Fire recurrence effects on Pinus halepensis Mill. communities of Catalonia

Memòria presentada per:

Màrcia Eugenio Gosalbo
Per optar al grau de Doctora

Amb el vist-i-plau del director de tesi:

Dr. Francisco Lloret Maya
Catedràtic d'Ecologia
Universitat Autònoma de Barcelona

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Fe de erratas

Nota: No aparecen recogidos los errores puntuales que no impiden la correcta comprensión del texto.

Mayores:

Capítulo 3

-No se especifica que las variables climáticas de temperatura y precipitación corresponden con la temperatura media anual y la precipitación anual acumulada (datos de serie climática, Atles Climàtic Digital de Catalunya).

Capítulo 4

-No se especifica que las variables climáticas de temperatura y precipitación corresponden con la temperatura media anual y la precipitación anual acumulada (datos de serie climática, Atles Climàtic Digital de Catalunya).

Capítulo 5

-No se especifica que los datos climáticos obtenidos a partir de la Xarxa Agrometeorològica de Catalunya corresponden a un mismo valor para zonas aparejadas.

Capítulo 6

-Los resultados de las regresiones en que se testa la correlación entre la densidad y la precipitación no aparecen recogidos en un apartado independiente (que es la pauta a lo largo del trabajo), sino en una frase añadida al primer párrafo de la Pág. 153, tras los resultados de densidad.

Capítulo 8

-Pág. 206, primer párrafo:
La frase "..., a lowe percentage of which was already reproductive 10 years alter the 1994 fire..." no debería aparecer, puesto que corresponde con un resultado del Capítulo 6 que finalmente no se incluyó en la tesis.

-Pág. 209:
De igual forma, aparecen tres párrafos que corresponden con resultados del Capítulo 7 que finalmente no se incluyeron en el trabajo. Los párrafos son consecutivos, y comienzan como sigue:
" At the regional level..."
"Relative abundance of Q.ilex..."
"Relative abundance of P.lentiscus..."

Menores:

Capítulo 3

-Pág.42, última frase del primer párrafo:
"...which would affect ecosystem productivity *and structure* (O'Connell 1987; Maggs 1988)"

-Pág. 52, última frase del primer párrafo:
"...the longer the time intervals between consecutive fires, the higher total vegetation cover, *irrespective of substrate type*"

Capítulo 4

-Pág.85, primera frase del primer párrafo:
"...,particularly where a thick layer of accumulated plant litter *or a layer of superficial stones* was not protecting it"

Capítulo 6

-Pág. 151:
El uso del término *crossdating* es erróneo (aparece dos veces en el texto), puesto que éste se refiere específicamente a la datación de árboles en base al uso de series preexistentes. El término correcto sería *dating*.

-Pág. 159, final del último párrafo:
"...not considered, and may *partly* explain..."

Capítulo 7

-Pág. 187, párrafo central:
"...(on the order of 10^2 m^2)..." debería ser "...(on the order of 100 m^2)..."

-Pág. 189, final del primer párrafo:
"...and P.lentiscus between paired *areas* (Chapter 5)..."

Chapter 1

General Introduction

1.1. Fire in Mediterranean-Type Ecosystems

Fire is a recurrent disturbance in Mediterranean-climate regions of the world, such as the Mediterranean Basin, southern California, the southwestern Cape of Africa, southwestern Australia, and the central zone of Chile. Natural fires are mainly ignited by lightning strikes resulting from thunderstorms, except in Chile (Kruger 1983; Bond & van Wilgen 1996). Such fires occur mostly along the warm and dry season that characterizes Mediterranean climate, when air humidity and fuel moisture are low (Keeley 1982; Vázquez & Moreno 1998).

Mediterranean vegetation is considered fire prone, which is related not only to primary productivity, but also to morphological and chemical features of individual plant species, and to structural characteristics of communities (Bond & van Wilgen 1996). Mediterranean landscapes are dominated by a variety of sclerophyllous shrublands, named in different regions as chaparral, coastal sage scrub, maquis, garrigue, matorral, kwongan, and fynbos, among others. Communities dominated by tree species are also abundant, and show dense shrubby understoreys and a vine layer (Hobbs et al. 1995). Consequently, fuel loads are generally high and fuels show vertical and horizontal continuity. Furthermore, fire is not usually initiated and sustained unless there is enough dead plant material, and Mediterranean plants tend to accumulate dead biomass, in such a way that the ratio of dead-to-live biomass increases with time since last fire (Christensen 1985). Fuel accumulation on the ground is enhanced by low decomposition rates (Mitchell et al. 1986). Moreover, vegetation flammability is promoted by the widespread presence of secondary compounds such as oils, fats, waxes, and terpenes, and by low plant tissue nutrient contents (Christensen 1985). Shape, size, and arrangement of plant parts also determines susceptibility to fire, which is higher at higher surface area-to-volume ratios: species showing finely divided leaves such as pines, grasses, and heaths, burn easily (Bond & van Wilgen 1996). As a consequence of all the above-mentioned, fires in Mediterranean regions are usually of moderate to high intensity, and consume all above-ground plant biomass and part of soil organic layers.

The term *fire regime* integrates several concepts related to temporal and spatial patterns of fire occurrence in a particular area, and also to its ecological effects. It was coined by Gill (1975), who also proposed four main components: intensity, extent, frequency, and seasonality. *Fire intensity* is determined both by maximum temperatures achieved and their time of residence, and is related to *fire severity* (White et al. 1996), the degree of damage caused to plants and soils. *Fire extent* alludes to the extent of burnt surface, whereas *fire seasonality* refers to the moment of the year in which the fire occurs. The use of the terminology related to temporal patterns of repeated fire occurrence has been particularly confusing: *fire frequency* has been applied both for stand-scale and regional-scale studies, as the mean number of fire events occurred along a certain time period, or also as the mean time length passing for the occurrence of a fire, which would be more accurately expressed as *average fire interval* (*sensu* Johnson 1992). The term *fire recurrence* has recently been proposed to avoid such ambiguity, and has been defined as accounting for the fires iterated in a geographic unit (Díaz-Delgado et al. 2004a). It alludes specifically to the number of fire events that have occurred at a certain site along a given time period, and is thus related to *fire interval* (Fox & Fox 1987), the elapsed time between two consecutive fires at a geographical location. *Fire period* (*sensu* Fox & Fox 1987) has been sometimes equaled to average fire interval, and more commonly to *fire cycle* (*sensu* Johnson 1992, and Johnson & Gutsell 1994), the length of time required for a certain surface to burn. Lastly, *fire history* (Fox & Fox 1987) summarizes to a greater extent fire occurrence in a place.

The idea that Mediterranean-type ecosystems are resilient to fire has been upheld for long on fire ecology literature (Trabaud & Lepart 1980; Kazanis & Arianoutsou 2002). *Resilience* is understood as the pace, manner, and degree of recovery of an ecosystem following disturbance (Westman 1986). The earliest approaches to the study of fire effects on vegetation revealed that Mediterranean plant species are able to survive fire or to reestablish after it. Hanes (1971) coined the term *autosuccession* to refer to post-fire vegetation succession in Californian chaparral, alluding to the fact that a serial substitution of communities was not observed, but rather a community that succeeded itself, characterized by the same species pool that it had immediately prior to disturbance. Two main post-fire regenerative strategies of plant species allow for such community recovery: o*bligate seeder species* are killed by fire and depend on seed reserves to recover populations, whereas *sprouter species* loose their aboveground phytomass and recover vegetatively from underground organs. Sprouter species were further subdivided into nonseeders and seeders (Zedler 1981), relying on whether they also show a fire-induced seeder strategy. Fire-induced recruitment of resprouters is very rare in the Mediterranean Basin, where most species either establish seedlings or resprout after fire, while it occurs in dominant species of other Mediterranean regions, such as Adenostoma fasciculatum in southern California chaparral.

Currently, fire regime characteristics are known to set limits to vegetation resilience, and are considered to largely determine vegetation dynamics in the Mediterranean Basin. High fire intensity or high fire severity can reduce regrowth ability of resprouter species (Lloret & López-Soria 1993) and seed viability of seeder species (Herranz et al. 1999), and usually enhance soil erosion (Giovannini et al. 2001; de Luís et al. 2003). Thus, it has been observed to negatively affect vegetation recovery (Moreno & Oechel 1994; Díaz-Delgado et al. 2003). High fire extent can impede arrival of seeds from unburnt sites to most of burnt surface, and thus negatively affect regeneration of seeder species (Rodrigo et al. 2004). Fire seasonality can diminish regrowth of resprouter species, if fire occurs when the levels of stored resources are low (Trabaud 1992; Cruz & Moreno 2001), and can prevent regeneration of seeder species, if fire occurs when seed banks have not yet been replenished (Domínguez et al. 2002) or when seeds have already germinated (Rodrigo et al. 2004).

A major concern of fire ecology in Mediterranean-type ecosystems remains to deal with fire frequency, or, more properly, with the effects on vegetation resilience of fire repetition and the time intervals at which it occurs. Mediterranean vegetation is thought to be able to recover when a certain time interval is allowed between fires, along which seeder species accumulate a sufficient seed bank and resprouter species replenish their underground reserves (Keeley 1986; Zammit 1988; Canadell & López-Soria 1998). However, relevant compositional and structural shifts could occur if fire intervals are particularly short (Zedler et al. 1983; Keeley et al. 1989). It has also been suggested that Fire repetition at short fire intervals may result in long-term cumulative effects on some ecosystem properties such nutrient cycling, and productivity, when nutrient losses exceed the rate of replacement by natural processes between consecutive fires (Carter & Foster 2004). Consequently, field studies addressing fire recurrence effects on plants and soils and considering the sequence and sum of fire events are required to gain further acknowledgement on resilience limits of Mediterranean-type ecosystems.

1.2. Fire Regime Characteristics in the Mediterranean Basin

In the Mediterranean Basin, natural fires are thought to have been occasionally present since the early Pleistocene, and to have significantly increased with the Mediterranean climate prevailing along the Holocene (Naveh 1999; Jalut et al. 2000; Carrión 2002). Moreover, man has been modifying its landscapes for more than 50,000 years (Naveh & Dann 1973), and using fire to facilitate hunting and gathering, to domesticate agricultural plants and to manage vegetation, particularly since the mid-Holocene (Naveh 1999; Quilès et al. 2002). Overall, it seems that burning was low in the western Mediterranean Basin during the early Holocene, and that humans became a major driver of fire occurrence 2,000 years ago (Carcaillet et al. 2002). Since then, many cultures have appeared and evolved, and have transformed landscapes by lighting fires, cutting, grazing, clearing, terracing, cultivating and abandoning arable lands (Naveh 1974, Pausas & Vallejo 1999). Thus, the disturbance regime has been long and intense in relation to other Mediterranean areas (Fox & Fox 1986).

Recent Fire Regimes

The study of recent fire regimes, mainly conducted through Landsat imagery and official fire databases extending up to middle 20th century, has revealed a general increase in fire recurrence and, in some areas, also in total burnt surface. Main factors involved are demographic patterns implying land-use changes, increasing climatic fire risk, and fire management policies.

In European countries of the Mediterranean Basin, such as Greece, Italy, Spain, and Portugal, an increase in the number of fires and in burnt surface has been observed along the last decades (Kaidilis 1992; Leone 1993; Baptista 1993; Xanthopoulos 1995; Vélez 1997; Moreno et al. 1998). In some Asiatic and African countries of the Mediterranean Basin, such as Turkey or Algeria, only the number of fires has been observed to increase (Anonymous 1993; Serez 1995). However, in the last 10 years the number of fires seems to have stabilized in Greece, Italy, Spain, and Portugal, and also in France and Morocco (Lloret et al. *in press*). Human demographic patterns and land-use changes, which differ among northern and southern areas, partly explain the observed shifts in fire regimes (Blondel & Aronson 1995). In southern areas, traditional land-uses remain to be the major socio-economic system, and growing populations are reducing forests and shrublands by overgrazing and extending arable lands. Contrastingly, in northern areas, the industrial development involved depopulation of rural areas and abandonment of crops, grazing lands and exploited forests (LeHouérou 1993). Subsequent afforestation processes have resulted in higher and more continuous fuel loads (Rego 1992), thus generating a trend of landscape homogenization that enhances fire occurrence (Lloret et al. 2002). Moreover, rural areas are being developed as suburbia or for vacation residence, which does not involve the recovery of traditional land management, but rather place humans as igniters near woodlands and shrublands.

Fire occurrence shows a strong correlation with certain meteorological variables, mainly related to precipitation and temperature (Vázquez & Moreno 1993; Viegas & Viegas 1994; Vázquez et al. 2002). Thus, lightning fires occur mostly along the warm and dry season, when temperature is high, and air humidity and fuel moisture are low (Vázquez & Moreno 1998). In the eastern Iberian Peninsula, the analysis of recent climatic trends has revealed the existence of an increasing climatic fire risk (Piñol et al. 1998; de Luís et al. 2001; Pausas 2004). The main detected climatic changes are temperature increases of around 0.30 °C per decade when only the second half of the 20_{th} century is considered, and of around 0.10 °C per decade when the whole century is considered (Piñol et al. 1998; Pausas 2004). Precipitation trends are less clear, since Mediterranean-climate regions are characterized by a high interannual variability of rainfall. However, a reduction in total rainfall and an increase in monthly rainfall concentration have been observed in València over the last 3 decades (de Luís et al. 2001). In Catalonia, the mean values of fire hazard indices (ICONA 1988; Carrega 1991) for the summer months increased by considering only temperature increases. The number of very high fire risk days also increased, and was proved to show a significant correlation with the number and area of wildfires (Piñol et al. 1998).

In southern California shrublands, fire suppression policies have been attributed to cause an increase in the extent and intensity of wildfires, through allowing the accumulation of continuous fuel beds constituted by high proportions of dead plant material. In order to avoid catastrophic wildfires, prescribed fires have been recommended as a suitable fuel management tool that allows generating a mosaic-like landscape (Minnich 1983, 1987, 2001). Such contention is part of an ongoing debate regarding shifts in recent fire regimes, main factors driving fire occurrence, and appropriate fire management tools. Alternatively, Keeley et al.'s contention (Keeley et al. 1999a, 2001; Moritz et al. 2004) is that the most catastrophic wildfires occur during particularly adverse climatic conditions, so they are not strictly dependent on fuel build-up. Consequently, prescribed fires are considered useful to manage exclusively certain strategic locations, namely the urban-wildland interface. These authors have reported similar shifts in fire regimes to those in the Mediterranean Basin: an increase in fire frequency and in total burnt surface along the 20th century, attributable to growing human populations and to land-use changes.

The prevalent fire management strategy in the Iberian Peninsula is fire suppression, despite prescribed fires are currently in progress. A recent model applied to northeastern Spain and central Portugal (Piñol et al. 2005) predicts that fire suppression would slightly enhance the dominance of large fires, whereas prescribed fires would greatly reduce their occurrence. However, total burnt surface would not vary as a consequence of extinguishing fires or using prescribed burns. A study on recent fire regimes in Catalonia supports the idea that ignition risk increases with forest stand age, but emphasizes that a plateau is rapidly reached: P.halepensis-dominated communities are developed enough after 15-16 years to undergo a new fire irrespective of the continuous increase in fuel loads, and the same can be stated for shrublands (Díaz-Delgado et al. 2004a). Accordingly, a recent model developed to test the fuel-driven and weather-driven hypotheses and applied to some particular areas of Catalonia did not support the fuel-driven assumption, and did not reject the null hypotheses of independence from previous fires (Salvador et al. 2005).

An important fact about the reported increase in fire recurrence is that fires are not randomly distributed: vegetation, climate, topography, and human activity determine their spatial pattern (Vázquez & Moreno 2001; Mouillot et al. 2003; Díaz-Delgado 2004b). Lightning fires are commonly clustered in certain geographical locations and show smaller maximum sizes than human-ignited fires (Vázquez & Moreno 1998). However, most current fires are human-ignited. In Spain, human action has accounted for 97% of the total number of fires and for 92.5% of the total burnt surface along the last quarter of the 20th century (Moreno et al. 1998). In Catalonia, human action has accounted for about 70% of summer fires and more than 80% of all year-long fires along the last decade (Departament de Medi Ambient i Habitatge, 2005). Thus, spatial patterns of fire occurrence are strongly determined by humans. Along the last quarter of the 20th century, 14% of the surface of Catalonia (32,000 km^2 extent), was burnt. Noticeably, fire recurrence was high, and 12% of the burnt area experienced at least one additional fire along the same time period. Recurrence was extremely high on some northern coastal areas, which were burnt at fire intervals shorter than 4 years (Díaz-Delgado et al. 2001, 2004a, 2004b).

Predictions on Future Fire Occurrence

Mediterranean regions are transitional climatic zones between the tropical and temperate ones, where it has been hypothesized that climatic changes may have the greatest effects (Lavorel et al. 1998). In the Mediterranean Basin, future climatic scenarios based on General Circulation Models predict summer temperature increases, namely warmer and drier conditions for vegetation (Kattenberg et al. 1996; Houghton et al. 2001). Despite there is no clear agreement in predictions on future precipitation trends, an increase in rainfall variability is expected, which may prolong and intensify summer drought, and also enhance the occurrence of intense rainfall events (Palutikof 1996).

Under such scenario, shifts in fire regimes involving higher fire occurrence and larger and more intense fires are expected (Piñol et al. 1998; Houghton et al. 2001). Shifts in fire regimes are thought to be capable of overshadowing direct effects of climatic changes on plant communities (Flannigan et al. 2000; McKenzie et al. 2003). In particular, fire recurrence has been suggested to be a major factor in determining future composition and structure of plant communities: simulation approaches combining scenarios of climatic change and functional models of vegetation dynamics predict shortened fire intervals that would lead to shrub-dominated landscapes (Mouillot et al. 2002).

Furthermore, major changes in vegetation may result in feedbacks on both climatic and fire regimes (Flannigan et al. 2000). For instance, enhanced CO_2 levels together with enhanced temperature could lead to changes in species composition, and thus in fuel loads and characteristics, which in turn would condition fire ignition and spread. In Catalonia, the existence of a positive feedback between increased fire recurrence at short fire intervals and the abundance of the invader Ampelodesmos mauritanica -a large, evergreen, resprouting tussock grass- has already been pointed (Grigulis et al. 2005).

1.3. Summary: Why Addressing Fire Recurrence Effects on Mediterranean Vegetation

Mediterranean-type ecosystems are considered to be resilient to fire, given both that fire has played a major ecological role in Mediterranean-climate regions for thousands of years, and that Mediterranean plant communities have been observed to recover pre-fire composition and structure in few years. However, fire regime characteristics such as intensity, extent, or seasonality strongly condition the ability of Mediterranean plant communities to recover. Particularly important are temporal patterns of fire occurrence, namely fire recurrence and the time intervals at which it occurs, since they may result in cumulative and deleterious effects on some ecosystem properties, such as vegetation regeneration, nutrient cycling and productivity. The natural temporal patterns of fire occurrence under which plant communities of the Mediterranean Basin were constituted is unknown, given that human-caused disturbance regime has been long and intense. Currently, most fires are not lightning-ignited, but human-ignited. Thus, temporal and spatial patterns of fire occurrence are strongly conditioned by human action. Fire occurrence has increased along the last decades of the century, both due to climatic shifts involving higher temperatures, and to human factors, including fire management policies and land-use changes. Consequently, very high fire recurrence levels are observed at some areas. Moreover, fire occurrence is expected to result further enhanced under predicted future climatic scenarios. Consequently, a new challenge for fire ecology is dealing with vegetation regeneration patterns not only after the occurrence of a fire, but as resulting from a particular sequence and sum of fire events.

1.4. Study Aim

I aimed to specifically address fire recurrence effects on Mediterranean vegetation regeneration. Consequently, I aimed to compare vegetation-related variables between sites which shared very similar environmental conditions, and which differed mainly in the number of fire events that had suffered along a certain time period.

Moreover, I hypothesized that fire recurrence may exert a control on composition and structure of plant communities, on structure and mass of soil organic horizons, and on population parameters and growth of some particular plant species. Thus, I considered a range of environmental conditions, including varying substrate types, and varying topographic and climatic conditions.

Consequently, I surveyed many study sites distributed over a large surface of Catalonia, such that every study site was conformed by two similar and nearby-located areas that had suffered a common last fire, but that differed in fire recurrence level along two decades.

1.5. Overview

The present work has addressed the effects of fire recurrence on post-fire regeneration of P.halepensis communities 8 to 11 years after fire.

The design was conceived to comparatively and synchronically assess fire recurrence effects at areas burnt once and twice along two decades. Once-burnt areas had not been burnt along at least 19 years, and twice-burnt areas showed fire intervals ranging from 1 to 16 years.

A total of 28 study sites placed over the range of distribution of P.halepensis communities in Catalonia were surveyed. Every study site was conformed by an area burnt once and an area burnt twice. Such areas were paired; they were located nearby, shared similar climatic and geomorphic conditions, and had been affected by the same last fire in 1994.

The aim of the study was to assess whether recent fire history (the occurrence of one *versus* two fires from 1975) resulted in common patterns of vegetation regeneration and soil organic horizons recovery throughout a range of climatic and geomorphic conditions.

Fire recurrence effects were addressed on:

Structural features of communities, by considering parameters such as height, cover, and fuel model (Chapter 3)

Floristic composition of communities, by considering parameters such as abundance, dominance, richness, diversity, and floristic similarity (Chapter 7)

Soil organic horizons, by considering parameters such as frequency, depth, dry mass, and nutrient contents (Chapter 4)

P.halepensis populations, by considering parameters such as density, height, diameter, radial growth patterns, and foliar nutrient contents (Chapter 6)

Plant growth of 3 common Mediterranean woody species, by considering parameters such as branch elongation, basal area increment, and foliar nutrient contents (Chapter 5)

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Chapter 2

Study Design and Study Site Characterization

2.1. Study Sites Selection

The study was conducted in Catalonia, a region 3,200,000 ha extent located on the northeastern Iberian Peninsula (Figure 1).

Figure 1. Location of Catalonia in the Mediterranean Basin.

Study sites were selected among areas that burnt for the last time in 1994. Such year has been considered as a turning point in the recent history of forest fires in Spain, since simultaneous and widespread very large fires occurred, favored by high summer temperatures and severe drought (Moreno et al. 1998). More than 400,000 ha were burnt, one of the highest yearly burnt surface along more than 3 decades, since there are good fire records (Anonymous 1995). In Catalonia, 1,217 fires occurred, which burnt more than 75,000 ha of forested surface. Noticeably, a single catastrophic wildfire accounted for more than 50% of total burnt surface: 39,000 ha (DARP 1999).

I worked on Mediterranean communities dominated by the seeder tree Pinus halepensis Mill. (Aleppo pine). Pine-dominated ecosystems constitute a main landscape feature in the Mediterranean Basin, where they cover more than 25% of forested surface (Barbéro et al. 1998). P.halepensis is the most abundant pine species in the western Basin, where it occupies 2.5 million ha (Quézel 2000). Moreover, pine forests have been reported to be more prone to burn than other vegetation types in Catalonia, since they are distributed under drier Mediterranean conditions (Díaz-Delgado et al. 2004b) (Figure 2).

Study sites were selected by conducting spatial analysis on digital maps. The Geographical Information System (GIS) MiraMon was used (Pons 1994-2006). Fire history and dominant vegetation maps were considered, which covered the period 1975-1995, and about 70% of the surface of Catalonia (except for the west end of Pyrenees Mountains). Such maps had been generated by R Díaz-Delgado along his PhD Thesis (see Díaz-Delgado & Pons 2001, Díaz-Delgado et al. 2004a, 2004b).

Figure 2. P.halepensis forests in southern Catalonia, at an area characterized by average temperatures of 13.8°C and annual precipitation of 680 mm (view to the northwest from Serra de Montalt, Ribera d'Ebre).

Fire History Maps

Fire history maps consisted of annual vector-structured maps showing fires larger than 30 ha that occurred during a particular year, and a vector-structured map plotting all fires larger than 30 ha that occurred between 1975 and 1995, which provided the level of fire recurrence along such period. Mapped fires were linked to an attribute table where ancillary data were stored, such as fire date, fire extent, fire perimeter, and affected municipalities. Thus, the map on fire recurrence allowed accessing such information for every fire that occurred at a certain geographical location along 1975-1995.

Fire history maps were generated by applying a semiautomatic methodology for mapping fire scars larger than 30 ha by subtracting consecutive NDVI (Normalized Difference Vegetation Index) images of Landsat MSS (Salvador et al. 2000). NDVI is a vegetation index that maximises the spectral vegetation response by showing high values in areas with dense vegetation cover. Thus, subtraction of consecutive temporal images yields negative values of large magnitudes in burnt areas. Moreover, fire history maps were completed by means of pre-existing cartography:

- fire cartography for 1994 and 1995, elaborated by the Institut Cartogràfic de Catalunya (ICC) through the use of CASI sensor and images from the satellites Landsat TM and SPOT, and supplied by Departament de Medi Ambient (DMA).
- fire cartography for 1986-1990: Mapa d'incendis forestals de Catalunya 1:500,000 (ICC 1992). It allowed including 14 additional fires, either not detected or out of the original study area.
- other thematic cartography, such as the Coordination of Information on the Environment (CORINE) map 1:250,000 (ICC 1991), and two Mapa d'usos del sòl de Catalunya 1:250,000 (ICC 1987, 1993). They provided 16 new fire patches not formerly detected.

Dominant Vegetation Maps

Dominant vegetation maps consisted of annual raster maps where dominant plant species or land cover present before the annual fires were mapped. Such maps were digitized over the source maps: Mapa de Cultivos y Aprovechamientos 1:50,000 (MAPA 1980) for years 1975 to 1985, and Mapa Forestal de Catalunya 1:100,000 (DARP 1996) for years 1986 to 1995.

Study Sites Identification

GIS layers showing fires occurred during 1994, fire recurrence level of 1 and 2 fires along 1975-1995, and P.halepensis as dominant plant species or land cover were isolated and overlaid. Spatial analysis was conducted to identify areas that met the following criteria: (1) dominated by P.halepensis before 1994 and burnt just in 1994; (2) dominated by P.halepensis before 1994 and burnt twice along 1975-1995, firstly between 1975 and 1993, and secondly in 1994. A total number of 30 study sites were defined by including adjacent areas burnt once and twice along 1975-1995, and both of them burnt by the same 1994 fire. Since 2 study sites were rejected during the field work, a final total number of 28 study sites were considered (Figure 3).

A global positioning system (GPS) was used to locate once- and twice-burnt areas on the field. Additionally, they were also recognized according to the presence of the following field indicators of fire history: (1) areas burnt once contained abundant remaining burnt branches and trunks of P.halepensis, and skeletons of resprouter species, which indicated fuel accumulation for at least 19 years before the 1994 fire, and (2) areas burnt twice contained noticeably fewer remaining burnt branches, trunks, and skeletons, since a previous fire had occurred some years (between 1 and 16) before the 1994 fire. They also contained old, decomposing, charred stumps that had burnt during the first fire.

A stand *ca.* 1 ha extent was selected in every once- and twice-burnt area, in such a way that paired stands were located nearby, were as similar as possible in relation to topographic (elevation, slope, aspect, position on hillside) and substrate characteristics, and were separated by a buffer area of 10 to 60 m in order to avoid errors in the location of the transition. Central points of stands were located and positioned by means of a GPS (Table 1).

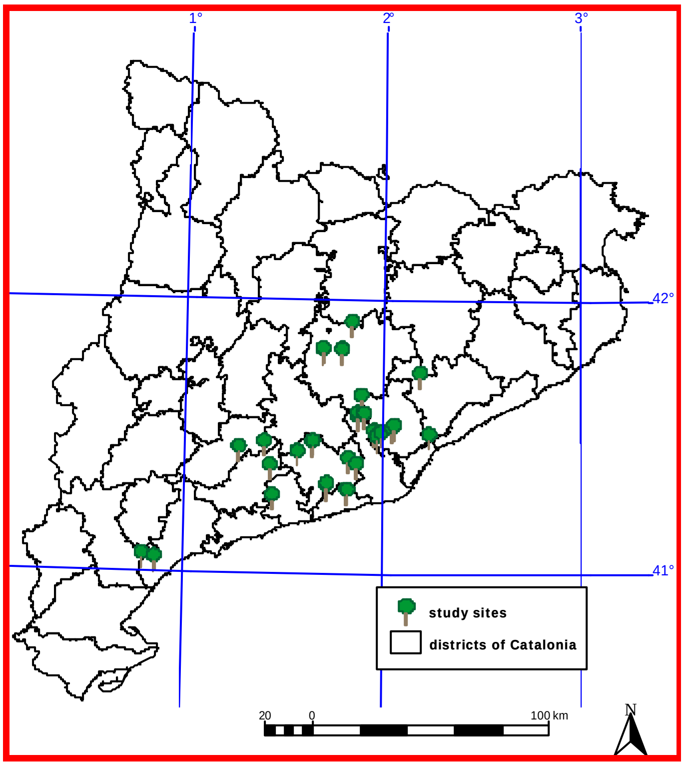

Figure 3. Location of study sites in Catalonia.

Study Site	**Municipality**	**District**	**UTM Coordinates**	
			Once-burnt	**Twice-burnt**
1	St. Quirze Safaja	Vallès Oriental	(0432093, 4619300)	(0432025, 4619306)
2	Tiana	Vallès Occidental	(0435882, 4594477)	(0435886, 4594509)
3	St. Quirze del Vallès	Vallès Occidental	(0420137, 4597203)	(0420418, 4597133)
4	St. Quirze del Vallès	Vallès Occidental	(0421130, 4598240)	(0421130, 4598274)
5	Rubí	Vallès Oriental	(0415664, 4595618)	(0415711, 4595330)
6	Ullastrell	Vallès Occidental	(0412718, 4596108)	(0412717, 4596165)
7	Castellbisbal	Vallès Occidental	(0413845, 4593965)	(0413779, 4593639)
9	Vacarisses	Vallès Occidental	(0408667, 4603201)	(0408306, 4603286)
10	Esparreguera	Baix Llobregat	(0405425, 4601920)	(0405327, 4601913)
11	Esparreguera	Baix Llobregat	(0405857, 4603435)	(0405978, 4603438)
12	Castellbell i el Vilar	Bages	(0407177, 4610430)	(0407313, 4610486)
13	Mediona	Baix Penedès	(0386543, 4591835)	(0386771, 4592049)
14	Mediona	Baix Penedès	(0386985, 4592157)	(0386993, 4592125)
15	Subirats	Alt Penedès	(0401825, 4585068)	(0401882, 4585018)
16	Subirats	Alt Penedès	(0404905, 4582792)	(0405131, 4582730)
17	Olivella	Garraf	(0400975, 4572358)	(0400881, 4572294)
18	Olivella	Garraf	(0401135, 4572089)	(0401328, 4572157)
19	Olèrdola	Alt Penedès	(0392355, 4574130)	(0392726, 4575015)
20	Torroelles de Foix	Alt Penedès	(0380358, 4588027)	(0380288, 4588086)
21	Sta. Perpètua de Gaià	Conca de Barberà	(0366493, 4592155)	(0366391, 4592142)
22	Querol	Alt Camp	(0368693, 4582589)	(0368629, 4582583)
24	La Bisbal del Penedès	Baix Penedès	(0369610, 4570280)	(0369710, 4570335)
25	Sarral	Conca de Barberà	(0355505, 4590150)	(0355758, 4590007)
26	Tivissa	Ribera d'Ebre	(0314713, 4546851)	(0314583, 4547065)
27	Pratdip	Baix Camp	(0319712, 4545637)	(0319842, 4545798)
28	Navàs	Bages	(0403162, 4640109)	(0402911, 4640061)
29	Callús	Bages	(0399323, 4629570)	(0399420, 4629254)
30	Sant Mateu de Bages	Bages	(0391274, 4620337)	(0391335, 4629795)

Table 1. Location characteristics of study sites. Note that study sites #8 and #23 do not exist: they were rejected along the field work.

2.3. Main Characteristics of Study Design

Regional Scale

The survey was not conducted at an only stand, but at several localities distributed over a large area.

Paired Design

Every study site was conformed by two study areas differing mainly in the number of fire events that had suffered along 1975-1994, since paired areas were selected to be:
(1) occupied by the same type of plant community,
(2) located nearby (thus sharing climatic conditions),
(3) as similar as possible in relation to geomorphic characteristics such as elevation, slope, aspect, position on hillside, and substrate, which are local factors strongly conditioning vegetation recovery (Díaz-Delgado et al. 2002),
(4) affected by the same last fire

Comparable Vegetation Successional Stages

Vegetation was at comparable successional stages in all stands, in order to avoid confusion between the pattern of changes over time since last fire and the pattern of changes generated by fire recurrence (Bond & van Wilgen 1996).

Medium-Term Effects of Fire

Survey was conducted between 8 and 11 years after the 1994 fires in order to avoid fire transient effects, namely those effects that are evidenced in the short term after fire and that last for time periods from some months to few years, such as higher availability of soil nutrients due to ash deposition (Hernández et al. 1997).

