that cork oak persistence is better understood when taking management variables into account. We have also determined that more than half of the landowners interviewed hold traditional beliefs that run contrary to current scientific knowledge and the results presented by this paper. Adequate reforestation programs, integrated policies and efficient government extension programs should be put in place, as well as knowledge exchange between scientists, technicians and landowners.

Key-words: *Cistus ladanifer*, forest transitions, agroforestry systems, wildfires, shrub encroachment, *Quercus suber*

Introduction

Mediterranean landscapes have long been shaped by a history of human management and ecological processes such as disturbance and succession (Aschmann 1973; Trabaud 1981; Conacher and Sala 1998). Understanding the dynamics of such landscapes and changes between different vegetation patch-types requires understanding how social and ecological factors interact, and how these interactions change over time (Lambin 2005; Perz 2007). Indeed, a landscape science or land use science has recently been born, integrating information from natural, social and geographic sciences (Plieninger and Schaar, 2008).

Since the 1960s, major socio-economic changes have led to a gradual abandonment of traditional agriculture and a rural exodus in Mediterranean Europe (Joffre and others 1991; Pinto-Correia 2000). Abandoned farmland has undergone a process of colonization by shrub and tree species, and a succession from fallow to forest was observed in many locations during the past 50 years (Mazzoleni and others 2004).

In southwestern Iberian Peninsula, a traditional agroforestry land use system dominates the landscape, where cork oak (*Quercus suber* L.), Holm oak (*Quercus ilex* L.) or a mixture of both, coexist with pastures and crops. Since the 1960s that rural exodus has caused abandonment of ploughing and herbivory in the understory of the oak trees (Pinto--Correia and Mascarenhas 1999; Alves and others 2003; Pinto-Correia and Vos 2004). In the absence of human management, the usual pathway of natural succession in agroforestry oak systems is through the gradual colonization of the understory by different shrub species (pioneer *Cistus* shrubs, followed by other shrub communities like *Arbutus* and *Erica*), mixed with oak natural regeneration, which will lead to forest recovery in the medium-term (Natividade 1950; Gonçalves 1991). However, several studies have reported decreasing oak density (Ferreira 2000; Vicente and Alés 2006; Vallejo *et al.*, 2009), high oak seedling mortality (Anon. 1990;

Montero and others 1994a), and lack of tree regeneration both in oak-dominated patches (Campos and others 1998; Montero and others 2000; Pulido and Díaz 2005), as well as in shrubland patches (Pons and Pausas 2006; Pausas and others 2006).

In Mediterranean agroforestry systems, persistency of some successional stages may be intrinsically related to management decisions affecting the ecological processes. Clearing of large areas for agriculture and pastures may eliminate "nurse" shrubs and increase drought stress on tree seedlings; it may also eliminate suitable dispersal sites and affect the habitats of the animal species responsible for seed dispersal. Also, livestock grazing contributes to seed and seedling predation (Herrera 1995, Pulido and Díaz 2002; Gómez and others 2003; Leiva and Fernández-Alés 2003). Management may interact with ecological processes and amplify limitations for seedling establishment, which consequences can be observed even after management has stopped.

There is some understanding of the ecological mechanisms responsible for patch persistency in Mediterranean ecosystems (Fuentes and others 1984; Westoby and others 1989; Puigdefábregas and Mendizabal 1998; Gonçalves 1991; Montero and others 1994a; Holmgren and others 2000; Acácio and others 2007), and some sociological work has been done on several Mediterranean forests (Pinto-Correia and Jorge 1996, Mazzoleni and others 2004). However, the interaction of ecological and social mechanisms is less understood and much work still needs to be done (Rindfuss and others 2004; Lambin 2005; Perz 2007).

Previous work in southern Portugal has shown that patches dominated by cork oak trees have been decreasing since 1985, with an important fraction becoming shrublands, that shrubland patches increased during the last 45 years, and that shrubland persistency has been promoted by wildfire, particularly at southern exposures in the last decade (Acácio and others 2009). Furthermore, shrubland patches have been found to be an arrested succession where cork oak recruitment is very difficult (Acácio and others 2007). Landscape changes were related with ecological variables (Acácio and others 2009) but management variables were not taken into account. From such departure point study, we now hypothesize that management variables can play an important role in explaining persistence of cork oak trees and might interact with topography and increasing wildfire frequency in the Iberian Peninsula (Pausas 2004; Anon. 2006).

The overall objective of this study was to assess the combined role of management practices and biophysical variables in explaining cork oak persistence in southern Portugal, and relate management decisions with landowner's perceptions. We use face-to-face interviews with landowners to collect information on management practices and social variables. We use aerial photographs and a Geographic Information System (GIS) to classify forest cover changes over a 45-year period and logistic regression to explain such changes based on collected management and biophysical variables. We further use information from interviews to discuss landowner's motivations regarding local forest problems, which allow better understanding of management decisions.

Methods

STUDY AREA

The study area is an 11,000 ha area in Serra do Caldeirão (37° 14´ N, 7° 56´ W), a mountain ridge in the northeastern part of the Algarve province in southern Portugal. The climate is Mediterranean, with average annual temperature of 16.6°C and average annual precipitation of approximately 900 mm (45-year period: 1958-2002, Barranco do Velho station). Altitudes range from 146 to 588 m. Predominant soil type is schist lithosols (National Center for Soil Survey and Land Planning). These soils are shallow, with a topsoil of approximately 15 cm, low fertility and prone to erosion. Cork oak (*Quercus suber*) is the dominant tree species in the study area.

HISTORICAL DESCRIPTION

Before the 15th century, southern Portugal was covered with cork oak forests, which were mainly used by kings and nobility to hunt large game, for firewood and for extensive grazing. Between the 15th and the 17th centuries the cork oak area in Portugal diminished substantially due to an increasing demand for wood for shipbuilding, agricultural land and pastures. Cork begun to be used for bottling wine after the 17th century, acquiring an increasing commercial value. From the 18th century onwards, cork oak forests were gradually transformed into an agroforestry system exploited for cork, crops and pastures (Mendes 2007). It is likely that the management of such agroforestry systems throughout the centuries also included protection of oak natural regeneration and artificially seedling or planting, in order to maintain cork production (Capelo and Catry 2007).

In the first half of the 20th century, traditional management of cork oak systems in the Iberian Peninsula included cork extraction, extensive grazing of pigs and sheep, and crop production. Shrub clearing and other operations were done by manual labour and trees were exploited in uneven-aged stands for natural regeneration (Soares and others 1998). From 1929 until the beginning of the sixties, most of the land in southern Portugal was cultivated for wheat, following a government policy known as The Wheat Campaign that strongly subsidized wheat production (Baptista 1993). During the 1950s wheat cultivation expanded to less suitable lands (Baptista 1993) with poor, shallow and lower productivity soils, such as oak forest lands, which tend to be more vulnerable to the detrimental effects of intensive cereal cultivation. At that time, most of the cork oak area in southern Portugal was exploited as an agroforestry system for cork, grazing and cropping. Stands age-structure included older trees from the 19th century and younger trees that had been planted in the beginning of the 20th century, when large reforestation projects with cork oak took place in the south (Costa and Pereira 2007a). Decades of The Wheat Campaign led to soil exhaustion (Pinto-Correia and Vos 2004), elimination of cork oak natural regeneration and the felling of many adult trees for cereal cultivation (Mendes 2007). Only forest areas located on steep slopes were not utilized as an agroforestry system because steepness made understory management for crop cultivation difficult or impossible.

Between the 1960s and 1970s, the national agricultural working population decreased by about one third (Baptista 1993) due to important national and international socio-economic changes (industrialization, immigration to cities and emigration) that took place by this time. After 1975 understory use had already been abandoned in the least productive lands and smaller properties in southern Portugal (study area included) and only cork was maintained as the single production component (Pinto-Correia and Mascarenhas, 1999). Presently in the study area, agriculture is only done for local family subsistence around the few scattered settlements and livestock is reduced to only few flocks of goats and sheep (approximately 500 animals) and is mainly based on fallow lands or shrublands (Pires 2000). Land holdings within the area are very fragmented and all under private tenure. Cork extraction is currently the main economic activity of the region, as it is the major economic asset of cork oak lands (Pereira, 2007b).

MANAGEMENT AND SOCIAL VARIABLES

Management and social data were derived from face-to-face interviews with landowners, and were carried out by a single interviewer. Landowners were defined as proprietors of the land and do not necessarily live in the study area. There is no information available on the ownership of the land at the study site, apart from landowners who are members of the Association of Forest Producers of Serra do Caldeirão (AFPSC), thus landowners were selected from this database. We were able to contact 20 landowners who owned 31 parcels (some landowners owned more than one). The landowner sample is considered representative of the study region, since it includes about 20% of all members of AFPSC and the sampled properties are spread throughout the study area.

The interviews included a combination of open-ended, qualitative questions along with closed, structured questions. Interviews were grouped in three main parts, each one with questions covering several variables:

i. Land management between 1958 and 2002, using the following variables: 1) understory management (crops cultivation and/or livestock); 2) total livestock units; 3) livestock composition; 4) cutting adult cork oak trees; 5) shrub clearing; 6) investments in land (including cork oak planting);
ii. Landowner profile, using the following variables: 1) age; 2) level of education; 3) type of management decisions (owner; others); 4) profession;
iii. Individual perceptions: 1) factors related with forest cover change (closed questions on cork oak natural regeneration and shrub encroachment, and open-ended questions on erosion, cork oak mortality, and wildfires); 2) open-ended questions on the main problems faced in local forest management; 3) open-ended questions on what is missing for local forest management.

When questions referenced a point in time that occurred many years ago, interviewees tend not to accurately recall their motivations and decisions, and owners of multiple parcels might be confused about which management has been implemented in each parcel (Rindfuss and others 2004). To account for this, national historical events (such as elections, governments, etc) were used as dates to help the landowner remembering of past management practices and management changes.

Since some of the management variables collected from the interviews were related or represented similar information, they were further combined. Total livestock units and livestock composition were simplified into a single variable indicating the presence or absence of livestock. However, the presence of livestock was positively associated with understory management (n= 35, $\chi^2 = 10.2$, $P = 0.0014$) thus we retained only the latter for further analysis.

Understory management existed only for the period before 1975 (for all parcels except one, owners stopped understory use for livestock or crops after 1975). Before 1975, the variable shrub clearing was also positively associated with understory management (n=35, $\chi^2 = 21.6$, $P < 0.001$), so it was excluded from further analysis. After 1975, shrub clearing was done at all parcels except for two, therefore it was excluded from further analysis. Finally, from all the investments in land (such as acquiring machinery and equipment, pruning trees, improving forest road network and building water points), tree planting was the one that could have a higher visible impact in forest cover changes. Tree planting only took place after 1985 following European Union subsidies. Adult cork oak trees were only cut after 1975, due to mortality.

Thus, from the initial six management variables, we derived a set of three management variables, related to the occurrence of: 1) understory management before 1975, 2) tree cutting after 1975; and 3) tree planting after 1985. Based on the interviews, we assumed that the parcels owned by the same interviewee were subjected to the same management practices.

COLLECTION OF DATA ON FOREST TRANSITIONS

Forest cover changes in the study area were characterised using aerial photographs from 1958 and orthophotos (rectified copy of an original aerial photograph) from 2002, thus covering a 45-year period. Aerial photographs were previously scanned and then orthorectified and georeferenced with ENVI 3.4 (Anon. 2001a) in order to produce geometrically correct images and project them onto the same coordinate references as the digital orthophotos (Transverse Mercator projection, datum WGS84). Digital elevation models with a spatial resolution of 8 meters were used for altitude coordinates (orthorectification process), and ground control points (between 10 and 15 per photo) were taken from the 2002-orthophoto for map coordinates (georeferentiation process). We obtained a RMS Error of about 10 meters. We overlaid a regular 0.5x0.5 km grid of points over the entire study area, and selected all the points that were contained inside landowners parcels. We selected 35 points from the 31 parcels (larger properties had more than one point) and photo interpreted on screen a 50 m-radius circle (sampling unit) around each photographic point. Photointerpretation was performed on a photo-by-photo basis. The grid was created with Arcview GIS 3.2 (Anon. 1999) and laid over the aerial photographs and orthophotos (imported into the GIS as scanned images).

For 1958 and 2002, each of the 35 sampling units was classified into one of the following five vegetation patch-types:

1– cork oak forests with high cork oak density (more than 100-150 trees/ha) and a diverse shrubby layer (e.g. *Arbutus unedo*, *Viburnum tinus*, *Erica arborea*, *Pistacia lentiscus*, *Rhamnus alaternus, Phillyrea latifolia*); this class corresponds to a tree cover higher than 30%;
2– cork oak savannas where cork oak density is lower than in forest patches (less than 100 trees/ha) with sparse shrubs in the understory; this class corresponds to a tree cover between 10% and 30%;
3– shrublands dominated by *Cistus ladanifer* shrubs, pure or mixed with *Ulex argenteus*, *Genista hirsuta* and *Lavandula stoechas* shrubs; in this class, less than 10% of the sampling unit is covered by trees;

4– grassland patches dominated by cultivated croplands, semi-natural pastures, or fallow land; in this class, less than 10% of the sampling unit is covered by trees;
5– others (e.g. plantations, pine forests, eucalyptus forests, riparian forests, and urban).

When more than one vegetation patch-type occurred in a sampling unit, it was classified based on the predominant type. Sampling units with only one type of patch-type were predominant (more than 50% of the total units) and when not, we could usually clearly assign one dominant class to each unit. We used tree cover percentage rather than tree density since in many cases it was not possible to count the number of trees on the photographs. Boundaries for forest cover (10% and 30% of ground cover) follow the National Forest Inventory norms (Anon. 2001b).

Before photo classification (2003) we visited the study area several times to familiarize ourselves with the different vegetation types and compare them with the patterns on the aerial photos of 2002. We estimated transitions between vegetation patch-types by counting the number of sampling units of any vegetation patch-type that changed into any other between 1958 and 2002. Transitions where there was maintenance or increase in tree cover were registered as cork oak persistence; transitions where there was absence or decrease in tree cover were registered as lack of cork oak persistence (Table 1). The sampling units classified as “others” were excluded from further analysis.

Table 1 – Types of vegetation transitions (1958-2002) grouped into cork oak persistence or lack of cork oak persistence (Fo: forest; Sa: savanna; Sr: shrubland; Gr: grassland)

Cork oak persistence (maintenance or increase in tree cover)	Lack of cork oak persistence: (absence or decrease in tree cover)
Fo→Fo	Sr→Sr
Sa→Sa	Gr→Sr
Sa→Fo	Fo→Sr
Sr→Fo	Sa→Sr
Sr→Sa	Fo→Sa
Gr→Fo	Gr→Gr
Gr→Sa	

BIOPHYSICAL VARIABLES

Three biophysical variables were collected for the study area: slope, exposure and wildfire occurrence. Slope is a relevant variable since it determines soil depth and erosion risk, thus determining tree growth and survival. Exposure determines the amount of sun and shade at a site, thus affecting vegetation succession and oak seedling survival (e.g. southern exposures are drier). Wildfire is a disturbance that will affect tree mortality and vegetation succession.

Topographical variables (slope and exposure) were derived from digital elevation models (Portuguese Military Geographic Institute) and stored as two Arcview GIS layers. We assigned one class of slope and exposure to each sampling unit based on the most common type. The slope categories were: low to medium (0-20%); steep (20-30%); very steep (>30%). The exposure categories were: north facing slopes (including NW, N and NE), south facing slopes (including SW, S and SE) and others (E and W). Wildfire occurrence was available as spatially referenced and digitized data for every year between 1984 and 2002 (General Directorate of Forests). The limits of the burned area per year were stored as an ArcView GIS layer and overlaid with the sampling units in order to identify the sampling units that were affected by fire between 1984 and 2002. The maximum number of times a unit was affected by fire in the period 1984-2002 was two.

STATISTICAL ANALYSES

To assess the relative importance of biophysical and management variables on the probability of cork oak persistence, we used an information--theoretical approach based on the Aikaike information criterion corrected for small sample sizes (AIC_c) (Burnham and Anderson 2003). This approach is based on formulating a series of empirical models that rely on an understanding of the system being studied, followed by an assessment of how the different putative models compare to the reality and explain the variation observed (Rushton and others 2004). The suite of candidate models is compared using the parameter AIC_c; the smaller the AIC_c value, the better the model fits the data. AIC_c differences (Δ_i) between each model and the model with the smaller AIC (AIC_{min}) can be used to assess the relative support for the different alternative models (Burnham and Anderson 2003).

Logistic regression (Hosmer and Lemeshow 2000) was used to evaluate the influence of biophysical and management variables on tree persistence (presence/absence) during the period 1958-2002. Due to the small sample size in the lower slope class, only 2 slope categories were considered, ≤ 30% and >30%. Exposure and wildfire were also assumed as categorical variables.

Models were built as follows. Firstly, for each set of biophysical and management variables we calculated separate models for each of the predictor variables (3+3 models), and 2 separate models for each set of 3 variables, and then built both forward and backward stepwise selection models (which yielded similar results, thus 2 models). Then, we built stepwise forward and backward selection models pooling all 6 variables. This resulted in a total of 12 different models.

For each model, AIC differences (Δ_i) and Akaike weights (w_i) were estimated; these correspond to weights of evidence in favour of each model being the nearest to reality, given the other models being considered (Burnham and Anderson 2003; Rushton and others 2004). The sum of w_i for all models equals to one. Subsequently, the set of models for which we have 95% confidence that it contains the best approximating model to the true model was identified by finding the subset of models for which the w_i sum to 0.95 (Burnham and Anderson 2003). The relative importance of each variable was also estimated by summing the Akaike weights across all models that contain that variable (Burnham and Anderson 2003).

Model fit and predictive performance of models were evaluated through the likelihood ratio statistic (full model χ^2) and by calculating the area under the receiver operating characteristics (AUC) curve (Pearce and Ferrier 2000). The calculation of the AUC and standard error was based on a non-parametric assumption.