2.4. Study Site Characterization

Vegetation Characterization: P.halepensis communities

In Catalonia, approximately 60% of the total surface, i.e., 2,000,000 ha, is considered as *forested surface*, since it shows other than urban, industrial, or agricultural land-uses. However, only about 38%, i.e., 1,200,000 ha, is constituted by forests or woodlands, namely a tree species constitutes the dominant land cover. P.halepensis communities occupy a total of 239,092 ha, and are thus considered the most frequent forest type (estimations based on the number of forestry plots where P.halepensis constituted more than 50% of total basal area over a total of 10,644 plots distributed throughout the forested surface of the region. Surveyed was conducted between 1988 and 1998) (Figure 4). In particular, they constitute more than 90% of forested surface at districts such as el Garraf, el Tarragonès, el Baix Penedès, les Garrigues, la Ribera d'Ebre, el Segrià, and l'Alt Penedès (IEFC. Gracia et al. 2004).

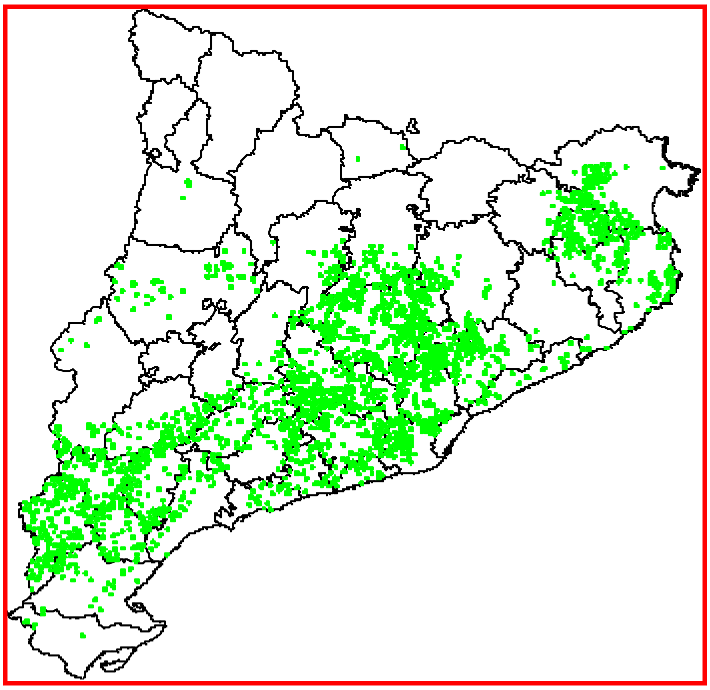

Figure 4. Forestry plots where P.halepensis was present in Catalonia (modified from www.creaf.uab.es/iefc/Introduccio/Especies/MapaPiBlanc.htm).

In Catalonia, P.halepensis is found from sea-level up to 1,000 m a.s.l., and both on calcareous and siliceous soils, despite sandy acidic soils are not suitable for it (Folch 1981). In a recent study dealing with determinants of distribution of pine species, spring rainfall lower than 190 mm allowed to predict 83% of the current distribution of P.halepensis in the region. Accuracy was improved to 92% by adding total rainfall (up to 830 mm) and minimum winter temperature (more than -1°C). However, geology and altitude were less useful (Rouget et al. 2001). Aleppo pine has expanded along the last century, both due to its widespread use in forestation programs and to its ability to colonize abandoned fields and grazing lands (Lepart & Debussche 1991; Barbéro et al. 1998).

In Catalonia, this species forms very homogeneous stands where it constitutes most of basal area. In 62% of forestry plots where it was present, it constituted more than 80% of basal area. Mean data for such type of stands at a regional level are: density around 700 pines$\cdot$ha^{-1}, basal area around 13 m$^{3}\cdot$ha^{-1}, and height around 11 m. Mean age of the 1,895 surveyed individuals was 42 years. However, territorial variability is high: wood production ranged between 1.5 m$^{3}\cdot$ha$^{-1}\cdot$any^{-1} and 5.5 m$^{3}\cdot$ha$^{-1}\cdot$any^{-1} (IEFC. Gracia et al. 2004). Biotic factors have been found to be important in predicting P.halepensis dominance: whereas it is excluded from dense stands of other pine species, it can be present in dense stands of oaks (Rouget et al. 2001). Where Aleppo pine is dominant, other common tree species are Quercus ilex, Arbutus unedo, Olea europaea, Ceratonia siliqua, Juniperus oxycedrus, and Phyllirea latifolia. P.halepensis communities usually show well-developed shrubby understoreys formed by species such as Pistacia lentiscus, Quercus coccifera, Rosmarinus officinalis, Ulex parviflorus, Rhamnus alaternus, Rhamnus lycioides, Cistus albidus, Cistus monspeliensis, Erica multiflora, or Genista scorpius. Widespread chamaephytes are Dorycnium pentaphyllum, Ononis natrix, Ononis spinosa, Polygala calcarea, Polygala rupestris, Fumana ericoides, Fumana thymifolia, or Helianthemum syriacum.

P.halepensis is a seeder and partially serotinous species that can both regenerate in the absence of fire and as a result of fire. Due to this dual strategy, it is not considered a fire-dependent species, but rather an opportunist species (Nathan & Ne'eman 2000). About 60% of the yearly seed crop is released in the absence of fire under dry and hot weather conditions (Daskalakou & Thanos 1996; Nathan et al. 1999). Subsequent seedling establishment occurs mainly in forest gaps or in adjacent, open sites, due to the shade-intolerant nature of the species (Broncano et al. 1999; Zavala et al. 2000). This and other traits such as early maturity, large seed crops, and good germination success enable P.halepensis to behave as an invader species (Thanos & Daskalakou 2000; Richardson 2000; Rouget et al. 2001). Moreover, it shows relatively efficient long-distance dispersal: despite only a small fraction of seeds (0.2%) reaches distances longer than 1 km, it is estimated that a small stand of 100 Aleppo pine individuals generates approximately one successful long-distance colonization event every year (Nathan & Ne'eman 2000). The rest of the yearly seed crop, about 40%, remains in the canopy within serotinous cones, and is thus added to a permanent and cumulative canopy seed bank. Seeds will be released when high fire temperatures force serotinous cones to open (Daskalakou & Thanos 1996). Post-fire regeneration of the species relies exclusively on such canopy seed bank, due both to the transient nature of the soil seed bank –seed viability is maintained for only around two years and seeds are submitted to high levels of predation- and to the destruction by fire of all seeds that are found on or near the soil surface (Daskalakou & Thanos 1996; Habrouk et al. 1999; Izhaki et al. 2000). Seed germination and seedling recruitment occur mostly shortly after the onset of the first post-fire rainy season in the resource-rich environment generated by the passage of fire, where light, space, and nutrients are largely available for plant recruits (Daskalakou & Thanos 2004).

Climatic Characterization

Study sites were characterized for temperature (annual, summer, and winter means), precipitation (annual and summer cumulative means) and real solar radiation. Temperature ranged from 12.9°C to 15°C (annual mean), 4.4°C to 8.7°C (winter mean), and 19.7°C to 22.9°C (summer mean); precipitation ranged from 523.9 mm to 772.4 mm (annual mean), and 105.5 mm to 185.1 mm (summer mean); and real solar radiation ranged from 9,950 kj·m^{-2}·d^{-1} to 16,170 kj·m^{-2}·d^{-1} (Table 2).

Study Site	**Mean Ann. Temp. (°C)**		**Mean Wint. Temp. (°C)**		**Mean Sum. Temp. (°C)**		**Ann. Cum. Precip. (mm)**		**Sum. Cum. Precip. (mm)**		**Mean Ann. RSR (Kj·m^{-2}·d^{-1})**	
	Once-burnt	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**
1	12.2	12.2	5.5	5.5	19.4	19.4	772.4	772.4	185.1	185.1	148.5	148.5
2	14.5	14.5	8.7	8.7	21.6	21.5	685.8	684.7	133.1	134.0	118.4	134.7
3	14.3	14.5	7.5	7.5	21.8	22.0	650.0	654.4	131.2	129.1	136.3	138.9
4	14.1	14.1	7.2	7.2	21.5	21.5	675.1	675.1	138.9	137.7	139.7	139.7
5	14.7	14.6	7.8	7.8	22.6	22.5	688.6	686.1	130.6	132.2	140.8	138.3
6	14.7	14.7	7.7	7.7	22.8	22.8	703.4	704.6	137.8	136.6	140.0	140.0
7	14.9	14.9	8.0	8.0	22.4	22.9	708.6	708.9	129.3	131.0	135.6	136.9
9	14.9	13.1	6.3	6.3	21.2	21.2	720.2	717.3	155.9	157.0	99.5	135.8
10	14.5	14.3	7.2	7.1	23.2	23.0	633.1	644.9	131.7	135.4	147.6	153.0
11	14.8	14.9	7.5	7.6	23.1	23.3	598.8	609.0	115.1	111.2	143.3	135.4
12	13.8	13.8	6.7	6.7	21.9	21.9	619.2	619.2	141.3	123.8	118.5	118.5
13	13.2	12.9	6.4	6.2	20.9	20.6	699.2	683.8	141.3	146.3	129.3	133.3
14	13.3	13.4	6.5	6.6	21.2	21.2	673.8	673.8	138.1	133.1	138.3	138.3
15	13.7	13.7	7.1	7.1	22.6	22.6	675.7	675.7	131.7	131.7	129.8	129.8
16	13.1	13.0	7.0	6.8	21.5	21.2	731.5	742.1	140.3	143.4	118.4	130.8
17	14.6	14.7	8.4	8.5	22.6	22.6	641.7	640.4	114.5	114.2	147.6	139.8
18	14.7	14.7	8.5	8.5	22.6	22.6	641.1	638.4	114.2	114.3	148.0	151.9
19	14.8	14.7	8.2	8.1	22.8	22.6	645.6	633.2	113.4	117.9	134.0	138.7
20	12.1	12.1	5.6	5.6	19.7	19.6	736.8	731.6	152.1	153.7	140.2	138.7
21	12.6	12.7	5.7	5.6	20.5	20.5	601.4	590.5	120.3	120.6	143.1	139.7
22	12.7	12.5	6.1	5.9	20.4	20.1	683.8	670.5	135.9	140.3	144.0	146.1
24	14.5	14.5	7.8	7.8	22.1	22.1	632.8	632.8	115.0	115.0	141.6	141.6
25	13.1	13.3	5.6	5.6	21.6	21.9	523.9	529.3	109.0	107.1	140.8	144.5
26	13.8	13.7	6.9	6.8	21.6	21.4	677.2	683.3	117.8	119.8	161.7	158.4
27	14.9	14.8	8.1	8.0	22.7	22.5	610.5	603.7	103.1	104.2	141.7	142.7
28	13.1	13.1	5.6	5.6	21.5	21.4	626.8	629.5	164.9	165.9	145.6	139.6
29	13.3	13.3	5.5	5.5	21.8	21.8	567.0	570.4	143.3	142.1	149.2	149.3
30	11.7	13.2	4.5	5.7	19.9	21.6	676.6	679.9	162.7	128.3	128.2	147.2

Table 2. Climatic characteristics of study sites. RSR= real solar radiation.

Such values were assigned to GPS-positioned central points of stands from Atles Climàtic Digital de Catalunya (Pons 1996; Ninyerola et al. 2000. http://magno.uab.es/atles-climatic), a collection of digital raster maps which display values of climatic variables for Catalonia with a 180-meter resolution. Temperature and precipitation maps display the values obtained from multiple regression analyses between meteorological data (covering the period 1950-1999) and geographical variables, afterwards corrected with residuals through GIS techniques. All profitable meteorological data were used, and final values of temperature and precipitation data were obtained from time series at least 20 year-long (Ninyerola et al. 2000). Real solar radiation reflects local levels of incoming solar radiation, and is a summarizing measure of factors such as latitude, altitude, and topography that has been considered a good indicator of site productivity in Mediterranean-type ecosystems (Safford & Harrison 2004). Real solar radiation maps display the values obtained by applying a model to calculate the incoming radiation on a 180-meter resolution Digital Elevation

Model. Final values of real solar radiation were obtained from time series at least 4 year-long (Pons 1996).

Geomorphic Characterization

Stands were characterized on the field for topography (altitude, aspect, slope, and position on hillside) and substrate (afterwards verified for GPS-positioned central points of stands from the digital Base Geològica 1:50,000 (ICC et al. 2002)). Elevation ranged from 156 m to 758 m, and slopes from 0° to 40°. About 90% of study sites were located on calcareous substrates. Most calcareous substrates (60%) were soft rocks (marls, clays, mudstones, argillites), and the rest were hard rocks (dolomites, limestones, conglomerates) (Table 3).

Study Site	**Elevation (m)**		**Slope (°)**		**Aspect (°)**		**Substrate Type**	
	Once-burnt	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**
1	677	657	15	20	230	220	marls	marls
2	233	230	25	15	150	140	granites	granites
3	259	273	15	25	230	220	clays	conglomerates
4	289	276	0	0	0	0	conglomerates	conglomerates
5	225	219	15	15	60	60	conglomerates	clays
6	247	252	0	0	0	0	clays	conglomerates
7	177	156	15	35	270	250	clays	clays
9	455	465	30	30	30	40	clays	argillites
10	275	285	40	40	180	170	argillites	limestones
11	192	239	30	25	270	280	clays	clays
12	270	273	30	15	350	220	argillites	conglomerates
13	555	502	15	15	20	10	dolomites	argillites
14	448	452	20	10	350	350	argillites	argillites
15	400	412	30	30	290	300	dolomites	dolomites
16	480	470	20	15	80	80	limestones	limestones
17	239	243	10	0	120	0	gravels	gravels
18	247	251	0	0	0	0	marls	marls
19	238	194	10	10	50	50	limestones	limestones
20	758	740	10	15	280	270	dolomites	dolomites
21	651	628	20	15	330	340	limestones	limestones
22	704	688	0	0	0	0	marls	marls
24	317	289	20	15	40	40	limestones	limestones
25	549	570	0	0	0	0	marls	marls
26	606	637	40	40	220	220	limestones	limestones
27	299	305	35	40	310	310	mudstones	mudstones
28	469	459	15	15	210	210	marls	marls
29	419	415	25	25	70	60	marls	marls
30	696	732	25	15	250	260	marls	gravels

Table 3. Geomorphic characteristics of study sites.

Fire Regime Characterization

Accurate spatial information on fire occurrence is not available in Catalonia previous to 1975. Basing on fire occurrence along 1975-1998, mean fire interval has been estimated in 23 to 42 years for surfaces between 8 and 80 km^2 (Díaz-Delgado et al. 2004a).

Fires considered in the present work ranged in extent from 11 ha to 6,191 ha (1975-1993 fires) and from 49 ha to 38,976 ha (1994 fires), and occurred mostly in summer (Díaz-Delgado & Pons 2001). Thus, fire interval in once-burnt areas was at least 19 year-long, and in many cases, field indicators -such as remnant burnt trees or surrounding, unburnt woodlands- suggested longer fire intervals. In twice-burnt areas, fire interval ranged from 1 to 16 years (Table 4).

Study Site	**1975-1993 Fire**			**1994 Fire**			**Fire Interval (y)**
	Extent (ha)	**Date**	**Season**	**Extent (ha)**	**Date**	**Season**	
1	434	1982	summer	2.692	04-07-94	summer	12
2	286	1982	unknown	914	10-08-94	summer	12
3	205	1982	unknown	346	04-07-94	summer	12
4	64	1991	unknown	346	04-07-94	summer	3
5	96	1982	unknown	1.388	04-07-94	summer	12
6	32	05-09-85	summer	1.388	04-07-94	summer	9
7	257	1991	unknown	1.388	04-07-94	summer	3
9	75	1981	unknown	3.165	04-07-94	summer	13
10	48	1986	unknown	3.165	04-07-94	summer	8
11	1.335	18-08-86	summer	3.165	04-07-94	summer	8
12	5.157	26-07-85	summer	335	22-08-94	summer	9
13	140	1978	unknown	406	10-08-94	summer	16
14	617	14-09-93	summer	406	10-08-94	summer	1
15	334	15-07-89	summer	70	07-04-94	spring	5
16	980	25-07-85	summer	83	02-07-94	summer	9
17	1.287	21-03-78	spring	4.594	09-04-94	spring	16
18	6.191	09-07-82	summer	4.594	09-04-94	spring	12
19	71	1984	autumn	1.153	04-07-94	summer	10
20	54	02-09-79	summer	159	20-07-94	summer	15
21	3.176	1981	unknown	261	10-04-94	spring	13
22	751	1978	unknown	49	18-09-94	summer	16
24	137	14-06-83	spring	1.360	02-04-94	spring	11
25	367	10-08-87	summer	448	27-07-94	summer	7
26	120	17-10-83	autumn	2.359	10-04-94	spring	9
27	4.073	11-12-81	winter	2.359	10-04-94	spring	13
28	1.078	01-08-83	summer	38.976	04-07-94	summer	11
29	619	28-07-83	summer	38.976	04-07-94	summer	11
30	11	08-07-93	summer	38.976	04-07-94	summer	1

Table 4. Fire regime characteristics at study sites.

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Chapter 3

Structural Features of Post-Fire *P.halepensis* communities: Height, Cover, and Fuel Models

Main contents of this chapter have been published as:
Eugenio M, Lloret F. 2004. Fire recurrence effects on the structure and composition of Mediterranean *Pinus halepensis* communities in Catalonia (northeast Iberian Peninsula). Écoscience, 11 (4): 446-454.

3.1. Introduction

A main theory of classic ecology is that vegetation succession is a deterministic process that leads to a final stage of maximum stability, in which plant communities are in equilibrium with environmental conditions, mainly climate (Clements 1916). Despite it has been criticized and modified along time, its importance in conforming traditional ecological acknowledgment has been enormous (Terradas 2001). After fire, Mediterranean communities were observed to do not undergo the serial substitution of communities described by Clements (1916), but rather to show the same pre-fire species pool (Hanes 1971). Other authors observed that the repeated occurrence of fire prevented vegetation from achieving such climax, and maintained it in which was named a *degradation stage* (Naveh 1974). Degradation stages were both characterized in terms of structural features and floristic composition. At them, structure was less developed and total biomass was lower than it could potentially be at the climax stage. In fact, fire recurrence was known from ancient times to result in important structural changes of plant communities, since men had been using fire for millennia to profitably manage vegetation.

Fire recurrence effects on phytomass production have been addressed in Q.coccifera (kermes oak) garrigues of the western Mediterranean Basin, and accord to reveal shifts in the structural features of such community. In southern France, Trabaud (1991) reported a decrease of biomass with increasing fire frequency which was mainly due to the lower production of woody species, given that herb phytomass increased. This fact was attributed to the depletion of Q.coccifera belowground carbohydrate reserves, since the regenerative capacity of the species was observed to be particularly low after autumn burns, when the proportion of carbohydrates contained in its root-system was lower. In eastern Spain, Delitti et al. (2005) underlined that the main effect of fire recurrence was a decrease in stem and total biomass of Q.coccifera, and in net primary production of garrigues, and attributed it to the dry climatic conditions of the region, which would reduce the regeneration capacity of kermes oak. Ferran et al. (2005), who addressed plant and soil nutrients at the same study sites, pointed to the depletion of Q.coccifera nutrient belowground reserves.

The likelihood of structural shifts in plant communities as resulting from high fire recurrence has also been pointed by a recent review on prescribed burning effects on pine forests of southern USA (Carter & Foster 2004), which has concluded that reduced nitrogen pools and lower annual aboveground net primary productivity (ANPP) may be the more significant long-term effects of repeated burning. Older works on prescribed burning effects on Eucalyptus forests and Pinus plantations in southwestern and eastern Australia, respectively, pointed that repeated losses of nitrogen and phosphorous due to periodic burning may accumulate and exceed inputs during inter-fire periods, which would affect ecosystem productivity and (O'Connell 1987; Maggs 1988).

In Catalonia, vegetation recovery after recurrent fires has been addressed at a landscape level through the use of Landsat imagery (Díaz-Delgado & Pons 2001; Díaz-Delgado et al. 2002). The NDVI (Normalized Difference Vegetation Index) exhibits a strong correlation with a number of vegetation characteristics, notably green biomass irrespective of plant species (Anderson et al. 1993; Duncan et al. 1993). In these studies, a slower NDVI recovery was observed after the second of two successive fires at fire intervals shorter than 11 years, implying a resilience loss that was detectable several years after fire. Moreover, green biomass after the second fire significantly increased at longer time intervals between fires, thus supporting the importance of vegetation regeneration after a given fire event in front of future disturbances (Díaz-Delgado et al. 2002).

3.2. Aim of the Chapter

The present study addresses structural features of post-fire P.halepensis communities in relation to fire recurrence. Since the study design comprises many and different study areas distributed throughout a large region, exhaustive techniques to assess vegetation structure or biomass production could not be used. Instead, two sound structural parameters providing an estimate on the vertical and horizontal structure of plant communities were selected: height and cover. Moreover, Rothermel's fuel models (Rothermel 1983), which both characterize vegetation structure and provide a rough estimate of fuel loads, were also attributed to every study area.

It is hypothesized that significant structural differences may exist between paired once- and twice-burnt areas several years after the last fire, as resulting from fire repetition at short fire intervals in twice-burnt areas. If fire recurrence exerts a control on vegetation regeneration, vegetation would be characterized by lower height, cover, and fuel loads in twice-burnt areas, and such pattern would be consistent throughout a variety of local environmental conditions. Furthermore, the existence of significant structural differences between paired areas may imply that fire recurrence affects floristic composition (Chapter 7), or relevant ecosystem processes such as nutrient cycling or primary productivity.

3.3. Methods

Field Survey

The survey was conducted at the 28 study sites and 8 years after the 1994 fire (Table 5).

Height Measures

? Height of herb, shrub and tree layers was visually estimated at the stand level.

Four transects 25 meter-long were placed perpendicularly to the slope in each stand. Along them, 1 m^2 quadrates were used as surveying units to record:

? estimated mean and maximum height of the overall community canopy,

? height of the tallest individual of P.halepensis, Quercus ilex (holm oak) and Quercus coccifera (kermes oak) present at the quadrate.

Cover Measures

? Cover percentage of herb, shrub and tree layers was visually estimated for the whole stand.

? Total plant cover was recorded in 15 randomly selected study sites by the point-interception sampling procedure, every 50 cm along transects.

Study Site	**Fire Interval (y)**	**Elevation (m)**		**Slope (°)**		**Aspect (°)**		**Substrate Type**	
		Once-burnt	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**
1	12	677	657	15	20	230	220	marls	marls
2	12	233	230	25	15	150	140	granites	granites
3	12	259	273	15	25	230	220	clays	conglomerates
4	3	289	276	0	0	0	0	conglomerates	conglomerates
5	12	225	219	15	15	60	60	conglomerates	clays
6	9	247	252	0	0	0	0	clays	conglomerates
7	3	177	156	15	35	270	250	clays	clays
9	13	455	465	30	30	30	40	clays	argillites
10	8	275	285	40	40	180	170	argillites	limestones
11	8	192	239	30	25	270	280	clays	clays
12	9	270	273	30	15	350	220	argillites	conglomerates
13	16	555	502	15	15	20	10	dolomites	argillites
14	1	448	452	20	10	350	350	argillites	argillites
15	5	400	412	30	30	290	300	dolomites	dolomites
16	9	480	470	20	15	80	80	limestones	limestones
17	16	239	243	10	0	120	0	gravels	gravels
18	12	247	251	0	0	0	0	marls	marls
19	10	238	194	10	10	50	50	limestones	limestones
20	15	758	740	10	15	280	270	dolomites	dolomites
21	13	651	628	20	15	330	340	limestones	limestones
22	16	704	688	0	0	0	0	marls	marls
24	11	317	289	20	15	40	40	limestones	limestones
25	7	549	570	0	0	0	0	marls	marls
26	9	606	637	40	40	220	220	limestones	limestones
27	13	299	305	35	40	310	310	mudstones	mudstones
28	11	469	459	15	15	210	210	marls	marls
29	11	419	415	25	25	70	60	marls	marls
30	1	696	732	25	15	250	260	marls	gravels

Table 5. Fire intervals and geomorphic characteristics of study sites. Note that #8 and #23 do not exist.

Fuel Models

Fuel models were visually assigned basing on field observations and photographic records by following the adaptation of Rothermel's types (Rothermel 1983) for the Spanish territory (ICONA 1987) and for Catalonia (IEFC. Gracia et al. 2004). Rothermel's fuel models characterize vegetation structure and provide a rough estimate of fuel loads. They are used as an approach to study fire propagation by USDA Forest Service, which considers 13 different fuel models classified in 4 groups: pastures, shrublands, litter under tree cover, and remains resulting from forest management practices. Within each group, respective models are based, among others, on vegetation structure (height and cover), flammability of main species, and fuel loads (dry, green, and fine). Clues to every model include a description and a set of pictures which help the assignment process (Figure 5). In the present survey, the photographic clues published for the main vegetation types in the Iberian Peninsula by ICONA (1987), and for the main vegetation types in Catalonia by IEFC (Gracia et al. 2004) were used; the stands surveyed corresponded to models 2, 4, 5, 6, and 7 (descriptions and photographic records in Appendix 1, pp. 61-70).

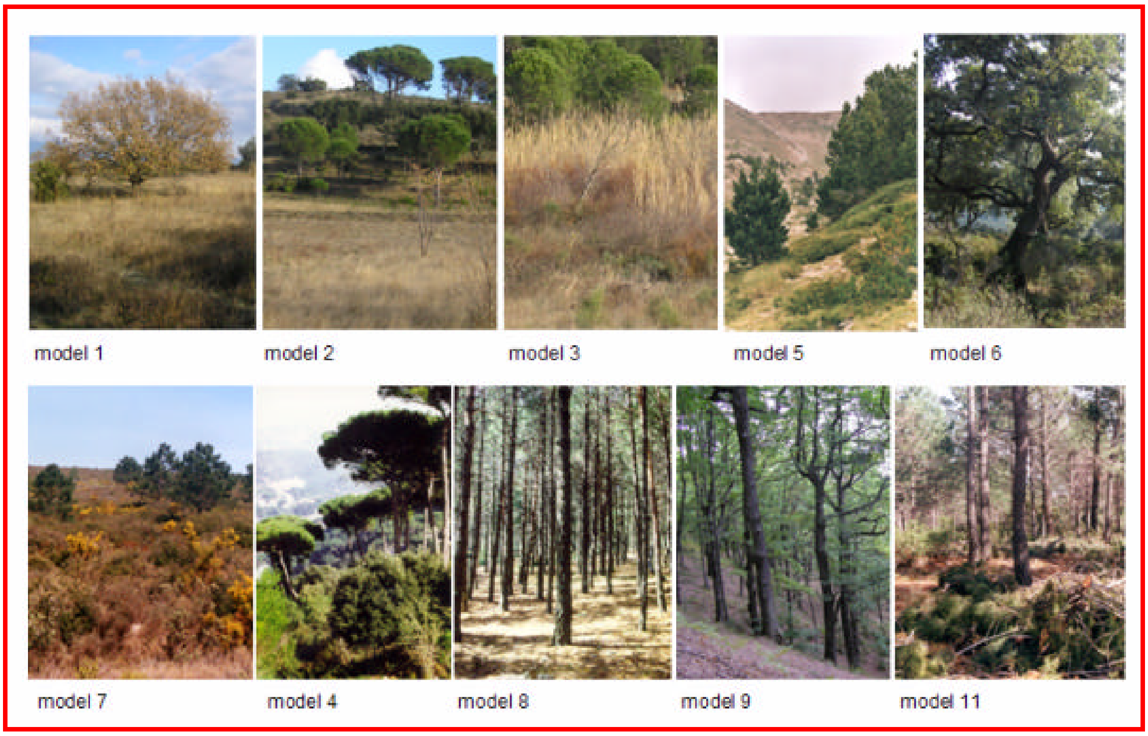

Figure 5. Photographic clues for the most common fuel models found in Catalonia. Models 1, 2, and 3 correspond to the group of pastures; models 5, 6, 7, and 4 correspond to the group of shrublands; models 8 and 9 correspond to the group of litter under tree cover, and are relatively similar to model 11, which corresponds to the group of remains resulting from forest management practices. Extracted from http://www.creaf.uab.es/iefc/Metodes/docs/I_aplicacions_modelscombus.htm.

Data Analyses

Fire Recurrence

Paired *t*-Student tests were performed to compare mean values of all height and cover measures between paired once- and twice-burnt stands. Whenever data did not meet the statistical assumptions required to perform such a test, nonparametric Wilcoxon rank tests were used. The sequential Bonferroni test (Holm 1979) was used to conduct simultaneous statistical inference; table-wide significance level was 5%.

A chi-square test was performed to analyze fuel model changes in relation to fire recurrence. Firstly, 3 fuel model categories were distinguished according to their corresponding fuel loads: (1) model 4 (25-35 t · ha^{-1}), (2) models 6 and 7 (10-15 t · ha^{-1}), and (3) models 2 and 5 (5-10 t · ha^{-1}) (Rothermel 1983). Afterwards, the number of cases in which fuel loads increased, decreased, or remained equal in twice-burnt stands in respect to paired once-burnt stands was calculated (observed values). Expected values were those obtained under a null hypothesis of no change after a second fire, namely, they were calculated assuming that the same proportion of areas was found in each category both after the first and the second fire.

Fire Interval

In order to test whether height and cover measures are correlated with the time interval between fires, simple linear regression models were performed. The dependent variables were mean and maximum canopy height, and total cover, which were considered both as: (1) values in twice-burnt areas, and (2) differences between paired areas ((once-burnt)-(twice-burnt)).

Climatic Variables: Precipitation, Temperature, and Real Solar Radiation

In order to test whether height and cover measures (mean and maximum canopy height; total cover) are correlated with climatic variables (temperature, precipitation, and real solar radiation), simple linear regression models were performed. Correlation was tested between: (1) differences in vegetation variables ((once-burnt)-(twice-burnt)) and mean value of climatic variables in paired areas, and (2) vegetation variables and climatic variables separately for once- and twice-burnt areas.

Substrate Type

Substrate type effect on total vegetation cover was tested by means of repeated measures ANOVA with fire recurrence as within-effect and substrate type (hard or soft) as between-effect on 12 study sites (total cover was recorded in 15 study sites, 12 of which showed the same substrate type in paired areas).

3.4. Results

Fire Recurrence

Significant differences between paired stands were found for all height measures Mean height of herb, shrub, and tree layers at the stand level; mean and maximum canopy height by quadrate; and height of the tallest individual of P.halepensis, Q.ilex and Q.coccifera by quadrate were significantly higher in once- than in paired twice-burnt areas (Figure 6) (Table 6).

Cover values (*arc sin* transformed) were also revealed to significantly differ between paired once- and twice-burnt stands (Figure 7) (Table 6). Total plant cover was significantly higher in once-burnt areas, and so were cover of herb layer and cover of tree layer. Only marginally significant differences were found in the cover of shrub layer, which was higher in twice-burnt areas.

				Once-burnt Stands		Twice-burnt Stands				
		Measure Unit	**n**	**Mean**	**SE**	**Mean**	**SE**	**test**	***t* / *Z* value**	***P* value**
Height Values (cm)	**Mean Canopy Height**	Quadrate	28	92.0	5.1	60.9	4.7	*t*-Student	6.33	<0.0001
	Maximum Canopy Height	Quadrate	28	137.2	5.2	100.8	5.4	*t*-Student	6.19	<0.0001
	Height of tallest P.halepensis	Quadrate	21	132.7	7.2	97.8	5.0	Wilcoxon	-3.22	0.001
	Height of tallest Q.ilex	Quadrate	10	171.7	9.7	140.6	8.5	Wilcoxon	-2.50	0.013
	Height of tallest Q.coccifera	Quadrate	18	93.3	4.7	78.2	4.3	Wilcoxon	-2.55	0.011
	Mean Height of Herb Layer	Stand	28	35.5	3.7	25.4	2.3	Wilcoxon	-2.51	0.012
	Mean Height of Shrub Layer	Stand	28	107.9	7.2	70.0	4.5	Wilcoxon	-4.28	<0.0001
	Mean Height of Tree Layer	Stand	28	149.6	7.3	92.0	17.4	Wilcoxon	-4.33	<0.0001
Cover Values (%) (*arc sin* transfor.)	**Mean Cover of Herb Layer**	Stand	28	43.8	4.6	33.2	4.7	*t*-Student	2.37	0.025
	Mean Cover of Shrub Layer	Stand	28	53.2	5.0	60.9	3.9	*t*-Student	-1.93	0.064
	Mean Cover of Tree Layer	Stand	28	32.9	4.2	13.4	3.0	Wilcoxon	-4.37	<0.0001
	Total Plant Cover	Transect	15	87.9	2.2	77.9	2.7	*t*-Student	3.69	0.002

Table 6. Summary of tests and results for height and cover values.

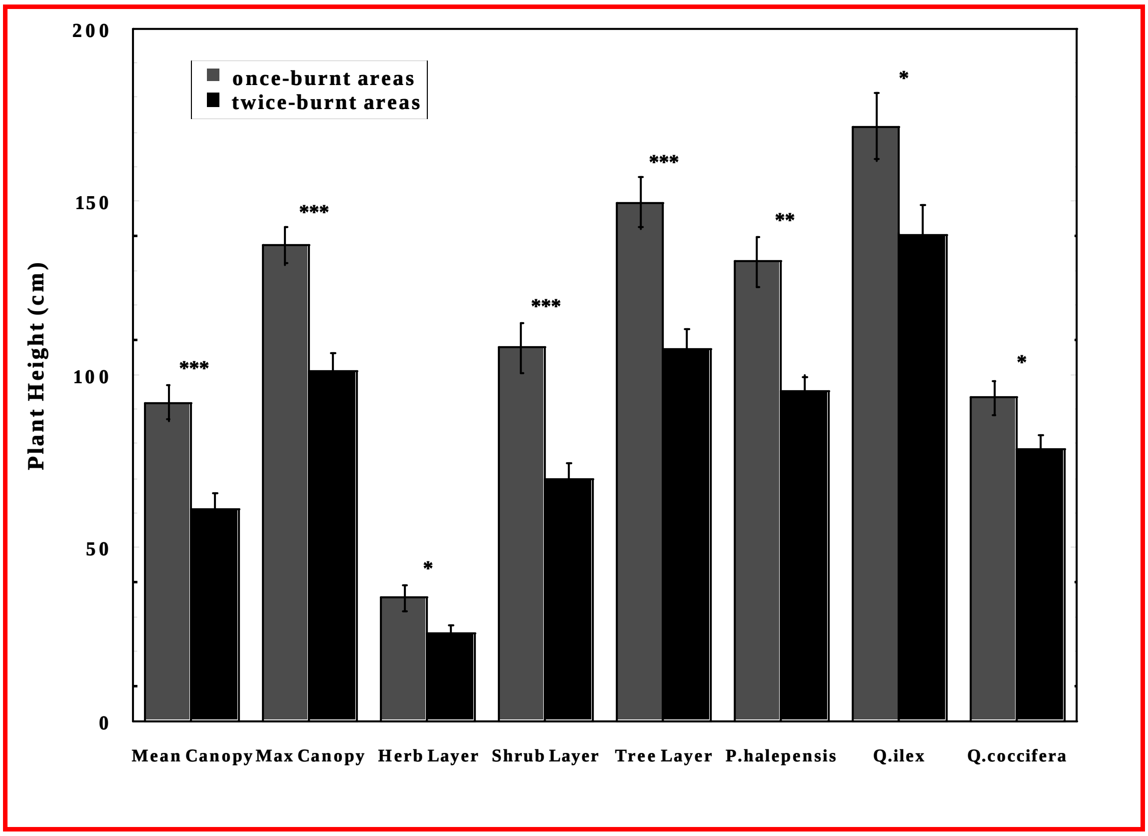

Figure 6. Height measures (± SE): mean and maximum canopy height by quadrate; mean height of herb, shrub and tree layers at the stand level; and height of the tallest individual of P.halepensis, Q.ilex and Q.coccifera by quadrate. Asterisks denote significance (*$P<0.05$, **$P<0.001$, ***$P<0.0001$) of differences between paired stands.

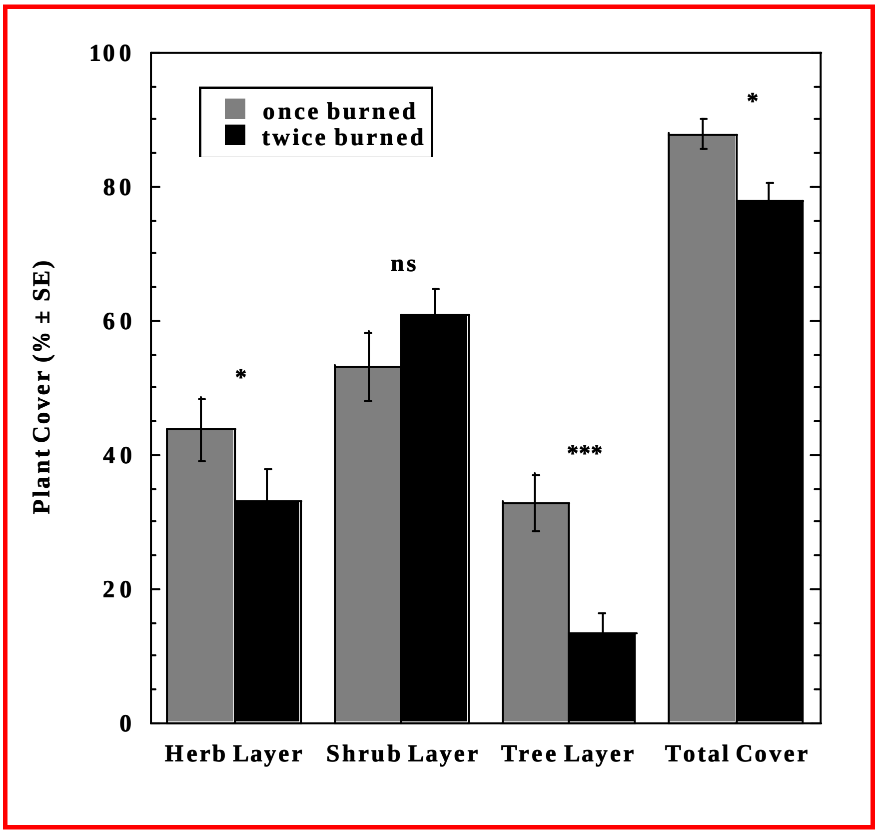

Figure 7. Estimated cover of herb, shrub, and tree layer at a stand level (n=28), and total plant cover as measured by the point-interception sampling procedure (n=15). Symbols above bars denote significance (ns= no significance, **P*<0.05, ***P*<0.001, ****P*<0.0001) of differences between paired stands.

Fuel Model Analysis

The pattern observed for changes in fuel models between paired areas was significantly different from that expected assuming a null hypothesis of no change in the proportion of cases corresponding to each of the 3 fuel load categories after the second fire ($?^? = 27.494$, $P < 0.0001$). After the second fire, half of the total study sites shifted to a model showing lower fuel loads and structural development, and the rest showed an equivalent model, whereas none of them shifted to a model showing higher fuel loads and structural development than after the first fire (Table 7).

	Same Fuel Load	**Lower Fuel Load**	**Higher Fuel Load**
Observed	14	14	0
Expected	19.36	4.32	4.32

Table 7. Frequency of changes in fuel models (categorized according to fuel loads) between paired once- and twice-burnt stands. Expected values were obtained assuming that the proportion of fuel loads categories found after one fire would remain constant after the second fire.

Fire Interval

A marginally significant, positive correlation was found between total cover in twice-burnt areas and fire interval (P = 0.052, R^2 = 0.26) (Figure 8). No significant correlations were found between height variables and fire intervals.

Climatic Variables: Precipitation, Temperature, and Real Solar Radiation

No significant correlations were found between vegetation variables (mean and maximum canopy height; total cover) and temperature, precipitation, or real solar radiation.

Substrate Type

No significant role of substrate type (hard or soft) was found on total cover. Repeated measures ANOVA revealed a significant role of fire recurrence (F = 9.13, P = 0.013), according to results obtained when comparing values of total cover between paired areas by means of a paired t-Student test.

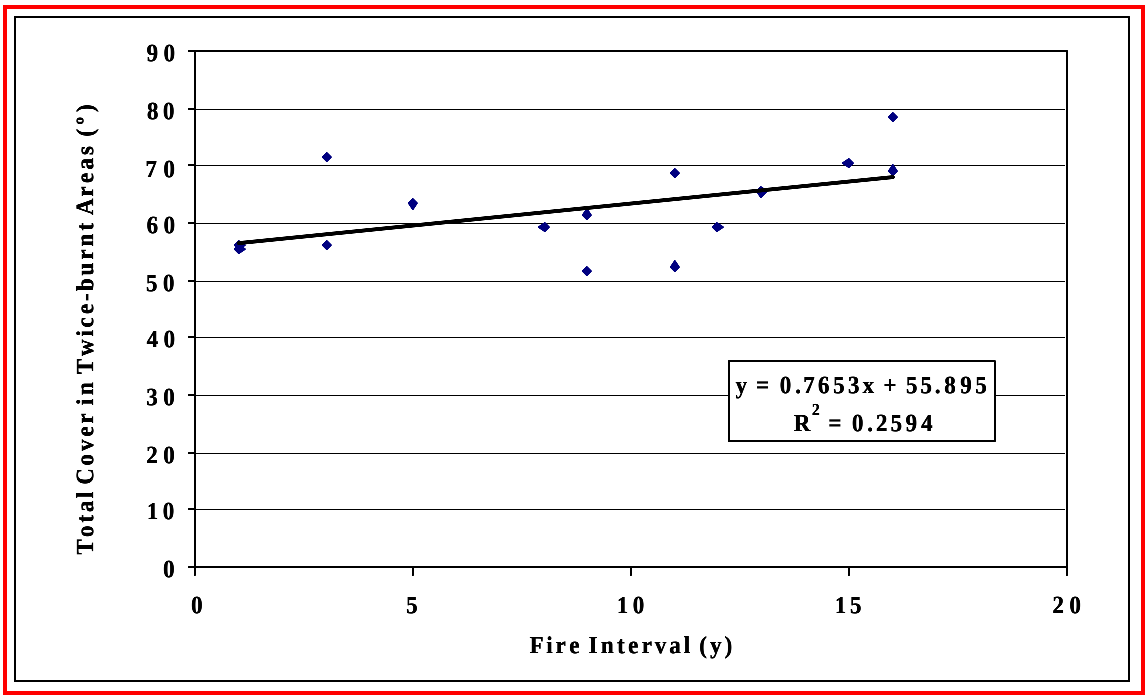

Figure 8. Marginally significant, positive correlation between total vegetation cover in twice-burnt areas (*arc sin* transformed) (°) and fire interval (years) (n = 15, $P = 0.052$).

3.5. Discussion

The occurrence of two fires along a 20 year-long period resulted in a structural simplification and in reduced biomass production of <u>P.halepensis</u> communities relative to the occurrence of a single fire along the same time period. Namely, 8 years after the last and common fire, areas that had been burnt only once showed higher mean and maximum vegetation height; higher mean height of herb, shrub, and tree layers; and higher total plant cover than paired areas burnt twice. Accordingly, half study sites shifted to fuel models characterized by lower fuel loads and less structural development after the second fire. Interestingly, total vegetation cover in twice-burnt areas relied on the time span between the two consecutive fires.

Such evidence agrees with previous hypotheses and observations on fire recurrence effects in Mediterranean communities. Overall, it supports the idea that repeated fires prevent vegetation to achieving a full structural development, thus reducing primary production (Naveh 1974). In particular, it confirms the loss of resilience observed in Mediterranean communities of Catalonia submitted to repeated fires by Díaz-Delgado et al. (2002). Such study was based on NDVI measures, which provide a rough estimation of green biomass, and considered the post-fire recovery of communities dominated both by resprouter trees (Quercus) and seeder trees (Pinus) *ca*. 6 years after the last fire; fire intervals in twice-burnt areas spanned 11 years as a maximum. It revealed that vegetation regrowth was lower after the second fire than after the first one, and that green biomass after the second fire significantly increased with longer fire intervals (Díaz-Delgado et al. 2002). Consequently, the present work makes such conclusions more specific; it provides field evidence on the loss of resilience experienced by Mediterranean communities dominated by the seeder P.halepensis and submitted to repeated fires at time intervals shorter than 17 years. Moreover, it shows that, the longer the time intervals between consecutive fires, the higher total vegetation cover.

The present work reports for the first time that a Mediterranean community dominated by a seeder tree species suffers similar structural and productivity changes to those observed in communities dominated by the resprouter shrub Q.coccifera (Trabaud 1991, 1992; Delitti et al. 2005). In both community types, fire recurrence enhanced smaller plant species characterized by shorter life cycles to the detriment of pre-fire dominant species: in P.halepensis communities, fire recurrence enhanced shrubs to the detriment of trees -as evidenced by their higher and lower cover in twice-burnt areas, respectively-, whereas in garrigues, fire recurrence enhanced subshrubs and herbs to the detriment of kermes oak (Trabaud 1992; Delitti et al. 2005). Furthermore, in garrigues, net primary production and Q.coccifera biomass decreased along with fire frequency, which was partly attributed to depletion of Q.coccifera underground reserves through consecutive resprouting (Trabaud 1991; Ferran et al. 2005). The structural and fuel load changes observed in P.halepensis communities also point to a decrease in biomass production due to fire recurrence. I suggest that other mechanisms than compositional changes could be underlying such pattern, such as pre-fire fuel load differences between paired areas resulting in different nutrient availability along the first post-fire years.

Fire causes an increase in the mobility and the availability of a variety of nutrients in the short-term, mainly due to direct mineral addition in ash (Christensen 1994): it was early observed that the use of fertilizers was ineffective after fire (DeBano & Conrad 1974), and that fire enhanced plant growth along some years (Christensen & Muller 1975). Nutrient increase rates are a function of fire temperature, and rely also on plant composition and soil type (Kutiel & Kutiel 1989; Kutiel & Shaviv 1992); a threshold is achieved at temperatures of 460 °C, over which fire effects on soil chemical and nutritional state are considered detrimental (Giovannini et al. 1989). Fire temperature, in turn, depends greatly on fuel loads and on vertical and horizontal distribution of fuel, among others (Whelan 1995). In this case, fuel loads and vertical and horizontal continuity of vegetation were likely higher in once- than in paired twice-burnt areas at the moment of the 1994 fire, since fire intervals had been longer in them and thus allowed further vegetation development. Consequently, higher pre-fire fuel loads would have resulted in higher post-fire nutrient availability in once-burnt areas than in twice-burnt areas, and thus in higher plant growth and biomass production along the first post-fire years. Previous work on P.halepensis post-fire regeneration supports this hypothesis: enhanced growth of pine seedlings has been observed near big burnt trees, where fire intensity and ash deposition are higher (Ne’eman et al. 1992; Ne’eman 1997), and at high fire severity sites, where post-fire soil nutrient availability was presumably higher, particularly of phosphorous (Pausas et al. 2003).

Furthermore, cumulative and deleterious effects of fire could have affected soils of twice-burnt areas, thus resulting in reduced chemical fertility. Fire generates direct nutrient losses by volatilization and ash convection, and thus, the repeated fire occurrence at short time intervals has been pointed as capable of generating depletion of soil nutrient reserves in the long term, particularly of nitrogen (O’Connell 1987; Maggs 1988; Carter & Foster 2004). Moreover, fire generates indirect nutrient losses by runoff, lixiviation, and erosion, particularly after rainfall events (Rubio et al. 1997; Giovannini et al. 2001; de Luís et al. 2003). In the eastern Iberian Peninsula, fires occur mostly in summer and are followed by autumn rains. Under such conditions, it has been suggested that indirect nutrient losses caused by fire could be more important that direct nutrient losses (Pausas & Vallejo 1999). In the present work, important cumulative nutrient losses directly resulting from fire repetition seem to be unlikely, given the scale considered (two fire events along 20 years). However, relevant nutrient losses resulting from repeated erosion events could have occurred in the short-term after fire, at least on certain soil types and locations.

Maximum height of 3 different species, the seeder P.halepensis, and the resprouters Q.ilex, and Q.coccifera, was reported to be lower in areas burnt twice than in paired areas burnt once. Regenerative strategies are closely tied with physiological attributes; thus, whereas resprouters store nutrients that use to regrow, seeders do not (Keeley 1998; Pausas 1999). Consequently, the lower height of Quercus sp. pl. in twice-burnt areas could be attributed to depletion of underground reserves through consecutive resprouting (Bowen & Pate 1993; Canadell & López-Soria 1998; Zammit 1998). However, other reasons should be adduced for the case of P.halepensis. The hypothesis of the existence of differences in growth between paired areas along the first post-fire years will be tested for the species through analyzing its radial growth patterns (Chapter 6).

Lastly, fire recurrence is thought to promote grasses and to reduce woody vegetation, particularly trees, in Mediterranean communities (Zedler et al. 1983; Trabaud 1991). In the present work, P.halepensis communities shifted to showing less developed structure and lower fuel loads after the occurrence of the second fire; moreover, tree cover was reduced and shrub cover increased, likely as a result of a competitive release. Such shifts in fuel characteristics and fuel loads may show feedbacks on fire regimes, in the sense of enhancing fire occurrence –unless horizontal continuity of fuel beds was broken- but at lower fire intensity. In that case, smaller species characterized by shorter life cycles, including grasses, would likely become more abundant (Trabaud 1991, 1992; Deliti et al. 2005). However, an increase in the cover of grass layer due to fire recurrence was not observed at the temporal scale considered.

3.5. Conclusions

The occurrence of two fires along two decades resulted in lower structural development and lower fuel loads of post-fire P.halepensis communities relative to the occurrence of a single fire. Eight years after fire, lower height and cover of vegetation, and fuel models characterized by lower fuel loads and less structural development evidenced such fact.

Consequently, a resilience loss is observed in P.halepensis communities submitted to fire recurrence levels of two fires at intervals shorter than 17 years.

Fire intervals played a significant role in determining total vegetation cover in areas burnt twice; the longer the time interval between consecutive fires, the higher the post-fire total vegetation cover in the medium term.

Reburning resulted in compositional changes, in the sense of reduced abundance of tree species, and enhanced abundance of shrub species. Herb species were not observed to be enhanced, as expected in MTEs. Such compositional changes caused, at least partly, the observed reduction of biomass production in areas burnt twice.

Moreover, other processes might have caused such pattern; in particular, pre-fire fuel load variability is hypothesized to influence post-fire plant growth in the short term after fire. Longer fire intervals would allow vegetation to further develop, and result in higher post-fire soil nutrient availability and biomass production in once-burnt areas. This hypothesis was supported by the fact that maximum height of the seeder P.halepensis was higher in them.

Additionally, the occurrence of repeated fires may promote soil nutrient deficits in soils, mainly through repeated erosion events, and thus negatively affect biomass production in the short-term after fire.

Lastly, reported shifts in fuel loads and characteristics may show positive feedbacks in fire regimes, thus enhancing fire occurrence at lower intensity.

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Chapter 4

Soil Organic Horizons: Frequency, Depth, Dry Mass and Nutrient Contents

Main contents of this chapter have been published as:
Eugenio M, Lloret F, Alcañiz JM. 2006. Regional patterns of fire recurrence effects on calcareous soils of Mediterranean *Pinus halepensis* communities. Forest Ecology and Management, 221: 313-318.

4.1. Introduction

Soils are a main factor in determining the distribution and productivity of plant communities. Thus, soil recovery after fire is of primary importance for the restoration of the ecosystem's components and functions. Fire shows effects on physical, chemical, and biological soil properties (Christensen 1994). Particularly, fire was early observed to strongly influence nutrient cycles, both through ash deposition, which fertilizes soils and enhances plant growth (DeBano & Conrad 1974; Christensen & Muller 1975), and through direct and indirect nutrient losses caused by volatilization, ash convection, and enhanced runoff, lixiviation, and erosion (DeBano & Conrad 1978; Raison et al. 1985). Studies dealing with fire effects on soils in the Mediterranean Basin have addressed short-term nutrient dynamics in mineral soils (Kutiel & Kutiel 1989; Carreira et al. 1997; Gimeno-García et al. 2000; Romanyà et al. 2001), post-fire formation of a water-repellent layer (Alcañiz et al. 1994), soil erosional responses after rainfall events (Rubio et al. 1997; Cerdà 1998; Andreu et al. 2001; De Luis et al. 2003; Pardini et al. 2004), recovery of organic horizons (Ferran & Vallejo 1992; Serrasolsas & Vallejo 1999), and depletion of microbial populations (Prodon et al. 1987; Dumontet et al. 1996; Hernández et al. 1997; Radea & Arianoutsou 2000). Such studies have been conducted after the occurrence of a single fire and at a local level.

However, fire effects on soils may be accumulated through consecutive fires, particularly when fire intervals do not allow the recovery of pre-fire conditions. On fire ecology literature, it has been repeatedly pointed that frequent fires may lead to cumulative nutrient losses, particularly of nitrogen and phosphorous, resulting in nutrient deficits in soils, and negatively affecting plant growth and primary production (Maggs 1988; O'Connell 1989; Carreira et al. 1996; Sardans 2004, 2005). Nutrients, together with water, are considered the main abiotic factors constraining plant growth in MTEs (Rundel 1982; McMaster et al. 1982; Witkowski et al. 1990). Thus, the existence of cumulative nutrient losses due to fire recurrence may have particularly relevant consequences on the structure and productivity of Mediterranean plant communities. The use of prescribed fires as a vegetation management tool has provided chances to observe the effects of fire repetition on soil properties, despite it is necessary to consider that prescribed fires are usually low-intensity fires conducted when fuel and soil moisture levels are moderate to high, and thus differ from wildfires, which are moderate to high-intensity fires that usually occur under particularly dry conditions. Early works on Pinus plantations and Eucalyptus forests in Australia pointed to the likeliness of cumulative nutrient losses, particularly of nitrogen, since lost nutrients might not be recovered during inter-fire periods (Maggs 1988; O'Connell 1989). A recent review on prescribed burning effects on pine forests of southeastern USA has emphasized that the main long-term effects of repeated fires may be a depletion of nitrogen pools and a reduction of the overall plant productivity (Carter & Foster 2004). In Mediterranean areas, direct nutrient losses caused by fire through volatilization and ash convection can be less important than indirect nutrient losses through runoff, lixiviation, and erosion, particularly when erosion is important (Pausas & Vallejo 1999). That is the case in the eastern Iberian Peninsula, where the fire season is followed by autumn, a rainfall season. Short and intense rainfall events have been observed to result in important losses of soil mass and soil nutrients (Rubio et al. 1997; Cerdà 1998; De Luis et al. 2003). Post-fire risk of soil erosion remains along the time required by vegetation to reach a critical value of projective cover that has been estimated in 30% (Thornes 1990).

Despite its potentially enormous ecological importance, few studies have specifically dealt with fire recurrence effects on soils in MTEs. Two studies have been conducted in the western Mediterranean Basin on hard calcareous substrates under Q.coccifera garrigues. Trabaud (1990) worked in southern France, and used spring and autumn prescribed fires every 2, 3, and 6 years to deal with the effects of fire frequency and fire season on soils. The experiment lasted for 19 years. Samples were collected from the first 5 cm of mineral soils at different times before and after fire occurrence. A decrease in organic carbon, a tendency towards the increase of available phosphorous, and no significant changes in total nitrogen or exchangeable potassium were observed. Ferran et al. (2005) have worked in València, and have considered the occurrence of 1, 2, and 3 wildfires along a 16 year-long period. Three and a half years after fire, soil organic horizons were not fully-recovered: despite L horizon masses were equivalent at all fire recurrence levels, F and H horizons were still not present. In relation to nutrient contents, no significant trend per surface unit was found either in organic horizons or in mineral soils. However, some site-dependent changes were observed: nitrogen concentration decreased in L horizons, and, at the first 0-2.5 cm of mineral soils, potentially mineralisable nitrogen increased and available phosphorous decreased.

Along the present work, twice-burnt areas have been observed to show less developed vegetation structure and lower fuel loads than once-burnt ones (Chapter 3); consequently, reconstruction of soil organic horizons may be delayed in them. During a fire, organic horizons can be partially or totally combusted, which mainly relies on fire temperatures, on their residence time, and on substrate characteristics (Ferran et al. 1992; Andreu et al. 1994). Upper horizons often result more intensely affected, whereas humiferous layers (H horizon) are only partially burnt, for instance when protected by a layer of superficial stones, as it occurs on limestones and schists (Ferran et al. 1992; Alcañiz et al. 1996; Serrasolsas & Vallejo 1999). Post-fire reconstruction of soil organic horizons relies basically on plant matter inputs to the remnant horizons. First inputs consist on dry or charred material; the incorporation of biggest burnt remains such as trunks occurs progressively and may take more than a decade (Mataix-Solera et al. 2002). Post-fire vegetation succession determines litter characteristics. In the first post-fire years, litter is mainly produced by herbs and subshrubs. As vegetation develops, the most quantitatively important inputs are produced by shrubs, and finally by trees (Ferran & Vallejo 1992). Furthermore, the reconstruction of H horizon relies also on the recovery of soil microorganism populations, which are responsible for litter decomposition. Post-fire recovery of soil biological activity has been estimated to require more than 20 years (Prodon et al. 1987), and the formation of humiferous layers is a slow processes that takes the order of several decades (Ferran & Vallejo 1992). Lastly, cumulative nutrient losses may have occurred as a consequence of repeated burning in twice-burnt areas, which might be evidenced in nutrient contents of mineral soils, foliar nutrient contents, plant growth, and overall productivity.

4.2. Aim of the Chapter

The present study addresses fire recurrence effects on soil organic horizons, and was conducted 9 years after fire in P.halepensis communities located on calcareous substrates. According to the general approach of my work (Chapter 2), soil organic horizons were surveyed synchronically in paired once- (in 1994) and twice- (once between 1978 and 1993, and again in 1994) burnt areas. Thus, I compared the selected variables between very similar areas differing mainly in their recent fire history.

The main question was whether the occurrence of two consecutive fires at time intervals equal or shorter than 16 years modified, relative to the occurrence of a single fire:

? the frequency of occurrence of soil organic horizons,
? the depth and dry masses of soil organic horizons,
? nutrient contents of soil organic horizons,

Moreover, I tested correlation between variables related to soil organic horizons (frequency of occurrence, dry masses), and fire interval, climatic factors (temperature, precipitation, real solar radiation), and substrate type.

Lastly, I aimed to characterize mineral soils in terms of nutrient contents, both to test their similarity in paired areas, and to estimate the ranges considered throughout the study area.

It is hypothesized that fire repetition may have resulted in a delayed reconstruction of soil organic horizons in twice-burnt areas relative to once-burnt ones, which would be observable several years after fire. If fire recurrence exerts a control on soil organic horizons recovery, those would be characterized by lower frequency, depth, and dry masses in twice-burnt areas. Moreover, such pattern would be consistent throughout a variety of local conditions.

4.3. Methods

Field survey

The survey was conducted 9 years after the 1994 fire at 15 randomly selected sites among those showing calcareous substrates (Table 8).

Study Site	**Fire Interval (y)**	**Elevation (m)**		**Slope (°)**		**Aspect (°)**		**Substrate Type**	
	Twice-burnt	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**
4	3	289	276	0	0	0	0	conglomerates	conglomerates
7	3	177	156	15	35	270	250	clays	clays
11	8	192	239	30	25	270	280	clays	clays
12	9	270	273	30	15	350	220	argillites	conglomerates
13	16	555	502	15	15	20	10	dolomites	argillites
14	1	448	452	20	10	350	350	argillites	argillites
15	5	400	412	30	30	290	300	dolomites	dolomites
18	12	247	251	0	0	0	0	marls	marls
20	15	758	740	10	15	280	270	dolomites	dolomites
21	13	651	628	20	15	330	340	limestones	limestones
22	16	704	688	0	0	0	0	marls	marls
26	9	615	637	25	40	260	220	mudstones	mudstones
28	11	493	485	0	0	0	0	marls	marls
29	11	419	415	25	25	70	60	marls	marls
30	1	696	732	25	15	250	260	marls	gravels

Table 8. Fire intervals and geomorphic characteristics of study sites considered for survey on soil organic horizons; all substrates were calcareous.

In each stand, 4 transects 25 meter-long were placed perpendicularly to the slope. The point-interception sampling procedure was used to record the occurrence of soil organic horizons every 50 cm along such transects, by considering four thickness categories: presence of a discontinuous layer formed by small amounts of litter (category 0), thickness up to 2 cm (category I), thickness 2 to 6 cm (category II), and thickness over 6 cm (category III).

In randomly selected points on such transects, sharp edge quadrates of 20 x 20 cm were used to obtain 10 samples of:

? pooled LF horizons, consisting of charred plant material left by fire and of post-fire plant material such as leaves, cones, acorns, branches, or bark, either unbroken or fragmented,

- ? H horizon, consisting of highly decomposed plant material and humiferous layers. Only 9 study sites showed recognizable H horizons in both once- and twice-burnt stands.

As we were interested in the variability that fire regimes could have generated between once- and twice-burnt stands but not within a particular stand, the 10 samples were pooled to obtain a single composite sample per stand of pooled LF horizons and of H horizon. Organic debris appear usually attached to small mineral particles, and thus, H horizons were sunk into water and stirred, and the light fraction was carefully collected. Consequently, small proportions of organic debris may have remained attached to the rejected fraction, and H horizon dry mass could have been underestimated. Pooled LF and H composite samples were oven-dried for 2 days at 60 °C and weighted. They were afterwards milled to <0.5 mm by means of a CYCLOTEC 1093 Sample mill FOS TECATOR, and analyzed at the Unit of Analyses of the Autonomous University of Barcelona, Barcelona, Spain. Analyses of total nitrogen and carbon were conducted after combustion with an elemental analyzer (Carlo Erba 1108, Milan, Italy); organic carbon was ascertained exclusively at LF horizons after digestion with HCl. Additionally, total phosphorous and potassium contents were ascertained in pooled FL horizons after digestion with HNO_3 and H_2O_2 through emission spectrometry in inductively coupled plasma (Perkin Elmer 4300, Norwalk, CT, USA).

In randomly selected points on transects, an Edelman auger was used to obtain 30 samples of mineral soil consisting of a constant volume up to 20 cm depth, after having carefully separated soil organic layers, surface stones, and rock fragments. The 30 samples were afterwards pooled, and a single composite sample of around 3 kg was obtained per stand. All composite samples were oven-dried for 2 days at 60°C. Afterwards, they were sieved to 2 mm in order to separate the coarse fragments. The fine soil fraction was analyzed following the common standard methods (Page et al. 1982) for total nitrogen (Kjeldahl), organic carbon (Walkey-Black), phosphorous (Olsen), potassium, magnesium, calcium, and sodium (ammonium acetate extract; ICP reading); pH and EC (25°C) values were also obtained. Total nitrogen was analyzed at the Soil Laboratory of the Center for Ecological Research and Forestry Applications

(CREAF, Autonomous University of Barcelona, Barcelona, Spain), and the rest of nutrient contents plus pH and EC were determined at the Laboratory on Analyses and Fertility of Soils (LAF, Diputació de Lleida, Lleida, Spain).

Data Analyses

Fire Recurrence

The frequency of occurrence of organic horizons (*arc sin* transformed) and the dry mass of LF horizons were compared between paired once- and twice-burnt areas by means of paired *t*-Student tests. A non parametric Wilcoxon rank test was used for the case of H horizon dry mass, since data transformation did not result in normal distributions.

Nutrient contents of soil organic horizons were compared between paired areas by means of paired *t*-Student tests (total nitrogen, total and organic carbon, phosphorous and potassium in LF horizons, and total nitrogen and total carbon in H horizon). Whenever data failed to meet the statistical assumptions of such test, nonparametric Wilcoxon rank tests were used (C/N ratio in LF horizons and in H horizon).

Similarly, nutrient contents of mineral soils were compared between paired areas by means of paired *t*-Student tests (total nitrogen, organic carbon, potassium, calcium) or nonparametric Wilcoxon rank tests (C/N ratio, phosphorous, magnesium, sodium).

Fire Interval

Simple linear regression models were used to test correlation between the difference in organic horizons variables (frequency of organic horizons, LF dry mass, H dry mass) in paired areas ((once-burnt)-(twice-burnt)) and fire interval. For the case of H horizon dry mass, such variable was *log* transformed in order to attain normality.

Climatic Variables: Temperature, Precipitation and Real Solar Radiation

Simple linear regression models were used to test correlation between soil organic horizons variables (occurrence of organic horizons, LF dry mass) and climatic variables (temperature, precipitation, and real solar radiation). Correlation was tested between: (1) differences in organic horizons variables ((once-burnt)-(twice-burnt)) and mean value of climatic variables for paired areas, and (2) organic horizons variables and climatic variables separately for once- and twice-burnt areas. For the case of H horizon dry mass, only (1) could be applied, by *log* transforming differences of dry mass in paired areas.

Substrate Type

A set of repeated measures ANOVA was performed to test the effects of substrate type (hard or soft calcareous substrate) on the frequency of occurrence of soil organic horizons and on LF horizon dry mass. Only 12 study sites were considered, those for which the same substrate type was found in paired stands. Such test could not be performed for the case of H horizon dry mass, due to the scarcity of data.

4.4. Results

Fire Recurrence

Fire recurrence significantly decreased the occurrence of organic horizons from 96% of the sampling points in once-burnt areas to 85% in twice-burnt ones (t= 4.21, P< 0.001). By categories, the frequency of the thickest organic layers (II and III) was significantly higher in once-burnt areas (t= 2.86, P= 0.013 and t= 3.74, P= 0.002, respectively), whereas the frequency of the thinnest organic layers (0 and I) was significantly higher in twice-burnt areas (t= -3.68, P= 0.003 and t= -2.14, P= 0.050, respectively) (Figure 9).

Fire recurrence also resulted in lower dry masses of soil organic horizons (mean ± SE) (Mg ha^{-1}): pooled LF organic horizons dry mass was 16.89 (± 1.98) in once-burnt areas and 10.85 (± 1.78) in twice-burnt ones (*t*= 3.27, *P*= 0.006); and H horizon dry mass was 0.98 (± 0.56) and 0.23 (± 0.12), respectively (*Z*= -2.43, *P*= 0.015).