Results

LAND MANAGEMENT AND LANDOWNER'S PROFILE

Before 1975, most landowners used their lands as an agroforestry system for cork, pastures and crops (70% of respondents at 26 sampling units). The size of herds was variable, usually between 50 and 100 animals, with mostly sheep and pigs. After 1975, adult dead trees were cut at 29 sampling units (about 80% of total sampling units) and after 1985, cork oak tree planting was carried out at 14 sampling units (40% of all sampling units). All interviewees were responsible for the decisions and implementation of their own land management practices, however, just 10% work directly on the land, 50% are retired, and 40% have a different profession than the land management. Most landowners were more than 60 years old (60% of interviewees), and only one (5% of interviewees) was less than 45 years old. Half of the interviewees had a low level of education (primary school) and 20% were college-educated.

LANDOWNER'S PERCEPTIONS

Table 2 shows the frequency (number and %) of landowner responses regarding individual perceptions on main causes of soil erosion, tree mortality and fire, changes in natural regeneration and changes in shrubland area since 1960. Table 3 shows direct quotations from landowners regarding difficulties and needs on local forest management.

The use of disk harrowing, rippers and heavy machinery was the most frequent answer (21,2%) for the main cause of soil erosion, followed by heavy rains. Opposite answers were given: cereal cultivation in the past and lack of cereal cultivation were pointed out as responsible for soil erosion in 15,2% and 9,1% of total causes, respectively. We also found that 35% of interviewees believe that there is no erosion at the study site (those landowners are not included under question 1 of Table 2).

Table 2 – Landowner's individual perceptions (frequency of responses) Total number of responses per question is higher than number of interviewees (20) because each interviewee usually gave more than one response to each question

Question asked	**Response**	**Frequency of response**	
		Number	**%**
Q1. What are the main causes of soil erosion at the study area? (open-ended)	Lack of fertilizer and lack of cereal cultivation	3	9,1
	Drought	5	15,2
	Cereal cultivation in the past	5	15,2
	Disk harrowing, use of rippers and heavy machinery	7	**21,2**
	Heavy rains	6	18,2
	Complete shrub clearing in steep terrains	2	6,1
	Decreasing tree density	1	3,0
	Wildfires	4	12,1
	Total	33	100,0
Q2. What are the main causes of cork oak mortality at the study area? (open-ended)	Disease	19	**24,4**
	Drought	10	12,8
	Wildfires	5	6,4
	Complete shrub clearing	3	3,8
	Lack of traditional land use with wheat cultivation and livestock (lack of fertilizer and manure)	12	15,4
	Pesticides	1	1,3
	Disk harrowing and ploughing, shrub clearing with heavy machinery	7	9,0
	Less soil water	1	1,3
	Old age of cork oak trees	1	1,3
	Soil erosion	6	7,7
	Pollution	5	6,4
	Clayey soils	2	2,6
	Inadequate human management	6	7,7
	Total	78	100
Q3. What are the main causes of wildfires at the study area? (open-ended)	Arson	19	**52,8**
	Lack of shrub clearing and fuel management	5	13,9
	Drought	3	8,3
	Lack of firemen capacity: bad coordination among firemen during combat; firemen lack forest fire fighting techniques and have bad knowledge of the terrain	5	13,9
	Negligence	2	5,6
	Accidents	2	5,6
	Total	36	100
Q4. How did cork oak natural regeneration change since 1960? (closed)	Increased	16	**80,0**
	Decreased	4	20,0
	Total	20	100
Q5. How did shrubland area change since 1960? (closed)	Increased	16	**80,0**
	Decreased	1	5,0
	No changes	3	15,0
	Total	20	100

Table 3 – Landowner's difficulties and needs related to local forest management. Table shows direct quotations from landowners

Interview Number	Main difficulties for local forest management	What is missing?
1	Properties are too small to invest	Government subsidies
2	Topography of the landscape	More shrub clearing to prevent wildfires
3	Wildfires, cork oak disease	(no answer)
4	Wildfires, lack of machines, high costs of shrub clearing	Roads, machines, seeding with selected acorns, prescribed burning in the winter
5	Wildfires and disease	Manpower
6	Cork oak mortality, lack of cadastre, small property	Landowner cooperatives and concerted management, scientific research; environmental instruments are too rigid concerning fuel management
7	Cork oak mortality, long time for subsidies payment; acorn production has been decreasing	More communication between landowners and researchers, livestock to feed on the grass and shrubs (fuel management)
8	Wildfires	(no answer)
9	(no answer)	(no answer)
10	Lack of land profitability land abandonment	(no answer)
11	Lack of land profitability, decreasing cork production because of disease	Compensations for restrictions from environmental instruments such as Natura 2000, cadastre
12	Bureaucracy (ex.; long time to get an authorization to cut a dead cork oak)	There are no subsidies for seeding (which are more successful than plantations), landowners cooperatives, more decision-making power for Associations of Forest Producers
13	Cork oak mortality (still without a cure for the disease), market competition with plastic stoppers	(no answer)
14	Lack of forest fire fighting techniques; too much bureaucracy for investments with subsidies and long time waiting for money	Subsidies for livestock (which is good for fuel management and fertilizing the soil); improvement of inspection
15	Cork oak mortality, decreasing cork production, money has to be invested before receiving subsidies	Find a cure for the cork oak disease
16	Cork oak mortality	Manpower, people working the land and living there
17	Land abandonment, lack of profitability of small landowners	Forest management, faster payment of subsidies and less bureaucracy
18	Small property and land fragmentation	Livestock for fuel management, landowners cooperatives, multiple-use forest management
19	Wildfires	Less taxes for managers and businesses; incite production
20	Wildfires	Landowner cooperation

A long list of responses was given for main causes of cork oak mortality at the study area but by far the most frequent cause referred by landowners was disease (24,4%), which was given by all interviewees except one. The disease that landowners are referring to is the one caused by the fungi *Phytophthora cinnamomi*, which has been correlated with cork oak decline in several recent studies (Moreira and Martins, 2005) Surprisingly, lack of traditional land use with wheat cultivation and livestock appeared as the second most frequent response (15,4%), corresponding to 60% of interviewees. Landowners further explained that wheat cultivation and livestock provided fertilizers and manure to the soil, and the lack of such is causing cork oak mortality. Drought and management changes (from traditional manual labor to the use of disk harrowing and heavy machinery) are the two next most frequent responses for cork oak mortality (12,8% and 9%, respectively).

Arson is pointed out by all landowners except one as the main responsible for wildfires (52,8% of total responses), followed by lack of firemen capacity to fight forest fires and lack of fuel management (both with 13,9% of total responses).

Most of interviewees (80%) reported that natural regeneration has been increasing since 1960 (after understory cultivation ceased), whereas 20% of the interviewees stated that natural regeneration has been decreasing since 1960. One landowner that answered that natural regeneration is increasing added that there is however high seedling mortality. Furthermore, most landowners stated that they do not protect natural regeneration during silvicultural interventions such as shrub clearing, which can lead to the destruction of seedlings. Landowners also claimed that the use of inadequate techniques (such as bad terrain preparation and insufficient supervision during the first years) in plantings was responsible for low seedling survival rates. Furthermore, during the course of the interviews, several landowners stated that direct oak seeding should be used instead of planting since it would allow higher seedling survival, but European Union (EU) programs have only been subsidizing planting operations. Two of those landowners included seedling with selected acorns and subsidies for seeding when asked about “what is missing for local forest management” (see Table 3).

Most of interviewees (80%) reported that *Cistus* shrubland area has been increasing since 1960 and only one affirmed that shrubland area has decreased because of subsidised shrub clearing in the last decades. Three respondents stated that there were no changes in shrubland area (Table 2).

Cork oak mortality (including disease) and wildfires were pointed out as the two main difficulties for local forest management by 35% and 30% of all respondents, respectively. Bureaucracy (to cut a dead cork oak tree and the long time for subsidies payment) (20%), small property--size and lack of land profitability (both with 15%) were the next most frequent answers. Many other issues were quoted as problems for local forest management, including: decreasing acorn and cork production, land abandonment, lack of cadastre, and market competition with plastic stoppers (Table 3).

Landowner cooperatives, subsidies (for seeding, livestock, and to compensate restrictions from environmental programs), livestock for fuel management, manpower, and communication between researchers and landowners were quoted as the most important necessities for local forest management (Table 3). Five landowners didn’t respond when asked on what is missing.

DETERMINANTS OF TREE PERSISTENCE: MANAGEMENT OR BIOPHYSICAL VARIABLES?

Forest transitions registered as tree persistence were observed at 23 sampling units (65,7% of all units) mostly due to persistence of forest and savannas (48% and 13%, respectively) and transitions from savannas to forests (13%). Forest transitions registered as lack of tree persistence were observed at 12 sampling units (34,3% of all units) mostly due to transitions from forests, savannas and grasslands to shrublands (33%, 17% and 17%, respectively), and shrublands persistence (17%).

The best model for tree persistence (persistence of forest and savannas, transitions from any patch-type to forests, and transitions from shrublands and grasslands to savannas) during the period 1958-2002, included both biophysical (slope and wildfire) and management variables (understory management and tree planting), and had an Akaike weight of 0.76 (Table 4). According to Burnham and Anderson (2003), models with AIC_c differences between 0 and 2 have substantial support, thus the second model (Δ_i=2.304) is also considered an alternative good fit to the data. This second model (Akaike weight of 0.24) is similar to the first one but with the exclusion of slope. All remaining models have much higher Δ_i and residual Akaike weights. The evidence for the first 2 models is expressed by summing their Akaike weights, showing that they represent an approximate 99% confidence set, i.e., we have 99% confidence that these 2 models contain the best model among the set of models compared. Wildfire occurrence, understory management before 1975, and cork oak planting were the most important variables in the set of models. These 3 variables were equally important, each with an Akaike weight of 0.99. Slope was second in importance (Akaike weight = 0.76). The remaining variables were not relevant for the models (Akaike weights <0.01).

The two best models presented a very good fit to the data (Table 4) and showed that tree persistence was more likely in the absence of wildfires, in steeper slopes, in areas where no understory management was carried out before 1975, and in areas where no tree planting was carried out after the 1980s.

Table 4 – Results of AIC_c-based model selection for tree recruitment models
For each model, the table shows the predictor variables entering the model and respective direction of association (positive + or negative –) with response variable (occurrence of tree recruitment), the AIC_c value, AIC_c differences (Δ_i) and Akaike weights (w_i), and model fit (full model χ^2 and area under curve (AUC±s.e.). Models are ordered by increasing Δi. Codes for management variables: underst= understory management pre 1975; cuttree= cut trees post 1975; planting= tree planting post 1985.

Model	Variables						AIC_c	Δ_i	w_i	χ^2	AUC
	exposure	slope	fire	underst	cuttree	planting					
1		+	–	–		–	22.618	0.000	0.759	34.45	0.98±0.019
2			–	–		–	24.922	2.304	0.240	29.41	0.95±0.035
3				–		–	37.062	14.444	0.001	14.71	0.83±0.069
4				–	–	–	38.583	15.965	0.000	15.75	0.85±0.066
5		+	–				39.933	17.315	0.000	11.84	0.80±0.084
6				–			40.265	17.647	0.000	9.11	0.69±0.087
7			–				41.612	18.994	0.000	7.76	0.73±0.097
8						–	43.947	21.329	0.000	5.43	0.70±0.096
9	– (S)[1]	+	–				44.481	21.863	0.000	12.59	0.81±0.080
10		+					45.902	23.284	0.000	3.47	0.66±0.100
11					–		48.278	25.660	0.000	1.01	0.56±0.100
12	– (S)[1]						51.661	29.043	0.000	0.12	0.52±0.103

[1] lower probability of tree recruitment in southern exposures, compared to other exposures

Discussion

CORK OAK PERSISTENCE EXPLAINED BY BOTH HUMAN MANAGEMENT AND BIOPHYSICAL VARIABLES

The analysis of alternative models to explain cork oak persistence showed that models including both biophysical and management variables constituted a much better fit to the data than models based on just biophysical or management variables. This shows that management is a significant driver of change observed at landscape–level in this Mediterranean forest landscape, and plays an important role to explain forest transition and tree persistence patterns. Previous work at the study area has shown that wildfire and exposure were the two most important biophysical variables explaining forest transitions (Acácio and others 2009). Our results now show that forest changes are better explained by also taking management variables into account. Cork oak persistence was more likely in areas where understory management (livestock and/or crops) and cork oak plantings were never carried out, in the absence of wildfires, and in steeper slopes.

MANAGEMENT FACTORS DETERMINING CORK OAK PERSISTENCE

The fact that tree persistence was found to be more likely in areas where understory management had not occurred in the past can be explained by several factors. It is well-documented how intensive wheat cultivation and grazing pressure under tree canopy in southern Portugal during decades led to a severe decrease in soil fertility, which can still be observed today (Natividade 1950; Oliveira 1955; Gonçalves 1991; Pinto-Correia and Vos 2004). Similar consequences for soil from past agroforestry practices are also observed for Spain (Montero and others 1994b). Indeed intensive understory use during decades caused decreasing understory vegetation cover due to continuous ploughing and cereal cultivation. A decreasing understory vegetation cover increased both water run-off and soil erosion and led to soil degradation through losses of soil moisture and nutrients (Lima and others 2000). Additionally, grazing causes soil compaction through trampling (Pulido and Díaz 2002), which also contributed to soil degradation. Very degraded soils and higher insulation (due to lower shading) make conditions for seedling survival very difficult and thus halt tree persistence.

We also observed that lack of tree persistence and transitions towards shrublands were more likely where cork oak planting had taken place, which appears to be a contradictory result. However, cork oak plantations in the Algarve province have registered very low survival rates, especially at drier exposures, with many young trees dying during the first months (Lima and others 2000). The use of inadequate techniques have been pointed out as an important cause of low plant survival in the Algarve, such as inadequate terrain preparation and shrub management and bad or no supervision during the first years (Lima and others 2000). The low genetic quality of the reproductive material used in many cork oak reforestation projects in Portugal has also been pointed out as one of the causes for low seedling survival (Almeida and others 2006). Also in Spain, oak plantings suffer from high plant mortality, mainly due to summer drought (Alloza and Vallejo 1999; Zamora and others 2001; Castro and others 2002).

Furthermore, initial vegetation clearings for plantations and other management interventions that are necessary during the first years of any reforestation project decrease vegetation diversity (Zavala and others 2004) and also destroy existing seedlings. As a result, if planted seedling mortality is high in the first months, there is less vegetation cover and the soil is quickly invaded by *Cistus* shrubs. Shrub encroachment competes with the remaining seedlings for soil water and nutrients, increasing oak mortality and subsequently decreasing tree persistence, particularly in low-fertility and erosioned soils.

BIOPHYSICAL VARIABLES DETERMINING CORK OAK PERSISTENCE

In the best model, cork oak persistence was found to be more likely in the absence of wildfires, which can be explained by several factors. Abandonment of traditional agroforestry land use led to shrub encroachment and the accumulation of dead wood, increasing the wildfire hazard (Piussi and Farrell 2000; Pausas and Vallejo 1999; Pardini and others 2004). Higher fire frequency increases the loss of soil fertility by accelerating erosion (Pardini and others 2004). Xerophytic *Cistus* shrubs are well-adapted to very poor soils (Gonçalves 1991) and are pyrophitic shrubs, which rely on fire to spread their seeds. On the other hand, either frequent fires or intense fires may kill adult cork oak trees, especially if the wildfire occurs immediately after cork extraction (Cabezudo and others 1995; Pausas 1997; Moreira and others 2007), which takes place in the summer, when the wildfire season begins in Mediterranean Europe. In such conditions cork oak recruitment is very difficult and the system may remain in an arrested sucessional stage dominated by pyrophitic *Cistus* shrubs.

The best model also shows that forest persistence is more likely on steeper slopes (although slope presents a lower Akaike weight than understory management and wildfire), probably because forests here were less subjected to human interventions on the understory, especially ploughing, which is more difficult or impossible on very steep slopes.

LANDOWNER'S PERCEPTIONS AS DETERMINANTS OF MANAGEMENT DECISIONS

We found surprising answers, which are not in accordance with scientific references: 15% of landowners believe that past intensive cereal cultivation was good for the soil and the lack of wheat cultivation is in fact responsible for soil erosion; 35% of landowners believe that there is no erosion at the study site; and more than half of landowners (60%) believe that the absence of traditional land use with wheat cultivation and livestock is responsible for cork oak mortality. Such beliefs run contrary to current scientific knowledge and the results found in this study.

Landowners are likely to have a landscape preference for agroforestry systems since this is the type of landscape that they perceive as the appropriate use for the territory, having difficulties in accepting a transformation of the landscape (Gómez-Limón and de Lucío Fernández 1999) and denying the existence of a problem (like soil erosion), thus creating ideological barriers. Such barriers can stop landowners from choosing adequate management practices (like adequate techniques for shrub clearing or protection of natural regeneration), which could certainly contribute to increase cork oak persistence in the study area.

Landowner behavior within the study area is also conditioned by the perception that their holding is too small and that further improvement through investment would not pay dividends. Some types of improvements are subsidized by the EU, which further condition the landowner's management practices. For example, although landowners believe that seeding is the best method for cork oak artificial reforestation at the study area, they chose to use planting operations instead because these are subsidized. Indeed subsidies are included on the list of needs for local forest management. Other studies have found that EU subsidies play an important role on management decisions, and can sometimes cause further degradation of tree cover (Pinto-Correia and Vos 2004). Planting was observed as one of the variables contributing to lack of tree persistence and many landowners recognized the use of bad or inefficient techniques.

Conclusion

Our results show that the forest changes at the study area are better understood if studied as a coupled human-environment system, which requires an integrated methodological approach that uses interdisciplinary tools (e.g. social sciences and ecology). We found that land management (intensive understory use and inadequate planting operations) in combination with biophysical factors (wildfire and slope) triggered shrub encroachment and decreased tree persistence. It is likely that the forest ecosystem lost capacity to recover from past practices damaging the soil and vegetation, and is now additionally threatened by more frequent wildfires (Zavala and others 2004). Natural succession is halted and the system remains in a pioneer state consisting of *Cistus* shrublands (Zavala 2003;

Acácio and others 2007). Cork oak forest recovery can become very difficult, be it through natural regeneration or even artificial reforestation (Natividade 1950; Zavala 2003; Acácio and others 2007).

Traditional attitudes and beliefs on the best management practices are not easy to change, especially with an aged and low-level educated rural population. Furthermore, when the property is small, management is frequently absent, and sales prices can be below land profit, which causes landowners to avoid investment. Moreover, cash losses make the renewal of cork oak woodlands economically unattractive to private landowners, which will not undertake such practices without subsidies (Ovando *et al.*, 2009). Integrated policies and efficient government extension programs should be put in place, as well as knowledge exchange between scientists, technicians and landowners. For example, at areas where tree density assures enough seed sources, it is essential to inform landowners on the protection of natural regeneration. Also, improvement of technical capacity and concerted actions for wildfire prevention and forest management can be put forward with landowners associations.

If the stands are uneven aged and the forest is well managed, cork production can be more or less constant every year, being cork extracted from trees with different ages (cognizant of the fact that cork can only be extracted every 9 years from each tree). If the cork oak systems are to be maintained, both in ecological and economical terms, additional regeneration is required and the most appropriate techniques and genetic material for each site should be carefully chosen and followed at all cork oak reforestation projects.

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Harvested cork stacked in piles in the open air to dry

Chapter 6

Synthesis

Mediterranean cork oak ecosystems have long been shaped by a combination of human management and ecological drivers that act upon vegetation dynamics. The current cork oak landscape in southern Portugal is the result of such interaction. As in other Mediterranean land use systems, overexploitation of the land and mismanagement have led to soil degradation and erosion, failures in cork oak recruitment and loss of woodlands. Areas with degraded soil conditions and drier sites are quickly invaded by pioneer heathland rockrose (*Cistus* spp.) shrubs, which constitute highly persistent patches. A hypothesis examined in this thesis is that the resulting shrublands constitute an alternative stable state of lower vegetation biomass at sites with degraded soils and dry conditions. Decades of overgrazing and intensive land use without protecting cork oak natural regeneration could have triggered feedback mechanisms that have led to a persistent shrub-dominated vegetation in which the establishment of cork oak seedlings and forest recovery had become very difficult. Shrublands could therefore represent an irreversible tree loss. It will be recalled that the dual objectives of this thesis were to evaluate if *Cistus* shrublands and cork oak forests were alternative stable states and to identify the land use and ecological mechanisms underlying their resilience and persistence.

In the research described in this thesis I used long-term observations (45 years), collected multidisciplinary data (ecological, land management and landowners' perceptions) and analysed multiple processes at broader (landscape) and smaller (plots) scales. In this thesis I have presented evidence that shrublands are an alternative stable state of lower vegetation biomass in former cork oak areas where forest recovery has been halted by multiple limitations to oak recruitment. I have also identified ecological and land use variables that drive landscape transitions and ecological feedbacks, contributing to forest regression and shrubland persistence and expansion.

Landscape changes

The analysis of landscape changes and patch type transitions over 45 years (1958-2002) showed that *Cistus* shrublands have been the most persistent patch type and have been expanding. Cork oak forests have also been persistent but, contrary to shrublands, have been decreasing since 1985. Savannas and grasslands have been less persistent (Chapter 2). Human intervention in cork oak savannas and grasslands has decreased since the 1960s, as a result of major socioeconomic changes (Alves *et al.*, 2003; Pinto-Correia and Vos, 2004), and therefore these two patch types have largely disappeared from the study area (particularly the grasslands), since they only survive if actively managed.

If the understorey of agro-silvopastoral systems such as pastures and crops under cork oak trees is not maintained in the Iberian Peninsula, it is expected that vegetation succession will follow the path towards forest recovery. Therefore, shrublands are usually assumed to be an intermediate phase before forest establishment in Mediterranean Europe (Mazzoleni *et al.* 2004). However, the research presented in this thesis shows that after an initial recovery following agriculture abandonment (1958-1984), since 1985 the cork oak savannas have been changing into shrublands six times faster than into forests (Chapter 2), which indicates that vegetation succession is not proceeding towards forest recovery and that shrub encroachment might be limiting oak regeneration in patches of savanna, especially under drier conditions. Furthermore, although cork oak forests represent the late successional stage of the system, since 1985 they too have been changing into shrublands, at an accelerating rate (Chapter 2). However, during the 45-year observation period, less than 10% of the shrublands changed into oak savannas or forests (Chapter 2). Several ecological and land use factors were found to influence the persistence and expansion of shrublands, and regression of cork oak forests and savannas in the study area.

Ecological and land use factors triggering transitions between patch types

The research results presented in preceding chapters show that shrubland is more persistent where wildfire has occurred, particularly on south-facing slopes. *Cistus* shrubs are active pyrophytes, thus their persistence can be supported by a positive feedback mechanism triggered by frequent wildfires, especially on southern aspects, where conditions are drier and more hostile for seedling recruitment and cork oak survival (Chapter 2). In addition, the results also show that post-fire survival of cork oak trees was lower on the slopes facing south to east in the study area (Chapter 4), which are more xerophitic and also the most exposed to the predominant hot summer winds in the region (Ribeiro *et al.*, 1987). On these sites the trees are therefore subjected to greater physiological stress. So, it seems that the combination of wildfire occurrence and aspect accounts for the lower post-fire survival rates of cork oak trees, since physiological stress will increase a tree's vulnerability to fire. As demonstrated (in Chapter 2), wildfires caused a decrease in forest persistence and triggered transitions from forests to shrublands after 1995. It will be recalled that it was argued that the observed transitions were probably reinforced and accelerated by the rise in mean annual temperatures since the 1970s (the six hottest recorded years occurred in the last 12 years of the period 1931-2000: Cabrinha and Santo, 2000, Miranda *et al.*, 2002) and increased frequency of wildfires in recent decades (Pausas, 2004; Anon., 2006) in southern Portugal.

From the findings presented in earlier chapters, patch type transitions at the landscape scale are determined not only by ecological processes, but also by human intervention, such as intensity of land use and management practices. Cork oak agro-silvopastoral systems are inherently unstable and have to be maintained by human management of the understorey. If the understorey under cork oak trees is not managed, it is expected to develop shrubs and cork oak trees, which will establish and lead to forest recovery. However, in Chapter 5 it was shown that for the 45-year observation period, the interactive effect of past understorey management, cork oak planting, wildfire occurrence and less steep slopes (although slope was less important than the other variables) correlated significantly with patches that underwent shrub encroachment, patches where tree cover diminished, and patches with no tree cover. It was concluded that the interaction of such management and ecological factors halted forest recovery and led to shrub encroachment.

Past understorey management in oak agroforestry systems of southern Portugal has been pointed out as a major reason for the current soil erosion and lack of fertility, particularly due to long-term intensive wheat cultivation from the 1930s to the 1960s (Baptista, 1993). In addition, it is also generally known that livestock grazing led to a gradual decrease in cork oak natural regeneration and seedling establishment. As livestock grazing pressure and understorey use intensified, the understorey vegetation cover gradually diminished, due to continuous ploughing, cereal cultivation and no protection of acorns or oak natural regeneration from grazing livestock. On already degraded soils, inadequate cork oak planting interventions will further increase soil erosion (Zavala *et al.*, 2004). Indeed, it has been reported that the use of inadequate techniques for cork oak planting combined with summer drought has led to high seedling mortality in southern Portugal (Almeida *et al.*, 2009). In addition, vegetation diversity and soil cover will decrease due to the vegetation clearings that are necessary for any reforestation project (Zavala *et al.*, 2004). As a result, if planted seedling mortality is high in the first months and remaining vegetation cover is sparse, and there is no project supervision, the soil is quickly invaded by *Cistus* shrubs. In infertile and degraded soils, *Cistus* shrubs will outcompete the remaining oak seedlings for soil water and nutrients, increasing oak mortality. If a wildfire occurs, *Cistus* shrubs will spread their seeds and expand, some cork oak seedlings will be destroyed, and the ones that are able to survive or recover will face several limitations to establish in shrubland patches (Chapter 3).

Figure 1 is a schematic depiction of the conclusions reached from the findings reported here, i.e. that the persistence of shrubland patches, absence of cork oak recruitment and regression of forests result from a combination of several management and ecological factors. As reported in Chapter 2, most of the changes are gradual and transitions between forests and shrublands are not immediate, instead, the tree canopy disappears gradually: forest patches first change into savannas and then these savannas change into shrublands. However, severe wildfires coupled with past intensive land use practices and drought may lead to abrupt transitions from forests to shrublands (Figure 1). Furthermore, as shown in Chapter 4, post-fire survival of adult cork oaks is also essentially determined by management decisions, namely when to start debarking and the timing of successive cork extractions. The reason Figure 1 does not include grasslands is because, as noted in Chapter 2, today they occupy very small and scattered patches in the landscape and are very unstable.

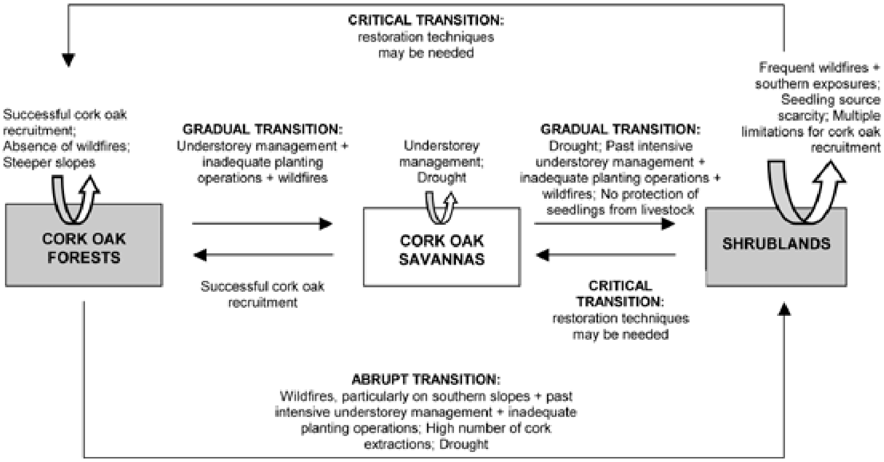

Figure 1 – Ecological and management factors that trigger transitions between cork oak forests, cork oak savannas and shrublands

Dashed lines indicate critical transitions, circular arrows indicate persistency of vegetation states and the symbol (+) indicates a combination of factors

The fate of seedling establishment in each patch type

The interaction of management practices with ecological processes restricts seedling establishment in different ways in each patch type. As Chapter 3 shows, the constraints to seedling establishment (namely, limited seed sources, dispersal, germination, and establishment) were significantly more severe in shrublands than in oak forests and savannas, hence oak seedling recruitment in shrubland was impeded in multiple ways during the early phases of the tree recruitment cycle.

In Chapter 3 it was shown that forest patches had more cork oak natural regeneration and fewer limitations for oak recruitment. It was argued that the higher tree density in forests enables a more benign microclimate with higher soil moisture and lower thermal stress, since oak requires shade for seed germination and seedling establishment (Callaway, 1992; Pulido *et al.*, 2001). The findings (Chapter 3) that dispersed seeds cached in forest patches germinated more easily, and that of all the sown acorns that germinated and grew into seedlings, the ones shaded by trees had the lowest mortality rates, imply that seedlings established in forest patches are more likely to survive severe summer droughts in future years. The lack of correlation between exposure and the transitions or persistence of forest patches also suggests that thermal stress is less important for seedlings growing in such patch types (Chapter 2). The results presented in Chapter 5 indicate that seedling survival will be greater in forest patches on steep slopes rarely or never subjected to intensive and prolonged understorey use or to planting operations, and where wildfires have not occurred. But, as argued in Chapter 4, in the event of wildfires, the shrubby understorey (fuel load) of forest patches will result in intense wildfires, more fire damage, and consequently lower post-fire cork oak survival, especially on southern slopes. It was indeed found that the most important ecological variable triggering transitions from forest to shrublands was wildfire.

Patches with lower cork oak density result from former agro-silvopastoral systems whose understorey use has been abandoned, or whose understorey is managed extensively. It was argued that because of the lower tree density the seedlings and saplings are exposed to higher irradiance and water stress than in forests. Indeed, established cork oak natural regeneration was found to be lower in savannas than in forest patches (Chapter 3). Savanna patch types were more persistent on aspects that did not face north, which, as argued in Chapter 2, implies that in drier sites the increased thermal stress on seedlings halts tree recruitment and forest recovery. The fuel load in savanna patches is usually much lower than in forests, particularly if the understorey is still managed. The lower fuel and larger space between the trees contributes to faster fires with lower intensity and a lower risk of crown fires, thus decreasing wildfire damage to seedlings and trees. Indeed, as reported in Chapter 2, wildfire did not appear to be primarily responsible for transitions or persistence of savannas. Even though observed seedling recruitment was not strongly limited in the savanna patches (Chapter 3), from the data collected on survival over 2 years it seems likely that the mortality of seedlings growing in full sun in savannas will increase in subsequent years due to summer drought.

Cistus shrubs usually invade cleared understorey patches, particularly on south-facing slopes exposed to long-term intensive land use and with low soil moisture and nutrient status (Gonçalves, 1991; Diniz, 1994; Latorre, 1996; Blanco *et al.*, 1997; Seng and Deil, 1999). The results reported in Chapter 3 show that several mechanisms limit cork oak recruitment in shrubland patches. Low cork oak acorn production and high rates of weevil infestation limit the first phase of the tree recruitment cycle, followed by lower rates of buried acorns (scatter-hoarded by mice), thus decreasing the likelihood of acorn germination. The germination of acorns that are effectively dispersed in shrublands is limited by high rates of post-dispersal predation. The seedlings that do successfully overcome the ecological constraints are less likely to survive. The findings that seedling mortality was significantly higher in shrublands than in forests and savannas, and that seedlings shaded by shrubs had lower survival rates than seedlings in full sun indicate that seedling growth is more constrained in *Cistus* shrublands than in open oak patches, and therefore competition between seedlings and *Cistus* is much stronger than facilitation. Other studies have shown that competition between *Cistus* and seedlings prevails over facilitation, in contrast to the facilitative effect of other shrubs (particularly late-successional shrubs) in Mediterranean environments (Gómez-Aparicio *et al.*, 2004; Pulido and Díaz, 2005; Pérez--Devesa *et al.*, 2008). Competition is likely to favour the shrubs, since *Cistus* spp. is physiologically well adapted to drought. It has also been reported that *Cistus* shrubs have allelopathic effects, aggravated by high temperatures and long photoperiods, which inhibit seedling germination and survival (Chaves *et al.*, 2001; Lobón *et al.*, 2002), but no information is available on the quantification of allelopathic effects between oak seedlings and *Cistus* shrubs.

Feedback mechanisms and critical thresholds leading to alternative stable states

The observed factors that trigger transitions can be grouped into disturbances that are external to the ecosystem (allogenic disturbances) such as human management, wildfires and drought, and disturbances within the ecosystem (autogenic disturbances) such as soil erosion and limitations in cork oak recruitment in shrubland patches. The net effect of the interaction among multiple disturbances determines the overall pathway of succession (Walker and Del Moral, 2009). In this study, the results indicate that the interaction between disturbances triggers feedback mechanisms that lead to persistent shrublands.

Land overexploitation in the past gradually disrupted the soil–vegetation system, reducing soil fertility, accelerating erosion and decreasing oak seedling establishment. Such management practices were followed by general land abandonment in the 1960s. Land abandonment led to shrub encroachment, particularly on southern slopes, which, coupled with increasing drought, led to changes in fire regimes – increasing fire frequency and intensity – in recent decades (Gomes, 2006; Silva and Catry, 2006; Mendes and Fernandes, 2007). In the event of a wildfire, *Cistus* shrubs will spread their seeds since they are active pyrophytes, and the patch type will persist and expand, as long as the interval between successive fires exceeds the time needed for seed bank restoration (3 years for *Cistus ladanifer* in Spain, Ferrandis *et al.*, 1999), which is the case for the study region. But, as demonstrated in Chapter 4, whereas wildfires benefit *Cistus* spp., they are serious threat to cork oak forests, killing many adult trees and seedlings, and lowering the capacity of resprouting of others, depending on the frequency and intensity of the fire, management practices, topography and climatic conditions. Oak post-fire survival will be lower on southern slopes, as shown in Chapter 4, where conditions for tree and seedling recovery are worst due to thermal stress. Other studies have shown that post-fire resprouting of trees may fail due to drought stress (Pereira *et al.*, 2009b).

Degraded soils with lack of vegetation cover, high incoming solar radiation and frequent wildfires make conditions for seedling survival very difficult, but maintain *Cistus* shrublands. In addition, on patches of shrubland, cork oak recruitment is severely limited. On more extensive shrublands, not only are fewer oak seeds available, but there are also higher densities of mice predating on the oak seeds, and the stronger competition between shrubs and oak seedlings further limits oak recruitment and favours the persistence of *Cistus* shrublands. After a critical threshold has been reached, feedback mechanisms of increased soil degradation and erosion, increased shrub encroachment and increased constraints to cork oak recruitment will prevent re-colonization by cork oak even after external disturbances have ceased: the vegetation biomass diminishes drastically, implying an irreversible tree loss (Figure 2). From this point on, cork oak establishment and forest recovery on the shrubland is severely threatened. In this study, the thresholds were described qualitatively, because they had not been quantitatively measured.

The first threshold probably occurs when disturbances from human management alter soil conditions to a point at which cork oak recruitment becomes difficult in savannas, particularly those on drier sites. From the results presented in Chapter 2 it can be inferred that because of the existence of this threshold, simply removing grazing livestock and understorey cultivation is unlikely to result in forest recovery. The second threshold occurs when mechanisms constraining seedling establishment on shrubland, coupled with the factors responsible for the first threshold, prevent the recovery of cork oak forests on patches of shrubland.