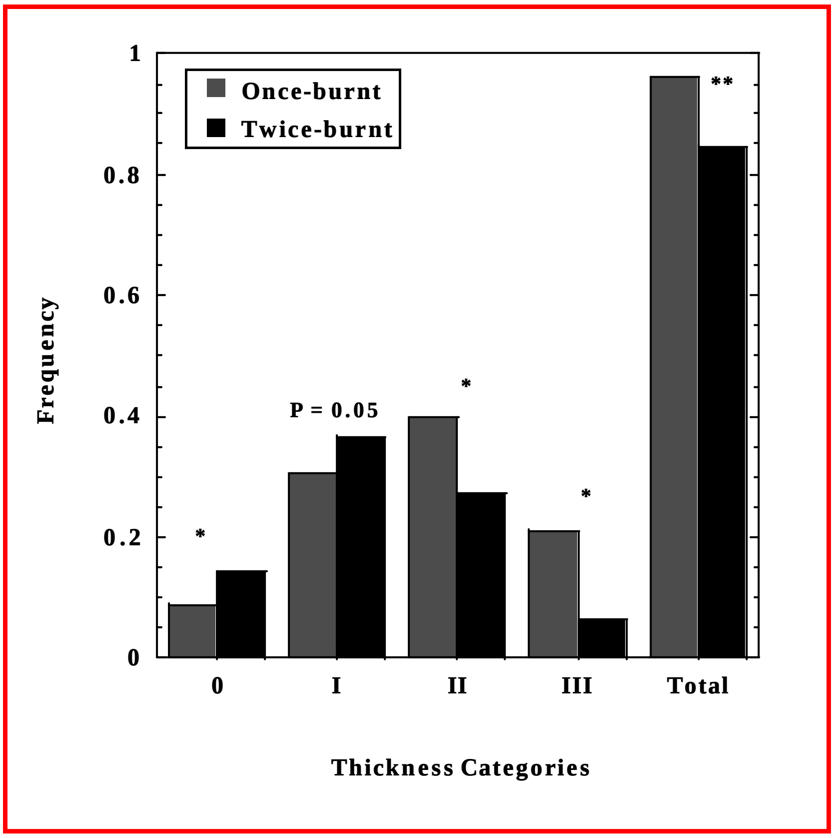

Figure 9. Total frequency of occurrence of soil organic horizons, and frequency of occurrence by thickness categories (category 0 = discontinuous layer formed by small amounts of litter, category I = thickness up to 2 cm, category II = thickness of 2-6 cm, and category II = thickness over 6 cm). Asterisks denote significance (**P*< 0.05, ** *P*< 0.001) of differences between paired stands.

There were significantly higher contents of total nitrogen and organic carbon in LF horizons of once-burnt areas relative to the same horizons of paired twice-burnt areas (*t*=2.25, *P*=0.041 and *t*=2.21, *P*=0.044, respectively), whereas no significant differences were found for total carbon, C/N ratio, phosphorous, or potassium (Appendix 2, pp. 97). Chemical analyses on H horizons revealed no significant differences for total nitrogen, total carbon, or C/N ratio (Appendix 2, pp. 99).

No significant differences in nutrient contents of mineral soils were found between paired once- and twice-burnt areas. Ranges of nutrients contents throughout the considered study sites were: 0.8 to 4.2 g · kg^{-1} for total nitrogen, 23.0 to 131.0 g · kg^{-1} for organic carbon, 7.7 to 41.3 for C/N ratio, 1 to 18 mg · kg^{-1} for phosphorous, 54 to 414 mg · kg^{-1} for potassium, 80 to 1,283 mg · kg^{-1} for magnesium, 4,512 to 10,676 mg · kg^{-1} for calcium, and 48 to 86 mg · kg^{-1} for sodium (Appendix 2, pp. 101).

Fire Interval

A significant, direct correlation was found between differences of H dry mass in paired areas and fire interval (R^2= 0.33, P= 0.026) (Figure 10). The differences in paired areas of the frequency of organic horizons or the dry mass of LF horizons were not correlated to fire interval.

Climatic Variables: Temperature, Precipitation and Real Solar Radiation

A significant, direct correlation was found between dry mass of LF horizons and precipitation, both in once-burnt (R^2= 0.38, P= 0.015) and in twice-burnt areas (R^2= 0.33, P= 0.025) (Figure 11). The dry mass of LF horizons was not correlated to temperature or real solar radiation. The frequency of occurrence of soil organic horizons and the dry mass of H horizon were not correlated to any climatic variable considered.

Substrate Type

No significant role of substrate type was found on the frequency of organic horizons or on FL horizon dry mass. In both cases, repeated measures ANOVA revealed a significant role of fire recurrence (P= 0.009 and P= 0.016, respectively), according to results obtained when comparing values between paired areas by means of a paired t-Student tests.

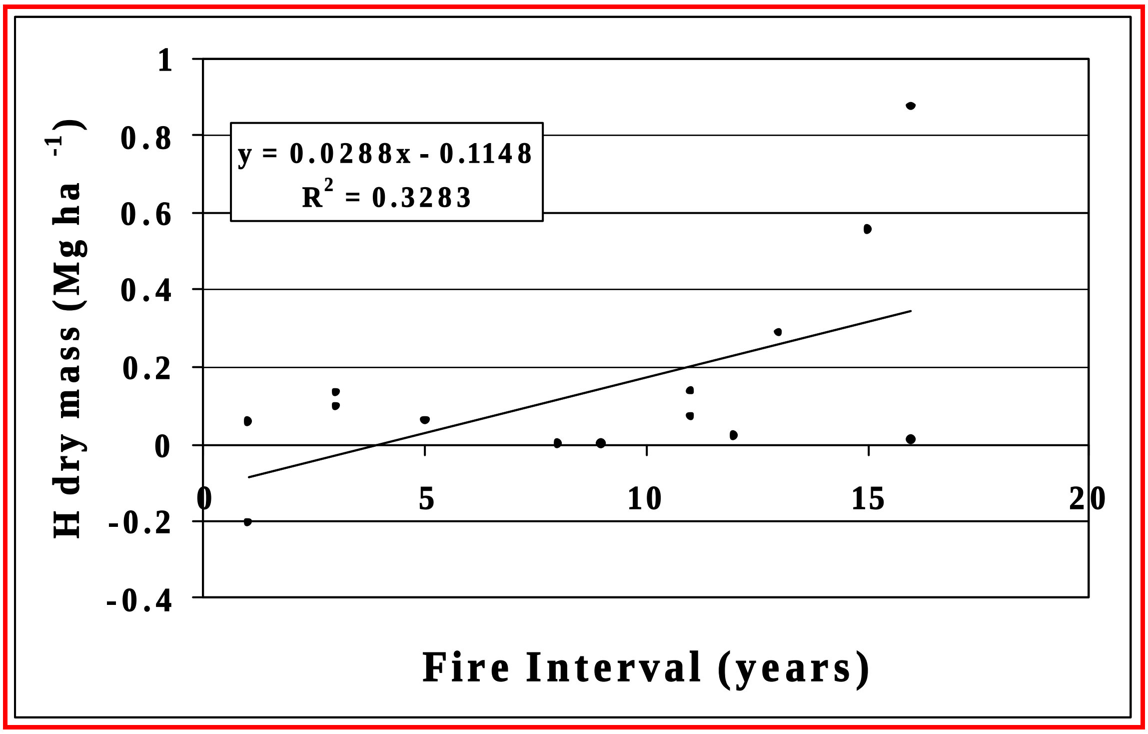

Figure 10. Correlation between differences of H horizon dry mass in paired areas (Mg · ha^{-1}) and fire interval (years) (*P*= 0.026).

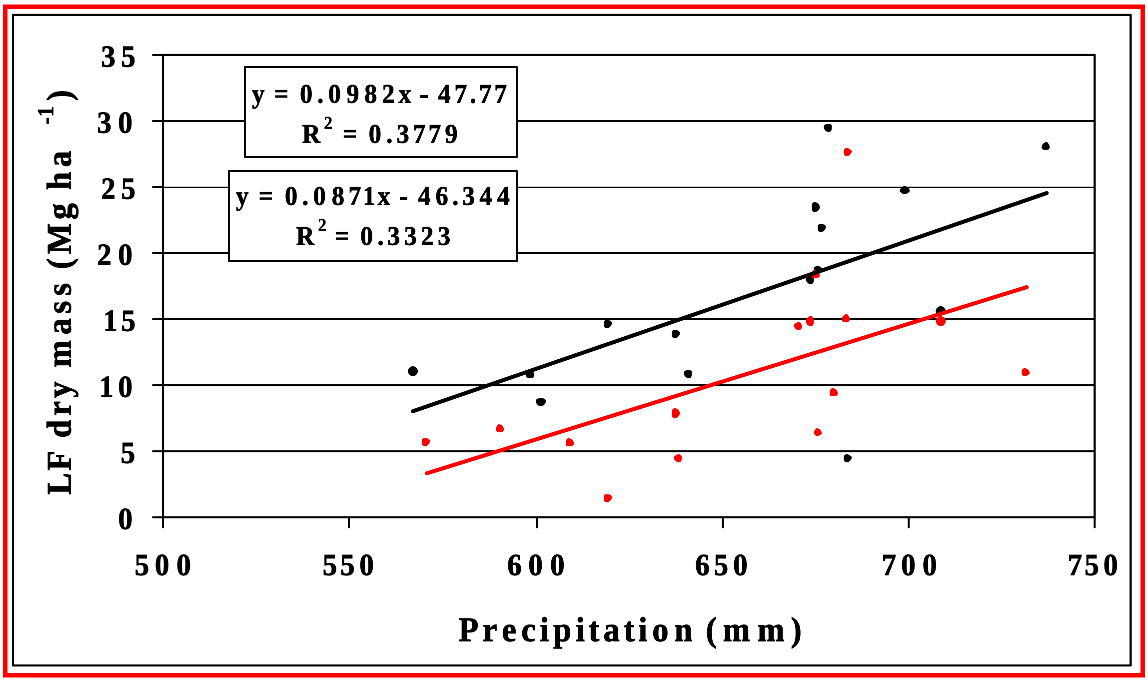

Figure 11. Correlations between LF horizon dry mass (Mg·ha^{-1}) and precipitation (mm) in once-burnt areas (black dots, upper line) (R^2= 0.38, *P*= 0.015) and in twice-burnt areas (red dots, lower line) (R^2= 0.33, *P*= 0.025).

4.5. Discussion

Structural features of soil organic horizons were modified by fire recurrence in such a way that, 9 years after the last fire, soil organic horizons covered a higher soil mineral surface and were deeper and more structured into layers in areas burnt only once relative to paired areas burnt twice along the same period. Consequently, masses of soil organic horizons per unit surface were higher in areas burnt once (*ca.* 18 Mg·ha^{-1}) than in areas burnt twice (around 11 Mg·ha^{-1}), most of which corresponded to LF horizons (94% and 98%, respectively). Accordingly, all areas showed LF horizons, while H horizons were not present in 3 once-burnt areas, and in 6 twice-burnt areas. It has been suggested that the state of soil organic horizons can be used as a sensitive indicator of the whole ecosystem recovery (Ferran & Vallejo 1992); in that sense, a loss of resilience was observed in twice-burnt areas.

The occurrence of a second fire at short fire intervals likely had the direct effect of further combusting soil organic horizons in twice-burnt areas, a fact that would be particularly relevant in the case of H horizon. Fire results in the total or partial combustion of soil organic horizons, which relies mainly on fire temperatures, on their residence time, and on substrate characteristics (Ferran et al. 1992; Andreu et al. 1994). Generally, upper organic horizons (L and F) are completely burnt, whereas humiferous layers are only partially burnt (Ferran et al. 1992; Serrasolsas & Vallejo 1999). In a study conducted on different substrate types, H horizon escaped the fire on limestones and schists, since it was protected by a layer of superficial stones. However, it was partially burnt on conglomerates, and completely burnt on marls (Ferran et al. 1992) (Appendix 3, pp. 105 and 107). In twice-burnt areas, the first fire likely combusted LF horizons at least partly, and thus resulted in more exposed H horizons. Such fire left ashes, which are incorporated to remnant organic horizons and upper mineral soils up to the second post-fire year (Serrasolsas & Vallejo 1999), and charred plant remains (Appendix 3, pp. 109). During a time span ranging from 1 to 16 years, plant litter accumulated and, together with charred plant remains, suffered subsequent decomposition processes. The 1994 fire would have combusted the newly-formed LF horizons, and further combusted the remaining H horizon, particularly where a thick layer of accumulated plant litter was not protecting it. Interestingly, a significant and direct correlation was found between differences of H horizon dry mass in paired areas and fire interval, which supports the importance of time spans between fires for keeping humiferous layers through accumulation of LH horizons. Post-fire formation of H horizon is very slow, and thus, it is not likely that the humiferous layers found 9 years after the 1994 fire were newly-formed (Ferran & Vallejo 1992). Given that H horizon plays a main role for mineral soil fertility, its direct reduction can be considered a relevant cumulative and deleterious effect of fire recurrence.

Moreover, the maintenance of humiferous layers is threatened by post-fire erosive processes, whose intensity relies on post-fire climatic conditions and on the degree of vegetation recovery (Ferran & Vallejo 1992; Thornes 1990). Erosion has been observed to result in the formation of an *erosive layer*, conformed by remains of H horizon mixed with mineral particles of eroded upper mineral soil, and enriched by ashes and charred organic remains, which is located without cohesion on the mineral soil surface. Chemically, such layer is characterized by contents of organic carbon higher than typical mineral soils but lower than typical H horizons (Ferran et al. 1992; Serrasolsas & Vallejo 1999). Namely, the occurrence of rainfall events shortly after the fire may result in the deconstruction of H horizons, which will only be recovered with time since last fire. In twice-burnt areas, the repeated occurrence of erosive events after consecutive fires may have contributed to further reduce humiferous layers.

Nine years after fire, mean dry mass of LF horizons in once-burnt areas, *ca*. 18 Mg·ha^{-1}, was similar to values reported for mature P.halepensis communities, which range from 12.5 Mg·ha^{-1} (near Alicante, in the València region) to 15.6 Mg·ha^{-1} (near Montpellier, in southern France) (Trabaud 1977; Pastor 1992; García-Plé et al. 1995). In twice-burnt areas, mean dry mass of LF horizons was of the same order, around 11 Mg·ha^{-1}, but significantly lower than in once-burnt ones, which is attributed to a lower growth of vegetation after the 1994 fire. LF horizons are formed by plant litter, and thus increase in depth and mass with time since last fire, along with vegetation regeneration (Mitchell et al. 1986; Ferran et al. 1992; Ferran & Vallejo 1999) (Appendix 3, pp. 111). In once-burnt areas, vegetation showed higher fuel loads and higher total cover (Chapter 3), which explains that soil organic horizons were deeper and heavier, and that they covered a higher soil mineral surface than in twice-burnt areas. The significant and direct correlation found between dry mass of LF horizons and precipitation both in once- and twice-burnt areas supports the role of vegetation growth in post-fire reconstruction of organic horizons, since water is a main abiotic factor limiting plant growth in MTEs (Dunn et al. 1977; Rundel 1982; Cherubini et al. 2003). Moreover, the development of the pine canopy is particularly important for the recovery of LF horizons mass: garrigues characterized by an overstorey of Aleppo pine have been observed to recover pre-fire values of litter mass only when the pine stratum is established. Litter mass values in the garrigue with pines were twice the values than in the garrigue without pines (Ferran et al. 1992). Consequently, the improved reconstruction of LF horizons in once-burnt areas may be partly due to the fact that tree cover was higher and Aleppo pine populations were denser in them (Chapters 3, 6).

In order to test the above-mentioned explanation for the better reconstruction of LF horizons in once-burnt areas, correlation was tested with variables provided by other surveys, in particular pine density (Chapter 6), total tree cover as estimated at a stand level (Chapter 3), and total vegetation cover as recorded by the point-interception sampling procedure (Chapter 3). LF showed a marginally significant, direct correlation with pine density (n=9) and tree cover (n=15) in once-burnt areas (R^2= 0.38, P= 0.075 and R^2= 0.24, P= 0.065, respectively), but no correlation with the same variables in twice-burnt ones (R^2= 0.03, P= 0.635 and R^2= 0.03, P= 0.561, respectively). Moreover, LF dry mass was significantly and directly correlated with total cover (n=15) in twice-burnt areas (R^2= 0.29, P= 0.038), but not in once-burnt ones (R^2= 0.04, P= 0.460). Similarly, the frequency of occurrence of soil organic was significantly and directly correlated with total cover in twice-burnt areas (R^2= 0.34, P= 0.023), but not in once-burnt ones (R^2= 0.12, P= 0.200). Such results support the role of vegetation in conforming organic horizons, particularly LF horizons, and underline the fact that Aleppo pine canopy is a major contributor to their reconstruction.

A further reason explaining the better reconstruction of LF horizons in once-burnt areas is that the 1994 fire likely left a greater amount of partially or totally combusted plant remains, since probably pre-fire fuel loads were higher and vegetation was more developed in these stands as a result of longer fire intervals. Contrastingly, in twice-burnt areas, the 1994 fire likely combusted the bigger charred plant remains left by the first fire which had not been incorporated to organic horizons, and likely resulted in lower amounts of big plant remains due to lower pre-fire fuel loads (Appendix 3, pp. 113).

Chemical analyses revealed significantly higher contents of total nitrogen and organic carbon in LF horizons of areas burnt once relative to paired areas burnt twice. In relation to nitrogen, previous works reported higher contents in L horizons of sites burnt less recurrently (Ferran et al. 2005). These authors conducted analyses in the short term after fire, and thus, differences were attributed to the initially higher decomposition and nutrient mineralization rates of the first post-fire leaves. In the medium term after fire, I hypothesize that differences in plant species composition between paired areas, in particular the higher abundance of P.halepensis in areas burnt once (Chapter 6), would have resulted in different nitrogen contents in LF horizons. Nitrogen content is particularly high in leaves (Sardans 1993), and pine needles constitute the major fraction of litter fall in P.halepensis communities (García-Plé et al. 1995). Consequently, and despite nutrient retranslocation before abscission is quantitatively important in pine species, and needle litter is characterized by low contents of some elements, including nitrogen (Moro et al. 1996; Moro & Domingo 2000), quantitative differences in pine needle litter production may account for the higher nitrogen contents in LF horizons of once-burnt areas. The alternative hypothesis of lower nutrient contents in leaves of plant species in twice-burnt areas –as resulting from soil nutrient deficits- is not supported by the chemical analyses conducted on 4 common plant species –P.halepensis, Quercus ilex, Pistacia lentiscus, and Rosmarinus officinalis-, which showed similar nutrient contents in paired areas (Chapters 5, 6). In relation to carbon, the higher contents found in LF horizons of once-burnt areas may be explained by the fact that charred plant remains -particularly burnt branches and trunks of P.halepensis, and skeletons of resprouter species (Appendix 3, pp. 113)- were more abundant in such areas, since carbon contents are particularly high in litter types such as bark, branches, or charred plant remains (Sardans 1993).

Fairly similar nutrient contents were found in mineral soils of paired areas, thus supporting the suitability of paired comparisons; the ranges of nutrient contents found throughout the study area reflect the variety of local conditions considered in the present study. No significant differences in nutrient contents were expected between paired areas as resulting from fire recurrence, since survey was conducted on the 20 upper cm of mineral soils and 9 years after fire, whereas fire affects a maximum soil depth of 5 cm (Giovannini 1994), and soil nutrient contents tend to recover pre-fire values in the short term (Kutiel & Kutiel 1989; Romanyà et al. 2001).

4.6. Conclusions

The occurrence of two fires along two decades resulted in less developed soil organic horizons of P.halepensis communities relative to the occurrence of a single fire. Nine years after fire, such fact was evidenced by a lower frequency of occurrence, presence of H horizon, depth, and dry mass.

Considering that the state of soil organic horizons can be used as a sensitive indicator of the whole ecosystem recovery, a loss of resilience is observed in P.halepensis communities submitted to fire recurrence levels of two fires at intervals shorter than 17 years.

The direct reduction of humiferous layers by fire repetition is a relevant cumulative and deleterious effect of fire recurrence on soils, given the slow rates of formation of such layers and the role that they play for the fertility of mineral soils. Fire intervals showed a positive and significant effect on H dry mass; the longer fire intervals, the higher masses of humiferous layers. After a fire, H horizon is likely to become more exposed and to result further combusted by the next fire if abundant litter accumulation is not allowed by fire intervals.

Fire recurrence also resulted in a lower reconstruction of LF horizons, as resulting from lower fuel loads and less developed structure of vegetation in areas burnt twice. Precipitation had a positive and significant effect on LF dry mass, thus underlining the role of plant growth in LF reconstruction.

Aleppo pine populations strongly conditioned post-fire recovery of LF horizons, since they produce quantitatively important amounts of litter, particularly needle litter, which resulted in higher masses of LF horizons, and higher nitrogen contents in them.

Higher organic carbon contents were also found in LF horizons of once-burnt areas, as resulting from the higher amounts of charred plant remains left by the 1994 in them.

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Chapter 5

Plant Growth: Branch Elongation, Basal Area Increment, and Foliar Nutrient Contents of *Quercus ilex*, *Pistacia lentiscus*, and *Rosmarinus officinalis*

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Eugenio M, Lloret F. Medium term effects of fire recurrence on plant growth in three Mediterranean woody species.

5.1. Introduction

In MTEs, growth rates within plant communities are slow compared to moister temperate regions (Margaris & Mooney 1981). Water and nutrient availability are two main abiotic factors limiting plant growth and primary production (Rundel 1982; McMaster et al. 1982; Spetch et al. 1983; Witkowski et al. 1990). In the Mediterranean Basin, phosphorous is considered the main limiting nutrient (Carreira et al. 1996, 1997; Sardans et al. 2004, 2005). Foliar nutrient contents are used as a biological index of soil nutrient availability (Van den Driessche 1974; Binkley 1986). The technique assumes that plants accumulate nutrients in excess of their immediate needs when they are freely available, so low foliar nutrient contents reflect soil nutrient deficiencies. However, growth may be negatively affected before foliar deficiencies appear, or plants may reduce foliage biomass while maintaining stable levels of foliar nutrient contents (Schlesinger & Gill 1980).

Plant growth is disrupted by fire: a common stand-replacing wildfire results in consumption of above-ground biomass and part of soil organic horizons, and generates a particularly resource-rich environment. Space and light become available for plant recruits, as well as nutrients, since soil chemical fertility is enhanced by ashes (DeBano & Conrad 1974; Christensen & Muller 1975). In the Mediterranean Basin, plants show two main regenerative strategies allowing post-fire community recovery: seeder species are killed by fire and recruit by seeds, whereas resprouter species regrow vegetatively from underground structures. Regenerative strategies are closely tied with physiological and morphological attributes (Keeley 1998; Verdú 2000), and thus, seeders and resprouters are expected to show different growth responses to post-fire conditions. Along the first post-fire years, resprouters may have a competitive advantage over seeders, since they use stored reserves to support growth (Bowen and Pate 1993, Canadell & López-Soria 1998) and already-developed root systems to access soil water reserves (Sardans et al. 2004; Clemente et al. 2005). However, in the medium-term, resprouters would show lower growth rates than seeders, as a result of the tradeoff between storage and growth (Bond & Midgley 2001; Pausas et al. 2004).

In the present study, vegetation of once-burnt areas was observed, 8 years after fire, to show more developed structure and higher fuel loads than vegetation of paired twice-burnt areas. It has been hypothesized that plant growth could have been comparatively higher in once-burnt areas exclusively along the first post-fire years, when soil nutrient availability may have been higher (Chapter 3). However, differences in plant growth between paired areas might persist several years after fire, thus determining patterns of vegetation structure and function over more prolonged periods of time. Moreover, different patterns of plant growth may also be found between seeders and resprouters, given that they show different resources-use strategies.

5.2. Aim of the Chapter

The present survey addresses comparatively plant growth of 3 common Mediterranean woody species in P.halepensis communities which differ in their recent fire history (burnt once *versus* twice along a 20 year-long period).

Basal area increment and branch elongation were surveyed 10 to 11 years after fire in the resprouter tree Quercus ilex, the resprouter shrub Pistacia lentiscus, and the seeder shrub Rosmarinus officinalis.

Foliar nutrient contents of current-year leaves (11 years after fire) of such species were also analyzed, since they are considered to provide clues on soil nutritional status.

5.3. Methods

The survey was conducted between 10 and 11 years after the fire at 13 randomly selected study sites among the total 28 study sites (Table 9).

Study Site	**Fire Interval (y)**	**Elevation (m)**		**Slope (°)**		**Aspect (°)**		**Substrate Type**	
		Once-burnt	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**
3	12	259	273	15	25	230	220	clays	conglomerates
9	13	455	465	30	30	30	40	clays	argillites
10	8	275	285	40	40	180	170	argillites	limestones
11	8	192	239	30	25	270	280	clays	clays
15	5	400	412	30	30	290	300	dolomites	dolomites
16	9	480	470	20	15	80	80	limestones	limestones
17	16	239	243	10	0	120	0	gravels	gravels
18	12	247	251	0	0	0	0	marls	marls
21	13	651	628	20	15	330	340	limestones	limestones
24	11	317	289	20	15	40	40	limestones	limestones
26	9	606	637	40	40	220	220	limestones	limestones
28	11	469	459	15	15	210	210	marls	marls
29	11	419	415	25	25	70	60	marls	marls

Table 9. Fire intervals and geomorphic characteristics of study sites considered for survey on plant growth.

Species Description

Q.ilex (Holm oak, Fagaceae) is distributed over an area extending 6,000 km from Portugal to Syria, and 1,500 km from Morocco to France (Terradas 1999). It is a tree up to 20 m tall, though it is shorter and multi-stemmed where it is submitted to frequent disturbances (Gracia et al. 1996). It shows evergreen, sclerophyllous leaves characterized by thick cuticles, abundant sclerification, and short spines on the margins (Sabaté et al. 1999). Q.ilex root-systems are quite extensive, very deep –over 4 m deep, whenever substrate can be penetrated-, and show dominant taproots, particularly under dry conditions (Canadell et al. 1999). After fire, Q.ilex resprouts from a lignotuber where buds, non-structural carbohydrates, and nutrients are stored (Canadell & Zedler 1995).

P.lentiscus (Mastic tree, Anacardiaceae) is distributed all over the Mediterranean Basin at low elevations (Quézel 1981). It is a shrub up to 5 m tall that shows composite, evergreen, sclerophyllous leaves. Resprouter shrubs usually show shallower root-systems than resprouter trees (Villar et al. 2004), but P.lentiscus root-systems are particularly deep -over 5 m deep (Oppenheimer 1957; Silva et al. 2003)-. After fire, P.lentiscus resprouts from a root crown.

R.officinalis (Rosemary, Labiaceae) is very widespread in the western Mediterranean Basin, where it dominates many shrubland communities on calcareous soils (Bolòs et al. 1990). It is a shrub up to 3 m tall, considered to show evergreen, sclerophyllous leaves by some authors (Clary et al. 2004) and drought semi-deciduous leaves by other ones (Ain-Lhout et al. 2004). R.officinalis is a seeder species which shows a shallow - under 1 m deep (Spetch 1998) - and laterally extended root-system.

Growth Measures

Twelve individuals of each species were randomly selected among average-sized individuals in each stand. R.officinalis was present in 12 study sites, P.lentiscus was present in 10 study sites, and Q.ilex was present in 5 study sites. Overall, 282 R.officinalis individuals, 238 P.lentiscus individuals, and 112 Q.ilex individuals were surveyed. Eight branches distributed all over the plant and located at medium plant height were selected per individual among outer, adult, and well-developed ones. Branches were permanently tagged and a line was painted, from which the branch was measured up to the apical growth. All stems were permanently tagged and a line was painted 20 cm above ground, on which diameter was measured with a digital metric caliper (Figure 12).

Survey was conducted firstly in winter-2004, and afterwards in summer-2005. Vegetative seasons in the Mediterranean Basin are spring and autumn, when temperatures are mild and water is available (Di Castri & Mooney 1973; Dunn et al. 1976), and thus, 3 vegetative seasons were considered. Individuals, branches, or stems that were found dead along the second survey were excluded from data. We considered absolute branch elongation, and relative basal area increment, since relative values of basal area are less influenced by initial size (Mayor & Rodà 1994).

Foliar Nutrient Contents

Samples of R.officinalis, Q.ilex, and P.lentiscus were collected in summer-2005 by harvesting current-year leaves at medium plant height in 6 individuals of each species randomly selected per stand. Samples were oven-dried for two days at 65°C. As we were interested in the variability that fire regimes could have generated between once- and twice-burnt areas but not within an area, a single composite sample was obtained for each species and stand. Composite samples were finely grounded and then analyzed at the Unit of Analysis of the Autonomous University of Barcelona, Barcelona, Spain. Analyses of total carbon, nitrogen, hydrogen, and sulphur were conducted after combustion with an elemental analyzer (Carlo Erba 1108, Milan, Italy). Analyses of iron, phosphorous, magnesium, potassium, and calcium, were conducted after digestion with HNO_3, H_2O_2 and HCl by emission spectrometry in inductively coupled plasma (Perkin Elmer 4300, Norwalk, CT, USA).

Figure 12. Tagged individuals of R.officinalis and P.lentiscus. Eight branches per individual and all stems were considered.

Data Analyses

Fire Recurrence

To compare growth between once- and twice-burnt areas, a set of GLMs (General Linear Models) was performed for each species. Mean values of absolute branch elongation and relative basal area increment for each individual were the dependent variables, and fire recurrence level and study site were fixed and random categorical predictors, respectively.

Paired *t*-Student tests (for R.officinalis) or Wilcoxon rank tests (for Q.ilex and P.lentiscus) were conducted to compare foliar nutrient contents between paired once- and twice-burnt areas. The sequential Bonferroni test (Holm 1979) was used to conduct simultaneous statistical inference.

Climatic Variables: Precipitation, Temperature, and Real Solar Radiation

To test correlation between climatic variables and basal area increment and branch elongation, simple linear regression models were performed separately in once- and twice-burnt areas.

Cumulative precipitation and mean temperature for the time period considered in growth survey (February-2004 to July-2005) were used as independent variables. Values corresponded to the nearest climatic station of the Xarxa Agrometeorològica de Catalunya (Departament de Medi Ambient 2006. http://xarxes.meteocat.com/xac).

Real solar radiation, which reflects local levels of incoming radiation, and is a summarizing measure of latitude, altitude, and topography that has been considered a good indicator of site climatic productivity in MTEs (Safford & Harrison 2004) was also used as an independent variable. Values were assigned to GPS-positioned central points of every once- and twice-burnt stand from the Atles Climàtic Digital de Catalunya (Pons 1996; Ninyerola et al. 2000. http://magno.uab.es/atles-climatic).

5.4. Results

Fire Recurrence

Mean absolute branch elongation of the 3 species was similar in areas burnt once and twice (Figure 13). Moreover, important variability in absolute branch elongation was found among locations, since study site was a significant factor for the 3 species. In the case of R.officinalis, the interaction between fire recurrence and study site was also significant (Table 10).

Mean relative basal area increment of the seeder shrub R.officinalis was significantly higher in twice-burnt areas than in paired once-burnt ones. No significant differences were found for the resprouter species Q.ilex and P.lentiscus (Figure 14). Moreover, relative basal area increment of R.officinalis was significantly influenced by study site. There was a significant interaction between fire recurrence level and study site for basal area increment of P.lentiscus (Table 11).

Comparison of foliar nutrient contents revealed that R.officinalis current-year leaves showed significantly higher sulphur content in once-burnt areas (t= 2.56, P= 0.027), and significantly higher iron content in twice-burnt ones (t= -2.29, Z= 0.043) (Appendix 4, pp. 135). However, such results lost significance after applying the sequential Bonferroni test. No significant differences were found in foliar nutrient contents of current-year leaves in P.lentiscus and Q.ilex (Appendix 4, pp. 137 and 139, respectively).

Climatic Variables: Precipitation, Temperature, and Real Solar Radiation

Basal area increment of P.lentiscus was marginally and inversely correlated to mean temperature along the growth period in once-burnt areas (P= 0.058, R^2= 0.38), but not in twice-burnt ones (P= 0.815, R^2= 0.02). No significant correlations were found between basal area increment or branch elongation of Q.ilex or R.officinalis and either mean temperature or cumulative precipitation along the growth period.

Basal are increment of Q.ilex was significantly and inversely correlated to real solar radiation in once-burnt areas ($P= 0.026$, $R^2= 0.85$), but not in twice-burnt areas ($P= 0.815$, $R^2= 0.02$). No significant correlations were found between basal area increment or branch elongation of P.lentiscus or R.officinalis and real solar radiation.

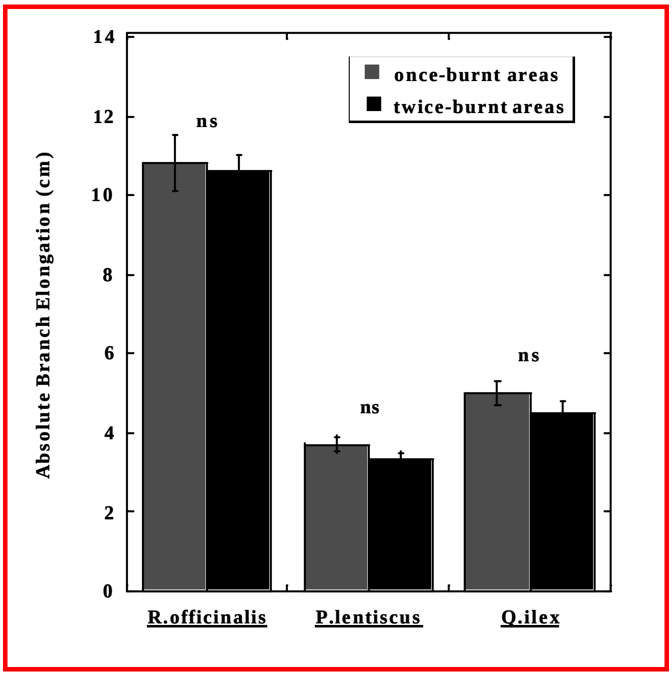

Figure 13. Comparison of mean absolute branch elongation (± SE) (cm) between areas burnt once and twice for R.officinalis, P.lentiscus, and Q.ilex. Symbols above bars denote significance of comparisons (*ns* = no significance).