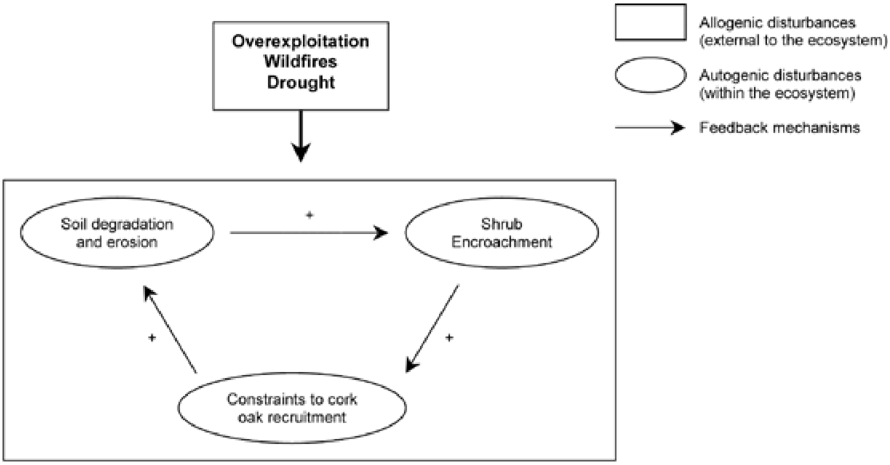

Figure 2 – Feedback mechanisms leading to the alternative stable state of shrublands
(Adapted from: Carpenter and Scheffer, 2009; Walker and Del Moral, 2009)

The inherently slow rates of unassisted forest recovery (oaks are long-lived species and recruitment can take two decades), and the long time needed for vegetation dynamics, which generally exceeds the time scale of human observation, throws into doubt the existence of alternative stable states; it could be that persistent shrubland is a long-term transient state (Didham *et al.*, 2005). However, in this study there is strong evidence to believe that thresholds exist and hence shrubland is an alternative stable state of lower vegetation biomass in former cork oak areas, namely: shrubland patches have been persistent for more than four decades and are expanding; forests and savannas have been changing into shrublands at an accelerating rate since 1985; cork oak recruitment is severely limited in shrubland, and there is strong competition between shrubs and seedlings (in this study, seedling survival was lowest under shrubs). Competitive interactions between species can retard succession by impeding species turnover, promoting stability of the existing community and arresting the succession (Walker and Del Moral, 2009). Given the above considerations, the evidence presented in this study strongly suggests that natural succession has been arrested and the system remains in a pioneer state of *Cistus* shrubland, which can be considered as an alternative stable state. The forest ecosystem has lost the capacity to recover from past practices damaging the soil and vegetation, and is now additionally threatened by more frequent wildfires and longer and more severe drought periods. To release the arrested succession and revert to the vegetation state of forests, it will be necessary to intervene with restoration techniques.

Implications for management and restoration

Knowledge and understanding of alternative stable states are fundamental for ecosystem restoration. In the case of this study, restoration implies destabilization of an unwanted attractor (shrubland) and manipulation to move the ecosystem into a preferred attractor (forest): for example, by simply expanding the size of the preferred attractor. To do so, it is necessary to have a good understanding of the underlying mechanisms that trigger the shifts and feedbacks and maintain the alternative states (or attractors) (Carpenter and Scheffer, 2009), and also to have information on the location and characteristics of the thresholds that are barriers preventing recovery from the degraded states (Standish *et al.*, 2009).

The drivers of transitions and the probable feedback mechanisms and thresholds identified in this study indicate that ecosystem restoration for forest recovery should include site amelioration (treatments to ameliorate soil properties and reduce soil losses: Vallejo *et al.*, 2006), inoculation of mycorrhizas to improve water uptake of seedlings and trees, and the simultaneous relief of multiple constraints to recruitment in the early life history of oaks. Management actions would need to simultaneously address the low seed availability, high rates of seed predation, low rates of seed germination and seedling survival found in shrubland as compared to other vegetation patches. The concrete actions that could be taken in shrubland patches include a combination of *Cistus* removal, seeding of acorns or seedling planting, planting of nurse shrubs to facilitate oak seed germination and seedling survival (Gómez-Aparicio *et al.*, 2004; Padilla and Pugnaire, 2006; Smit *et al.*, 2008), facilitating predators of rodents, and perch trees to attract long-distance dispersers like jays (Walker and Del Moral, 2009). In savanna and forest patches, protection of acorns and oak seedlings from grazing (from livestock or wild herbivores, if present) is also necessary to ensure seedling establishment in the medium term. Furthermore, late-successional shrubs should not be cleared from large areas, because they may provide some protection when oak seedlings are establishing (Gómez-Aparicio *et al.*, 2004; Pulido and Díaz, 2005; Pérez--Devesa *et al.*, 2008).

In Chapter 5 it was shown that cork oak planting has been highly unsuccessful and that some landowners prefer oak seeding. Many restoration projects based on artificial regeneration may fail because of post--planting water deficits. In Mediterranean-climate regions, drought is the main threat to the survival of nursery-raised seedlings (Vallejo, 2009), so nursery and field techniques must be devised to improve seedling performance in such dry conditions, especially in the face of climate change. Techniques to improve the success of cork oak seeding and seedling planting can be found in Cortina *et al.* (2009) and references therein, and Vallejo *et al.* (2006). In the event of a wildfire, post-fire restoration techniques should be implemented at burned sites as soon as possible, in order to prevent soil loss and erosion (Vallejo *et al.*, 2006) and increase the post-fire survival of cork oaks.

Management actions are not effective if implemented at the patch or farm level; to relieve the multiple constraints on cork oak recruitment such actions must be implemented at landscape scale, thus by the concerted actions of landowners, perhaps through existing associations of forest producers.

Landowners' perceptions and management decisions

It was found (Chapter 5) that landowners' perceptions of forest management and the land use system clearly influence the management decisions that are impeding forest recovery. Though several landowners interviewed demonstrated good understanding of the ecological problems in the study area, more than half of interviewees claimed that cereal cultivation in the past was good for the soil and the lack of it was in fact responsible for soil erosion and tree mortality. Some landowners (35% of interviewees) also claimed that there was no soil erosion in the study area. Ignoring the existence of an ecological problem such as soil erosion and the effects of the traditional land use system on soil properties and natural regeneration can stop landowners from opting for adequate management practices and restoration actions. Most of the landowners interviewed also stated they do not protect natural regeneration during silvicultural interventions that can damage established seedlings. It will be recalled that the management decisions of the landowners in the study area are also conditioned by the perception that their holding is too small and that further improvement through investment would not be profitable. Indeed, if sales prices are too low for profit, landowners will avoid investment, and in the worst scenario they will abandon their current management practices. Furthermore, cash losses make the renewal of cork oak woodlands economically unattractive to private landowners; this means that management and restoration actions will not be undertaken without subsidies (Ovando *et al.*, 2009). The Common Agricultural Policy (CAP) and cork prices are therefore important socio-economic factors at the macro-level; they act upon the vegetation dynamics in the study area by influencing management decisions and landowners' profit. Since the only improvements undertaken by landowners are those subsidized by the European Union (EU), the CAP greatly influences the landowners' management options. In this study, it was found (Chapter 5) that despite their preference for seeding as a management option, landowners opt for cork oak planting instead of seeding because planting is subsidized. Other studies have also found that EU subsidies greatly influence management decisions and can sometimes cause further degradation of tree cover (Pinto-Correia and Vos, 2004). The landowners' reluctance to invest has been aggravated by the fall in cork prices in recent years (Cork Information Bureau, 2008).

How resilient is the cork oak land use system?

This study presents evidence that the future of the cork oak land use system in the study area is severely threatened by loss of ecological resilience (shrub encroachment, difficulties in cork oak recruitment and lack of forest recovery) and loss of social and economical resilience (lack of investment and profit, lack of adequate and concerted management). Higher--scale drivers such as macroeconomics, regulatory policies and regional social norms can reinforce the loss of social and economic resilience by limiting the economic capacity and adaptability of the socioecological system. In addition, climate change will probably reinforce the loss of ecological resilience by contributing to the expansion of *Cistus* shrubland and regression of cork oak forests (Pereira *et al*., 2002).

Resilience could be enhanced by building human adaptive capacity by means of combining scientific knowledge with traditional local knowledge (King and Whisenant, 2009). The future of cork oak forests and cork oak land use systems will depend on people's willingness and capacity to undertake concerted management actions and restoration programmes and on the development of entrepreneurial skills to develop multipurpose businesses, which generate additional income, so that ecological and socio-economic thresholds can be overcome. Unless such actions are undertaken in the short-term, the cork oak land use systems in the study area will not be sustainable. Further research is needed to unveil the mechanisms that maintain feedbacks and thresholds in cork oak land use systems, for example by enlarging the sample size of the field experiments and data collected in this study, in order to relate specific landscape changes with local ecological conditions, management and social aspects.

Cork oak tree at the study site

References

Acácio, V., Holmgren, M., Jansen, P.A., Schrotter, O. 2007. Multiple recruitment limitation causes arrested succession in Mediterranean cork oak systems. Ecosystems 10:1220–1230.

Acácio, V., Holmgren, M., Rego, F., Moreira, F., Mohren, G.M.J. 2009. Are drought and wildfires turning Mediterranean cork oak forests into persistent shrublands? Agroforestry Systems 76:389-400.

Aguiar, C. and Pinto, B. 2007. Paleo-história e história antiga das florestas de Portugal continental – até à Idade Média. *In*: Sande Silva, J. (ed). Floresta e Sociedade. Uma história comum. Árvores e Florestas de Portugal 7. Público, Comunicação Social SA & Fundação Luso-Americana para o Desenvolvimento. Lisboa. 107-113 pp.

Alés, R.F. 1999. Dehesas y Montados**.** Bases Ecologicas para su Gestión. Revista de Biologia (Lisboa). Vol. 17. Núm. 1-4:147-157

Alloza, J.A. and Vallejo, R. 1999. Relación entre las características meteorológicas del año de plantación y los resultados de las repoblaciones. Ecología 13:173-187.

Almeida, M.H., Merouani, H., Costa e Silva, F., Cortina, J., Trubat, R., Chirino, E., Vilagrosa, A., Khaldi, A., Stiti, B., El Alami, S.L., Vallejo, V.R. 2009. Germplasm selection and nursery techniques. *In*: Aronson, J., Pereira, J.S., Pausas, J.G. (ed). Cork oak woodlands on the edge. Ecology, adaptive management, and restoration. Society for Ecological Restoration International. Island Press. Washington D.C. 129-137 pp.

Almeida, M.H., Sampaio, T., Lourenço, M.J., Merouami, H., Costa e Silva, F., Nunes, A.M., Chambel, M.R., Branco, M., Faria, C., Varela, M.C., Pereira, J.S. 2006. Influência da qualidade dos materiais de reprodução na reflorestação com sobreiro. *In*: Espejo, M., Martin, M., Matos, C., Mesias, F.J. (ed). Gestión ambiental y económica del ecosistema dehesa en la Península Ibérica. Junta de Extremadura, Consejería de Infraestructuras y Desarrollo Tecnológico. Mérida. 173-176 pp.

Alonso, I., Luis, E., Tárrega, R. 1992. First phases of regeneration of *Cistus laurifolius* and *Cistus ladanifer* after burning and cutting in experimental plots. International Journal of Wildland Fire 2(1):7-14.

Alves, A.L., Carvalho, N.S., Silveira, S., Castel-Branco, S., Marques, J.P., Costa, Z., Horta, A.L. 2003. O abandono da actividade agrícola. Grupo de Trabalho Agro-Ambiental. Acção 2.2.1. Ministério da Agricultura, Desenvolvimento Rural e Pescas. Lisboa.

Amo, E. and Chacón, C. 2003. Recomendaciones selvícolas para alcornocales afectados por el fuego. Cuadernos Forestales. IPROCOR. Mérida.

Anon. 1990. Inventário florestal do sobreiro. Estudos e Informação n.° 300. Direcção Geral das Florestas. Lisboa.

Anon. 1999. Arcview GIS 3.2. Environmental Systems Research Institute. Redlands.

Anon. 2001a. ENVI 3.4. Research systems. Boulder.

Anon. 2001b. Inventário Florestal Nacional: Portugal Continental. 3.ª revisão 1995–1998. Relatório final. Direcção Geral das Florestas. Lisboa.

Anon. 2006. Incêndios Florestais. Relatório de 2005. Direcção Geral dos Recursos Florestais. Lisboa.

Aronson, J., Pereira, J.S., Pausas, J.G. 2009. Cork oak woodlands on the edge. Ecology, adaptive management, and restoration. Society for Ecological Restoration International. Island Press. Washington D.C..

Aschmann, H. 1973. Man‘s impact on the several regions with Mediterranean climates. *In*: Di Castri, F., Mooney, H.A. (ed). Mediterranean type ecosystems. Origin and structure. Springer-Verlag. Berlin. 363–371 pp.

Baptista, F. 1993. A política agrária do Estado Novo. Edições Afrontamento. Lisboa.

Barberis, A., Dettori, S., Filigheddu, M.R. 2003. Management problems in Mediterranean cork oak forests: post-fire recovery. Journal of Arid Environments 54:565–569.

Barbero, M., Bonin, G., Loisel, R., Quézel, P. 1990. Changes and disturbances of forest ecosystems caused by human activities in the western part of the Mediterranean Basin. Vegetatio 87:151-173.

Baskin, J.M. and Baskin, C.C. 1989. Physiology of dormancy and germination in relation to seed bank ecology. *In*: Leck, M.A., Thomas, V.T., Simpson, R.L. (ed). Ecology of soil seed banks. Academic Press. San Diego, California. 53-66 pp.

Bellarosa, R., Simeone, M., Papini, A., Schirone, B. 2005. Utility of ITS sequence data for phylogenetic reconstruction of Italian *Quercus* spp. Molecular Phylogenetics and Evolution 34:355-370.

Berrahmouni, N., Regato, P., Ellatifi, M., Daly-Hassen, H., Bugalho, M., Bensaid, S., Díaz, M., Aronson, J. 2009. Ecoregional planning for biodiversity conservation. *In*: Aronson, J., Pereira, J.S., Pausas, J.G. (ed). Cork oak woodlands on the edge. Ecology, adaptive management, and restoration. Society for Ecological Restoration International. Island Press. Washington D.C.. 203-216 pp.

Blanco, E., Casado, M.A., Costa, M., Escribano, R., García, M., Génova, M., Gómez, A., Gómez, F., Moreno, J.C., Morla, C., Regato, P., Sáinz, H. 1997. Los bosques ibéricos. Una interpretación geobotánica. Planeta. Madrid.

Bond, W.J. and Van Wilgen, B.W. 1996. Fire and plants. Chapman & Hall. London.

Borchert, M.I., Davis, F.W., Michaelsen, J., Oyler, L.D. 1989. Interactions of factors affecting seedling recruitment of blue oak (*Quercus douglasii*) in California. Ecology 70:389–404.

Bossema, I. 1979. Jays and oaks: an eco-ethological study of a symbiosis. Behaviour 70:1–117.

Branco, M., Branco, C., Merouani, H., Almeida, M.H. 2002. Germination success, survival and seedling vigour of *Quercus suber* acorns in relation to insect damage. Forest Ecology and Management 166:159–64.

Branco, A. and Parejo, F. 2008. Incentives or obstacles? The institutional aspects of the cork business in the Iberian Peninsula (1930-1975). Revista de Historia Económica – Journal of Iberian and Latin America Economic History 1:17-44.

Branco, M. and Ramos, A.P. 2009. Coping with pests and diseases. *In*: Aronson, J., Pereira, J.S., Pausas, J.G. (ed). Cork oak woodlands on the edge. Ecology, adaptive management, and restoration. Society for Ecological Restoration International. Island Press. Washington D.C.. 103-111 pp.

Bugalho, M., Plieninger, T., Aronson, J., Ellatifi, M., Crespo, D.G. 2009. Open woodlands: a diversity of uses (and overuses). *In*: Aronson, J., Pereira, J.S., Pausas, J.G. (ed). Cork oak woodlands on the edge. Ecology, adaptive management, and restoration. Society for Ecological Restoration International. Island Press. Washington D.C.. 33-41 pp.

Bugalho, M.N., Lecomte, X., Pile, S., Caldeira, M.C. 2006. Efeitos do pastoreio por cervídeos na regeneração arbórea e composição florística de uma pastagem. Revista de Ciências Agrárias 29:145-157.

Burnham, K.P. and Anderson, D.R. 2003. Model Selection and Multi--Model Inference: A Practical Information-Theoretic Approach. Springer-Verlag. New York.

Cabezudo, B., Pérez Latorre, A., Nieto, J.M. 1995. After fire regeneration in a *Quercus suber* forest in the South of Spain (Istán, Málaga). Acta Botanica Malacitana 20:143-151.

Cabrinha, V. and Santo, F.E. 2000. Drought tendencies in mainland Portugal. *In*: Wilhite, D.A., Sivakumar, M.V.K., Wood, D.A. (ed). Early warning systems for drought preparedness and drought management. Proceedings of an expert group meeting. Lisbon. 169–81 pp.

Callaway, R.M. 1992. Effect of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. Ecology 73:2118-2128.

Calvão da Silva, M., 1996. Contributo para o estudo da qualidade da cortiça. Universidade de Trás-os-Montes e Alto Douro. Secção de Engenharia Florestal. Vila Real.

Calvão, T. and Palmeirim, J.M. 2004. Mapping Mediterranean scrub with satellite imagery: biomass estimation and spectral behaviour. International Journal of Remote Sensing 25:3113–3126.

Campbell, J.B. 2002. Introduction to Remote Sensing. Third Edition. Taylor & Francis. London.

Campos, P., Díaz, M., Pulido, F.J. 1998. Las dehesas arboladas. Un equilibrio necesario entre explotación y conservación. Quercus 147:31–5.