	Absolute Branch Elongation					
	R.officinalis **n = 282**		**P.lentiscus** **n= 238**		**Q.ilex** **n = 112**	
	F	***P***	***F***	***P***	***F***	***P***
Study Site	4.73	0.008	7.54	0.003	24.2	0.005
Fire Recurrence	0.1	0.762	1.59	0.239	4.46	0.102
Site*Recurrence	1.9	0.04	1.63	0.109	0.7	0.593

Table 10. Results of the GLM; mean values of absolute branch elongation for each individual were the dependent variable, and fire recurrence level and study site were fixed and random categorical predictors, respectively.

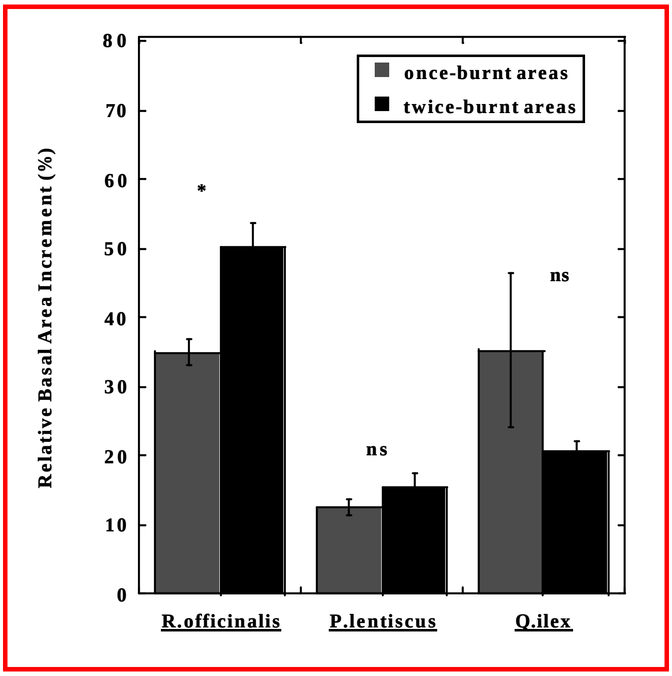

Figure 14. Comparison of mean relative basal area increment (± SE) (%) between paired areas for R.officinalis, P.lentiscus, and Q.ilex. Symbols above bars denote significance of comparisons (*ns* = no significance, * $P < 0.05$).

	Relative Basal Area Increment					
	R.officinalis **n = 282**		**P.lentiscus** **n= 238**		**Q.ilex** **n = 112**	
	F	***P***	***F***	***P***	***F***	***P***
Study Site	6.6	0.002	1.93	0.171	1.43	0.369
Fire Recurrence	12.86	0.004	0.83	0.387	1.86	0.244
Site*Recurrence	1.65	0.086	2.24	0.021	1.12	0.353

Table 11. Results of the GLM; mean values of relative basal area increment for each individual were the dependent variable, and fire recurrence level and study site were fixed and random categorical predictors, respectively.

5.5. Discussion

R.officinalis basal area increment between 10 and 11 years after fire was promoted in areas affected by two fires in relation to paired areas affected by one fire along the same time period. Moreover, R.officinalis basal area increment showed a significant variability among sites. It is hypothesized that enhanced basal area growth of the species may be due to the competition release generated through fire repetition in twice-burnt areas. Between 8 and 10 years after the last fire, twice-burnt areas have been observed to show lower tree cover and Aleppo pine abundance (Chapters 3, 6, 7), higher shrub cover and shrub abundance (Chapters 3, 7), and, overall, shorter and more open vegetation (Chapter 3). Namely, the occurrence of the 1994 fire at fire intervals shorter than 17 years resulted in lower post-fire recruitment of P.halepensis. Such reduction was accompanied by an increase in shrub abundance. Consequently, shrubs in twice-burnt areas can benefit from higher space availability and higher access to soil resources than shrubs in paired once-burnt areas. Foliar nutrient patterns in R.officinalis were broadly accordant with growth patterns, since enhanced growth results in greater iron allocation to leaves due to higher photosynthetic demands, and in a subsequent dilution effect on sulphur (Sardans et al. 2005). However, such results lost significance after applying the Bonferroni test. Moreover, foliar nutrient contents of R.officinalis did not reveal the existence of phosphorous deficiencies in soils. Phosphorous contents averaged 0.68 mg·g^{-1} in areas burnt once, and 0.64 mg·g^{-1} in areas burnt twice. Thus, both values were higher than those previously reported in current-year leaves of the species, ranging between o.34 and 0.56 mg·g^{-1}, as observed in a 5 year-old shrubland burnt 3 times along 20 years (Sardans et al. 2005).

Contrastingly, no significant differences in basal area increment or foliar nutrient contents were found for the resprouters Q.ilex and P.lentiscus. According, foliar nutrient contents were similar in paired once- and twice-burnt areas in both species. Resprouter species show a more conservative resource-use strategy than seeder species: whereas seedlings of seeders use the space released by fire for establishing, resprouter individuals held their sites through vegetative regrowth (Keeley 1986). Moreover, resources that are stored in underground organs might support growth also several years after fire, since Q.ilex growth responses to phosphorous addition have been observed up to 6 years later (de la Fuente et al. 1997). Resprouters also have deeper root-systems than seeders, and thus show a higher potential for the absorption of nutrients and water, particularly during summer drought (Silva et al. 2003).

Branch elongation was higher in once-burnt areas for the 3 considered species, but differences were not significant. Such pattern could indicate that, a decade after fire, vegetation is not submitted to notably different levels of competition for light in areas burnt once and twice. Commonly, light availability is not a limiting factor in MTEs. On the contrary, plants exhibit a range of morphological and physiological adaptations to cope with high light intensity together with heat and drought (Martínez-Ferri et al. 2000; Ain-Lhout et al. 2004). Moreover, light photosynthetic utilization is constrained by water and nutrient availability (Lambers et al. 1998). In addition, branch elongation patterns evidence a modular response rather than a whole-plant response, as evidenced by the fact that study site showed a significant influence on branch elongation for the 3 considered species.

Basal area increment of the resprouter species were observed to rely on climatic variables in once-burnt areas, but not in twice-burnt ones, where the constraint produced by fire repetition seemed to prevail. Higher mean temperatures along the growth period resulted in lower basal area increment of P.lentiscus in once-burnt areas. Similarly, higher real solar radiation, i.e., lower climatic productivity, resulted in lower basal are increments of Q.ilex in such areas. Growth of the seeder R.officinalis was not observed to rely on climatic variables. However, the absence of significant correlations with cumulative precipitation or mean temperature along the considered growth period may be due to the fact that data corresponded to the nearest climatic station, and thus did not specifically characterize the geographical locations considered.

5.6. Conclusions

A decade after fire, differences in growth between once- and twice-burnt areas were not present in resprouter species such as Q.ilex and P.lentiscus, whose post-disturbance growth is largely controlled by stored resources in surviving underground organs. However, the growth of the seeder R.officinalis was higher in twice-burnt areas, suggesting that competition release resulting from reburning at short fire intervals remains several years after fire. Such effect was observed in basal area increment, but not in branch elongation, which is more likely determined by competition for light.

Accordingly, significantly different levels of foliar nutrient contents were found only in R.officinalis, as related to the higher basal area increment of the species in twice-burnt areas. However, such results lost significance after applying the sequential Bonferroni test. Overall, fire repetition at fire intervals shorter than 17 years was not observed to result in soil nutrient deficits, as indicated by foliar nutrient contents and observed 11 years after fire.

Basal area increment of resprouter species was inversely correlated to climatic variables such as mean temperature along the growth period and climatic productivity in once-burnt areas, but not in twice-burnt ones. This, fire repetition likely resulted in a stronger constraint for growth that overshadowed the effects of climatic variables.

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Chapter 6

***P.halepensis* Populations: Post-Fire Recruitment, Population Structure, and Radial Growth**

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Eugenio M, Verkaik I, Lloret F, Espelta JM. 2006. Recruitment and growth decline in *Pinus halepensis* populations after recurrent wildfires in Catalonia (NE Iberian Peninsula). Forest Ecology and Management, 231: 47-54.

6.1. Introduction

P.halepensis populations are submitted to recurrent stand-replacing fires. Since Aleppo pine is a seeder species, its regeneration relies on the recruitment of a post-fire cohort of seedlings. Moreover, Aleppo pine is a partially serotinous species: *serotinity*, also named *bradychory*, consists in the retention of mature seeds into closed cones that constitute a canopy seed bank, in such a way that seed dispersal is induced by fire (Lamont et al. 1991). P.halepensis individuals carry both non-serotinous and serotinous cones, and thus seed release occurs also in the absence of fire, particularly under hot and dry conditions (Nathan & Ne'eman 2000), and is followed by recruitment whenever environmental conditions are favorable. It has been estimated that about 60% of the abundant yearly seed crop is released during summer, and the rest, about 40%, is retained into serotinous cones and is annually added to the canopy seed bank (Daskalakou & Thanos 1996; Nathan et al. 1999; Habrouk et al. 1999). Post-fire population recovery of Aleppo pine relies exclusively on the germination and establishment of seeds dispersed after fire from such canopy seed bank, since soil seed bank shows a transient nature -seed viability is maintained only for around two years, and seeds are submitted to high levels of predation- , and, moreover, seeds that are found on or near the soil surface are killed by fire (Daskalakou & Thanos 1996).

Consequently, post-fire regeneration of P.halepensis may partly or completely fail when time intervals between fires are not long enough as to allow a critical storage of viable seeds (Enright et al. 1998; Keeley et al. 1999). This phenomenon has been named *immaturity risk* (Zedler 1995). Despite some Aleppo pine individuals can produce viable seeds as soon as 7 years after fire (Verkaik & Espelta, personal communication), it is considered that an entire even-aged population may not end the juvenile phase up to 12-20 years after fire (Thanos et al. 1998). The length of time required to accumulate a sufficient seed bank to ensure post-fire recovery at similar densities to those of parent populations is still unknown, despite it has been suggested that two decades might be necessary (Papió 1994; Pausas 2001).

Post-fire seed germination of Aleppo pine takes place in the resource-rich environment generated by the passage of fire, where light, space, and nutrients are largely available. It occurs almost exclusively during the first post-fire autumn and winter seasons (Trabaud et al. 1985; Saracino et al. 1993; Ne'eman et al. 1995; Thanos et al. 1996; Thanos 1999; Arianoutsou & Ne'eman 2000; Leone et al. 2000). Sporadic seedling emergence has been observed during subsequent years in some cases (Herranz et al. 1997). In a recent study dealing specifically with seedling recruitment dynamics along the first post-fire year, seed germination and seedling emergence took place in the form of a massive wave shortly after the onset of the first post-fire rainy season, in such a way that most germinable seeds were transformed into seedlings during winter; at some particular locations, this phenomenon was delayed or showed a bimodal pattern with a second maxima in spring following fire (Daskalakou & Thanos 2004a).

Seedling mortality shows two peaks along the first post-fire year, which is crucial for seedling survival (Saracino et al. 1993; Thanos et al. 1996; Daskalakou & Thanos 1997): firstly at the stage of cotyledon expansion, and secondly during the first post-fire summer (Thanos et al. 1996; Daskalakou & Thanos 2004b). Relevant seedling mortality has also been reported at some locations during the second post-fire year (Ne'eman et al. 1995), and can occur later due to factors such as competition, pests, and herbivory. In the eastern Mediterranean Basin, density of regenerating P.halepensis forests has been reported to decrease constantly up to about 10 years after fire (Arianoutsou & Ne'eman 2000). However, in southern France, initial density has been observed to increase up to a maximum at 10 to 15 years after fire, and then to decrease (Trabaud et al 1985; Trabaud 2000).

Post-fire P.halepensis populations range widely in density, which can be considered site-specific. In the western Mediterranean Basin, densities of tens to thousand hundreds of pines per hectare have been reported for 8 year-old populations (Trabaud et al. 1985; Papió 1994, Pausas et al. 2004). Densities of adult populations are on the order of hundreds to thousands of pines per hectare: in Catalonia, populations about 30 year-old, which are characterized by a mean height of 6 m and correspond to a diameter class of 5 to 10 cm, averaged

350 pines·ha^{-1} (IEFC. Gracia et al. 2004). The role of pre-fire density of adult pines in determining density of regenerating P.halepensis populations has been repeatedly pointed (Abbas et al. 1984; Trabaud et al. 1985; Papió 1994; Sracino & Leone 1993). Environmental factors, mainly those related to water availability, have also been observed to play a role (Papió 1994; Daskalakou & Thanos 2004b). In the eastern Iberian Peninsula, post-fire density has been observed to rely mainly on the amount of pre-fire pine biomass, on the amount of branches and trunks covering the soil surface, and, to a lesser extent, on water-related variables such as precipitation and slope (Pausas et al. 2004).

Height of P.halepensis individuals increases linearly along the first post-fire decade, and despite variability is high, the average rate has been estimated in 10 and 7 cm·year^{-1} in the western and eastern Mediterranean Basin, respectively (Trabaud 2000; Arianoutsou & Ne'eman 2000). Thereafter, growth is faster and fits a power function: in Catalonia, the average height for a 40 year-old individual is about 9 m (IEFC. Gracia et al. 2004). Height growth is correlated with a variety of factors such as position on the hillside, shrub cover, and rockiness, among others (Papió 1994; Tsitsoni 1997). Thus, this parameter alone is usually not sufficient to characterize Aleppo pine development. For instance, in dense stands, pine trees might be taller but might also show lower biomass and reproductive capacity (Arianoutsou & Ne'eman 2000).

P.halepensis is thought to show a rather plastic growth response to environmental conditions, particularly rainfall and temperature, as shown by dendrochronological studies (Gindel 1944; Oppenheimer 1945; Messeri 1953; Lueck & Ans 1972; Ans 1973, 1976; Lev-Yadun et al. 1981; Liphschitz et al. 1984; Attolini et al. 1986, 1990; Nicault et al. 2001). In Catalonia, radial growth patterns of P.halepensis have been specifically addressed: a regional-scale study basing on wood cores concluded that precipitation accounted for about 65% of the variability in radial growth between provenance regions (Ferrio et al. 2003). Moreover, a local-scale study basing on the use of dendrometers conducted at Garraf (41°20'26'' N, 01°50'38'', 300 m a.s.l.) concluded that cambial activity was explained by mean temperature and precipitation, and occurred from mid-February to mid-December, with maxima in May and October. It stopped due to low winter temperatures, and was only reduced in summer, usually not involving latewood formation (Ribas et al. 2003).

6.2. Aim of the Chapter

Firstly, I aimed to test whether the occurrence of two consecutive fires at time intervals shorter than 17 years compromises post-fire recovery of Aleppo pine populations. Thus, density was recorded and compared between paired once- and twice-burnt areas.

Secondly, I aimed to test whether post-fire Aleppo pine populations show structural differences in once- and twice-burnt areas. In Chapter 3, it was reported that maximum height achieved by P.halepensis individuals was significantly higher in once- than in paired twice-burnt areas, thus pointing that populations' structure and biomass production of the dominant tree species could have resulted notably affected by fire repetition. In the present chapter, height and diameter of Aleppo pine individuals were measured in order to characterize populations' structures and to compare them between paired areas.

Thirdly, I aimed to test whether radial growth of Aleppo pine individuals differs between once- and twice-burnt areas. In Chapter 3, it was hypothesized that pre-fire fuel load variability between paired areas may have resulted in different post-fire soil nutrient availability in the short term after fire, which in turn may have caused a differential plant growth along the first post-fire years. Such hypothesis can be tested for the particular case of the dominant tree species, P.halepensis, through the use of dendrochronological techniques. Thus, dendrochronological analyses were conducted, which allowed comparing patterns of radial growth along 10 years (1994-2004) between paired areas. Additionally, foliar nutrient contents of current-year leaves of the species were analyzed, since they provide clues on soil nutritional status (Binkley 1986).

Lastly, temporal patterns of post-fire recruitment of Aleppo pine populations were characterized after ageing the trees surveyed for radial growth through dendrochronological techniques.

6.3. Methods

The survey was conducted 10 years after the 1994 fire at 14 randomly selected sites among the total 28 study sites (Table 12).

Study Site	**Fire Interval (y)**	**Elevation (m)**		**Slope (°)**		**Aspect (°)**		**Substrate Tpe**	
	Twice-burnt	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**
3	12	259	273	15	25	230	220	clays	conglomerates
5	12	225	219	15	15	60	60	conglomerates	clays
7	3	177	156	15	35	270	250	clays	clays
10	8	275	285	40	40	180	170	argillites	limestones
11	8	192	239	30	25	270	280	clays	clays
13	16	555	502	15	15	20	10	dolomites	argillites
15	5	400	412	30	30	290	300	dolomites	dolomites
16	9	460	460	0	0	0	0	limestones	limestones
20	15	758	740	10	15	280	270	dolomites	dolomites
21	13	651	628	20	15	330	340	limestones	limestones
24	11	317	289	20	15	40	40	limestones	limestones
26	9	606	637	40	40	200	220	limestones	limestones
28	11	469	459	15	20	210	210	marls	marls
29	11	419	415	25	25	70	60	marls	marls

Table 12. Fire intervals and geomorphic characteristics of study sites considered for survey on P.halepensis populations.

Field survey

In each stand, 4 transects 25 meter-long were placed perpendicularly to the slope. Along them, 1 m^2 quadrates were used as surveying units to record Aleppo pine density. Thus, the number of P.halepensis individuals was counted on a total surface of 100 m^2 per stand.

Transects were also used to randomly select 30 pine individuals per stand, which were sawed at their base (Figure 15). Their height and base diameter were measured with a metric tape and a digital metric caliper, respectively. Lastly, a base disk about 3 cm wide was obtained. In order to have a more reliable estimate of height growth, 20 extra pine individuals randomly selected per stand were also measured; those were not removed.

(a) (b)

Figure 15. The tallest and the shortest individuals of P.halepensis sawed at (a) once-burnt and (b) twice-burnt area of study site #29.

Leaf Nutrient Contents

Leaf samples of P.halepensis were collected in summer-2005 (11 years after fire) by harvesting current-year leaves at medium plant height in 6 individuals randomly selected per stand. Such samples were collected in half of study sites. They were oven-dried for 2 days at 65°C. As we were interested in the variability that fire regimes could have generated between once- and twice-burnt areas but not within an area, a single composite sample was obtained for each stand. Composite samples were finely grounded and then analyzed at the Unit of Analysis of the Autonomous University of Barcelona, Barcelona, Spain. Analyses of total carbon, nitrogen, hydrogen, and sulphur were conducted after combustion with an elemental analyzer (Carlo Erba 1108, Milan, Italy). Analyses of iron, phosphorous, magnesium, potassium, and calcium, were conducted after digestion with HNO_3, H_2O_2 and HCl by emission spectrometry in inductively coupled plasma (Perkin Elmer 4300, Norwalk, CT, USA).

Dendrochronological analyses

Dendrochronology is a widely used tool in temperate climates, since cambial activity of trees and shrubs stops during the cold season, and annual tree rings are formed (Fritts 1976). Under Mediterranean conditions, cambial activity may stop not only due to low winter temperatures, but also due to summer drought; this is the so-called *Mediterranean double stress*, which leads to the formation of *false* or *double rings*. However, Mediterranean tree species can still be used for dendrochronological purposes (Cherubini et al. 2003). In particular, P.halepensis cambial activity and radial growth patterns have been widely addressed at different locations in the Mediterranean Basin (Gindel 1944; Oppenheimer 1945; Messeri 1953; Lueck & Ans 1972; Ans 1973, 1976; Lev-Yadun et al. 1981; Liphschitz et al. 1984; Attolini et al. 1986, 1990; Nicault et al. 2001), including the eastern Iberian Peninsula (Raventós et al. 2001, 2004; Ferrio et al. 2003; Ribas et al. 2003).

Aleppo pine base disks were dried naturally in the laboratory and afterwards fine-sanded. For dating purposes, they were separated into two groups, corresponding to two provenance regions. A provenance region defines an adaptative unit in which phenotypically or genetically similar stands are found (European Council Directive 1999/105/EC; Ferrio et al. 2003). The first provenance corresponded to a coastal north-to-south strip up to 50 km wide, and comprised 7 study sites which showed an average annual precipitation of 657 mm and an average annual temperature of 14.4°C; the second provenance corresponded to an inland area and comprised also 7 study sites, which showed an average annual precipitation of 664 mm and an average annual temperature of 13.0°C (Atles Climàtic Digital de Catalunya (Pons 1996; Ninyerola et al. 2000. http://magno.uab.es/atles-climatic)).

Firstly, base disks were observed under a magnifying glass to distinguish true rings from false rings basing on latewood morphology and coloration: whereas latewood of real annual rings is characterized by intense brown color and well-defined boundaries, latewood of false rings -which are not formed by true dormancy of cambial activity, but rather during a period of droughtimposed rest (Borchert 1991, 1994) - shows light brown color and diffuse boundaries. During this first step, those rings that showed particular morphological characteristics recognizable in most individuals of a certain location were also identified (*pointer rings*, Schweingruber 1988).

Secondly, a *skeleton* of the tree ring sequence was plotted for up to 6 individuals of each study site, including both individuals from once- and twice-burnt areas. Skeleton plots corresponding to every study site were used to construct a *master chronology* for each provenance region. Both master chronologies were characterized by the same pointer rings, corresponding to years 1996 –particularly wide earlywood and thin latewood- and 1999 –characterized by a false ring very near the true latewood-. Pointer rings were dated directly by considering that outer ring corresponded to year 2004, when trees were sawed, and thus, no matching with other tree series was necessary.

Since earlywood width (i.e. radial growth) is related with precipitation patterns, and false rings are formed due to severe drought or to abnormally low temperatures, meteorological data were checked. Precipitation data for year 1996 were available only for 8 study sites over the total 14 study sites: in all cases, 1996 was a particularly rainy year, and, in some cases, annual cumulative precipitation of 1996 doubled that of 1995 (data kindly ceded by M. Ninyerola, and obtained from the Spanish Instituto Nacional de Meteorología). Temperature data for year 1999 revealed a pattern that could be related with the formation of a false ring near the real latewood: in all study sites, November temperature was around 1.5º-2ºC lower than average November temperature for the period 1996-2004 (Departament de Medi Ambient 2006. http://xarxes.meteocat.com/).

Lastly, all base disks were visually crossdated, and thus, time of recruitment was assigned. Three different cohorts were identified, corresponding to trees established in years 1994, 1995, and 1996.

Radial growth patterns were analyzed on 15 base disks per stand, which were randomly selected among those corresponding to the older cohort -10 years- in order to avoid errors resulting from age-related growth patterns. Two lines corresponding to the shortest and the longest distances from the bark to the pith were marked on each disk. Base disks were afterwards scanned at resolutions of either 800 DPI or 1200 DPI (Figure 16). Two strip images corresponding to previously-marked longest and shortest transects were obtained per base disk, on which ring width was recorded to ±0.01 mm by using the CooRecorder software (Cybis Elektronik & Data AB 2004). Since tree ring series were only 10 year-long, statistical assessment of crossdating and measurement accuracy could not be performed –series at least 30 year-long are required-. However, the fact that series were so short greatly avoided the likeliness of crossdating errors. As a caution measure, growth was not considered and compared among paired areas for every ring, but for rings grouped as marked by pointer 1999, which moreover allowed us to compare radial growth patterns between once- and twice-burnt areas in two different scenarios: a post-fire scenario (1994-1999), when soil nutrient availability is particularly high, and some years after fire (2000-2004), when soil nutrients have presumably recovered their pre-fire levels. Total radial growth along 1994-2004 was also considered.

Data analyses

Fire Recurrence

Comparisons between paired once- and twice-burnt areas were conducted by means of paired *t*-Student tests. In order to obtain the normal distributions required to perform such test, data were *log* transformed (density, height, diameter, and radial growth), or *arc sin* transformed (percentages of trees corresponding to each cohort). Foliar nutrient contents were compared between paired areas by means of Wilcoxon rank tests.

Kolmogorov-Smirnov tests were used to test normality of height and diameter frequency distributions. Values of skewness and kurtosis were also calculated. Chi-Square tests were used to compare height and diameter frequency distributions between paired areas.

(a)

(b)

Figure 16. Scanned images of 15 randomly selected base disks corresponding to individuals 10 year-old. They correspond to (a) once-burnt area, and (b) twice-burnt area of study site #5. Two strip images were afterwards obtained, corresponding to the longest and shortest transect from the bark to the pith, on which radial growth was measured to ±0.01 mm.

Precipitation after Fire

Correlation was tested between density of P.halepensis populations and precipitation following fire. In particular, correlation was tested between density in twice-burnt areas and precipitation after the first fire (by considering two time periods: September to December following fire, and September to June following fire), and between density in both once-burnt and twice-burnt areas and precipitation after the 1994 fire (by considering two time periods: September to December following fire, and September to June following fire). Precipitation values corresponded to the nearest climatic station of the Instituto Meteorológico Nacional, and were kindly ceded by M Ninyerola.

6.4. Results

Field survey

Aleppo pine density (mean ± SE) was significantly higher in once-burnt areas (25,389 ± 12,677 pines·ha^{-1}) than in paired twice-burnt areas (14,121 ± 10,131 pines·ha^{-1}) (t= 4.58, P< 0.001) (Table 13). Density of Aleppo pine was not correlated with precipitation following fire either in once- or twice-burnt areas.

Mean height of Aleppo pine individuals (mean ± SE) was significantly higher in once-burnt areas (168.8 ± 10.9 cm) than in twice-burnt ones (142.0 ± 13.0 cm) (t= 2.83, P= 0.014) (Table 13). Accordingly, mean annual increase along the first 10 post-fire years ranged from 9.1 to 23.1 cm·yr^{-1} in once-burnt areas, and from 8.7 to 23.0 cm·yr^{-1} in twice-burnt areas. It averaged (16.9 ± 1.1 cm·yr^{-1}) and (14.2 ± 1.3 cm·yr^{-1}), respectively.

Mean diameter of Aleppo pine individuals (mean ± SE) was significantly higher in once- (25.88 ± 1.54 mm) than in twice-burnt areas (23.26 ± 1.99 mm) (t= 2.26, P= 0.043) (Table 13), and so was mean basal area: 651.46 (± 70.33) mm^2 in once-burnt areas, and 541.03 (± 99.04 mm^2) in twice-burnt areas (t= 2.28, P= 0.042).

Height frequency distributions were significantly different between once- and twice-burnt areas (Chi-Square= 92.08, df= 16, P< 0.0001). In once burnt areas, height frequency distribution followed a normal pattern (d= 0.047, P< 0.10), and was only slightly platykurtic (-0.21 ± 0.18) and positively skewed (0.40 ± 0.92). In twice burnt areas, height frequency distribution did not follow a normal pattern (d= 0.105, P< 0.01); it was slightly leptokurtic (0.27 ± 0.21), and more prominently positively skewed, i.e., it showed a longer tail to larger height classes (0.85 ± 0.10) (Figure 17).

Diameter frequency distributions were not significantly different between once- and twice-burnt areas (Chi-Square= 20.78; df= 14, P= 0.107). Diameter frequency distributions did not follow a normal pattern either in once- or in twice burnt areas (d= 0.082, P< 0.01 and d= 0.091, P< 0.01, respectively). In both cases they were leptokurtic (1.58 ± 0.24 and 5.91 ± 0.27, respectively) and positively skewed (1.01 ± 0.12 and 1.66 ± 0.14, respectively), but such patterns were more prominent in twice–burnt areas (Figure 18).

Leaf Nutrient Contents

Comparison of foliar nutrient contents did not reveal significant differences between once- and twice-burnt areas for carbon, hydrogen, nitrogen, sulphur, iron, phosphorous, magnesium, potassium, or calcium (Appendix 5, pp. 171).

Study Site	**Density ($pines \cdot ha^{-1}$)**		**Height (cm)**		**Diameter (mm)**	
	Once-burnt	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**
3	1,300	300	212.1	193.2	32.18	29.19
5	14,500	600	156.3	103.4	23.10	15.88
7	4,500	1,400	174.3	201.0	28.27	31.40
10	3,200	500	189.7	192.4	31.94	36.11
11	5,400	1,300	163.3	125.5	25.30	22.68
13	112,900	35,800	231.2	230.1	29.04	27.58
15	3,800	7,300	108.9	87.9	19.06	21.40
16	12,400	2,700	177.1	102.5	25.19	18.78
20	156,600	141,800	118.0	119.0	18.69	17.87
21	2,700	600	91.1	86.6	13.90	12.78
24	11,200	400	205.3	100.1	29.49	13.99
26	7,400	500	178.7	110.0	24.62	17.70
28	150	100	152.9	158.4	27.02	28.62
29	19,400	4,400	203.4	178.5	34.57	31.71
Mean	25,389	14,121	168.8	142.0	25.88	23.26
SE	12,677	10,131	10.9	13.0	1.54	1.99

Table 13. Average density, height, and diameter of P.halepensis populations in once- and twice-burnt stands.

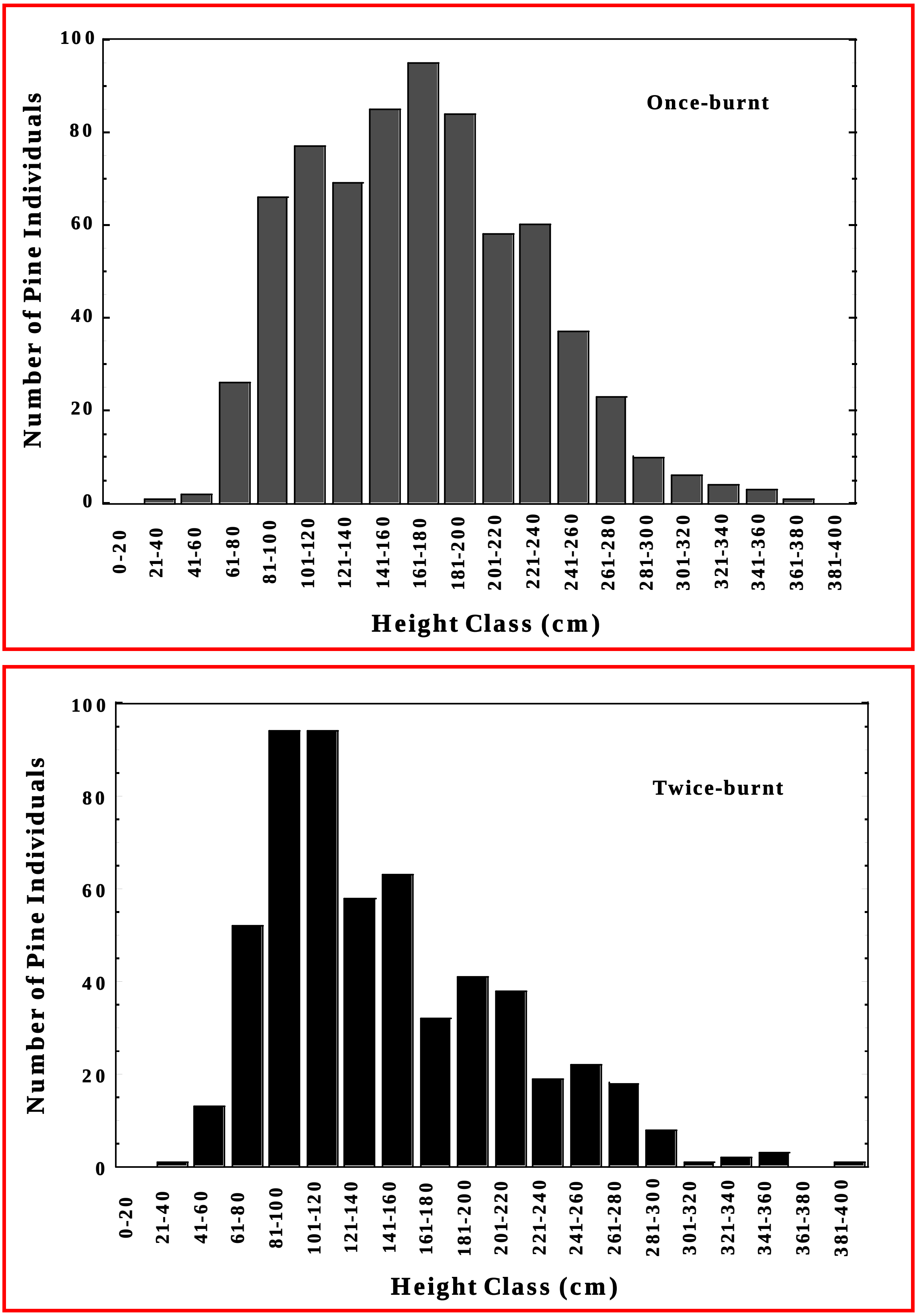

Figure 17. Height distributions of P.halepensis populations 10 years after fire in once-burnt areas (n = 707; mean ± SE = 168.8 ± 10.9 cm) and in twice-burnt areas (n = 560; mean ± SE = 142.0 ± 13.0 cm). Data from all stands were pooled.