Campos, P., Ovando, P., Caparrós, A. 2006. La economía del "secuestro del carbono" por parte de los bosques: reforestación y regeneración natural de encinares y alcornocales. *In*: workshop proceedings Los Bosques Españoles y el Cambio Climático. November 15. Fundación Gas Natural/Junta de Castilla y León. Valladolid. www.fundaciongasnatural.org

Capelo, J. and Catry, F. 2007. A distribuição do sobreiro em Portugal. *In*: Sande Silva, J. (ed). Os Montados. Muito para além das árvores. Árvores e Florestas de Portugal 3. Público, Comunicação Social SA & Fundação Luso-Americana para o Desenvolvimento. Lisboa. 107-113 pp.

Carpenter, S.R. and Scheffer, M. 2009. Critical transitions and regime shifts in ecosystems: consolidating recent advances. *In*: Hobbs, R.J., Suding, K.N. (ed). New models for ecosystem dynamics and restoration. Island Press. Washington D.C.. 22-32 pp.

Carrión, J.S., Parra, I., Navarro, C., Munuera, M. 2000. Past distribution and ecology of the cork oak (*Quercus suber*) in the Iberian Peninsula: a pollen-analytical approach. Diversity and Distributions 6: 29-44.

Castro, E., González, M., Tenorio, M., Bombín, R., Antón, M., Fuster, M., Manzaneque, A., Manzaneque, F., Saiz, J., Juaristi, C., Pojares, P., Ollero, H. 1997. Los bosques ibéricos. Una interpretación geobotánica. Editorial Planeta. Barcelona.

Castro, J., Zamora, R., Hódar, J.A., Gómez, J.M. 2002. The use of shrubs as nurse plants: a new technique for reforestation in Mediterranean mountains. Restoration Ecology 10:297-305.

Castro, J., Zamora, R., Hódar, J.A., Gómez, J. M., Gómez-Aparicio, L. 2004. Benefits of using shrubs as nurse plants for reforestation in Mediterranean mountains: a 4-year study. Restoration Ecology 12:352–358.

Catry, F.X., Rego, F.C., Bugalho, M.N., Lopes, T., Silva, J.S., Moreira, F. 2006. Effects of fire on tree survival and regeneration in a Mediterranean ecosystem. *In*: Viegas, X. (ed). Proceedings of the V International Conference on Forest Fire Research, ADAI. Figueira da Foz.

CELIÈGE. 2005. Código Internacional das Práticas Suberícolas. *In*: DGRF, ICMC (ed). Subernova Project - Interreg III A, Portuguese ed. Évora and Mérida.

CESE. 1996. O Sector Florestal Português. Conselho Ensino Superior Empresa. Grupo de Trabalho sobre o Sector Florestal, 4-5 Outubro. Póvoa de Varzim.

Chaves, S. and Escudero, T. 2001. Plant growth inhibiting flavonoids in exudates of *Cistus ladanifer* and in associated soils. Journal of Chemical Ecology 27(3): 623-631.

Clark, S.C. 1996. Mediterranean Ecology and an Ecological Synthesis of the Field Sites. *In*: Brandt, C. J., Thornes, J. B. (ed). Mediterranean Desertification and Land Use. John Wiley & Sons. Chichester. 271-301 pp.

Coelho, I.S. and Campos, P. 2009. Mixed cork oak-stone pine woodlands in the Alentejo region of Portugal. *In*: Aronson, J., Pereira, J.S., Pausas, J.G. (ed). Cork oak woodlands on the edge. Ecology, adaptive management, and restoration. Society for Ecological Restoration International. Island Press. Washington D.C.. 153-161 pp.

Conacher, A.J. and Sala, M. 1998. Land degradation in Mediterranean environments of the world. Nature and extent, causes and solutions. Wiley. Chichester.

Congalton, R.G. and Green, K. 1999. Assessing the accuracy of remotely sensed data: principles and practices. CRC Press. New York.

Cork Information Bureau. 2008. Sector da cortiça em números 2008.

Corral, R., Perez Garcia, F., Pita, J. 1989. Some aspects of seed germination in four species of *Cistus*. Seed Science & Technology 18: 321-325.

Correia, O., Oliveira, G., Martins-Loução, M. A., Catarino, F.M. 1992. Effects of bark-stripping on the water relations of *Quercus suber* L. *Scientia Gerundensis* 18:195-204.

Cortina, J., Maestre, F.T., Vallejo, R., Baeza, M.J., Valdecantos, A., Pérez-Devesa, M. 2006. Ecosystem structure, function and restoration success: Are they related? Journal for Nature Conservation 14:152-160.

Cortina, J., Pérez-Devesa, M., Vilagrosa, A., Abourouh, M., Messaoudène, M., Berrahmouni, N., Silva, L.N., Almeida, M.H., Khaldi, A. 2009. Field techniques to improve cork oak establishment. *In:* Aronson, J., Pereira, J.S., Pausas, J.G. (ed). Cork oak woodlands on the edge. Ecology, adaptive management, and restoration. Society for Ecological Restoration International. Island Press. Washington D.C.. 141-149 pp.

Costa, A. and Pereira, H. 2007a. Montados e sobreirais: uma espécie, duas perspectivas. *In*: Sande Silva, J (ed). Os Montados. Muito para além das árvores. Árvores e Florestas de Portugal 3. Público, Comunicação Social SA & Fundação Luso-Americana para o Desenvolvimento. Lisboa. 17-37 pp.

Costa, A. and Pereira, H. 2007b. A silvicultura do sobreiro. *In*: Sande Silva, J (ed). Os Montados. Muito para além das árvores. Árvores e Florestas de Portugal 3. Público, Comunicação Social SA & Fundação Luso-Americana para o Desenvolvimento. Lisboa. 39-58 pp.

Costa, A., Pereira, H., Oliveira, A. 2004. The effect of cork-stripping damage on diameter growth of *Quercus suber* L. Forestry 77: 1–8.

Cox, D.R. 1972. Regression models and life tables. Journal of the Royal Statistical Society Ser B 34:187–220.

Cruz, M.G., Butler, B.W., Alexander, M.E., Forthofer, J.M., Wakimoto, R.H. 2006. Predicting the ignition of crown fuels above a spreading surface fire. Part I. model idealization. International Journal of Wildland Fire 15:47–60.

Cubash, U., Von Storch, H., Waskewitz, J., Zorita, E. 1996. Estimates of climate change in Southern Europe derived from dynamical climate model output. Climate Research 7:129–149.

Del Tredici, P. 2001. Sprouting in temperate trees: a morphological and ecological review. Botanical Review 67:121–140.

Den Ouden, J., Jansen, P.A., Smit, R. 2005. Jays, mice and oaks: predation and dispersal of *Quercus robur* and *Q. petraea* in North-western Europe. *In*: Forget, P.M., Lambert, J.E., Hulme, P.E., Vander Wall, S.B. (ed). Seed fate: predation, dispersal and seedling establishment. CAB International. Wallingford. 223–39 pp.

DGF. 1990. Inventário Florestal do Sobreiro. Estudos e Informação n.º300. Lisboa.

DGF. 2001. Inventário Florestal Nacional. Portugal Continental. 3.ª Revisão, 1995-1998. Direcção-Geral das Florestas. Lisboa.

DGRF. 1999. Manual de instruções para o trabalho de campo do Inventário Florestal Nacional. Direcção-Geral dos Recursos Florestais. Lisboa.

DGRF. 2007. Resultados do Inventário Florestal Nacional 2005-2006. Direcção-Geral dos Recursos Florestais. Lisboa.

DGRF, APIF. 2005. Incêndio florestal S. Barnabé (Almodôvar). Relatório da Direcção-Geral dos Recursos Florestais e da Agência para a Prevenção de Incêndios Florestais. Lisboa.

Díaz, M., Pulido, F., Marañón, T. 2003. Diversidad biológica en los bosques mediterráneos ibéricos: relaciones con el uso humano e importancia para la sustentabilidad de los sistemas adehesados. *In:* Campos, P., Montero, G. (ed). Beneficios Comerciales y Ambientales de la Repoblación del Arbolado del Monte Mediterráneo. CIFOR-INIA. Madrid. 33-44 pp.

Díaz-Delgado, R., Lloret, F., Pons, X., Terradas, J. 2002. Satellite evidence of decreasing resilience in Mediterranean plant communities after recurrent wildfires. Ecology 83:2293-2303.

Díaz-Fernandez, P.M., Climent, J., Gil, L. 2004. Biennial acorn maturation and its relationship with flowering phenology in Iberian populations of *Quercus suber*. Trees - Structure and Function 18: 615-621.

Didham, R.K., Watts, C.H., Norton, D.A. 2005. Are systems with strong underlying abiotic regimes more likely to exhibit alternative stable states? Oikos 110: 409-416.

Dikinson, M.B. and Johnson, E.A. 2001. Fire effects on trees. *In*: Johnson, E.A., Miyanishi, K. (ed). Forest Fires: Behaviour and Ecological Effects. Academic Press. New York. 477–525 pp.

Diniz, A.C. 1994. Os solos do montado e aptidão suberícola nos concelhos de Grândola, Santiago do Cacém e Sines. Correlações com a Morte Prematura do Sobreiro. Silva Lusitana 2(2):247-267.

Esteban-Parra, M.J., Pozo-Vázquez, D., Rodrigo, F.S., Castro-Díez, Y. 2003. Temperature and precipitation variability and trends in Northern Spain in the context of the Iberian Peninsula Climate. *In*: Bolle, H.J. (ed). Mediterranean Climate Variability and Trends. Springer Verlag. Berlin. 259-276 pp.

FAO. 2001a. FRA global forest fire assessment 1990-2000. Forest Resources Assessment Programme, Working Paper 55. FAO. Rome.

FAO. 2001b. Protection des forêts contre l'incendie. Fiches techniques pour les pays du bassin méditerranéen. Cahier FAO Conservation, 36. FAO and CEMAGREF. Rome.

Ferrandis, P., Herranz, J.M., Martínez-Sánchez, J.J. 1999. Effect of fire on hard-coated *Cistaceae* seed banks and its influence on techniques for quantifying seed banks. Plant Ecology 144:103–114.

Ferreira, F. 2000. The cork oak condition in Portugal. *In*: Oszako, T., Delatour, C. (ed). Recent advances on oak health in Europe. Forest Research Institute. Warsaw. 121-130 pp.

Fonseca, F., Louzada, J.L., Silva, M.E. 1994. Crescimento e qualidade da cortiça. Potencialidades da microdensitometria. *In*: Páscoa, F., Pinheiro, L., Isidoro, A. (ed). Actas III Congresso Florestal Nacional, SPCF. Lisboa. 267–279 pp.

Friedel, M.H. 1987. A preliminary investigation of woody plant increase in the Western Transvaal and implications for veld assessment. Journal of the Grassland Society of Southern Africa 4:25-30.

Friedel, M.H. 1991. Range condition assessment and the concept of thresholds: a viewpoint. Journal of Range Management 44(5):422-426.

Fuentes, E.R., Otaiza, R.D., Alliende, M.C., Hoffmann, A., Poiani, A. 1984. Shrub clumps of the Chilean matorral vegetation: structure and possible maintenance mechanisms. Oecologia 62: 405-411

Gomes, J.F.P. 2006. Forest fires in Portugal: how they happen and why they happen. International Journal of Environmental Studies 63:109-119.

Gómez, J.M. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. Ecography 26:573–84.

Gómez, J.M., García, D., Zamora, R. 2003. Impact of vertebrate acorn and seedling predators on a Mediterranean *Quercus pyrenaica* forest. Forest Ecology and Management 180:125–134.

Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J., Baraza, E. 2004. Applying plant facilitation to forest restoration in Mediterranean ecosystems: a meta-analysis of the use of shrubs as nurse plants. Ecological Applications 14:1128–1138.

Gómez-Gutiérrez, J.M. and Pérez-Fernández, M. 1996. The "dehesas": silvopastoral systems in semiarid Mediterranean regions with poor soils, seasonal climate and extensive utilisation. *In*: Etienne, M. (ed). Western European Silvopastoral Systems. INRA Editions. Paris. 55-70 pp.

Gómez-Limón, J., de Lucío Fernández, J.V. 1999. Changes in use and landscape preferences on the agricultural-livestock landscapes of the central Iberian Peninsula (Madrid, Spain). Landscape and Urban Planning 44:165-175.

Gonçalves, J. 1991. Fitocenoses espontâneas dos sobreirais alentejanos: factores ambientais e dinâmica da vegetação associada a condições de mortalidade das árvores. Relatório Final do Curso de Eng. Silvicultor. Instituto Superior de Agronomia. Universidade Técnica de Lisboa. Lisboa.

Gould, J.S., Knight, I., Sullivan, A.L. 1997. Physical modelling of leaf scorch height from prescribed fires in young *Eucalyptus sieberi* regrowth forests in South-eastern Australia. International Journal of Wildland Fire 7:7–20.

Graça, J. and Pereira, H. 2000. Methanolysis of bark suberins: analysis of glycerol and acid monomers. Phytochemical Analysis 11:45-51.

Hengst, G.E. and Dawson, J.O. 1994. Bark properties and fire resistance of selected tree species from the central hardwood region of North America. Canandian Journal of Forest Research 24:688–696.

Herrera, J. 1995. Acorn predation and seedling production in a low--density population of cork oak (*Quercus suber* L.). Forest Ecology and Management 76:197-201.

Hobbs, R.J. and Suding, K.N. 2009. New models for ecosystem dynamics and restoration. Island Press. Washington D.C..

Holling, C.S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1-23.

Holmgren, M. 2002. Exotic herbivores as drivers of plant invasion and switch to ecosystem alternative states. Biological Invasions 4:25-33.

Holmgren, M. and Scheffer, M. 2001. El Niño as a window of opportunity for the restoration of degraded arid ecosystems. Ecosystems 4:151-159.

Holmgren, M., Scheffer, M., Huston, M. 1997. The interplay of facilitation and competition in plant communities. Ecology 78(7):1966-1975.

Holmgren, M., Segura, A.M., Fuentes, E.R. 2000. Limiting mechanisms in the regeneration of the Chilean matorral: experiments on seedling establishment in burned and cleared mesic sites. Plant Ecology 147:49–57.

Hosmer, D.W. and Lemeshow, S. 1989. Applied logistic regression. Wiley. New York.

Huntsinger, L. and Bartolome, J.W. 1992. Ecological dynamics of *Quercus* dominated woodlands in California and southern Spain: a state transition model. Vegetatio 99-100:299-305.

ICMC. 2005. Curso Restauración de Alcornocales incendiados. Proyecto SUBERNOVA. ICMC. Unpublished. Mérida.

INE. 2001. Censos 2001. Recenseamento Geral da População. Instituto Nacional de Estatística. Lisboa.

Joffre, R., Hubert, B., Meuret, M. 1991. Les systèmes agro-sylvopastoraux méditerranéens: enjeux et réflexions pour une gestion raisonnée. Dossier MAB 10, UNESCO. Paris.

Joffre, R., Rambal, S., Ratte, J.P. 1999. The dehesa of southern Spain and Portugal as a natural ecosystem mimic. Agroforestry Systems 45:57-79.

Keeley, J. 2006. Fire severity and plant age in postfire resprouting of woody plants in sage scrub and chaparral. Madroño 53(4):373-379.

King, E.G. and Whisenant, S. 2009. Thresholds in ecological and linked social-ecological systems: application to restoration. *In*: Hobbs, R.J., Suding, K.N. (ed). New models for ecosystem dynamics and restoration. Island Press. Washington D.C.. 63-77 pp.

Klein, J.P. and Moeschberger, M.L. 1997. Survival analysis: techniques for censored and truncated data. Springer. New York.

Köhl, M., Innes, J.L., Kaufmann, E. 1994. Reliability of differing densities of sample grids used for the monitoring of forest condition in Europe. Environment Monitoring Assessment 29:201–220.

Lambin, E.F. 2005. Conditions for sustainability of human-environment systems: information, motivation and capacity. Global Environmental Change 15:177-180.

Lamey, A. 1893. Le chêne-liège, sa culture et son exploitation. Berger--Levrault et Cie éditeurs. Paris, Nancy.

Latorre, A.V.P. 1996. Restauración del alcornocal en Andalucía. Elección y manejo de especies Ecología 10:9-19.

Laycock, W.A. 1991. Stable states and thresholds of range condition on North American rangelands: a view point. Journal of Range Management 44:427-433.

Leiva, M.J. and Fernández-Alés, R. 2003. Post-dispersive losses of acorns from Mediterranean savannah-like forests and shrublands. Forest Ecology and Management 176:265–271.

Li, H. and Zhang, Z. 2003. Effect of rodents on acorn dispersal and survival of the Liaodong oak (*Quercus liaotungensis* Koidz.). Forest Ecology and Management 176:387–96.

Lima, M.B., Bernardo, D.A.F., Madeira e Madeira, M.E.B., Graça, J.M., Félix, A.L.T., Rita, F., Custódio, S.I.G., Varela, J.J.L.M., da Silva, I.C.C.P., Bouça, J.E.. 2000. Sistemas agrários tradicionais no Algarve – contributos para o seu estudo. Direcção Regional de Agricultura do Algarve. Faro.

Lobón, N.C., Gallego, J.C., Díaz, T.S., García, J.C. 2002. Allelopathic potential of *Cistus ladanifer* chemicals in response to variations of light and temperature. Chemoecology 12:139-145.

Lumaret, R., López de Heredia, U., Soto, A. 2009. Origin and genetic variability. *In*: Aronson, J., Pereira, J.S., Pausas, J.G. (ed). Cork oak woodlands on the edge. Ecology, adaptive management, and restoration. Society for Ecological Restoration International. Island Press. Washington D.C.. 25-32 pp.

Magri, D., Fineschi, S., Bellarosa, R., Buonamici, A., Sebastiani, F., Schirone, B., Simeone, M.C., Vendramin, G.G. 2007. The distribution of *Quercus suber* chloroplast haplotypes matches the palaeogeographical history of the western Mediterranean. Molecular Ecology 16:5259-5266.

Marañón, T. 1988. Agro-sylvo-pastoral systems in the Iberian Peninsula: dehesas and montados. Rangelands 10(6):255-258.

Mazzoleni, S., Di Pasquale, G., Mulligan, M., Di Martino, P., Rego, F. 2004. Recent dynamics of the Mediterranean vegetation and landscape. Wiley. Chichester.

McCarthy, J.J., Canziani, O.F., Leary, N.A., Dokken, D.J., White, K.S. 2001. Climate change 2001: impacts, adaptation and vulnerability. Cambridge University Press. Cambridge.

McHugh, C.W. and Kolb, T.E. 2003. Ponderosa pine mortality following fire in northern Arizona. International Journal of Wildland Fire 12:7–22.

Mendes, A.C. 2002. A Economia do sector da cortiça em Portugal. Evolução das actividades de produção e de transformação ao longo dos séculos XIX e XX (Documento de Trabalho). Universidade Católica Portuguesa. Porto.

Mendes, A.C. 2007. O sobreiro ao longo dos tempos. *In*: Sande Silva, J. (ed). Os montados. Muito para além das árvores. Árvores e Florestas de Portugal 3. Público, Comunicação Social SA & Fundação Luso-Americana para o Desenvolvimento. Lisboa. 77-106 pp.

Mendes, A.C., Carvalho, M., Dias, R., Tavares, M., Feliciano, D. 2004. Evaluating financing of forestry in Europe – Portugal. Country Report. Faculdade de Economia e Gestão, Universidade Católica Portuguesa. Porto.

Mendes, A.M.S.C. and Fernandes, L.C.R.M. 2007. Políticas e instituições florestais em Portugal – desde o final do Antigo Regime até à actualidade. *In*: Sande Silva, J. (ed). Floresta e Sociedade. Uma história comum. Árvores e Florestas de Portugal 7. Público, Comunicação Social SA & Fundação Luso-Americana para o Desenvolvimento. Lisboa. 77-125 pp

Mendes, A.M.S.C. and Graça, J.A.R. 2009. Cork bottle stoppers and other cork products. *In*: Aronson, J., Pereira, J.S., Pausas, J.G. (ed) Cork oak woodlands on the edge. Ecology, adaptive management, and restoration. Society for Ecological Restoration International. Island Press. Washington D.C.. 59-69 pp.

Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: synthesis. Island Press. Washington, D.C..

Miller, M. 2000. Fire autecology. *In*: Brown, J.K., Smith, J.K. (ed). Wildland fire in ecosystems: effects of fire on flora. Gen. Tech. Rep. RMRS-GTR-42- vol. 2. Ogden, UT, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 9–34 pp.

Miranda, P., Coelho, F.E.S., Tomé, A.R., Valente, M.A. 2002. 20th century Portuguese climate and climate scenarios. *In*: Santos, F.D., Forbes, K., Moita, R. (ed). Climate change in Portugal. Scenarios, impacts and adaptation measures - SIAM Project. Gradiva. Lisboa. 23–83 pp.

Montero, G. 1988. Modelos para cuantificar la producción de corcho de los alcornocales (*Quercus suber* L.) en función de la calidad de estación y de los tratamientos selvícolas. PhD thesis, INIA, Ministerio de Agricultura, Pesca y Alimentación. Madrid.

Montero, G., San Miguel, A., Cañellas, I. 2000. Systems of Mediterranean Silviculture: La Dehesa. Grafistaff. S.L. Madrid.

Montero, G., Torres, E., Cañellas, I. 1994a. Regeneración de alcornocales. Síntesis bibliográfica. Ecologia 8:271–283.

Montero, G., Torres, E., Cañellas, I., Ortega, C. 1994b. Aspectos selvícolas, económicos y sociales del alcornocal. Agricultura y Sociedad 73:137-193.

Montgomery, K.R. and Strid, T.W. 1976. Regeneration of introduced species of *Cistus* (*Cistaceae*) after fire in Southern California. Madrono 23:417–427.

Mooney, H., Cropper, A., Reid, W. 2005. Confronting the human dilemma. Nature 434:561–562.

Moreira, A.C. and Martins, M.S. 2005. Influence of site factors on the impact of *Phytophthora cinnamomi* in cork oak stands in Portugal. Forest Pathology 35:145-162.

Moreira, F., Duarte, I., Catry, F., Acácio, V. 2007. Cork extraction as a key factor determining post-fire cork oak survival in a mountain region of southern Portugal. Forest Ecology and Management 253:30-37.

Moreno, J.M., Vázquez, A., Vélez, R. 1998. Recent history of forest fires in Spain. *In:* Moreno, J.M. (ed). Large Forest Fires. Backhuys Publishers. Leiden. 159-185 pp.

Mulligan, M., Burke, S.M., Concepción Ramos, M. 2004. Climate change, land-use change and the "desertification" of Mediterranean Europe. *In*: Mazzoleni, S., Di Pasquale, G., Mulligan, M., Di Martino, P., Rego, F. (ed). Recent dynamics of the Mediterranean vegetation and landscape. Wiley. Chichester.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B., Kent, J. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853-858.

Nathan, R. and Muller-Landau, H.C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecololy and Evolution 15:278–85.

Natividade, J.V. 1948. Os fundamentos científicos da cultura racional do sobreiro. Boletim da Junta Nacional da Cortiça 113: 381-391.

Natividade, J.V. 1950. Subericultura. Ministério da Agricultura, Pescas e Alimentação, Direcção-Geral das Florestas Lisboa.

Naveh, Z. 1974. Effects of fire in the Mediterranean region. *In:* Kozlowski, T.T., Ahlgren, C.E. (ed). Fire and Ecosystems. Academic Press. New York. 401-434 pp.

Naveh, Z. 1990. Fire in the Mediterranean – a landscape ecological perspective. *In*: Goldammer, J.G., Jenkins, M.J. (ed). Fire in ecosystem dynamics. Mediterranean and Northern perspectives. SPB Academic Publishing. The Hague. 1-20 pp.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4:25-51.

Nuñez, E., Cabzas, J., Escudero, J.C. 1986. Relación de matorrales en la formación de dehesas. Función de la jara, valoración de su bimasa y su utilización industrial. *In*: Campos, P., Bellido, M. (ed). Conservación y desarrolo de las dehesas portuguesa y española. Secretaría

General Técnica, Ministerio de Agricultura, Pesca y Alimentación. Badajoz. 111-118 pp.

Oliveira, A. and Costa, A. 1992. Metodologias do ordenamento do montado de sobro. *In*: Actas do II Encontro sobre os Montados de Sobro e Azinho. Universidade de Évora, 4-5 Junho, Évora. 26-33 pp.

Oliveira, AFL. 1955. Subsídios para o estudo da vegetação espontânea da Serra do Caldeirão (freguesia de Salir). Relatório final do curso de Eng.º Agrónomo. Lisboa: Instituto Superior de Agronomia, Universidade Técnica de Lisboa. Lisboa.

Oliveira, R. 1998. Causas para a desertificação e degradação da floresta – Estudo-caso para o concelho de Mértola – Portugal. Mediterrâneo 12-13:75-94.

Olson, D.M. and Dinerstein, E. 2002. The global 200: priority ecoregions for global conservation. Annals of the Missouri Botanical Garden 89:199-224.

Ovando, P., Campos, P., Oviedo, J.L., Montero, G. 2009. Cost-benefit analysis of cork oak woodland afforestation and facilitated natural regeneration in Spain. *In*: Aronson, J., Pereira, J.S., Pausas, J.G. (ed). Cork oak woodlands on the edge. Ecology, adaptive management, and restoration. Society for ecological Restoration International. Island Press. Washington D.C.. 177-188 pp.

Padilla, F.M. and Pugnaire, F.I. 2006. The role of nurse plants in the restoration of degraded environments. Frontiers in Ecology and the Environment 4:196–202.

Pampiro, F., Pintus, A., Ruiu, P.A., 1992. Interventi di recupero di una giovane sughereta percorsa da incêndio. *In*: Instituto de Promoción del Corcho (ed). Simpósio Mediterrâneo sobre Regeneración del Monte Alcornocal. Mérida. 174–177 pp.

Pardini, G., Gispert, M., Dunjó, G. 2004. Relative influence of wildfire on soil properties and erosion processes in different Mediterranean environments in NE Spain. Science of the Total Environment 328:237-246.

Paskoff, R.P. 1973. Geomorphological Processes and Characteristic Landforms. *In*: Di Castri, F., Mooney, H. A. (ed). Mediterranean Type Ecosystems. Origin and Structure. Springer-Verlag. New York. 53-60 pp.

Pausas, J.G. 1997. Resprouting of *Quercus suber* in NE Spain after fire. Journal of Vegetation Science 8:703-706.

Pausas, J.G. 2004. Changes in fire and climate in the Eastern Iberian Peninsula (Mediterranean Basin). Climate Change 63:337–350.

Pausas, J.G., Marañón, T., Caldeira, M., Pons, J. 2009a. Natural regeneration. *In*: Aronson, J., Pereira, J.S., Pausas, J.G. (ed). Cork oak woodlands on the edge. Ecology, adaptive management, and restoration. Society for ecological Restoration International. Island Press. Washington D.C.. 115-124 pp.

Pausas, J.G., Ouadah, N., Ferran, A., Gimeno, T., Vallejo, R. 2003. Fire severity and seedling establishment in *Pinus halepensis* woodlands, eastern Iberian Peninsula. Plant Ecology 169:205–213.

Pausas, J.G., Pereira, J.S., Aronson, J. 2009b. The tree. *In*: Aronson, J., Pereira, J.S., Pausas, J.G. (ed). Cork oak woodlands on the edge. Ecology, adaptive management, and restoration. Society for Ecological Restoration International. Island Press. Washington D.C.. 11-21 pp.

Pausas, J.G., Pons, J., Vallejo, R. 2004. Cork oak restoration: developing techniques to enhance establishment of a threatened ecosystem (Spain). Ecological Restoration 22:289–90.

Pausas, J.G., Ribeiro, E., Dias, S.G., Pons, J., Beseler, C. 2006. Regeneration of a marginal Cork oak (*Quercus suber*) forest in the eastern Iberian Peninsula. Journal of Vegetation Science 17:729-738.

Pausas, J.G. and Vallejo, V.R. 1999. The role of fire in European Mediterranean ecosystems. *In*: Chuvieco, E. (ed). Remote sensing of large wildfires in the European Mediterranean Basin. Springer-Verlag. Berlin. 3-16 pp.

Pearce, J. and Ferrier, S. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling 133:225–245.

Pereira, H. 2007a. A cortiça – um material único. *In*: Sande Silva, J. (ed). Os Montados. Muito para além das árvores. Árvores e Florestas de Portugal 3. Público, Comunicação Social SA & Fundação Luso--Americana para o Desenvolvimento. Lisboa. pp 59-75.

Pereira, H. 2007b. Cork: biology, production and uses. Elsevier Science. Amsterdam.

Pereira, H. and Tomé, M. 2004. Cork oak. *In*: Burley, J., Evans, J., Youngquist, J.A. (ed). Encyclopedia of Forest Sciences. Elsevier. Oxford. 613–620 pp.

Pereira, J.M.C. and Santos, M.T.N. 2003. Fire risk and burned area mapping in Portugal. Direcção Geral das Florestas. Lisboa.

Pereira, J.S., Conceição, M., Rodrigues, J. 1999. As causas da mortalidade do sobreiro revisitadas. Revista Florestal, vol12, 1/2:20-23.

Pereira, J.S., Correia, A.V., Correia, A.P., Pereira, J.M.C., Caldeira, M.C., Freit, A.C., Bugalho, M.N. *et al.* 2002. Forests and biodiversity. *In*: Santos, F.D., Forbes, K., Moita, R. (ed). Climate change in Portugal. Scenarios, impacts and adaptation measures. SIAM Project. Gradiva. Lisboa.

Pereira, J.S., Correia, A.V., Joffre, R. 2009a. Facing climate change. *In*: Aronson, J., Pereira, J.S., Pausas, J.G. (ed). Cork oak woodlands on the edge. Ecology, adaptive management, and restoration. Society for ecological Restoration International. Island Press. Washington D.C.. 219-226 pp.

Pereira, J.S., Kurz-Besson, C., Chaves, M. 2009b. Coping with drought. *In*: Aronson, J., Pereira, J.S., Pausas, J.G. (ed). Cork oak woodlands on the edge. Ecology, adaptive management, and restoration. Society for ecological Restoration International. Island Press. Washington D.C.. 73-80 pp.

Perez, M.R. 1990. Development of Mediterranean agriculture: an ecological approach. Landscape and Urban Planning 18:211-220.

Pérez-Devesa, M., Cortina, J., Vilagrosa, A., Vallejo, R. 2008. Shrubland management to promote *Quercus suber* L. establishment. Forest Ecology and Management 255:374:382.

Perez-Trejo, F. 1994. Desertification and land degradation in the European Mediterranean. European Commission. Luxembourg.

Perz, S.G. 2007. Grand theory and context-specificity in the study of forest dynamics: forest transition theory and other directions. The Professional Geographer 59 (1):105-114.

Petersen, T. 2002. Put a cork in it! WWF Newsroom Dec 6, 2002. (www.panda.org)

Pignatti, S. 1978. Evolutionary trends in Mediterranean flora and vegetation. Vegetatio 37:175-185.

Pignatti, S. 1995. Successioni. *In*: Pignatti, S. (ed). Ecologia vegetale. Unione Tipografico Editrice Torinese (UTET). Torino.

Pinto-Correia, T. 2000. Future development in Portuguese rural areas: how to manage agricultural support for landscape conservation? Landscape and Urban Planning 50:95–106.

Pinto-Correia, T. and Fonseca, A.M. 2009. Historical perspective of montados: the example of Évora. *In*: Aronson, J., Pereira, J.S., Pausas, J.G. (ed). Cork oak woodlands on the edge. Ecology, adaptive management, and restoration. Society for Ecological Restoration International. Island Press. Washington D.C.. 49-56 pp.

Pinto-Correia, T. and Jorge, R. 1996. Rural marginalization in Southern Portugal: farmers reactions to European Policies and current land use changes. *In*: Jongman, R.H.G. (ed). Ecological and Landscape Consequences of Land Use Change in Europe. ECNC Publication Series on Man and Nature 2. Tilburg. 286-297 pp.

Pinto-Correia, T. and Mascarenhas, J. 1999. Contributing to the extensification/intensification debate: new trends in the Portuguese Montado. Landscape and Urban Planning 46:125-131.

Pinto-Correia, T. and Vos, W. 2004. Multifunctionality in Mediterranean landscapes: past and future. *In*: Jongman, R. (ed). The New Dimensions of the European Landscape. Wagenigen UR Frontis Series Vol 4. Springer. Dordrecht. 135-164 pp.

Pires, A. 2000. A caprinicultura na Serra do Caldeirão. *In*: Direcção Regional de Agricultura do Algarve, Associação IN LOCO. (ed). Valorização da caprinicultura na Serra do Caldeirão. Universidade do Algarve. Faro. 19-55 pp.

Piussi, P. and Farrell, E.P. 2000. Interactions between society and forest ecosystems: challenges for the near future. Forest Ecology and Management 132:21-28.

Plieninger, T. and Pulido, F. 2009. Livestock grazing in dehesas: a self--destruct mechanism? *In*: Aronson, J., Pereira, J.S., Pausas, J.G. (ed). Cork oak woodlands on the edge. Ecology, adaptive management, and restoration. Society for Ecological Restoration International. Island Press. Washington D.C.. 42-45 pp.

Plieninger, T., Pulido, F.J., Konold, W. 2003. Effects of land-use history on size structure of holm oak stands in Spanish dehesas: implications for conservation and restoration. Environmental Conservation 30:61-70.

Plieninger, T. and Schaar, M. 2008. Modification of land cover in a traditional agroforestry system in Spain: processes of tree expansion and regression. Ecology and Society 13(2):25.

Pons, J. and Pausas, J.G. 2006. Oak regeneration in heterogeneous landscapes: the case of fragmented *Quercus suber* forests in the eastern Iberian Peninsula. Forest Ecology and Management 231:196-204.

Pons, J. and Pausas, J.G. 2007. Rodent acorn selection in a Mediterranean oak landscape. Ecological Research 22:535–541.

Puigdefábregas, J. 1995. Desertification: stress beyond resilience, exploring a unifying process structure. Ambio 24(5):311-31.

Puigdefábregas, J. and Mendizabal, T. 1998. Perspectives on desertification: western Mediterranean. Journal of Arid Environments 39:209-224.

Pulido, F.J. 1999. Herbivorismo y regeneración de la encina (*Quercus ilex*) en bosques y dehesas. PhD Thesis. Universidad de Extremadura. Cáceres.

Pulido, F.J. and Díaz, M. 2002. Dinámica de la regeneración natural del arbolado de encina y alcornoque. *In*: Pulido, F., Campos, P., Montero, G. (ed). 2002. La gestión forestal de las dehesas. Historia, ecología, selvicultura y economia. Instituto del Corcho, la Madera y el Carbón Vegetal (ICMC). Junta de Extremadura. Mérida. 39–62 pp.

Pulido, F.J. and Díaz, M. 2005. Regeneration of a Mediterranean oak: a whole-cycle approach. Écoscience 12:92–102.

Pulido, F.J., Díaz, M., Hidalgo de Trucios, H. 2001. Size structure and regeneration of Spanish holm oak *Quercus ilex* forests and dehesas: effects of agroforestry use on their long-term sustainability. Forest Ecology and Management 146:1-13.

Putz, F.E. and Canham, C.D. 1992. Mechanisms of arrested succession in shrublands: root and shoot competition between shrubs and tree seedlings. Forest Ecology and Management 49:267–275.

Quero, J.L., Villar, R., Marañón, T., Zamora, R. 2006. Interactions of drought and shade effects on seedlings of four *Quercus* species: physiological and structural leaf responses. New Phytologist 170:819-834.