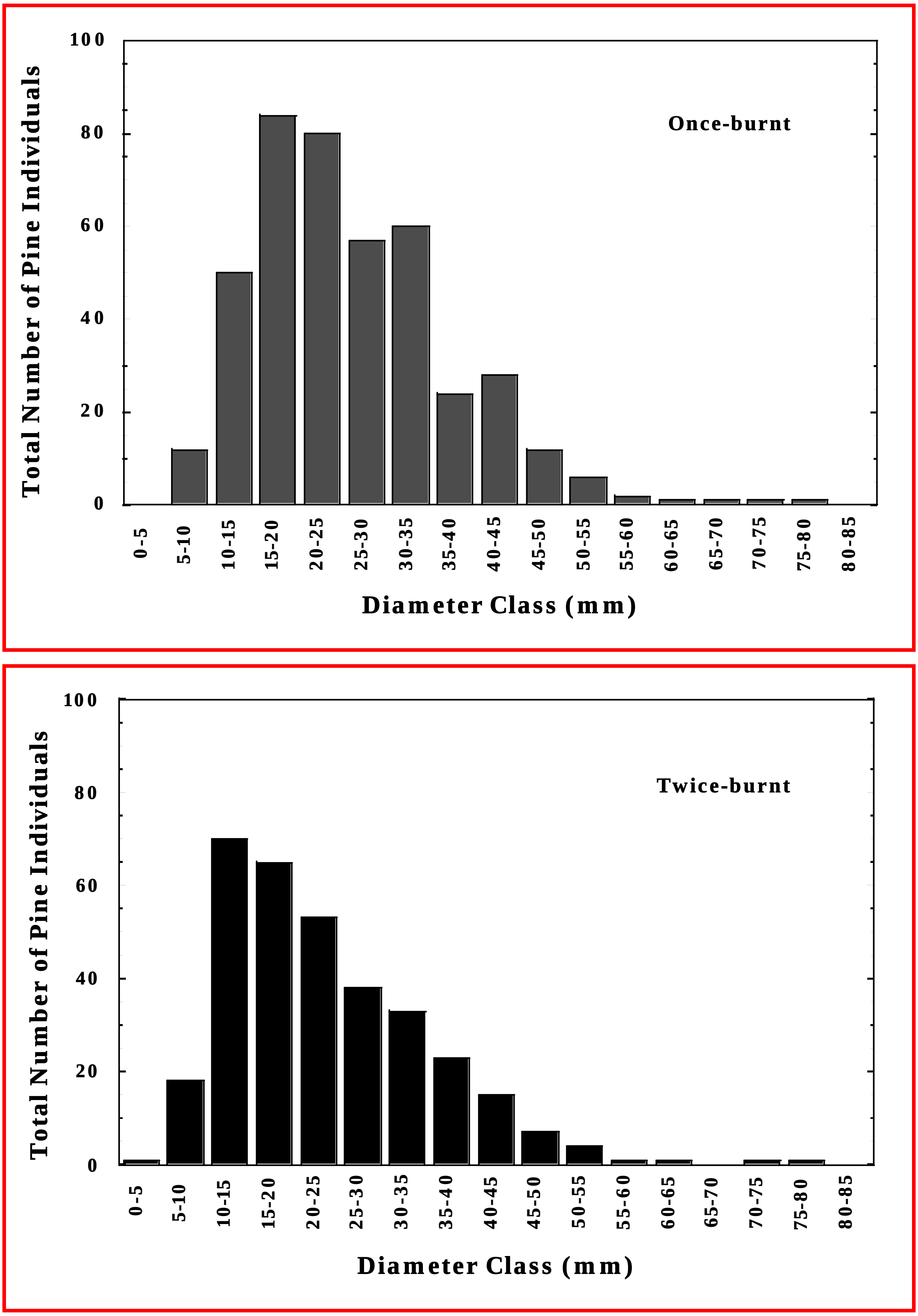

Figure 18. Diameter distributions of P.halepensis populations 10 years after fire in once-burnt areas (n = 419; mean ± SE = 25.88 ± 1.54 mm) and in twice-burnt areas (n = 332; mean ± SE = 23.26 ± 1.99 mm). Data from all stands were pooled.

Dendrochronological analyses

The 87.9 (± 3.6) % of pines in once-burnt areas and the 85.9 (± 3.4) % in twice-burnt ones were 10 year-old (1994-cohort). The 11.3 (± 3.5) % in once-burnt areas and the 13.0 (± 3.3) % in twice-burnt ones were 9 year-old (1995-cohort). Finally, the 0.8 (± 0.6) % in once-burnt areas and the 1.0 (± 0.8) % in twice-burnt ones were 8 year-old (1996-cohort). No significant differences were found between paired once- and twice-burnt areas in the percentages of trees corresponding to the 1994 or the 1995 cohorts. The 1996-cohort was only represented in two once-burnt and in two twice-burnt areas, so statistical comparison between paired areas was not performed.

Total radial growth accumulated from 1994 to 2004 was significantly higher in once-burnt areas than in twice-burnt ones (*t*= 2.37, *P*= 0.036). Growth patterns, however, were not constant along the studied period: radial growth was significantly higher in once-burnt areas along the period 1994-1999 (*t*= 2.75, *P*= 0.018), whereas no significant differences were found along the period 2000-2004 (*t*= 0.35, *P*= 0.733) (Table 14).

Study Site	**Growth per periods (mm)**					
	1994-1999		**2000-2004**		**1994-2004**	
	Once-burnt	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**
3	5.40	4.82	8.81	10.63	14.21	15.45
5	4.06	2.13	4.90	5.00	8.97	7.13
7	3.20	4.36	10.41	9.60	13.62	13.96
10	3.43	3.84	11.88	13.17	15.32	17.00
11	5.61	3.06	5.34	6.87	10.95	9.93
13	6.48	4.86	6.10	6.72	12.58	11.58
16	3.89	2.45	7.02	5.80	10.91	8.25
20	3.84	2.81	3.93	4.34	7.78	7.15
21	1.90	2.01	4.09	4.08	5.99	6.09
24	3.68	2.13	6.11	4.04	9.79	6.17
26	3.55	2.63	7.59	7.51	11.14	10.14
28	4.69	4.61	9.02	7.44	13.71	12.05
29	4.73	4.25	11.27	10.26	16.00	14.51
Mean	4.19	3.38	7.42	7.34	11.61	10.72
SE	0.32	0.29	0.71	0.76	0.80	0.99

Table 14. Mean radial growth of P.halepensis in once- and twice-burnt areas along the periods 1994-1999, 2000-2004, and total (1994-2004).

6.5. Discussion

The occurrence of two fires at fire intervals shorter than 17 years resulted in a density and growth decline of post-fire P.halepensis populations relative to the occurrence of a single fire, as observed 10 years after fire. In areas burnt twice, P.halepensis populations were significantly less dense, and were characterized by a greater number of shorter and thinner individuals. Moreover, radial growth of the species was lower along the first post-fire years (1994-1999) in such areas.

Time of recruitment of P.halepensis was not affected by fire repetition. Both in once- and twice-burnt areas, recruitment occurred mainly the same year of the fire (1994), when 87% of pine individuals established. Only 12% of individuals established along the next year (1995), and very few individuals established later (1996), accounting for 1% of the total. This result agrees with previous studies concluding that seed germination and seedling emergence occur mostly in the form of a massive wave during the first post-fire growing season. Thus, the majority of seeds are transformed into seedlings in the same year of the fire (November-December). At some locations, delayed seedling establishment (January-February), or a bimodal pattern of establishment with peaks in winter and spring following fire were also reported (Daskalakou & Thanos 1996, 2004a). Such field observations agree with previous laboratory studies showing optimum germination temperatures of 15-20 ºC, and the achievement of maximum germination values (80-100%) in 2 or 3 weeks either in darkness or white light (Thanos 2000). Under field conditions, a time lag is expected: seedling emergence occurs in about 4 to 6 weeks after fire, and thus is first observed at least one month after the onset of the rainy season (Daskalakou & Thanos 2004a). Fall-winter germination has been considered an adaptation to Mediterranean climatic conditions, since when seed germination is achieved early during autumn, seedlings can take advantage of most of the wet season before summer drought (Thanos & Skordilis 1987; Skordilis & Thanos 1995).

Density of post-fire P.halepensis populations ranged widely, between hundreds (100 pines·ha^{-1} was the minimum value) and thousands of hundreds (156,600 pines·ha^{-1} was the maximum value). Such range is similar to that previously reported for 8 year-old stands in the eastern Iberian Peninsula: 60 to 204,000 pines·ha^{-1} (Pausas et al. 2004). Density significantly declined due to fire repetition, and most study sites showed densities one or two levels of magnitude lower in twice- than in paired once-burnt areas. Thus, average density of Aleppo pine populations was 55% higher in areas burnt only once. Such decline is mainly related to the reproductive traits of the species, which is a seeder whose regeneration depends exclusively upon post-fire release and establishment of seeds kept in a canopy seed bank (Daskalakou & Thanos 1996). Namely, P.halepensis populations require a certain time interval between consecutive fires to accumulate a sufficient seed bank allowing post-fire regeneration at similar densities to parent populations (Keeley et al. 1999).

P.halepensis is characterized by an early maturity: in Catalonia, the earliest production of viable seeds has been observed as soon as 7 years after fire (Verkaik & Espelta, personal communication). An entire even-aged population of P.halepensis is estimated to be reproductive about 12-20 years after fire (Thanos et al. 1998). In the present survey, fire intervals in twice-burnt areas ranged between 3 and 16 years. I suggest that 15 years would be the minimum fire interval required for maintenance of P.halepensis populations. The only study site where density was of the same order in both types of areas was characterized by a fire interval 15 year-long, and nearby, unburnt mature forests that could act as seed sources were not present. However, the twice-burnt area corresponding to site #13, characterized by a fire interval 16 year-long, showed much lower pine density than its paired once-burnt area. Post-fire density of P.halepensis populations has been observed to be highly site-specific, and to rely on a variety of factors such as topography, pre-fire pine biomass, amount of pine remains covering the soil, competition, pests, and herbivory, which were not considered, and which may explain the variability observed among study sites (Tsitsoni 1997; Saracino & Leone 1993; Papió 1994, Arianoutsou & Ne'eman 2000; Pausas et al. 2004). In the present study, post-fire precipitation along one and two growing seasons was not observed to determine post-fire density either in once- or in twice-burnt areas. However, other environmental factors might have played a relevant role.

Noticeably, growth of Aleppo pine declined in areas burnt twice, as previously observed in relation to maximum height of the species (Chapter 3). Mean height was 26.7 cm lower and mean diameter was 2.62 mm smaller than in paired areas burnt only once. Consequently, population structure differed, in such a way that lower and thinner pine individuals were more represented in twice-burnt areas. P.halepensis is a shade intolerant species: in many cases, suppressed individuals of shade intolerant species tend to etiolate (quickly extend in height towards the light) to approach the height of more competitive individuals and thus compete for light (Morgan & Smith 1979; Hara et al. 1991). Thus, in dense stands, Aleppo pine individuals have been reported to be higher, but also thinner (Arianoutsou & Ne'eman 2000). Consequently, competition for light does not explain the patterns observed in the present survey. Even if such density-dependent effects would have occurred, our results imply higher biomass production in once- relative to paired twice-burnt areas.

According to radial growth patterns, size differences observed 10 years after fire derive from a differential growth of P.halepensis in paired areas along the first post-fire years (1994-1999). Given that paired once- and twice-burnt areas are very similar as for environmental conditions, radial growth differences are not likely to result from differences in water availability. I hypothesize that they might be attributed to differential soil nutrient availability between paired areas during the first years after fire (Chapter 3). Longer fire intervals in once-burnt areas would have allowed further vegetation development and higher fuel accumulation, a fact which would have resulted in higher soil organic matter mineralization and ash deposition (Giovannini et al. 1989; Kutiel & Kutiel 1989; Romanyà et al. 2001), thus enhancing plant growth in the short-term (Christensen & Muller 1975) comparatively more than in twice-burnt areas. As soil nutrient contents recovered pre-fire levels in both types of areas (Giovannini et al. 1989; Kutiel & Kutiel 1989; Serrasolses & Vallejo 1999), growth would have equaled, as observed from year 2000. Eleven years after fire, foliar nutrient contents of P.halepensis were similar in paired areas, thus supporting the absence of growth differences revealed by radial growth patterns.

Post-fire P.halepensis growth has been previously related to pre-fire fuel loads through ash effects, in such a way that, the higher the pre-fire fuel loads, the higher the ash amounts and the faster the growth. At Mount Carmel (Israel), pine seedlings grew faster when they occupied the microsites left by mother trees, which was attributed to the fact that big burnt trees result in higher amounts of ashes (Ne’eman et al. 1992; Ne’eman & Izhaki 1999). In València, pine seedlings grew faster when they occupied sites burnt at high fire severity, which was attributed to higher post-fire soil nutrient availability, particularly of phosphorous (Pausas et al. 2003). Our results show provide further evidence on the existence of a relation between post-fire growth of P.halepensis and pre-fire fuel load variability, in this case as related to recent fire history.

The foliar nutrient contents observed in current-year leaves of P.halepensis agreed well with the normal ranges found in the Iberian Peninsula and reported by the FFCC (in brackets) (Stefan et al. 1997). Phosphorous was 0.73 in once-burnt areas and 0.79 $mg·g^{-1}$ in twice-burnt areas (0.60-1.07 $mg·g^{-1}$), potassium was 3.7 and 4.0 $mg·g^{-1}$ (3.57-6.88 $mg·g^{-1}$), magnesium was 1.9 and 1.8 $mg·g^{-1}$ (1.49-2.74 $mg·g^{-1}$), and calcium was 6.7 and 6.5 $mg·g^{-1}$ (3.28-7.22 $mg·g^{-1}$). Only nitrogen content was slightly lower than normal, 9.4 $mg·g^{-1}$ in both types of areas (9.88-14.98 $mg·g^{-1}$). Carbon contents were high, as expected for current-year leaves (López-Serrano et al. 2005).

6.6. Conclusions

The occurrence of two fires at fire intervals shorter than 17 years resulted in a density and growth decline of post-fire P.halepensis populations relative to the occurrence of a single fire, and thus, in a reduced biomass production of the species. Ten years after fire, P.halepensis populations were significantly less dense, and were characterized by a greater number of shorter and thinner individuals in twice-burnt areas. Density decline was related to life history traits of the species. It is suggested that fire intervals at least 15 year-long are required by Aleppo pine populations to accumulate a critical seed storage allowing successful post-fire regeneration.

Growth decline resulted from a lower growth of the species in twice-burnt areas along the first post-fire years, from 1994 to 1999. It is hypothesized that it this pattern might be related to pre-fire fuel load variability between paired areas, as resulting from varying fire intervals. Radial growth equaled in both types of areas from the year 2000 on, which is attributed to the recovery of pre-fire levels of soil nutrients. Foliar nutrient contents were similar in paired areas 11 years after fire, thus supporting the absence of current growth differences.

As a consequence of all the above-mentioned, a resilience loss is observed in P.halepensis populations submitted to fire recurrence levels of two fires at intervals shorter than 17 years.

Time of recruitment did not vary in relation to recent fire history, and occurred mainly the same year of the fire (1994) in both types of areas.

Density was observed to widely vary among sites, namely, to be highly site-specific. It did not show correlation with precipitation shortly after fire.

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Chapter 7

Floristic Composition of Post-Fire *P.halepensis* Communities: Richness, Diversity, Dominance, and Abundances

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7.1. Introduction

Reburning at short fire intervals has been evidenced to show relevant effects on the floristic composition of Mediterranean communities. Particularly, it can lead to the local elimination of some species that completely fail to regenerate (Zedler et al. 1983; Haidinger & Keeley 1993; Yates et al. 2003). Subsequent local differences in vegetation composition are thought to remain for a long time, since depleted species will need to establish from surrounding, unburnt patches (Zedler et al. 1983). In Californian chaparral and coastal sage scrub, substantial declines in the frequency of 4 common species showing different regenerative strategies (Ceanothus oliganthus, an obligate seeder; Xylococcus bicolor, a sprouter non-seeder; and Adenostoma fasciculatum and Salvia apiana, sprouter seeders) were reported after the occurrence of two fires at an interval of 1 year (Zedler et al. 1983). Moreover, an expansion of subshrubs and herbs was qualitatively observed, which considered capable of enhancing spread of future fires. Similar results were found by Haidinger & Keeley (1993) on sites burnt once, twice, or three times along a 6 year-long period, since post-fire establishment of the dominant A.fasciculatum and S.apiana was reduced, and the abundance of exotic herb species was enhanced. Yates et al. (2003) considered the impact of two consecutive wildfires at an interval of 3 years on granite outcrop vegetation in southwestern Australia, and reported reduced seedling densities of all taxa, and complete regeneration failure of some species.

Several later studies have also suggested that high fire recurrence may result in shifts in fuel characteristics that promote fire propagation (*positive fire/grass feedback*) (Trabaud 1991; Keeley et al. 1999). This topic is well-addressed for the case of invaders (see Brooks et al. 2004 for a review). When introduced grasses invade sites otherwise dominated by woody species, they create a more continuous and flammable fuel that enhances fire recurrence, and, sometimes, fire intensity (D'Antonio & Vitousek 1992). In the northeastern Iberian Peninsula, field studies and modeling predictions have confirmed the existence of a fire/grass positive feedback in P.halepensis communities where the large, exotic, resprouting tussock grass A.mauritanica is enhanced by fire recurrence (Vilà et al. 2001; Lloret et al 2003; Grigulis et al 2005).

Fire repetition at varying fire intervals may result in differing species richness. The intermediate disturbance hypothesis, which states that diversity will be the highest at some intermediate frequency of disturbance preventing competitive exclusion (Connell 1978; Huston 1994), was tested in South African fynbos by Schwilk et al. (1997). The study design was conceived to compare sites at the same stage of post-fire succession, and fire intervals of more than 40 years, around 15 years, and between 4 and 6 years were considered. Fire frequency was reported to result in contrasting effects on species richness at different spatial scales, which was ascribed to patterns of spatial heterogeneity generated through fire repetition. Intermediate fire intervals of around 15 years, which are commonly used to manage large proteoid shrubs, were not found to generate the highest species richness.

Fire recurrence effects on floristic composition have been specifically addressed on Q.coccifera garrigues of the western Mediterranean Basin. In southern France, Trabaud (1991, 1992) used prescribed fires in a long-term experiment to deal with the effects of fire season and frequency, and considered sites burnt in spring or autumn every 2, 3, and 6 years. According to classical autosuccessional approaches, the community was considered highly resilient to fire, since whatever the fire regime, 53% of species present before the fires were also present 19 years later. Fire recurrence was observed to favor subshrubs and herbs, and to disfavor some phanaerophytes. In the eastern Iberian Peninsula, the occurrence of 1, 2, or 3 wildfires along 16 years has been considered by Delitti et al. (2005). Three and a half years after fire, species richness was enhanced by the increase of herb and subshrub species at sites showing both the highest level of fire recurrence and short time intervals before the last fire. However, other species, such as U.parviflorus, were depleted at such sites.

Lastly, modeling approaches based on plant functional types have been widely used in MTEs to simulate vegetation dynamics under fire regimes characterized by varying fire intervals. Modeling allows for predicting shifts in composition and structure of plant communities that would be hard to detect basing on field studies, since information on fire occurrence at a location usually extends for fer decades, whereas the longevity of some species and the length of fire intervals can be on the order of several decades (Franklin et al. 2004). In the eastern Iberian Peninsula, the models FATE (Moore & Noble 1990) and BROLLA (Pausas 1998), despite based on different approaches, have produced quite similar outputs (Pausas 1999; Lloret et al. 2003). The repeated occurrence of fire at short time intervals –every 5 or 10 years- and over time periods on the order of hundreds of years enhanced the abundance of lower-structured and shorter-lived species, thus resulting in a total biomass decrease (Pausas 1999), promoted the alien A.mauritanica, decreased the abundance of the resprouter tree Quercus and eliminated the seeder tree Pinus (Lloret et al. 2003).

Overall, previous works dealing with the effects of fire repetition on the floristic composition of Mediterranean communities have reported the local extinction of some particular species, the promotion of subshrubs and herbs to the detriment of shrubs, and altered spatial patterns of species richness. The likelihood of shifts in fuel characteristics resulting in enhanced fire occurrence has been particularly stressed. Moreover, and on a long time scale, modeling approaches predict shifts in the abundance of plant functional types.

In the present work, fire repetition at fire intervals shorter than 17 years was observed to result in reduced biomass production and structural simplification of post-fire P.halepensis communities (Chapter 3). It was hypothesized that such fact may be due to lower soil nutrient availability along the first post-fire years in twice-burnt areas, as deriving from lower pre-fire fuel loads than in once-burnt areas. The hypothesis was tested for the dominant tree species: P.halepensis showed a significantly lower growth in twice-burnt areas exclusively along 1995-1999, which resulted in an overall lower growth along 1994-2004 (Chapter 6). However, other evidences point to the existence of shifts in floristic composition towards the greater abundance of shorter-sized species that may also explain the patterns observed at community level in twice-burnt areas, such as the higher cover of shrub layer, the lower cover of tree layer (Chapter 3), and the density decline of P.halepensis populations (Chapter 6).

7.2. Aim of the Chapter

The present study addresses fire recurrence effects on floristic composition of P.halepensis communities in Catalonia, and was conducted 10 years after fire.

Relative to previous works considering the effects of fire repetition on composition of Mediterranean plant communities, it provides:

(1) a regional approach, since 14 study sites were surveyed, which were distributed over a large area of Catalonia, and showed a range of climatic and geomorphic conditions,

(2) a design which specifically addresses the effects of fire recurrence at paired areas that share very similar climatic and geomorphic conditions, and differ mainly in the number of fire events that have suffered along 20 years,

(3) a synchronic approach that allows surveying vegetation at the same successional stages, and thus avoids confounding fire recurrence effects with the effects of time since last fire.

Importantly, the suitability of the autosuccessional model, proposed by Hanes (1971) for describing post-fire recovery of Mediterranean plant communities, will be tested in the particular case of P.halepensis communities, which are currently submitted to scenarios of high fire recurrence levels.

The main question was whether the occurrence of two consecutive fires at time intervals shorter than 17 years modified, relative to the occurrence of a single fire along, at least, 19 years:

? species richness in nested plots,
? species-area correlations,
? diversity and equitability,
? dominance,
? relative abundance of single species,
? relative abundance of species grouped according to regenerative strategy and Raunkjaer biological types,

7.3. Methods

Field survey

The survey was conducted 10 years after the 1994 fire along the flowering period (mid-March to mid-June), at 14 randomly selected study sites over the total 28 study sites (Table 15).

Study Site	Fire Interval (y)	Elevation (m)		Slope (°)		Aspect (°)		Substrate Type	
	Twice-burnt	Once-burnt	Twice-burnt	Once-burnt	Twice-burnt	Once-burnt	Twice-burnt	Once-burnt	Twice-burnt
3	12	259	273	15	25	230	220	clays	conglomerates
5	12	225	219	15	15	60	60	conglomerates	clays
9	13	455	465	30	30	30	40	clays	argillites
10	8	275	285	40	40	180	170	argillites	limestones
13	16	555	502	15	15	20	10	dolomites	argillites
15	5	400	412	30	30	290	300	dolomites	dolomites
16	9	480	470	20	15	80	80	limestones	limestones
17	16	239	243	10	0	0	120	gravels	gravels
18	12	247	251	0	0	0	0	marls	marls
20	15	758	740	10	15	280	270	dolomites	dolomites
25	7	549	570	0	0	0	0	marls	marls
26	9	606	637	40	40	220	220	limestones	limestones
28	11	469	459	15	15	210	210	marls	marls
29	11	419	415	25	25	70	60	marls	marls

Table 15. Fire intervals and geomorphic characteristics of study sites considered for survey on floristic composition of P.halepensis communities.

In each once- and twice-burnt area, an area 375 m^2 was selected around the GPS-positioned central point of stand. Four transects 25 meter-long were placed in it, perpendicularly to the slope and in such a way that they were separated 5 meters from each other. Over such area, and at nested plots of 1, 5, 10, 25, 125, 250, and 375 m^2, all vascular species present were recorded. Along such transects, the point-interception sampling procedure was used to record, every 50 cm, all vascular species present.

Data analyses

Floristic composition of plant communities was assessed by considering:

(1) Species richness (*S*) in nested plots (data *log* transformed);

(2) Species-area regressions for *log* transformed data from nested plots;

(3) Shannon's Diversity Index ($H' = -?\ p_i \cdot \log_2 p_i$, where $p_i = N_i / N$, N_i = number of interceptions of a single species, N = total number of interceptions) (Shannon & Weaver 1964), and Equitability following Shannon ($J = H' / H'_{max} = -?\ p_i \log_2 p_i / \log_2 S$, where S = total number of species) (from transect records);

(4) Dominance indices:
(a) of the most abundant species ($DI(1) = 100\ (N_I / N)$),
(b) of the two more abundant species ($DI(2) = 100\ (N_I + N_{II} / N)$),
where N_I and N_{II} were the number of contacts of the first and second most abundant species, respectively, and N was the total number of interceptions of all species sampled (from transect records, data *log* transformed);

(5) Relative abundance of 23 species, those present at least in half study areas (from transect records, data *log* transformed);

(6) Relative abundance of the 3 regenerative strategies (resprouter, seeder, and resprouter-seeder following Clemente et al. 1996; Cavero & Ederra 1999; Lloret et al. 2003), obtained by grouping all species according to their ability to regenerate after fire (from transect records, data *log* transformed);

(7) Relative abundance of Raunkjaer biological types (Raunkjaer 1934), based on the position and degree of protection of permanent buds: macrophanerophytes (trees), nanophanerophytes (shrubs), other phanerophytes (palms and vines), chamaephytes (scrubs), geophytes, hemicriptophytes (perennial forbs and grasses), and therophytes (annuals)

(after Bolòs et al. 1990). Obtained by grouping all species according to such types (from transect records, data *log* transformed).

Values obtained for paired once- and twice-burnt areas were afterwards compared by means of paired *t*-Student tests.

Floristic composition similarity between paired once- and twice-burnt areas was assessed by calculating the quantitative Jaccard's Similarity Index (Jaccard 1912) for all vascular species as $JI = S_{12} / (S_{12} + S_1 + S_2)$, where S_1 = number species present only in once-burnt areas, S_2 = number of species present only in twice-burnt areas, and S_{12} = number of species common to once- and twice-burnt areas. *JI* was afterwards used as the dependent variable in a forward stepwise multiple regression model to test correlation with climatic variables (annual and summer temperature, annual and summer precipitation, and real solar radiation) and fire interval.

7.4. Results

No significant differences in species richness (*S*) were found between paired once- and twice-burnt areas for any plot size considered. The highest difference corresponded to the 10 m^2 plot (t= -1.83; P= 0.091), whereas the 25 m^2 plot accounted for the lowest difference (t= 0.24; P= 0.811) (Table 16).

Study Site	**1 m^2**		**5 m^2**		**10 m^2**		**25 m^2**		**125 m^2**		**250 m^2**		**375 m^2**	
	Once-burnt	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**
3	7	9	8	12	13	13	22	20	26	26	32	29	35	30
5	10	15	18	19	19	23	32	25	37	30	46	34	48	40
9	14	10	20	25	22	32	35	37	48	49	58	57	63	58
10	4	7	10	15	15	22	25	29	30	33	35	35	39	39
13	5	18	12	29	16	29	23	43	34	53	47	61	53	66
15	12	13	27	24	31	30	49	37	61	48	64	56	65	59
16	4	10	10	20	19	28	26	30	29	36	33	40	34	42
17	11	10	19	24	27	27	32	32	44	46	50	50	53	52
18	10	8	16	13	19	18	24	25	35	34	38	40	39	42
20	8	16	15	27	23	35	41	46	51	56	54	60	55	61
25	10	9	21	15	28	20	31	23	54	45	59	52	75	55
26	10	13	21	18	26	26	33	32	43	36	50	40	51	40
28	9	4	14	8	22	18	31	20	44	30	47	34	49	38
29	8	10	18	23	27	30	38	39	46	47	48	55	54	57
Mean	8.7	10.9	16.4	19.4	21.9	25.1	31.6	31.3	41.6	40.6	47.2	45.9	50.9	48.5
SE	0.8	1.0	1.4	1.7	1.4	1.7	2.0	2.2	2.7	2.6	2.6	2.9	3.1	2.9

Table 16. Species richness (*S*) in nested plots of 1, 5, 10, 25, 125, 250, and 375 m^2.

Log-log linear regressions well described the species-area correlations for every once- and twice-burnt area (R^2 ranged from 0.85 to 0.99; all $P < 0.005$) (Table 17). However, slopes were significantly higher in once- than in twice-burnt areas (t= 2.73, $P= 0.017$). No differences were found for intercepts.

Study Site	**Once-burnt areas**					**Twice-burnt areas**				
	Slope	**Intercept**	R^2	F	P	**Slope**	**Intercept**	R^2	F	P
3	0.290	0.817	0.94	78.28	<0.001	0.216	0.944	0.98	200.50	<0.001
5	0.259	1.046	0.96	126.27	<0.001	0.153	1.181	0.98	254.86	<0.001
9	0.263	1.129	0.99	363.09	<0.001	0.267	1.138	0.90	46.27	0.001
10	0.360	0.733	0.92	60.88	0.001	0.261	0.975	0.88	37.27	0.002
13	0.377	0.777	0.98	252.76	<0.001	0.214	1.281	0.98	213.69	<0.001
15	0.272	1.191	0.91	52.86	0.001	0.241	1.185	0.96	131.65	<0.001
16	0.333	0.775	0.85	29.34	0.003	0.215	1.117	0.88	36.08	0.002
17	0.256	1.103	0.97	140.04	<0.001	0.254	1.117	0.92	59.08	0.001
18	0.231	1.032	0.99	357.17	<0.001	0.272	0.945	0.98	204.28	<0.001
20	0.328	0.985	0.92	59.00	0.001	0.219	1.275	0.94	73.96	<0.001
25	0.314	1.064	0.98	210.65	<0.001	0.313	0.960	0.99	645.27	<0.001
26	0.258	1.097	0.94	82.68	<0.001	0.189	1.161	0.92	59.13	0.001
28	0.293	0.994	0.96	115.46	<0.001	0.363	0.708	0.92	57.85	0.001
29	0.296	1.033	0.90	45.08	0.001	0.268	1.125	0.91	51.59	0.001
Mean	0.295	0.984				0.246	1.079			
SE	0.011	0.039				0.014	0.042			

Table 17. Slopes, intercepts and significance of *log-log* linear regressions for species-area curves ($\log S = z \log A + \log w$, where S = species richness and A = area)

Shannon's Diversity Index (*H'*) and Equitability following Shannon (*J*) for transect records were not significantly different between paired once- and twice-burnt areas (Table 18).

Dominance indices, *DI(1)* and *DI(2)* were both significantly higher in twice-burnt areas (t=-2.435, P=0.03 and t=-2.462, P=0.029, respectively) (Table 19).

Study Site	**Shannon (*H'*)**		**Equitativity (*J*)**	
	Once-burnt	**Twice-burnt**	**Once-burnt**	**Twice-burnt**
3	3.53	3.27	0.77	0.80
5	3.48	2.81	0.77	0.67
9	3.74	3.75	0.74	0.78
10	2.38	2.90	0.58	0.63
13	3.11	3.54	0.68	0.72
15	4.35	3.47	0.84	0.71
16	3.39	3.04	0.77	0.65
17	3.72	3.47	0.79	0.74
18	3.76	4.02	0.83	0.85
20	3.49	3.74	0.73	0.74
25	3.62	3.93	0.74	0.79
26	3.16	3.45	0.70	0.75
28	3.08	2.32	0.70	0.65
29	3.61	3.46	0.78	0.74
Mean	**3.46**	**3.37**	**0.74**	**0.73**
SE	**0.12**	**0.12**	**0.02**	**0.02**

Table 18. Values of Shannon's Diversity Index ($H'= -?\ p_i \cdot \log_2 p_i$, where $p_i = N_i / N$, N_i = number of interceptions of a single species, N = total number of interceptions), and equitability following Shannon ($J= H'/\ H'_{max} = -?\ p_i \log_2 p_i\ /\ \log_2 S$, where S= total number of species) in once- and twice-burnt areas.

Comparisons of relative abundance of species revealed that:
(a) among the 23 species present al least in half study areas, only one showed significantly different values of abundance: P.halepensis was more abundant in once-burnt areas than in twice-burnt ones (*t*= 3.61, *P*= 0.003) (Table 20),
(b) when species were grouped according to their regenerative strategy, there were no significant differences for any category considered (Table 21);
(c) when species were grouped according to their Raunkjaer biological type, there were significant differences in the abundances of macrophanerophytes, which were significantly more abundant in once-burnt areas (*t*= 3.07, *P*=0.009), and nanophanerophytes, which were significantly more abundant in twice-burnt ones (*t*= -2.69, *P*= 0.022) (Fig. 19). P.halepensis was afterwards excluded from the analysis, and differences disappeared for macrophanerophytes, whereas nanophanerophytes remained to be significantly more abundant in twice-burnt areas (*t*= -2.23, *P*= 0.044).

Study Site	**Once-burnt areas**			**Twice-burnt areas**		
	Dominant species	***DI(1)***	***DI(2)***	**Dominant species**	***DI(1)***	***DI(2)***
3	Ulex parviflorus Rosmarinus officinalis	21.30	35.08	Ulex parviflorus Pistacia lentiscus	28.12	39.11
5	Rosmarinus officinalis Pistacia lentiscus	18.82	35.42	Rosmarinus officinalis Pistacia lentiscus	41.04	55.78
9	Brachypodium phoenicoides Rubia peregrina	22.66	35.79	Brachypodium phoenicoides Dorycnium pentaphyllum	26.98	40.06
10	Rosmarinus officinalis Brachypodium retusum	41.30	70.65	Rosmarinus officinalis Brachypodium retusum	37.11	65.63
13	Pinus halepensis Rubus ulmifolius	35.36	50.42	Pinus halepensis Rubia peregrina	27.13	42.53
15	Brachypodium phoenicoides Rosmarinus officinalis	17.21	27.60	Brachypodium retusum Quercus coccifera	26.82	48.40
16	Quercus coccifera Rosmarinus officinalis	27.02	41.67	Quercus coccifera Brachypodium retusum	39.60	63.01
17	Ampelodesmos mauritanica Brachypodium retusum	20.70	39.49	Quercus coccifera Brachypodium retusum	28.83	51.84
18	Brachypodium retusum Pinus halepensis	17.42	30.93	Ampelodesmos mauritanica Pinus halepensis	14.77	28.00
20	Pinus halepensis Quercus coccifera	21.06	36.98	Brachypodium retusum Pinus halepensis	22.78	40.39
25	Ulex parviflorus Rosmarinus officinalis	19.35	34.44	Brachypodium phoenicoides Ulex parviflorus	20.92	38.51
26	Quercus coccifera Ulex parviflorus	29.23	51.86	Quercus coccifera Brachypodium retusum	24.60	43.13
28	Rosmarinus officinalis Brachypodium phoenicoides	34.54	49.00	Rosmarinus officinalis Thymus vulgaris	54.84	64.52
29	Pinus halepensis Dorycnium pentaphyllum	16.99	31.64	Brachypodium phoenicoides Brachypodium retusum	27.69	42.42
Mean		24.50	40.78		30.09	47.38
SE		2.08	3.03		2.69	3.01

Table 19. Dominant species and values of dominance indices: *DI(1)* considers only the most abundant species (*DI(1)*= 100 (N_I / N)), whereas *DI(2)* considers the two most abundant species (*DI(2)*= 100 ($N_I + N_{II}$ / N)) (N_I and N_{II} were the number of contacts of the first and second most abundant species, respectively, and N was the total number of interceptions of all species sampled).

Species Name	**Regenerative Strategy**	**Biological Type**	**Relative Abundance**			
			Once-burnt		**Twice-burnt**	
			Mean	**SE**	**Mean**	**SE**
Aphyllantes monspeliensis	Resprouter-seeder	Hemicriptophyte	0.026	0.008	0.027	0.009
Arbutus unedo	Resprouter	Macrophanerophyte	0.012	0.005	0.003	0.002
Bupleurum fruticescens	Seeder	Nanophanerophyte	0.007	0.003	0.010	0.003
Brachypodium phoenicoides	Resprouter	Hemicriptophyte	0.080	0.019	0.082	0.027
Brachypodium retusum	Resprouter	Chamaephyte	0.121	0.020	0.140	0.026
Carex hallerana	Resprouter	Hemicriptophyte	0.004	0.002	0.002	0.001
Daphne gnidium	Resprouter	Nanophanerophyte	0.002	0.001	0.001	0.001
Dorycnium pentaphyllum	Resprouter-seeder	Chamaephyte	0.055	0.016	0.051	0.011
Erica multiflora	Resprouter	Nanophanerophyte	0.008	0.005	0.011	0.006
Fumana ericoides	Seeder	Chamaephyte	0.017	0.010	0.011	0.006
Genista scorpius	Seeder	Nanophanerophyte	0.015	0.006	0.030	0.011
Juniperus oxycedrus	Resprouter	Macrophanerophyte	0.006	0.002	0.005	0.003
Ononis minutissima	Seeder	Chamaephyte	0.019	0.009	0.011	0.005
Pinus halepensis	Seeder	Macrophanerophyte	0.087	0.027	0.055	0.022
Pistacia lentiscus	Resprouter	Macrophanerophyte	0.054	0.016	0.042	0.013
Polygala rupestris	Resprouter-seeder	Chamaephyte	0.007	0.003	0.006	0.002
Quercus coccifera	Resprouter	Nanophanerophyte	0.069	0.027	0.097	0.036
Quercus humilis / faginea	Resprouter	Macrophanerophyte	0.007	0.004	0.008	0.004
Quercus ilex	Resprouter	Macrophanerophyte	0.011	0.004	0.014	0.005
Rhamnus alaternus	Resprouter	Nanophanerophyte	0.003	0.002	0.006	0.003
Rosmarinus officinalis	Seeder	Nanophanerophyte	0.125	0.033	0.129	0.047
Rubia peregrina	Resprouter-seeder	other Phanerophytes	0.048	0.013	0.032	0.011
Rubus ulmifolius	Resprouter-seeder	other Phanerophytes	0.022	0.013	0.014	0.008

Table 20. Regenerative strategy, Raunkjaer biological type, and mean relative abundance of the 23 species present at least in half study areas.

Study Site	**Resprouter**		**Seeder**		**Resprouter-seeder**	
	Once-burnt	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**
3	0.369	0.524	0.491	0.406	0.140	0.070
5	0.579	0.408	0.365	0.588	0.055	0.004
9	0.614	0.691	0.060	0.131	0.325	0.178
10	0.511	0.467	0.474	0.459	0.015	0.075
13	0.335	0.336	0.370	0.370	0.295	0.294
15	0.541	0.643	0.289	0.228	0.170	0.129
16	0.699	0.757	0.250	0.150	0.051	0.092
17	0.494	0.757	0.237	0.080	0.269	0.163
18	0.456	0.310	0.189	0.307	0.354	0.384
20	0.391	0.466	0.449	0.389	0.160	0.144
25	0.262	0.391	0.605	0.462	0.133	0.147
26	0.559	0.639	0.412	0.316	0.029	0.045
28	0.362	0.151	0.585	0.735	0.053	0.114
29	0.534	0.703	0.305	0.112	0.016	0.184
Mean	0.479	0.517	0.363	0.338	0.148	0.145
SE	0.033	0.050	0.041	0.051	0.032	0.026

Table 21. Abundance of species as grouped according to their regenerative strategy (resprouter, seeder, and resprouter-seeder; Zedler 1977, 1981) following Clemente et al. (1996), Cavero & Ederra (1999), and Lloret et al. (2003).

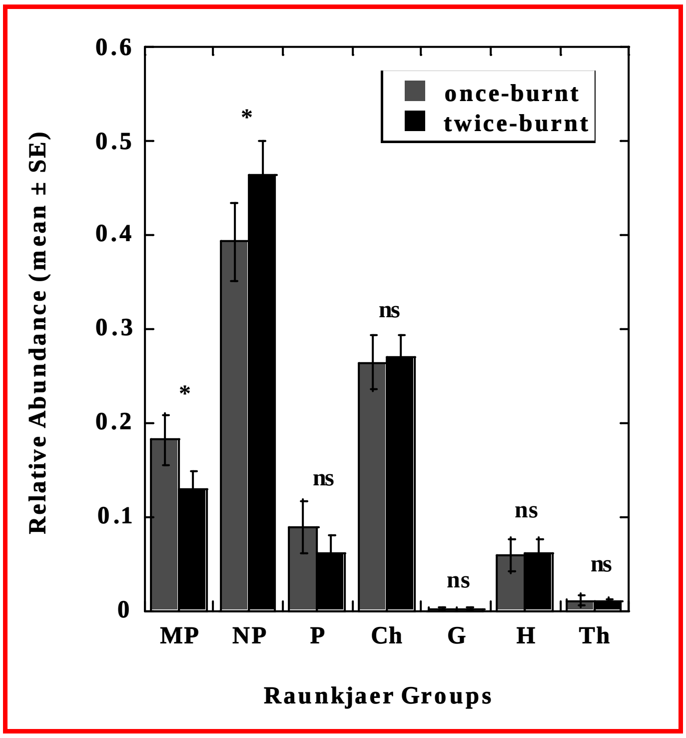

Figure 19. Relative abundance of species as grouped according to Raunkjaer biological types (Raunkjaer 1934): macrophanerophytes (MP), nanophanerophytes (NP), other phanerophytes (P), chamaephytes (Ch), geophytes (G), therophytes (Th). Symbols above-bars denote significance (ns = no significance, * *P* < 0.005) of differences between paired once- and twice-burnt areas (paired *t*-Student tests).

Jaccard's Similarity Index (*JI*) ranged between 0.426 and 0.761. The forward stepwise multiple regression resulted in the selection of real solar radiation and annual precipitation as predictive variables. Such model was not significant (R^2= 0.36, *P*= 0.085), but revealed a significant role of real solar radiation (*P*=0.030). A simple linear regression model considering only such predictive variable was marginally significant (R^2= 0.28, *P*=0.051): similarity between paired once- and twice-burnt areas tended to be higher in study sites characterized by higher values of real solar radiation, namely, less productive or more Mediterranean in terms of climatic conditions.

7.5. Discussion

Ten years after the last fire, richness and diversity of plant species found after two fires did not significantly differ from those found after a single fire, as expected for Mediterranean-type vegetation (Hanes 1971; Keeley 1986). That is, regenerative strategies linked to life-history traits ensure that most species are able to persist even after the occurrence of two fires at short fire intervals.

However, species-area correlations revealed that the rate of species increase with area was significantly higher in once-burnt areas. In fact, although comparisons were not statistically significant, mean species richness was higher at the smallest plots in twice-burnt areas. Richness became similar in both types of areas at the 25 m^2 plot, and become lower in twice-burnt areas at larger scales. In South African fynbos, fire frequency was also reported to result in contrasting effects on species richness at different spatial scales, which was explained by patterns of spatial heterogeneity generated through consecutive fires (Schwilk et al. 1997). At our study sites, fire intervals before the 1994 fire had been longer in once-burnt areas, and likely, vegetation structure was more developed and fuel loads were higher when such fire occurred. Contrastingly, fuel loads were probably lower in twice-burnt areas. Thus, patches of varying fire intensity would have resulted in higher post-fire spatial heterogeneity at the larger spatial scales (on the order of 10^2 m^2) in once-burnt areas, whereas higher post-fire spatial heterogeneity would have resulted at the smaller spatial scales in twice-burnt areas (on the order of 10 m^2). Such patterns of spatial heterogeneity allowed the presence of a higher number of plant species at the smaller scales in twice-burnt areas, while in once-burnt areas the number of plant species increased readily as more extent surfaces were considered. This argument is consistent with the less developed vertical and horizontal structure and the lower fuel loads observed in twice-burnt areas (Chapter 3).

Although floristic similarity between paired once- and twice-burnt areas remained high, some interesting patterns emerged when analyzing these differences in relation to the regional climatic gradient. Thus, floristic similarity between paired areas was correlated with climatic productivity, in such a way that the less climatically productive sites were the most resilient and showed more similar paired areas in relation to plant composition. Safford and Harrison (2004) also observed that fire effects on diversity in serpentine chaparral (typically slow growing, stunted, and xeromorphic) were less pronounced although longer lasting than in sandstone chaparral, a similar but more productive community-type. Recently, a study considering several types of Mediterranean plant communities and conducted 8 years after fire at a regional level in Catalonia provided similar results in relation to floristic similarity. Post-fire recovery of floristic composition was observed to be more successful at localities characterized by higher water deficit along summer months, which was attributed to the fact that a higher proportion of seeder species was present at them (Arnan 2006). Consequently, a relation may exist between the ability of plant communities to withstand drought and to recover after fire, which would imply that communities growing under particularly marked Mediterranean conditions are more capable of successfully withstanding features such as drought and fire occurrence. Otherwise, such observations may indicate that coexistence is enhanced in less productive sites since competitive exclusion is prevented, which results in weaker effects of disturbance (Huston 1994). Lastly, previous studies conducted on a single stand and considering particularly short fire intervals revealed marked changes in Californian chaparral composition (Zedler et al 1983; Haidinger & Keeley 1993). Although correlation between fire interval and floristic similarity was directly tested in the present study, no significant results were found.

Significant differences between paired once- and twice-burnt areas were rarely found for single species. P.halepensis was the only species greatly affected by reburning, and its abundance was significantly reduced in twice-burnt areas. As discussed in Chapter 6, P.halepensis populations require a minimum fire interval, estimated in *ca*. 15 years, to accumulate a sufficient seed bank that ensures regeneration at pre-fire densities, and most twice-burnt areas showed shorter fire intervals. P.halepensis determined the abundance pattern found for the group of macrophanerophytes, which was significantly higher in once-burnt areas. When this species was excluded from the group, the rest of it (Arbutus unedo, Ceratonia siliqua, Olea europaea, or Quercus ilex, among others) showed similar abundances in paired once- and twice-burnt areas. Most tree species present in the studied communities, except for P.halepensis, show a resprouter post-fire regenerative strategy, which seems to be an efficient mechanism to withstand the occurrence of two consecutive fires at intervals shorter than 17 years, as shown by the absence of the absence of growth differences in Q.ilex and P.lentiscus between paired (Chapter 5), and by the absence of changes in the abundance of reprouter species after the second fire relative to the occurrence of a single fire.

Some contrasting patterns between once- and twice-burnt areas were observed when species were grouped according to Raunkjaer biological type. Ten years after fire, when transient species have already disappeared, the group of nanophanerophytes (R.officinalis, Q.coccifera, Erica multiflora, or Cistus sp. pl., among others) was significantly more abundant in twice-burnt areas, likely due to a competitive release associated with P.halepensis decline. Such shift towards the higher abundance of shorter-sized species may also explain the higher species richness at the smallest spatial scales in twice-burnt areas. The abundance of chamaephytes (scrubs), geophytes, hemicriptophytes (perennial forbs and grasses), and therophytes (annuals) did not vary with reburning.

Changes in species composition were also more apparent when analyzing dominance patterns than for abundances of single species. Dominance was intensified by reburning, since it was shown to be higher in twice-burnt areas, both by one and two species. Interestingly, whereas in most once-burnt areas dominant species were shrubs such as Q.coccifera, R.officinalis, or Ulex parviflorus, in most twice-burnt areas dominant species were scrubs such as Dorycnium pentaphyllum or Thymus vulgaris, and grasses such as Brachypodium retusum. This pattern agrees with previously reported structural simplification in more recurrently burnt areas (Chapter 3). These results highlight the fact that some species gained dominance as a result of reburning, and thus became the most abundant species in the stand. In particular, R.officinalis decreased its dominance in twice-burnt areas relative to once-burnt ones, whereas B.retusum showed the opposite pattern. B.retusum is a rhizomatous perennial grass which shows great post-fire regeneration capacity, since its below-ground organs are buried deep enough to survive fire, and its sexual reproduction is enhanced during the first post-fire year (Caturla et al. 2000). It has been observed to dominate during the first stages of post-fire recovery, and thus to play an important role for soil protection (Caturla et al. 2000; De Luis et al. 2004). Our results show that reburning enhanced this species up to 10 years after fire, which would facilitate future fire lighting and propagation, since B.retusum produces abundant, fine, and dry fuels by necromass accumulation. Hence, the present work provides further evidence to an idea that has been long upheld for MTEs: fire recurrence at short fire intervals promotes herb dominance and thus may result in a *positive herb/fire feedback* (Zedler et al. 1983; Trabaud 1991; Haidinger et al. 1993; Keeley et al. 1999; Vilà et al. 2001; Lloret et al. 2003; Delitti et al. 2005; Grigulis et al. 2005).

Although resprouter species were more abundant in twice-burnt areas and the opposite pattern was found for seeder species, no statistically significant differences were observed in the relative abundances of regenerative groups. In fire-prone ecosystems, vegetation dynamics is strongly influenced by vital attributes such as regenerative strategy (Noble & Slatyer 1980). Models based on such concepts have been used to simulate the effects of different fire regimes on floristic composition (Pausas 1999; Franklin et al. 2001; Lloret et al. 2003). The absence of changes in relative abundance of regenerative strategies in this study is presumably due to two different facts. Firstly, life cycle explains the pattern of P.halepensis, whose abundance declined where fire intervals where shorter than the time span needed to accumulate a sufficient seed bank (Chapter 6). However, most of seeder species reach maturity much more rapidly, and thus their post-fire abundance did not result limited by fire intervals, which explains the absence of overall differences in the group of seeder species between once- and twice-burnt areas. Secondly, persistence capability of resprouter species has been widely described in MTEs (Keeley 1986; Bond & van Wilgen 1996). Despite resprouting is diminished by repeated disturbances at short fire intervals (Canadell & López-Soria 1998; Bowen & Pate 1993), we considered the occurrence of two fires along two decades, which is probably a short time scale to observe differences as for changes in the abundance of resprouter species.

7.6. Conclusions

The present study provides further evidence supporting the paradigm of resilience in Mediterranean vegetation, since plant species richness and diversity were similar in communities burnt once and twice along the same time period (*ca.* 20 years).

However, spatial patterns of species richness differed between once- and twice-burnt areas. In twice-burnt areas, a higher number of plant species was present at smaller spatial scales (on the order of 10 m^2). Contrastingly, in once-burnt areas the number of species was lower at such scales, but readily increased along with surface, and was higher at larger spatial scales (on the order of 10^2 m^2). Such trends were attributed to patterns of spatial heterogeneity generated through fire repetition. Moreover, the higher abundance of shorter-sized species may also partly explain that a higher number of species were present at the smaller spatial scales in twice-burnt areas.

The most Mediterranean study sites in terms of climatic conditions were revealed to show the most similar floristic composition in paired once- and twice-burnt areas. Thus, drought resistance and post-fire resilience of Mediterranean plant communities may be closely related.

Reburning resulted in an important decline of the dominant tree species, P.halepensis, in higher abundance of nanophanaerophytes, and in higher dominance both by one and two species, which moreover shifted from being shrubs to scrubs and the perennial grass B.retusum. These compositional changes partly explain the less developed structure and lower fuel loads previously observed in twice-burnt areas (Chapter 3).

The occurrence of two fires at fire intervals shorter than 17 years did not significantly alter the abundance of regenerative groups, despite they are expected under fire regimes characterized by short fire intervals along longer time spans.

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Appendix 6

List of Species Present at Study Sites

Species Name	**Family Name**
Agrimonia eupatoria	Rosaceae
Alyssum alyssoides	Brassicaceae
Amelanchier ovalis	Rosaceae
Ampelodesmos mauritanica	Poaceae
Anacamptis pyramidalis	Orchidaceae
Anagallis arvensis	Primulaceae
Andryala ragusina	Asteraceae
Anthyllis tetraphylla	Fabaceae
Aphyllantes monspeliensis	Liliaceae
Arbutus unedo	Ericaceae
Argyrolobium zanonii	Fabaceae
Aristolochia pistolochia	Rafflesiaceae
Arrhenatherum elatius	Poaceae
Aspargus acutifolius	Liliaceae
Asperula cynanchica	Rubiaceae
Asphodellus albus	Liliaceae
Aster sedifolius	Asteraceae
Asteriscus spinosus	Asteraceae
Astragalus incanus	Fabaceae
Atractylis humilis	Asteraceae
Avenula sp. pl.	Poaceae
Biscutella laevigata	Brassicaceae
Blackstonia perfoliata	Gentianaceae
Bonjeania hirsuta	Fabaceae
Brachypodium phoenicoides	Poaceae
Brachypodium retusum	Poaceae
Brachypodium sp. pl.	Poaceae
Bupleurum fruticescens	Apiaceae
Bupleurum rigidum	Apiaceae
Calluna vulgaris	Ericaceae
Carex hallerana	Cyperaceae
Carthamus lanatus	Asteraceae
Catananche caerulea	Asteraceae
Catapodium rigidum	Poaceae
Centaurea linifolia	Asteraceae
Centaurium pulchellum	Gentianaceae
Centaurium quadrifolium	Gentianaceae
Cephalantera longifolia	Orchidaceae
Cephalanthera rubra	Orchidaceae
Ceratonia siliqua	Fabaceae
Chamaerops humilis	Arecaceae
Cirsium arvense	Asteraceae
Cistus albidus	Cistaceae
Cistus monspeliensis	Cistaceae
Clematis flammula	Ranunculaceae
Clematis vitalba	Ranunculaceae
Colutea arborescens	Fabaceae
Colutea sp. pl.	Fabaceae
Conium maculatum	Apiaceae
Conopodium majus	Apiaceae
Convolvulus althaeoides	Convulvulaceae
Convulvulus arvensis	Convulvulaceae
Convolvulus lanuginosus	Convulvulaceae
Conyza sp. pl.	Asteraceae
Coriaria myrtifolia	Coriariaceae
Coris monspeliensis	Primulaceae
Coronilla minima	Fabaceae
Crataegus monogyna	Rosaceae
Cytisus sessilifolius	Fabaceae

Dactylis glomerata	Poaceae
Daphne gnidium	Thymelaeaceae
Dorycnium pentaphyllum	Fabaceae
Echinops ritro	Asteraceae
Echium vulgare	Boraginaceae
Erica multiflora	Ericaceae
Erucastrum nastortiifolium	Brassicaceae
Eryngium bourgatii	Apiaceae
Eryngium campestre	Apiaceae
Euphorbia amygdaloides	Euphorbiaceae
Euphorbia characias	Euphorbiaceae
Euphorbia exigua	Euphorbiaceae
Euphorbia falcata	Euphorbiaceae
Euphorbia flavicoma	Euphorbiaceae
Euphorbia peplus	Euphorbiaceae
Euphorbia serrata	Euphorbiaceae
Filago sp.pl.	Asteraceae
Foeniculum vulgare	Apiaceae
Fumana ericoides	Cistaceae
Fumana laevipes	Cistaceae
Fumana thymifolia	Cistaceae
Galactites tomentosa	Asteraceae
Galium lucidum	Rubiaceae
Galium maritimum	Rubiaceae
Galium parisiense	Rubiaceae
Genista hispanica	Fabaceae
Genista monspessulana	Fabaceae
Genista scorpius	Fabaceae
Geranium robertianum	Geraniaceae
Geranium sylvaticum	Geraniaceae
Globularia alypum	Globulariaceae
Globularia vulgaris	Globulariaceae
Hedera helix	Araliaceae
Helianthemum appeninum	Cistaceae
Helianthemum oelandicum	Cistaceae
Helianthemum syriacum	Cistaceae
Helichrysum stoechas	Asteraceae
Hieracium pilosella	Asteraceae
Hippocrepis comosa	Fabaceae
Hypericum perforatum	Clusiaceae
Juniperus oxycedrus	Cupressaceae
Lactuca serriola	Asteraceae
Lathyrus filiformis	Fabaceae
Lathyrus inconspicus	Fabaceae
Lathyrus sylvestris	Fabaceae
Lavandula latifolia	Labiaceae
Leontodon taraxacoides	Asteraceae
Leucanthemum coronarium	Asteraceae
Leuzea conifera	Asteraceae
Linum narbonense	Linaceae
Linum strictum	Linaceae
Linum tenuifolium	Linaceae
Lithospermum fruticosum	Boraginaceae
Lollium perenne o rigidum	Poaceae
Lonicera etrusca	Caprifoliaceae
Lonicera implexa	Caprifoliaceae
Lotus pedunculatus	Fabaceae
Marrubium vulgare	Labiaceae
Medicago polimorpha	Fabaceae
Melilotus altissima	Fabaceae
Odontides lutea	Scrophulariaceae
Onobrychis saxatilis	Fabaceae
Ononis minutissima	Fabaceae
Ononis natrix	Fabaceae

Ononis spinosa	Fabaceae
Olea europaea	Oleaceae
Origanum vulgare	Labiaceae
Orobanche sp. pl.	Orobanchaceae
Oryzopsis miliacea	Poaceae
Petrorhagia prolifera	Caryophyllaceae
Peucedanum officinale	Apiaceae
Phillyrea angustifolia	Oleaceae
Phillyrea latifolia	Oleaceae
Picris hieracioides	Asteraceae
Pinus halepensis	Pinaceae
Pistacia lentiscus	Anacardiaceae
Plantago lanceolata	Plantaginaceae
Phlomis lychnitis	Labiaceae
Polygala calcarea	Polygalaceae
Polygala rupestris	Polygalaceae
Polypodium sp. pl.	Polypodiaceae
Potentilla neumanniana	Rosaceae
Prunella laciniata	Labiaceae
Prunus domestica	Rosaceae
Prunus mahaleb	Rosaceae
Prunus spinosa	Rosaceae
Psoralea bituminosa	Fabaceae
Quercus coccifera	Fagaceae
Quercus humilis	Fagaceae
Quercus faginea	Fagaceae
Quercus ilex	Fagaceae
Rhamnus alaternus	Rhamnaceae
Rhamnus lycioides	Rhamnaceae
Rosa sp. pl.	Rosaceae
Rosmarinus officinalis	Labiaceae
Rubia peregrina	Rubiaceae
Rubus sp. pl.	Rosaceae
Ruta graveolens	Rutàcia
Sarothamnus scoparius	Fabaceae
Sanguisorba minor	Rosaceae
Satureja montana	Labiaceae
Scabiosa columbaria	Dipsacàcia
Scabiosa stellata	Dipsacàcia
Scorpiurus muricatus	Fabaceae
Scorzonera angustifolia	Asteraceae
Scorzonera hispanica	Asteraceae
Sedum sediforme	Crassulàcia
Sideritis hirsuta	Labiaceae
Smilax aspera	Smilacaceae
Sonchus oleracerus	Asteraceae
Sonchus sp. pl.	Asteraceae
Sonchus tenerrimus	Asteraceae
Sorbus domestica	Rosaceae
Stachys officinalis	Labiaceae
Staehelina dubia	Asteraceae
Symphytum sp. pl.	Boraginaceae
Teucrium chamaedrys	Labiaceae
Teucrium polium	Labiaceae
Thalictrum tuberosum	Ranunculaceae
Thesium humifusum	Santalaceae
Thymelaea tinctoria	Thymelaeaceae
Thymus vulgaris	Labiaceae
Torilis sp.1	Apiaceae
Ulex parviflorus	Fabaceae
Urospermum dalechampii	Asteraceae
Valerianella sp. pl.	Valerianaceae
Verbascum sp. pl.	Scrophulariaceae
Viburnum tinus	Caprifoliaceae
Vicia cracca	Fabaceae
Vicia sativa	Fabaceae
Vincetoxicum hirundinaria	Asclepiadaceae
Viola alba	Violaceae
Viola hirta	Violaceae
Vulpia unilateralis	Poaceae

Chapter 8

General Discussion and Conclusions

8.1. Summary of Main Results

Fire recurrence level was shown to exert a regional control on vegetation regeneration and soil organic horizons recovery in P.halepensis communities, since significant shifts in the considered parameters were observed in areas burnt twice relative to paired areas burnt once throughout a range of climatic and geomorphic conditions.

At the community level, shifts were observed in relation to vegetation structural features and to floristic composition. Reburning resulted in a less developed vertical and horizontal structure of vegetation, and in lower fuel loads, as observed 8 years after the 1994 fire (Chapter 3). Such shifts involved a decrease in overall biomass production. Fire repetition resulted in a density decline of the dominant tree species, P.halepensis, in an increase of nanophanerophytes' abundance, and in enhanced dominance by one and two species, particularly scrubs such as Dorycnium pentaphyllum or Thymus vulgaris, and grasses such as Brachypodium retusum, as observed 10 years after the 1994 fire (Chapter 7). Overall, such compositional changes involved a shift towards lower-structured and more open communities. Consequently, the shifts that fire repetition generated on vegetation structural features and on floristic composition concurred to result in communities that are less productive, less structurally complex, shorter, more open, and shrub-dominated, where P.halepensis is present at low densities, or is even absent. Other processes different than shifts in floristic composition may have concurred to generate the observed decrease in biomass production; those will be discussed later.

According to changes reported at the community level, soil organic horizons were less developed in areas burnt twice, i.e., were less frequent and shallower, and thus showed lower dry masses, as observed 9 years after the 1994 fire (Chapter 4). In such areas, lower fuel loads, less developed vegetation structure, and reduced density of P.halepensis resulted in lower plant litter inputs to LF organic horizons. Additionally, the second fire had the direct and relevant effect of further combusting humiferous layers.

Reburning resulted in P.halepensis populations that were less dense and characterized by shorter and thinner individuals, a lower percentage of which was already reproductive 10 years after the 1994 fire (Chapter 6). The density decline was related to the reproductive traits of the species, which needs certain fire intervals to accumulate a sufficient seed bank that ensures density recover after fire. The growth decline was observed to have occurred exclusively along the first post-fire years, since radial growth of the species was lower in twice-burnt areas exclusively from 1994 to 1999, but not afterwards. This evidence supports the hypothesis that other processes different than compositional changes may have concurred to generate an overall decline in biomass production, which may have been lower along the first post-fire years, when soil nutrient availability was presumably lower due to lower pre-fire fuel loads.

Fire repetition indirectly resulted in promoted growth of the seeder R.officinalis in twice-burnt areas, as observed 10 to 11 years after the 1994 fire (Chapter 5). Since density of P.halepensis populations was significantly lower in such areas, the competition release likely benefited shrub species such as R.officinalis. However, the resprouter species Q.ilex and P.lentiscus, which have a more conservative resource-use strategy, grew similarly in paired areas. Q.ilex was observed to show lower maximum height in areas affected by two fires (Chapter 3), suggesting that this species grew less along the first post-fire years, as observed for the case of P.halepensis.

Foliar nutrient contents were analyzed in P.halepensis, Q.ilex, P.lentiscus, and R.officinalis 11 years after the 1994 fire (Chapters 5, 6). Differences were only found in R.officinalis (they lost significance after applying the sequential Bonferroni test), in agreement with its higher growth in twice-burnt areas. The absence of differences in foliar nutrient contents between paired areas would involve that fire repetition did not result in lower nutrient uptake by plants, in agreement with the observed absence of growth differences.

8.2. Other Results

Chapter 3

A clear pattern was found for vegetation height in relation to fire recurrence level: all considered height parameters were significantly higher in once-burnt areas relative to paired twice-burnt areas, including the maximum height achieved by the species P.halepensis, Q.ilex, and Q.coccifera.

Half study sites shift to a fuel model characterized by less structural complexity and lower fuel loads after the occurrence of the second fire. The rest showed an equivalent fuel model in once- and twice-burnt areas.

Total vegetation cover in twice-burnt areas was significantly and directly correlated with fire intervals: the longer the fire intervals, the higher the total vegetation cover in twice-burnt areas.

Chapter 4

Total litter mass values observed in once-burnt areas were similar to those previously reported for mature P.halepensis communities. Total litter mass values observed in twice-burnt areas were of the same order, but significantly lower than in once-burnt areas. Thus, a loss of resilience was supported in twice-burnt areas.

The direct combustion of humiferous layers was a relevant cumulative effect of reburning. The difference in dry mass of humiferous layers between paired areas was significantly and inversely correlated to fire interval, since longer fire intervals allow for higher plant litter accumulation in LF horizons, which likely results in higher protection of humiferous layers against a new fire.

Vegetation growth played a main role in determining the reconstruction of LF organic horizons, as shown by the fact that where precipitation was more abundant, dry mass of LF horizons was higher in both types of areas.

Tree layer, which was mainly constituted by P.halepensis, importantly conditioned the reconstruction of LF horizons in once-burnt areas, as pointed by the existence of marginally significant, direct correlations between LF dry mass and tree layer cover and P.halepensis density in such areas.

In twice-burnt areas, where total cover of tree layer and density of P.halepensis populations were significantly lower, both the frequency of occurrence of soil organic horizons and LF dry mass were significantly and directly correlated with total vegetation cover.

In once-burnt areas, LF horizons showed significantly higher contents of total nitrogen and organic carbon. The quantitatively higher production of pine needle litter may explain the higher nitrogen contents. The higher amounts of charred organic remains likely left by the 1994 fire relative to paired twice-burnt areas may explain the higher organic carbon contents.

Chapter 5

No significant differences in branch elongation were found in R.officinalis, Q.ilex, or P.lentiscus, probably because vegetation is not submitted to notably different levels of competition for light in paired areas.

Q.ilex basal area increment was significantly and inversely correlated to real solar radiation in once-burnt areas, but not in twice-burnt ones.

Similarly, P.lentiscus basal area increment showed a marginally significant, inverse correlation with temperature in once-burnt areas, but not in twice-burnt ones.