Quézel, P. and Barbero, M. 1990. Les forêts méditerranéennes. Problèmes posés par leur signification historique, écologique et leur conservation. Acta Botanica Malacitana 15:145-178.

R Development Core Team. 2006. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna. http://www.R-project.org.

Raven, P.H. 1973. The Evolution of Mediterranean Floras. *In*: Di Castri, F., Mooney, H.A. (ed). Mediterranean Type Ecosystems. Origin and Structure. Springer-Verlag. New York. 213–224 pp.

Rego, F., Pereira, J., Trabaud, L. 1993. Modelling community dynamics of a *Quercus coccifera* L. garrigue in relation to fire using Markov chains. Ecological Modelling 66:251–260.

Retana, J., Espelta, J.M., Gracia, M., Riba, M. 1999. Seedling recruitment. *In*: Rodà, F., Retana, J., Gracia, C., Bellot, J. (ed). The Ecology of Mediterranean Evergreen Oak Forests. Springer-Verlag. Berlin. 89-103 pp.

Ribeiro, O., Lautensach, H., Daveau, S., 1987. Geografia de Portugal. Edições João Sá da Costa. Lisboa.

Rietkerk, M., Van de Bosch, F., Van de Koppel, J. 1997. Site-specific properties and irreversible vegetation changes in semi-arid grazing systems. Oikos 80(2):241-252.

Rietkerk, M. and Van de Koppel, J. 1997. Alternate stable states and thresholds effects in semi-arid grazing systems. Oikos 79:69-76.

Rigolot, E. 2004. Predicting postfire mortality of *Pinus halepensis* Mill. and *Pinus pinea* L. Plant Ecology 171:139–151.

Rindfuss, R.R., Walsh, S.J., Turner, B.L., Fox, J., Mishra, V. 2004. Developing a science of land change: challenges and methodological issues. PNAS 101(39):13976-13981.

Rivas-Martínez, S., Lousa, M., Díaz, T.E., Fernández-González, F., Costa, J.C. 1990. La vegetación del sur de Portugal (Sado, Alentejo y Algarve). Itinera Geobotanica 3:5–126.

Rothermel, R. 1983. How to predict the spread and intensity of forest and range fires. General Technical Report INT-143, Forest Service, United States Department of Agriculture.

Rousseau, O. and Lepart, J. 2000. Positive and negative interactions at different stages of a colonizing species (*Quercus humilis*). Journal of Ecology 88:401-412.

Rushton, S.P., Ormerod, S,J,, Kerby, G. 2004. New paradigms for modelling species distributions? Journal of Applied Ecology 41:193-200.

Ryan, K.C. 1990. Predicting prescribed fire effects on trees in the interior west. *In*: Alexander, M.E., Bisgrove, G.F. (ed). The Art and Science of Fire Management: Proceedings of the Interior West Fire Council Annual Meeting, October 24–27, 1988, Kananiskis Village, Alberta. Info. Rep. NOR-X-309. Edmonton, Forestry Canada, Northern Forestry Centre. Alberta. 148–162 pp.

Ryan, K.C. and Reinhardt, E.D. 1988. Predicting post-fire mortality of seven western conifers. Canadian Journal of Forest Research 18:1291–1297.

Sarmiento, F.O. 1997. Arrested succession in pastures hinders regeneration of Tropandean forests and shreds mountain landscapes. Environmental Conservation 24:14–23.

Sauvage, C. 1961. Recherches géobotaniques sur les Subéraies marocaines. Travaux de l´Institut Scientifique Chérifien, Série Botanique, Rabat 21:1-462.

Saveland, J.M. and Neueschwander, L.F. 1990. A signal detection framework to evaluate models of tree mortality following fire damage. Forest Science 36:66–76.

Scarascia-Mugnozza, G., Oswald, H., Piussi, P., Radoglou, K. 2000. Forests of the Mediterranean region: gaps in knowledge and research needs. Forest Ecology and Management 132:97-109.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B. 2001. Catastrophic shifts in ecosystems. Nature 413: 591-596.

Schupp, E.W., Milleron, T., Russo, S.E. 2002. Dissemination limitation and the origin and maintenance of species-rich tropical forests. *In*: Levey, D.J., Silva, W.R., Galetti, M. (ed). Seed dispersal and frugivory: ecology, evolution and conservation. CAB International. Wallingford. 19–33 pp.

Schwilk, D.W., Knapp, E.E., Ferrenberg, S.M., Keeley, J.E., Caprio, A.C. 2006. Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. Forest Ecology and Management 232:36–45.

Seng, M. and Deil, U. 1999. Forest vegetation types in the Serra de Monchique (Portugal): anthropogenic changes of oak forests. Silva Lusitana 7(1):71-92.

Silva, J.S. and Catry, F. 2006. Forest fires in cork oak (*Quercus suber* L.) stands in Portugal. International Journal of Environmental Studies 63(3):235-257.

Smit, C., Den Ouden, J., Díaz, M. 2008. Facilitation of holm oak recruitment by shrubs in Mediterranean open woodlands. Journal of Vegatetaion Science 19:193–200.

Soares, P., Carvalho, P., Tomé, M. 1998. Agrosilvopastoral and agrisilvicultural systems in Portugal. *In*: Pukkala, T., Eerikäinen, K. (ed). Modelling the growth of tree plantations and agroforestry systems in South and East Africa. Proceedings of the meeting in Finland 24 - 28 August 1998. Research Notes 80. University of Joensuu, Faculty of Forestry. Joensuu. 24-33 pp.

SPSS, 2004. SPSS for Windows. SPSS Inc. Chicago.

Standish, R.J., Cramer, V.A., Wild, S.L., Hobbs, R.J. 2007. Seed dispersal and recruitment limitations are barriers to native recolonisation of old--fields in Western Australia. Journal of Applied Ecology 44:435-445.

Standish, R.J., Cramer, V.A., Yates, C.J. 2009. A revised state-and-transition model for the restoration of woodlands in Western Australia. *In*: Hobbs, R.J., Suding, K.N. (ed). New models for ecosystem dynamics and restoration. Island Press. Washington D.C.. 169-188 pp.

Stephens, S.L. and Finney, M.A. 2002. Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor consumption. Forest Ecology and Management 162:261–271.

Thirgood, J.V. 1981. Man and the Mediterranean Forest. A history of resource depletion. Academic Press. New York.

Tomaselli, R. 1981. Relations with other Mediterranean ecosystems: temperate evergreen forests, Mediterranean coniferous forests, savannahs, steppes and desert shrublands. *In*: Di Castri, F., Goodall, D.W., Specht, R.L. (ed). Mediterranean-Type Shrublands. Ecosystems of the World 11. Elsevier. Amsterdam. 95-106 pp.

Tomé, M., Coelho, M.B., Lopes, F., Pereira, H. 1998. Modelo de produção para o montado de sobro em Portugal. *In*: Pereira, H. (ed). Cork Oak and Cork, European Conference on cork-oak and cork. Centro de Estudos Florestais. Lisboa. 22–46 pp.

Torre, I. and Díaz, M. 2004. Small mammal abundance in Mediterranean post-fire habitats: a role for predators? Acta Oecologica 25:137–42.

Toumi, L. and Lumaret, R. 1998. Allozyme variation in cork oak (*Quercus suber* L.): the role of phylogeography and genetic introgression by other Mediterranean oak species and human activities. Theoretical and Applied Genetics 97:647-656.

Trabaud, L. 1981. Man and fire: impacts on Mediterranean vegetation. *In*: Di Castri, F., Goodall, D.W. (ed). Ecosystems of the World 11. Mediterranean-Type Shrublands. Elsevier. Amsterdam. 479-521 pp.

Trabaud, L. 2003. Towards a sounder fire ecology. Forum. Frontiers in Ecology and the Environment 1(5):274-275.

Trabaud, L. and Galtié, J.F. 1996. Effects of fire frequency on plant communities and landscape pattern in the Massif des Aspres (southern France). Landscape Ecology 4:215–224.

Trabaud, L. and Oustric, J. 1989. Heat requirements for seed germination of three *Cistus* species in garrigue of southern France. Flora 183: 321-325.

Usher, M.B. 1981. Modelling ecological succession with particular reference to Markovian models. Vegetatio 46:11–18.

Vallejo, R., Aronson, J., Pausas, J.G., Cortina, J. 2006. Restoration of Mediterranean Woodlands. *In*: Van Andel, J., Aronson, J. (ed). Restoration Ecology: The New Frontier. Blackwell Science. Oxford. 193-207 pp.

Vallejo, V.R. 2009. Restoration in practice. *In*: Aronson, J., Pereira, J.S., Pausas, J.G. (ed). Cork oak woodlands on the edge. Ecology, adaptive management, and restoration. Society for ecological Restoration International. Island Press. Washington D.C.. 127-128 pp.

Vallejo, V.R., Aronson, J., Pausas, J.G., Pereira, J.S., Fontaine, C. 2009. The way forward. *In*: Aronson, J., Pereira, J.S., Pausas, J.G. (ed). Cork oak woodlands on the edge. Ecology, adaptive management, and restoration. Society for Ecological Restoration International. Island Press. Washington D.C.. 235-245 pp.

VanWagner, C.E. 1973. Height of crown scorch in forest fires. Canadian Journal of Forest Research 3:373–378.

VanWagner, C.E. 1977. Conditions for the start and spread of crown fire. Canadian Journal of Forest Research 3:373–378.

Vicente, A.M. and Alés, R.F. 2006. Long term persistence of dehesas. Evidences from history. Agroforestry Systems 67:19–28.

Viegas, X. 2004. Slope and wind effects on fire propagation. International Journal of Wildland Fire 13:143–156.

Walker, L.R. and Del Moral, R. 2009. Transition dynamics in succession: implications for rates, trajectories, and restoration. *In*: Hobbs, R.J., Suding, K.N. (ed). New models for ecosystem dynamics and restoration. Island Press. Washington D.C.. 33-49 pp.

Walsh, T.A. and Burk, T.E. 1993. Calibration of satellite classifications of land area. Remote Sensing of Environment 46:281-290.

Walter, H. 1973. Vegetation of the Earth. In relation to climate and the eco-physiological conditions Heidelberg Science Library, Vol.15, Springer-Verlag. New York.

Wang, B.C. and Smith, T. 2002. Closing the seed dispersal loop. Trends in Ecology and Evolution 8:379–85.

Werner, C., Correia, O.A., Ryel, R.J., Beyschlag, W. 1998. Modeling wholeplant primary production of macchia species: assessing the effects of photoinhibition and foliage orientation. Revista de Biologia 16:247–57.

Westoby, M., Walker, B., Noy-Meir, I. 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management 42:266-274.

Whelan, R.J. 1995. The Ecology of Fire. Cambridge University Press. Cambridge.

WWF (World Wild Fund). 2006. Cork screwed? Environmental and economic impacts of the cork stoppers market. A WWF Report, May 2006. WWF/MEDPO.

Xiao, Z., Jansen, P.A., Zhang, Z. 2006. Using seed-tagging methods for assessing post-dispersal seed fate in rodent-dispersed trees. Forest Ecology and Management 223:18–23.

Zamora, R., Castro, J., Gómez, J.M., García, D., Hódar, J.A., Gómez, L., Baraza, E. 2001. Papel de los matorrales en la regeneración forestal en ambientes mediterráneos: aplicaciones para la restauración. Quercus 187:40-47.

Zapata, S., Parejo, F.M., Branco, A., Gutierrez, M., Blanco, J.I.J., Piazzetta, R., Voth, A. 2009. Manufacture and trade of cork products: an international perspective. *In*: Aronson, J., Pereira, J.S., Pausas, J.G. (ed). Cork oak woodlands on the edge. Ecology, adaptive management, and restoration. Society for Ecological Restoration International. Island Press. Washington D.C.. 189-200 pp.

Zavala, M.A. 2003. Dinámica y sucesión en bosques mediterráneos: modelos teóricos e implicaciones para la silvicultura. *In*: Rey-Benayas, J.M., Espigares, T., Nicolau, J.M. (ed). Restauración de Ecosistemas Mediterráneos. Universidad de Alcalá de Henares. Alcalá de Henares. 43-63 pp.

Zavala, M.A., Zamora, R., Pulido, F., Blanco, J.A., Imbert, J.B., Marañón, T., Castillo, F.J., Valladares, F. 2004. Nuevas perspectivas en la conservación, restauración y gestión sostenible del bosque mediterráneo. *In*: Valladares, F. (ed). Ecología del bosque mediterráneo en un mundo cambiante. Ministerio de Medio Ambiente, EGRAF, S.A. Madrid. 509-529 pp.

Summary

The landscape in southern Portugal is dominated by a distinctive Mediterranean land use system in which cork oak (*Quercus suber* L.) is the main tree species; this area constitutes the largest cork oak habitat in the world. The cork oak land use system of today is the result of long-term combined ecological and land use dynamics that have shaped the landscape. In some cases, overexploitation of the land has led to soil degradation and erosion and a lack of natural regeneration of cork oak. Areas of degraded soil are commonly invaded and dominated by rockrose (*Cistus* spp.) shrubs; the resulting shrubby vegetation is very persistent and can be interpreted as a stage of regressive succession of the original forest. Succession has traditionally been thought of as a relatively linear process, but evidence from a variety of ecosystems indicates that persistent alternative vegetation states may occur, particularly after disturbances. The existence of alternative stable states causes discontinuous responses to increasing disturbances; such responses are often difficult to reverse.

In this thesis I hypothesized that cork oak forests and *Cistus* shrublands (i.e. scrub) in southern Portugal are alternative stable states, which change slowly or not at all in the absence of human intervention. *Cistus* shrubland could represent an alternative persistent state of lower vegetation biomass on the most degraded soils and drier areas. I also hypothesized that overexploitation could have triggered feedback mechanisms that led to decreasing cork oak natural regeneration and, in the long-term, to a persistent shrub-dominated vegetation, in which the establishment of cork oak seedlings has become very difficult, especially in very dry conditions. The overall objective of this thesis was thus twofold: to evaluate if cork oak forests and shrublands represent alternative stable states in

southern Portugal, and to ascertain the ecological and land use mechanisms underlying their resilience and persistence. The fieldwork presented in this thesis was conducted in a site in Serra do Caldeirão, a mountain range in the northeastern part of the Algarve province, southern Portugal. All the data analysed for this thesis were collected at this site.

Chapter 1 is a general introduction, presenting the overall hypotheses and objectives of the thesis and describing briefly the evolution, ecology, human management and socio-economics of the cork oak land use system in Portugal, with a final focus on overall resilience.

Chapter 2 analyses and explains vegetation changes at a landscape scale. The cork oak landscape at the study site was conceived of as a mosaic of four main types of vegetation patches: 1) cork oak forests (more than 100 trees/ha, without understorey management); 2) cork oak savannas (40 to 100 trees/ha, with understorey management), 3) shrublands dominated by *Cistus* spp; 4) and grasslands dominated by annual herbaceous species (native or improved pastures). I used aerial photographs from a period of 45 years (1958–2002) to quantify the persistence and rates of transitions between vegetation patch types, and logistic regression to relate transitions with topographical features (aspect and slope) and wildfire history. Chapter 2 reveals that *Cistus* shrublands have been the most persistent patch type in the study area for the 45 years and have been expanding at the expense of the other vegetation patch types. Cork oak forests have also been persistent but, contrary to shrublands, have been decreasing since 1985; savannas and grasslands have been less persistent. Chapter 2 shows that wildfires triggered transitions from forests to shrublands after 1995 and contributed to maintain shrubland patches, particularly on south-facing slopes. *Cistus* shrubs are active pyrophytes and are well adapted to drought through physiological responses, thus their persistence can be supported by a positive feedback mechanism triggered by frequent wildfires, especially on south-facing slopes, where conditions are drier and more limiting for seedling recruitment and cork oak survival. Forests persisted longer on steeper slopes, probably because they were less accessible to human interventions.

Chapter 3 analyses and explains patch-type changes at a local scale by quantifying mechanisms that limit cork oak recruitment in different patch types. Using a combination of field studies and experiments I quantified cork oak natural regeneration, seed production, seed removal and dispersal, seed survival and germination, and seedling establishment and survival for the three dominant vegetation patch types in the study area: cork oak forests, cork oak savannas and *Cistus* shrublands. All four forms of cork oak recruitment limitation (namely, source, dispersal, germination, and establishment limitations) were significantly more severe in shrublands than in oak forests and savannas, hence cork oak seedling recruitment in shrubland was impeded in multiple ways. Seed source scarcity and establishment failure seemed to be the major limitations to tree recruitment in shrubland patches. The findings of Chapter 3 explain the persistence of *Cistus* shrubland patches. Succession in these patches appears arrested, and unable to progress towards forest recovery due to severe constraints to cork oak recruitment during the early phases of the recruitment cycle. Although the recruitment constraints are equally strong in forests and savannas, seedling survival was significantly lower in full-sun conditions than under tree shade, suggesting that forests provide better establishment conditions than savannas. It is likely that in the following years, summer drought stress will increase seedling mortality in the savanna patches.

Chapter 4 assesses the survival rates and variables affecting cork oak survival 18 months after a large wildfire had occurred in the study area. The focus is on the management of bark exploitation. In this Chapter it is shown that fire resistance in cork oak is essentially determined by management decisions. Survival rate was 84% and the most important factors affecting survival were related to the management of cork extraction: stripped trees, trees with thinner bark and trees with larger diameter (correlated with the number of stripping operations) showed lower survival. Survival also decreased with increasing charring height (an indicator of fire damage). It was also found that post-fire survival of stripped cork oak trees was lower on the south to east oriented slopes, which are more xerophitic. So, it seems that the combination of wildfire occurrence and aspect accounts for the lower post-fire survival rates of cork oak trees, since a physiologically stressed tree is more vulnerable to fire. Based on these insights a survival model was built for managers to use to identify areas vulnerable to future fires, where fire prevention is crucial.

In Chapter 5 the cork oak landscape is viewed as a social–ecological system in which patch-type transitions are explained by a combination of management and biophysical variables. I used face-to-face interviews with landowners to collect information on management practices and landowners' individual perceptions, and the biophysical variables quantified in Chapter 2 (wildfire, slope and exposure). Patch-type transitions were grouped into cork oak persistence (maintenance or increase in tree cover) or lack of cork oak persistence (absence of or decrease in tree cover). Logistic regression was used to evaluate the influence of collected biophysical and management variables on patch-type transitions during 45 years (1958-2002). The best model for tree persistence included both biophysical and management variables and showed that cork oak persistence was more likely in areas where there had been no understorey management before 1975, no cork oak plantings had been carried out since the 1980s, wildfires were absent and slopes were steeper. It was found that over half of the landowners interviewed hold traditional beliefs that run contrary to current scientific knowledge; this suggests that landowners' perceptions of the land use system clearly influence management decisions that hamper forest recovery. I argue that landowners' behaviour within the study area is conditioned by the perception that their holding is too small and that further improvement through investment would not pay dividends, so landowners avoid investment and, in the worst-case scenario, abandon management.

Chapter 6 is a synthesis of the findings. The main findings are discussed in a wider perspective and it is concluded that shrubland is an alternative stable state of lower vegetation biomass in former cork oak areas. Here, the natural succession is arrested and the system remains in a pioneer state of *Cistus* shrubland. In Chapter 6 I also show the theoretical and practical relevance of the results of this thesis towards the resilience and sustainability of cork oak land use systems. My findings suggest that the future of the cork oak land use system in the study area is severely threatened by loss of ecological resilience (shrub encroachment, difficulties in cork oak recruitment and lack of forest recovery) and loss of social and economic resilience (lack of investment and profit, lack of adequate and concerted management), and that cork oak land use systems in the study area are not sustainable if adequate management actions and restoration programmes are not enforced in the short term.

Samenvatting

Het landschap in Zuid Portugal wordt gedomineerd door een landsgebruiksysteem met kurkeik (*Quercus suber* L.) als belangrijkste boomsoort. Dit gebied herbergt tevens het grootste kurkeikenhabitat in de wereld. Het kurkeik landsgebruiksysteem is ontstaan door een combinatie van langdurige ecologische en landgebruiks-dynamiek die het landschap hebben gevormd. In sommige gevallen heeft overexploitatie echter geleid tot bodemdegradatie en erosie en tot een gebrekkige natuurlijke verjonging van kurkeik. Gedegradeerde gebieden worden vaak begroeid en later gedomineerd door rotsroos (*Cistus* spp.). De zo ontstane vegetatie blijkt zeer persistent en kan worden beschouwd als een vroege successiefase van het oorspronkelijke bos. Traditioneel werd sucessie vaak gezien als een lineair process, maar nadere analyse van verscheidene ecosystemen wijst erop dat er verschillende persistente alternatieve vegetaties kunnen voorkomen in een gebied, vooral na verstoring. Het bestaan van alternatieve stabiele vegetaties veroorzaakt discontinue reacties op verhoogde verstoring die vaak moeilijk ongedaan te maken zijn.

In dit proefschrift stel ik de hypothese dat kurkeikenbos en *Cistus*-gedomineerde vegetatie twee alternatieve stabiele vegetatietypen zijn, die niet of nauwelijks veranderen bij uitblijven van menselijk ingrijpen. *Cistus*-vegetatie kan worden gezien als een alternatief met een lagere biomassa voor de meest gedegradeerde en droogste gebieden. Ik verwacht verder dat overexploitatie een feedbackmechanisme in werking heeft gezet dat leidt tot een afname van de natuurlijk regeneratie van kurkeik en, op lange termijn, zal leiden tot het ontstaan van een persistente struik-gedomineerde vegetatie, waar de vestiging van kurkeik zaailingen wordt bemoeilijkt, vooral onder droge condities.

In hoofdstuk 1 geeft ik een algemene inleiding met de hypothesen en doelstellingen van het proefschrift en beschrijf ik kort de ontstaansgeschiedenis, ecologie, het beheer en de sociaaleconomische aspecten van het kurkeik landgebruiksysteem in Portugal. Tevens wordt er aandacht besteed aan de algehele veerkracht van het systeem.

In hoofdstuk 2 worden de vegetatieveranderingen op landschapsniveau geanalyseerd en beschreven. Het kurkeiklandschap van het onderzoeksgebied wordt voorgesteld als een mozaïek met fragmenten van vier belangrijke vegetatietypen, te weten: 1) kurkeikbos (meer dan 100 bomen/ha, zonder beheer van de ondergroei); 2) kurkeiksavannes (40 tot 100 bomen/ha, met beheer van de ondergroei); 3) struikvegetatie gedomineerd door *Cistus* soorten.; 4) en grasland gedomineerd door eenjarige kruiden (zowel oorspronkelijke als verbeterde weilanden). Ik gebruikte luchtfoto's gemaakt over een periode van 45 jaar (1958-2002) om de persistentie en transitiesnelheid tussen fragmenten van de verschillende vegetatietypen te kwantificeren. Met behulp van logistische regressie werd de vegetatietransitie gerelateerd aan topografische aspecten (oriëntatie en helling) en brandgeschiedenis. In hoofdstuk 2 laat ik zien dat door *Cistus* gedomineerde vegetatie, gedurende de 45 jaar, de meest persistente fragmenten in het onderzoeksgebied vormt en dat het in areaal is toegenomen ten koste van de andere vegetatie fragmenten. Kurkeikenbos was ook persistent maar, in tegenstelling tot de struikvegetatie, was er een afname in areaal sinds 1985. Savanne en grasland waren minder persistent. Hoofdstuk 2 laat zien dat bosbranden na 1985 de transitie van bosnaar struikvegetatie bevorderden en bijdroegen aan de instandhouding van struik fragmenten, vooral op zuidelijke hellingen. *Cistus*-soorten zijn vuur-resistent en fysiologisch goed aangepast aan droogte. Zodoende wordt hun persistentie ondersteund door een positief feedback mechanisme, veroorzaakt door terugkerende bosbranden, vooral op zuidelijke hellingen, waar de condities droger zijn en meer limiterend voor de verjonging en overleving van kurkeik. Bossen persisteren langer op steilere hellingen, waarschijnlijk omdat ze daar minder toegankelijk zijn voor menselijk ingrijpen.

In hoofdstuk 3 worden de veranderingen in typen vegetatiefragmenten op lokale schaal geanalyseerd en beschreven door middel van het kwantificeren van de mechanismen die kurkeikverjonging tegengaan in de verschillende typen fragmenten. Door gebruik te maken van zowel veldstudies als experimenten kwantificeerde ik de natuurlijke regeneratie, de productie, verwijdering, verspreiding, overleving en kieming van zaden, als ook zaailingvestiging en -overleving voor de drie dominante vegetatietypen in het onderzoeksgebied; kurkeikenbos, kurkeiksavanne en *Cistus*-gedomineerde struikvegetatie. De vier voornaamste beperkingen voor de natuurlijke verjonging van kurkeik (namelijk aanwezigheid van zaadbronnen, en beperkingen voor verspreiding, kieming en vesting) waren aanzienlijk sterker in struikvegetatie dan in eikenbossen en eikensavannes, waardoor de verjonging van kurkeik in struikvegetaties op verschillende manieren belemmerd wordt. Schaarste aan zaadbronnen en het mislukken van vestiging van zaailing bleken de voornaamste beperkingen voor de verjonging in struikvegetatie fragmenten. De bevindingen van hoofdstuk 3 verklaren de persistentie van de fragmenten van de met *Cistus* gedomineerde struikvegetatie. Door ernstige beperkingen op de kurkeikverjonging gedurende de eerste levensstadia wordt de successie geremd en komt hergroei van het oorspronkelijke bos niet tot stand, Hoewel de beperkingen voor natuurlijke verjonging even sterk zijn in bossen en in savannes, was de overleving van zaailingen aanzienlijk lager in de volle zon dan in de schaduw van bomen, wat suggereert dat bossen betere omstandigheden voor de vestiging van zaailingen bieden dan de savannes. Waarschijnlijk vergroot de zomerdroogte de zaailingsterfte in de daarop volgende jaren.

In hoofdstuk 4 evalueer ik de overlevingkans en de factoren van invloed op de overleving van kurkeik 18 maanden na een grote bosbrand in het onderzoeksgebied, met speciale aandacht voor de kurkexploitatie. In dit hoofdstuk wordt aangetoond dat vuurbestendigheid van het kurkeikenbos sterk wordt bepaald door het gevoerde beheer. De kans op overleven was 84% en de belangrijkste factoren van invloed op overleving werden sterk bepaald door het beheer van het kurkeikenbos en de kurkextractie. Bomen waarvan de kurkschors recent was geoogst, bomen met een dunne schors en bomen met een grote diameter (en waarvan relatief vaak schors is geoogst) hadden een agere overlevingskans. Overleving nam ook af met de hoogte van verbranding van de stam (een indicator van vuurschade). Verder werd gevonden dat de overleving van gestripte kurkeiken lager was op de drogere zuid- tot oost-georiënteerde hellingen. Zodoende lijkt het dat de combinatie van terugkerende branden en de hellingsrichting verantwoordelijk is voor de lagere overlevingskans van kurkeiken na een initiële bosbrand, daar een fysiologisch gestresste boom vatbaarder is voor vuur. Op basis van deze inzichten werd er een overlevingsmodel ontwikkeld voor gebruik door beheerders bij de identificatie van gebieden die vatbaar zijn voor toekomstige branden en waar de vuurpreventie cruciaal is.

In hoofdstuk 5 wordt het kurkeikenlandschap gezien als een sociaaleconomisch systeem waar de transities tussen vegetatiefragmenten verklaart worden door een combinatie van beheer en biofysische variabelen. Ik gebruikte interviews met landeigenaren om informatie te verzamelen over beheerspraktijken en individuele opvattingen van grondbezitters, en dit te combineren met de biofysische variabelen uit hoofdstuk 2 (brand, hellingsoriëntatie en expositie). Transities tussen vegetatie fragmenten werden gegroepeerd als kurkeikpersistentie (behoud of toename van boombezetting) of het gebrek aan kurkeik persistentie (afwezigheid of afname van de boombezetting). Logistische regressie werd gebruikt om de invloed van de verzamelde biofysische- en beheervariabelen op de transities tussen vegetatiefragmenten gedurende 45 jaar (1958-2002) in kaart te brengen. Het beste model omvatte zowel biofysische als beheervariabelen en liet zien dat de persistentie van kurkeik waarschijnlijker is in gebieden waar voor 1975 geen beheer van de ondergroei en geen aanplant van kurkeik heeft plaatsgevonden, bij het uitblijven van bosbranden, en op steilere hellingen. Er werd gevonden dat meer dan de helft van de landeigenaren er traditionele overtuigingen op na hielden die tegenstrijdig zijn met de huidige wetenschappelijke kennis, hetgeen suggereert dat de opvattingen van eigenaren van dit landgebruiksysteem de besluiten omtrent het beheer beïnvloeden en het natuurlijk herstel van het bos tegenwerken. Ik constateer dat het gedrag van landeigenaren in het onderzoeksgebied is geconditioneerd door het idee dat hun bedrijven te klein zijn en dat verdere verbetering door middel van investering niet rendabel zou zijn. Daarom vermijden eigenaren verdere investering en zien in het uiterste geval af van enig actief beheer.

Hoofdstuk 6 is een synthese van de bevindingen. De belangrijkste resultaten worden bediscussieert in een breder perspectief en er wordt geconcludeerd dat struikvegetatie een alternatief evenwicht met een lagere biomassa vormt in gebieden die voorheen gedomineerd werden door kurkeik. De natuurlijke successie wordt daardoor geremd en het systeem blijft in een pioniersstadium gedomineerd door *Cistus* soorten. In hoofdstuk 6 laat ik ook de theoretische en praktische relevantie van de resultaten van dit proefschrift zien voor de veerkracht en duurzaamheid van kurkeik landgebruiksystemen. Mijn bevindingen suggereren dat de toekomst van het kurkeik land gebruiksysteem ernstig in gevaar is door verlies aan ecologische veerkracht (door invasie van struiken, moeilijkheden met verjonging van de eiken, en achterblijvend herstel van het bos) en het verlies aan sociale en economische veerkracht (gebrek aan investering en winst, gebrek aan duidelijk en adequaat beheer). De kurkeiksystemen in het onderzoeksgebied zijn niet duurzaam als er niet op korte termijn adequate beheersmaatregelen worden getroffen en herstelprogramma's worden doorgevoerd.

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Short Biography

Vanda Acácio was born on the 1st of December 1971 in Lisbon, Portugal. She finished her high school education in 1989 in Lisbon and entered Instituto Superior de Agronomia, Universidade Técnica de Lisboa (Higher Institute of Agronomy, Technical University of Lisbon), for a 5-year course on Forestry Engineering from 1990 to 1996. While at the university she coordinated the editing of the magazine of the Portuguese Forestry Students Association for two years. In 1996 she completed her degree with an internship at a natural park in southwestern Portugal, from which she wrote her degree dissertation on wild boar management.

After graduating she was employed as a consultant and project coordinator by a Portuguese private company working in the field of environment and natural resources. She coordinated different kinds of projects, such as forest inventory and forest management, the writing and editing of technical forestry handbooks, forest certification, watershed management plans, and forest fire prevention plans. At this company she also coordinated the making of a CD-ROM focusing on the Portuguese cork oak, for the Third Ministerial Conference on the Protection of Forests in Europe (in 1997).

In 2001 she moved to the United States (San Francisco, California), where she lived for one year. In 2002 she was awarded a fellowship from the Portuguese Foundation for Science and Technology to do a PhD in the Forest Ecology and Forest Management Group of the Centre for Ecosystem Studies, at Wageningen University, The Netherlands, and she moved from San Francisco to the Netherlands. From 2002 to 2006 she carried out her Sandwich PhD, alternating between Wageningen University and the Centro de Ecologia Aplicada Prof. Baeta Neves (Centre for

Applied Ecology, Higher Institute of Agronomy in Lisbon). The PhD research resulted in this thesis.

From 2005 to 2006 she worked for the Portuguese Directorate of Forest Resources (Portuguese Ministry of Agriculture and Fisheries) to coordinate a European Union project (Interreg IIB-Medoc RECOFORME) on cooperation actions and information exchange on European Mediterranean forests. In 2007 she worked at a Forest Producers Association, where she coordinated several forest fire prevention and management plans for municipalities south of Lisbon. At present she lives in Lisbon and is a member of the research team at Centro de Ecologia Aplicada Prof. Baeta Neves (Higher Institute of Agronomy, Technical University of Lisbon), while she also develops projects for the private company in which she worked after graduating. This allows her to combine her passion for research and the theoretical aspects of science with the more practical side of project consultancy.

List of Publications

Published in peer reviewed journals:

Acácio, V. Holmgren, M., Rego, F., Moreira, F. Mohren, G.M.J. 2009. *Are drought and wildfires turning Mediterranean cork oak forests into persistent shrublands?* Agroforestry Systems 76: 389-400.

Catry, F., Moreira, F., Duarte, I., **Acácio**, V. 2009. *Factors affecting post-fire crown regeneration in cork oak (Quercus suber L.) trees*. European Journal of Forest Research 128: 231-240.

Moreira, F., Catry, F., Duarte, I., **Acácio**, V., Sande Silva, J. 2009. *A conceptual model of sprouting responses in relation to fire damage: an example with cork oak (Quercus suber L.) trees in Southern Portugal.* Plant Ecology 201: 77-85.

Acácio, V. Holmgren, M., Jansen, P., Schrotter, O. 2007. *Multiple recruitment limitation causes arrested succession in Mediterranean cork oak systems*. Ecosystems 10: 1220-1230.

Moreira, F., Duarte, I., Catry, F., **Acácio**, V. 2007. *Cork extraction as a key factor determining post-fire cork oak survival in a mountain region of southern Portugal.* Forest Ecology and Management 253: 30-37.

Submitted to peer reviewed journals:

Acácio, V. Holmgren, M., Moreira, F., F. Mohren, G.M.J. *Interactive effects of human and ecological factors determine persistence of cork oak forests in southern Portugal.* (Submitted to Ecology and Society)

PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of Literature (5.6 ECTS)

- Sustainable management of agro-forestry systems in the Mediterranean; state of the art on cork oak: species, ecosystem, human management and disturbances; alternative stable states and resilience (2002)

Writing of Project Proposal (7 ECTS)

- The dynamics of cork oak systems in Portugal: the role of ecological and land use factors (2003)

Post-Graduate Courses (4.4 ECTS)

- Basic and Advanced Statistics; PE&RC (2002/03)
- Multivariate analysis; PE&RC (2005)
- Tropical Forest Ecology and Management; PE&RC (2006)

Competence Strengthening / Skills Courses (3.2 ECTS)

- Techniques for writing and presenting scientific papers; Mansholt Institute (2003)
- Critical Reflection on Science/Technology, Values and Sustainability; Mansholt Institute (2003)

- Time Planning and Project Management; Mansholt Institute (2004)
- Scientific Publishing; Mansholt Institute (2004)

Discussion Groups / Local Seminars and Other Scientific Meetings (7 ECTS)

- Discussion group Forest and Conservation Ecology (2002/06)
- Weekly chair group scientific meetings and presentations (2002/06)

PE&RC Annual Meetings, Seminars and the PE&RC Weekend (0.3 ECTS)

- PE&RC Annual Meeting - Ethics in Science (2002)

International Symposia, Workshops and Conferences (5.9 ECTS)

- First Colloquium on Flora and Fauna of Montados; Portugal (2002)
- European Congress of the International Association for Landscape Ecology: Landscape Ecology in the Mediterranean. Inside and outside approaches; Portugal (2005)
- Seminar: The vitality of cork oak and Holm oak stands. Current situation, state of knowledge and actions to take; Portugal (2006)
- The International Mediterranean Ecosystems Conference; Perth, Australia (2007)

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