Growth of the seeder R.officinalis was more dependent on space availability, since it was enhanced in twice-burnt areas and basal area increment was significantly affected by study site. However, growth of the resprouters Q.ilex and P.lentiscus was controlled by stored resources, and significantly affected by climatic variables.

Chapter 6

Time of recruitment of post-fire P.halepensis populations was not influenced by fire recurrence level. Recruitment occurred mostly along 1994 in both types of areas. Only 13% of individuals were established later, mainly in 1995.

P.halepensis populations of twice-burnt areas were estimated to have required at least 15 years for recovering levels of density similar to paired once-burnt areas.

Chapter 7

Reburning did not alter species richness or diversity.

The more Mediterranean sites in terms of climatic productivity showed higher resilience in relation to floristic composition.

No significant changes in the relative abundance of resprouters and seeders were found as resulting from fire recurrence.

At the regional level, resprouter species were more abundant at moister sites, whereas seeder species were more abundant at drier sites. These trends existed only in once-burnt areas.

Relative abundance of Q.ilex was significantly and inversely correlated to real solar radiation in once-burnt areas. The pattern did not exist in twice-burnt areas.

Relative abundance of P.lentiscus was significantly and directly correlated to temperature in both types of areas.

The dominant tree species, P.halepensis, determined the pattern of abundance of the group of macrophanerophytes. When it was not considered, the relative abundance of such group was similar in paired areas.

8.3. General Discussion

Loss of Resilience under High Fire Recurrence

A general trend of resilience loss was observed in P.halepensis communities burnt twice at fire intervals shorter than 17 years relative to those burnt only once along at least 19 years. Eight to eleven years after fire, P.halepensis communities of twice-burnt areas showed less developed vertical and horizontal structure, lower fuel loads, lower densities of P.halepensis, and less developed soil organic horizons that P.halepensis communities of once-burnt areas.

A loss of resilience after repeated burning was also reported at a regional level in Catalonia by Díaz-Delgado et al. (2002), who based on NDVI measures, namely on estimations of green biomass from Landsat imagery. Seventy months after the last fire, Mediterranean communities -both dominated by Pinus tree species (seeders) and by Quercus tree species (resprouters)- burnt twice along 12 years were observed to show lower green biomass than communities burnt only once. Moreover, green biomass after the second fire significantly increased with longer fire intervals, and was directly correlated to mean rainfall, and inversely correlated to solar radiation.

Similarly, total vegetation cover in twice-burnt areas was directly correlated to fire interval. Moreover, an inverse correlation was found between dry mass of humiferous layers and fire interval. Fire interval was expected to affect P.halepensis density in twice-burnt areas and floristic composition similarity between paired areas, but correlations were not evidenced. Such fact may be due to the short range of fire intervals considered, to the fact that no replicates were available for most fire interval spans, and to the fact that areas characterized by similar fire intervals showed different climatic and geomorphic characteristic, which are local factors strongly conditioning vegetation recovery (Díaz-Delgado et al. 2002). In fact, rainfall directly conditioned dry mass of LF horizons, and inverse correlations were found between climatic parameters and growth of Q.ilex and P.lentiscus, but only in once-burnt areas. The effects of fire repetition likely overshadowed those of climatic variables in twice-burnt areas.

The Role of the Dominant Tree Species

The patterns that fire repetition generated on populations of the dominant tree species, P.halepensis, played a main role for the loss of resilience observed at the community level. Shifts in P.halepensis populations explained at least partly some shifts in structural features (less vertical complexity, lower tree cover, and lower fuel loads), some shifts in floristic composition (higher abundance of shrubs), and lower recovery of LF organic horizons. A recent study conducted at a regional level in Catalonia has reached to similar conclusions: post-fire recovery of several types of Mediterranean communities has been observed to rely on the recovery of the dominant tree or shrub species (Arnan 2006). Vegetation dynamics are driven by life history attributes of plant species such as regenerative strategy, age to maturity, shade tolerance, or plant longevity, which involve differences in resilience to fire intervals of various lengths (Noble & Slatyer 1980; Keeley 1986; Bond & van Wilgen 1996). Life history attributes of the dominant tree species are particularly relevant, since such species provide main compositional and structural traits.

Resprouter species have been traditionally considered to be resilient to a wider range of fire intervals than seeder species, and to gain dominance over them in the absence of fire (Keeley 1992; Enright et al. 1998; Pausas 2001). However, depletion of resprouters' underground reserves has been observed as a result of recurrent disturbances at short time intervals (Canadell & López-Soria 1998; Zammit 1998), and some studies have shown that large and long-lived resprouters may loss resilience after consecutive fires (Zedler et al. 1983; Delitti et al. 2005). In the eastern Iberian Peninsula, simulation approaches based on plant functional types point to a decrease in the abundance of Quercus at high fire recurrence, and to its dominance when fires become rare (Pausas 1999; Lloret et al. 2003). In Catalonia, and basing on estimations of green biomass from Landsat imagery, overall resilience after two fires at intervals shorter than 12 years was higher in Quercus-dominated forests, despite Pinus-dominated forests showed lower resilience decrease after the second fire (Díaz-Delgado et al. 2002).

Seeder species have been traditionally considered to show reproductive cycles specialized to fire, and to peak at intermediate fire frequencies (Keeley 1986; Hilbert 1987; Burgam & Lamont 1992). In fact, later studies have shown that in the Mediterranean Basin, seeder species evolved in the Quaternary, under Mediterranean conditions characterized by fire occurrence, whereas resprouter species correspond to older lineages that evolved in the Tertiary under tropical conditions (Herrera 1992; Verdú 2000; Verdú et al. 2003). In the eastern Iberian Peninsula, simulation approaches predict seeder shrubs to peak at intermediate levels of fire recurrence (Lloret et al. 2003). Local extinction of Pinus is observed when fire intervals are particularly short, 5 or 10 year-long (Pausas 1999; Pausas & Ramos 2004). Seeder species that show fire-dependent regeneration face two potential threats along their lifecycle: a *senescence risk* associated with infrequent fires and an *immaturity risk* associated with high fire recurrence. In the first case, fire intervals would exceed the longevity of the seed bank, whereas in the second, fire intervals would be too short to accumulate a sufficient seed bank (Zedler 1995; Keeley et al. 1999a).

P.halepensis is a partially serotinous species that can both regenerate in the absence of fire and as a result of fire. About the 40% of the yearly cone crop remains in the canopy within serotinous cones, and is thus added to a permanent and cumulative canopy seed bank. Seeds will be released when high fire temperatures force serotinous cones to open (Daskalakou & Thanos 1996). Serotinity is considered to be a fire-dependent strategy (Lamont et al. 1991; Enright et al. 1996; Keeley et al. 1999a), since the retention of mature seeds up to fire occurrence ensures seedling recruitment in the best environmental conditions, namely when resources such as space, light, and nutrients are largely available as a result of the passage of fire. Thus, P.halepensis populations face the above-mentioned immaturity risk. The present study revealed that fire intervals at least 15 year-long are required by this species to show successful post-fire regeneration. Namely, on a time scale of many generations, the local viability of P.halepensis populations would be conditioned by the occurrence of fire events at time intervals longer than 15 years.

Future Predictions

In those areas of Catalonia where consecutive fires occur at time intervals shorter than 15 years, P.halepensis communities are prone to shift towards less productive, lower and more open, shrub-dominated communities, where Aleppo pine may be present at low densities, or may even be absent. Such shifts would result in relevant changes in the functioning of ecosystems and in the physiognomy of landscapes. Basing on a study on recent fire history in Catalonia, the total burnt area along 1975-1998 was 1,673,244 ha, 12% of which was reburnt along such time span (Díaz-Delgado et al. 2004). Consequently, about 200,789 ha of forested surface suffered two fires in 24 years, at different fire intervals. Considering that P.halepensis communities are the most frequent forest type (covering about 239,092 ha (Gracia et al. 2004)) and are more prone to burn that other vegetation types in this region (Díaz-Delgado et al. 2004), the reported shifts could affect large surfaces of forested area.

The results of the present study agree with modeling predictions based on the response of plant functional types for the eastern Iberian Peninsula (Pausas 1998, 1999b; Lloret et al. 2003; Pausas & Ramos 2004). Such models have been considered appropriate tools for testing the consequences of different fire scenarios on vegetation dynamics in MTEs (Malanson et al. 1992; Rego et al. 1993; Franklin et al. 2001, 2005), and allow predicting shifts in the composition and structure that are hard to detect by field studies (Franklin et al. 2004). FATE (Moore & Noble 1990) and BROLLA (Pausas 1998) have been applied to simulate dynamics of up to 7 coexistent types of plant species under different levels of fire recurrence (fire intervals of 5 to 100 years) during long time spans (up to 500 years). FATE and BROLLA predict similar vegetation responses to high fire recurrence: the occurrence of fire at intervals of 5 to 10 years would enhance the abundance of lower-structured and shorter-lived species such as Cistus and Erica, and also of the alien resprouter grass A.mauritanica. Short fire intervals would also reduce the abundance of Quercus; and would eliminate or markedly reduce the abundance of Pinus, thus resulting in a decrease of total biomass (Pausas 1998, 1999b; Lloret et al. 2003; Pausas & Ramos 2004).

Moreover, the observed shifts in structural features and floristic composition may show positive feedbacks on fire regimes. Fuel characteristics such as dryness, continuity, presence of secondary compounds, tissue nutrient contents, and shape, size and arrangement of plant parts are of the main importance for fire ignition and spread (Bond & van Wilgen 1996). On fire ecology literature, it has been repeatedly stressed that an *herb/fire positive feedback* may exist (Zedler et al. 1983; Trabaud 1991; Haidinger & Keeley 1993; Keeley et al. 1999b; Delitti et al. 2005). The topic has been widely addressed for the case of invaders effects on fire regimes (see Brooks et al. 2004 for a revision). Increases in fire frequency have been reported when alien grasses invade sites otherwise dominated by shrubs, since they create a more continuous and flammable fuel bed (D'Antonio & Vitousek 1992). In Catalonia, the herb/fire positive feedback caused by the invader <u>A.mauritanica</u> in <u>P.halepensis</u> communities of the Garraf area has been well-documented (Vilà et al. 2001; Lloret et al. 2003; Grigulis et al. 2005). In our study, the observed higher dominance of <u>B.retusum</u>, which produces abundant thin and dry fuels through necromass accumulation (Caturla et al. 2000; De Luis et al. 2004), may promote future fire occurrence. Moreover, since overall fuel loads have been observed to decrease after repeated fires, it is likely that future fires would be less intense.

Lastly, future climatic scenarios based on General Circulation Models predict warmer and drier conditions for vegetation in the Mediterranean Basin (Kattenberg et al. 1996; Houghton et al. 2001), namely higher fire risk (Piñol et al. 1998; Houghton et al. 2001). In fact, it is hypothesized that direct effects of climatic changes on plant communities may be less evident than indirect changes deriving from promoted fire occurrence (Flannigan et al. 2000; McKenzie et al. 2003). An increase of rainfall variability is also expected, which may prolong and intensify summer drought (Palutikof 1996). Simulation approaches combining scenarios of climatic change and functional models of vegetation dynamics have predicted shortened fire intervals that would lead to shrub-dominated landscapes in the western Mediterranean Basin, and have underlined that fire recurrence could be the major factor determining future composition and structure of plant communities (Mouillot et al. 2002).

Fire Intervals and Overall Post-Fire Biomass Production

The lower biomass production and the less developed vertical and horizontal structure of vegetation that was observed in areas burnt twice seemed to be at least partly caused by shifts in floristic composition. However, other processes may also have concurred to generate such trends: along the present work, I hypothesized that fire intervals may influence post-fire biomass production.

Longer time intervals between fires allow further structural development of vegetation and higher fuel accumulation, in such a way that greater amounts of nutrients are allocated in phytomass and can be released by fire. Moreover, higher pre-fire biomass usually involves higher fire intensity, and both factors have been observed to result in higher soil organic matter mineralization and ash deposition (Raison 1979; Giovannini et al. 1989; Kutiel & Kutiel 1989; Romanyà et al. 2001). Fire is an important mineralizing factor in MTEs, where decomposition rates are low due to water scarcity and low tissue nutrient contents (Mitchell et al. 1986). Ash beds can be considered as reservoirs of nutrients that improve soil fertility and enhance plant growth (Giovannini 1994). Ashes are particularly rich in phosphorous, base cations, and nitrogen (Kutiel & Kutiel 1989; Kutiel & Shaviv 1992; Christensen 1994; Serrasolsas & Vallejo 1999). Enhanced phosphorous availability in the short-term after fire has been considered particularly relevant for plant growth (Sardans et al. 2004, 2005a; Pausas et al. 2003). Thus, I hypothesize that where vegetation was more developed and fuel loads were higher at the moment of the 1994 fire, post-fire soil nutrient availability would have been higher, and plant growth would have been promoted. Such effect would occur only in the short term after fire, since in the medium term, soil nutrients contents tend to recover their pre-fire levels (Giovannini et al. 1989; Kutiel & Kutiel 1989; Gimeno-García et al. 2000).

Direct assessment of such process could not be performed, since the present study was conducted several years after fire. However, indirect evidence resulted from the analysis of P.halepensis radial growth patterns. An overall higher radial growth of the species was observed in once-burnt areas, which was due to the higher radial growth that occurred exclusively along 1995-1999.

Previous studies provide similar evidences on growth responses of P.halepensis to post-fire conditions. Pausas et al. (2003) worked on post-fire regeneration of Aleppo pine populations affected by different fire severities in València, and found higher growth and biomass of seedlings at the high fire severity plots. Foliar analyses of the first post-fire year needles revealed a tendency towards higher phosphorous contents at such plots. Ne'eman (1997) worked on post-fire regeneration of Aleppo pine forests along the first 4 post-fire years on Mount Carmel (Israel), and observed that growth of pine seedlings was enhanced under big burnt trees, where fire intensity and ash deposition were presumably higher. Lastly, recent fertilization experiments on P.halepensis saplings, both under field and garden conditions, have revealed a strong capacity of the species to quickly respond to sudden increases of phosphorous. Even 3 years after phosphorous addition, biomass production was enhanced and phosphorous contents in stems and leaves were higher (Sardans et al. 2004, 2005b).

The present study provided further indirect evidence supporting the hypothesis of higher soil nutrient availability in once-burnt areas along the first post-fire years. Overall maximum height of Q.ilex was higher in once-burnt areas, despite 10 to 11 years after fire, growth of this species was similar in both types of areas, both in terms of branch elongation and basal area increment. Q.ilex grows markedly in height up to the third or fourth year after fire; afterwards its height growth slows down (Gratani & Amadori 1991). Noticeably, enhanced growth of holm oaks has been observed up to 6 years after phosphorous addition under field conditions (Sardans 1997; de la Fuente et al. 1997). Such fact might be attributed to phosphorous storage in the lignotuber and subsequent use along extended periods, as suggested by later works (Sardans et al. 2004).

An outstanding question refers to the time duration of growth enhancement effects. In our study, two time periods where differentiated when analyzing radial growth patterns in P.halepensis, basing on the pointer year 1999. The selection of such methodology was a caution measure, since considering post-fire growth along shorter time periods could have introduced measurement errors. It is generally considered that main nutrient changes in soils occur along some months, up to 2 years after fire (Kutiel & Kutiel 1989; Kutiel &Shaviv 1992; Christensen 1994; Serrasolsas & Vallejo 1999). However, growth of Aleppo pine seedlings has been observed to result enhanced along the fourth post-fire year (Ne'eman 1997), and positive growth responses to phosphorous fertilization have been observed in the third year after addition in P.halepensis and in the sixth year after addition in Q.ilex (Sardans 2004, 2005b; de la Fuente et al. 1997). Overall, it seems reasonable to consider that enhanced plant growth may be observed for at least some years after fire, as suggested by our results.

The hypothesis of enhanced growth along the first years after fire could explain some of the observed patterns. However, it needs to be tested directly in the short term after fire, by survey on nutrient contents in mineral soils and leaves, and on plant growth. Moreover, several arguments limit such hypothesis. Despite higher fire intensity results in higher ash deposition and nutrient mineralization, it also generates effects such as:

(1) higher nutrient losses by volatilization and ash convection during burning, which are positively and linearly correlated with fuel consumption (Hough 1981; Raison et al. 1985).

(2) further combustion of soil organic horizons, particularly H horizons (Ferran & Vallejo 1992).

(3) higher temperature rises, residence time, and penetration of heat into mineral soils, and thus, higher affection of their chemical, physical, and biological properties.

(4) the formation of a water-repellent layer that enhances erosion risk. Water repellency occurs in soils heated over 200°C, and lasts for several years after a severe fire in summer season (Alcañiz et al. 1994; DeBano 2000).

(5) higher post-fire soil erosion (Gimeno-García et al. 2000).

Cumulative Effects of Fire Recurrence

Zedler et al. (1983), in a study dealing with effects of reburning at a fire interval of 1 year on chaparral and coastal sage scrub composition, underlined the fact that consecutive fires at short fire intervals may result in cumulative and deleterious effects on ecosystem properties, particularly under arid conditions.

I also hypothesized that soils of twice-burnt areas may be affected by cumulative and deleterious effects of fires. Firstly, fire intervals ranged from 1 to 16 years, and thus insufficient time spans were available for the recovery of soil organic horizons before the occurrence of the second fire (Ferran & Vallejo 1992), which likely had the direct effect of further reducing them. Secondly, soil nutrient losses could have accumulated through consecutive erosion events. On the eastern coast of Spain, intense fires occur mostly in the drought season, which is followed by autumn rainfalls. Consequently, the ash layer, organic soil remains, and upper mineral soil are likely to be readily washed (Rubio et al. 1997; Soto et al. 1997; Gimeno-García et al. 2000; De Luis et al. 2003). Lastly, quantitatively important losses of nitrogen, phosphorous, sulphur, and basic cations -mainly potassium, calcium, and magnesium- occur as a direct result of burning (DeBano & Conrad 1978; Arianoutsou & Margaris 1981; Serrasolses & Vallejo 1999). Whenever fire intervals do not allow the ecosystem to recover pre-fire contents through nutrient inputs (such as atmospheric deposition or biological fixation), the occurrence of consecutive fires could result in cumulative nutrient losses (O'Conell 1987; Maggs 1988; Carter & Foster 2004).

In the present study, humiferous layers were observed to be negatively affected by cumulative effects of repeated burning. However, the existence of cumulative nutrient losses in mineral soils was not evidenced.

8.4. Conclusions

A loss of resilience is observed in Mediterranean P.halepensis communities submitted to a fire recurrence level of 2 fires along 2 decades relative to those submitted to a single fire. Reburning is observed, 8 to 11 years after fire, to have resulted in shorter and more open communities, where P.halepensis populations are less dense, shrubs are more abundant, and soil organic horizons are less developed. Overall, shifts observed in structural features and in floristic composition suggest a decrease of biomass production.

Such shifts, including the lower recovery of soil organic horizons, were strongly conditioned by the density decline of the dominant tree species. Populations of P.halepensis require a certain time interval between fires to store a sufficient seed pool to recover pre-fire density. In the present work, such critical fire interval has been estimated in 15 years.

Fire intervals were shown to have a relevant role in determining post-fire recovery at the community level: it significantly influence total vegetation cover in twice-burnt areas, and the difference in dry mass of humiferous layers between paired areas. Despite the present study failed to detect other significant correlations, fire interval is known to condition the recovery of pre-fire density of P.halepensis, and probably influences shifts in floristic composition.

Moreover, fire interval is hypothesized to condition post-fire vegetation growth, and thus, to affect also other structural features than total vegetation cover. Pre-fire fuel load variability between paired areas may have resulted in different levels of soil nutrient availability along the first post-fire years, and thus, in differential plant growth. P.halepensis was shown to have grown comparatively more in once-burnt areas along 1994-1999, which resulted in higher overall growth of the species. Pre-fire fuel loads had likely been higher in such areas, since longer fire intervals allowed further vegetation development. There was some evidence for a similar growth pattern in Q.ilex, despite it was not demonstrated through direct analysis.

Soil nutrient contents are thought to recover pre-fire levels few years after fire. Radial growth of P.halepensis was shown to be similar in paired areas from the year 2000 on. Basal increments of the resprouters Q.ilex and P.lentiscus were similar in paired areas 10 to 11 years after fire. Accordingly, foliar nutrient contents of such 3 species did not differed, as observed 11 years after fire.

Overall, fire recurrence has been evidence to condition post-fire vegetation regeneration and soil organic horizons recovery at a landscape level, since common patterns regarding structural features, floristic composition, soil organic horizons and P.halepensis populations, have been observed in areas burnt only once and in areas burnt twice throughout a range of climatic and geomorphic conditions. Interestingly, the effect of fire repetition even prevailed over the effect of climatic variables on several vegetation-related parameters.

Consequently, the study design, which allowed synchronic survey in paired areas differing mainly in fire recurrence level, and comprised 28 study sites distributed over the P.halepensis dominated surface of Catalonia, has been proved useful for addressing fire recurrence effects.

Lastly, the results of the present study pointed to:

The existence of shifts in floristic composition that may show feedbacks on fire regimes, particularly a higher abundance of shrubs and a higher dominance by scrubs and herbs. Given that fuel loads were lower after the second fire, it is likely that future fires would be more recurrent and less intense.

The existence of cumulative effects as a result of fire repetition at short fire intervals, both on vegetation regeneration (local extinction of P.halepensis) and on soil organic horizons (lower reconstruction of soil organic horizons).

The fact that, under current fire regimes characterized by high levels of fire recurrence, important shifts in the physiognomy and functioning of P.halepensis communities would occur in the Mediterranean Basin.

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Appendix 1

Structural Features of Vegetation

Group	**Model**	**Description**	**Estimated Fuel Loads ($t \cdot ha^{-1}$)**
Pastures	**model 2**	Fine, dry, and low pasture. 1/3-2/3 covered by woody species. Fuel constituted by herbaceous material, litter, and fallen branches	5 to 10
Shrublands	**model 4**	Mature shrubland or young, dense plantation (over 2 m tall) containing dry branches. Fuel constituted by fine, dry, woody material and flammable leaves	25 to 35
	model 5	Dense and green shrubland (under 1 m tall). Fuel constituted by low amounts of dry fuel and leaves showing low contents of flammable compounds. Plant cover near 100%	5 to 8
	model 6	Mature shrubland similar to model 5 but containing more flammable species, and taller plants, despite no so tall as in model 4.	10 to 15
	model 7	Shrubland constituted by particularly flammable species, 0.5 to 2 m tall. When a coniferous tree overstorey exists, flammability is enhances by their leaves	10 to 15

Description of fuel models according to USDA Forest Service.

Study site #24, located on hard calcareous substrate at La Bisbal del Penedès (Baix Penedès).
Once-burnt area was assigned fuel model number 6 (left).
Twice-burnt area was assigned fuel model number 5 (right). It was characterized by a fire interval of 11 years.

Study site #20, located on hard calcareous substrate at Torroelles de Foix (Alt Penedès).
Once-burnt area was assigned fuel model number 6 (left).
Twice-burnt area was also assigned fuel model number 6 (right). It was characterized by a fire interval of 15 years.

Study site #26, located on steep slopes on hard calcareous substrate at Tivissa (Ribera d'Ebre).
Once-burnt area was assigned fuel model number 7 (left).
Twice-burnt area was assigned fuel model number 5 (right), and was characterized by a fire interval of 9 years.

Appendix 2

Nutrient Contents in Mineral Soils and Soil Organic Horizons

Study Sites	**Total N (g kg^{-1})**		**Total C (g kg^{-1})**		**Organic C (g kg^{-1})**		**C/N ratio**		**P (g kg^{-1})**		**K (g kg^{-1})**	
	Once-burnt	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**
4	9,7	11,0	428,6	321,6	412,4	313,1	42,4	28,4	0,35	0,69	1,22	2,43
7	11,8	6,9	416,5	316,4	405,7	310,7	34,5	44,8	0,47	0,40	1,97	2,44
11	7,6	8,0	403,9	355,8	393,5	336,0	51,9	41,8	0,29	0,21	2,28	1,14
13	9,6	7,0	418,1	374,7	397,9	362,0	41,6	51,7	0,38	0,30	1,74	1,67
12	8,1	7,6	414,8	449,1	408,8	439,0	50,6	57,6	0,40	0,31	3,43	2,72
14	9,2	7,9	380,8	417,8	368,8	406,0	40,0	51,1	0,38	0,41	2,80	2,49
15	8,9	7,7	384,2	390,2	372,2	342,8	42,0	44,3	0,37	0,27	2,55	1,48
18	6,5	5,3	406,6	369,0	393,0	356,2	60,7	66,7	0,24	0,19	0,93	1,28
20	5,5	8,2	358,3	408,5	337,7	385,3	61,4	46,9	0,24	0,31	1,12	2,15
21	10,5	8,5	399,1	388,0	397,6	375,7	37,9	44,5	0,37	0,33	2,43	1,79
22	11,0	8,6	426,5	450,5	423,8	440,9	38,6	51,2	0,29	0,38	1,70	2,55
26	11,8	7,5	428,4	432,2	426,2	425,8	36,0	56,5	0,24	0,29	1,10	1,92
28	8,3	8,1	410,4	387,1	385,5	364,3	46,3	44,8	0,48	0,51	2,61	2,12
29	9,8	10,1	430,8	379,3	424,2	362,5	43,3	35,9	0,41	0,44	2,52	2,57
30	9,2	7,8	469,2	413,9	461,6	398,3	49,9	51,0	0,45	0,32	2,85	1,45
Mean	9,2	8,0	411,7	390,3	400,6	374,6	45,1	47,8	0,36	0,36	2,08	2,01
SE	0,5	0,3	6,7	10,4	7,5	10,7	2,1	2,4	0,02	0,03	0,20	0,13

Nutrient contents in pooled organic LF horizons, constituted of charred plant material left by fire and of post-fire plant material such as leaves, cones, acorns, branches, or bark, either unbroken or fragmented. Samples were collected 9 years after fire. Chemical analyses were conducted in oven-dried and milled composite samples and considered total nitrogen, total carbon, phosphorous, and potassium.

Study Sites	**Total N (g kg^{-1})**		**Total C (g kg^{-1})**		**C/N ratio**	
	Once-burnt	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**
13	15,5	16,5	403,4	414,3	26,1	25,1
14	14,7	14,8	428,4	374,6	29,2	25,4
15	13,1	12,1	410,8	441,1	31,4	36,6
18	12,8	9,3	438,4	433,5	34,4	46,6
20	16,1	14,4	433,2	399,9	26,9	27,9
21	15,9	13,4	418,3	426,9	26,3	32,0
22	17,2	15,8	401,8	420,2	23,4	26,6
28	13,7	13,4	373,1	342,9	27,2	25,6
30	10,9	13,4	343,5	391,3	31,7	29,2
Mean	14,4	13,7	405,6	405,0	28,5	30,5
SE	0,5	0,5	7,9	8,1	0,9	1,8

Nutrient contents in organic H horizons, consisting of highly decomposed plant material and humiferous layers. Samples were collected 9 years after the last fire; only 9 study sites showed recognizable H horizons in paired once- and twice-burnt stands. Chemical analyses were conducted in oven-dried and milled composite samples and considered total nitrogen, and total carbon.

Study Sites	**Total N ($g\ kg^{-1}$)**		**Organic C ($g\ kg^{-1}$)**		**C/N ratio**		**P ($mg\ kg^{-1}$)**		**K ($mg\ kg^{-1}$)**		**Mg ($mg\ kg^{-1}$)**		**Ca ($mg\ kg^{-1}$)**		**Na ($mg\ kg^{-1}$)**		**pH**		**EC ($dS\ m^{-1}$)**	
	Once-burnt	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**
4	1,4	1,5	41	40	28,7	26,1	6	3	59	68	121	150	7.882	7.860	58	61	8,2	8,1	0,27	0,25
7	1,5	0,8	26	23	17,0	28,8	1	4	120	68	384	170	6.279	6.056	58	51	8,3	8,3	0,23	0,23
11	1,4	1,9	41	49	30,1	25,3	9	12	122	123	325	345	6.632	8.222	54	86	8,4	8,4	0,25	0,30
12	1,7	3,1	56	24	32,5	7,7	3	1	131	120	376	195	6.900	7.028	51	52	8,0	8,4	0,40	0,27
13	2,8	1,4	94	43	33,3	29,7	7	7	291	239	196	174	10.656	8.005	65	53	8,2	8,3	0,31	0,27
14	2,4	2,2	60	60	25,0	27,7	2	5	258	206	412	409	7.305	6.502	54	48	8,1	8,1	0,29	0,28
15	2,1	2,7	74	73	34,7	26,8	12	9	181	179	625	571	6.088	6.144	56	56	8,0	8,0	0,45	0,42
18	2,5	2,2	89	89	35,1	41,3	12	12	221	179	172	174	9.382	10.676	66	63	8,2	8,2	0,29	0,34
20	3,7	4,2	131	130	35,5	30,7	3	8	414	245	1.241	1.283	6.614	6.237	57	55	7,9	8,0	0,48	0,41
21	3,7	2,3	111	75	30,1	32,3	10	3	253	189	831	317	9.134	8.648	85	61	8,1	8,2	0,39	0,31
22	2,4	2,0	40	60	17,0	29,4	2	3	234	334	147	165	7.719	8.246	58	68	8,2	8,2	0,25	0,28
26	2,0	2,6	52	86	25,5	32,5	9	18	241	263	159	182	8.023	9.195	54	57	8,3	8,2	0,27	0,35
28	1,1	3,5	23	33	20,6	9,3	1	3	64	54	80	105	4.512	6.662	50	60	8,3	8,3	0,20	0,22
29	1,8	1,5	45	45	25,4	29,2	5	3	169	192	210	273	7.451	7.386	56	57	8,1	8,2	0,40	0,35
30	2,3	2,1	75	68	32,7	31,6	5	6	192	189	329	398	8.268	8.141	56	54	8,1	8,2	0,32	0,30
Mean	2,2	2,3	63,9	59,9	28,2	27,2	5,8	6,5	196,7	176,5	373,9	327,4	7.523,0	7.667,2	58,5	58,8	8,2	8,2	0,32	0,31
SE	0,2	0,2	8,1	7,3	1,6	2,2	1,0	1,2	23,9	20,3	81,0	75,8	387,7	332,3	2,2	2,4	0,03	0,03	0,02	0,02

Nutrient contents, pH, and EC of mineral soils. Survey was conducted 9 years after the fire and up to 20 cm depth. Chemical analyses were conducted in oven-dried and milled composite samples and considered total nitrogen, organic carbon, phosphorous, potassium, magnesium, calcium, and sodium

Appendix 3

Soil Pictures

A fire happened about 2 years ago on a community dominated by Q.coccifera and located on dolomites (hard substrate). LF horizons kept into a layer of superficial stones survived the fire; humiferous layers are still protected below them.

Soils developed on marls show fine texture and poor aggregation, and are thus easily eroded. Usually post-fire vegetation shows low cover values, and soil organic horizons are scarce. Pictures were taken 12 years after fire.

A fire happened about 2 years ago, and left charred organic matter remains,
which will be progressively incorporated into remnant soil organic horizons and upper mineral soil.

Soil organic horizons on conglomerates in a once-burnt area and 9 years after fire, at the moment of the survey.

The 1994 fire left higher amounts of big plant remains, such as trunks, in once-burnt areas.
Such remains are slowly incorporated to soil organic horizons (picture was taken 12 years after fire).
In twice-burnt areas, they were likely combusted by the 1994 fire.

Appendix 4

Leaf Nutrient Contents of Q.ilex, P.lentiscus, and R.officinalis

Study Site	**C ($mg·g^{-1}$)**		**H ($mg·g^{-1}$)**		**N ($mg·g^{-1}$)**		**S ($mg·g^{-1}$)**		**Fe ($mg·g^{-1}$)**		**P ($mg·g^{-1}$)**		**Mg ($mg·g^{-1}$)**		**K ($mg·g^{-1}$)**		**Ca ($mg·g^{-1}$)**	
	Once-burnt	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**
3	514	527.45	67.6	70.6	9.8	9.8	1.5	1.9	0.09	0.10	0.79	0.98	2.2	2.4	12.5	11.5	13.0	14.7
9	516.8	514.5	68	68.05	9.0	7.5	1.5	1.3	0.09	0.14	0.97	0.61	1.9	2.2	14.4	12.8	11.0	14.6
10	513	517.65	66.05	67.05	8.8	9.2	1.5	1.3	0.21	0.23	0.51	0.64	2.2	2.2	8.5	9.4	13.2	15.1
11	519.6	522.8	67.35	68.6	7.2	7.4	1.5	1.5	0.22	0.30	0.55	0.48	2.8	2.5	7.9	9.0	17.5	16.2
15	516.5	512.85	68.95	67.55	9.7	8.7	2.1	1.3	0.08	0.12	0.56	0.60	2.0	2.1	10.0	11.8	10.9	11.6
16	527.95	505.55	68.8	65.85	8.8	8.8	1.4	1.4	0.08	0.13	0.91	0.69	1.7	1.6	13.0	13.3	10.0	12.8
17	523.55	512.7	68.55	65.95	8.2	7.9	1.6	1.5	0.18	0.21	0.52	0.53	2.2	2.1	9.1	10.4	15.9	16.1
18	522.25	500.8	67.7	65.55	6.2	7.6	2.2	2.0	0.13	0.13	0.50	0.53	2.4	2.3	10.2	11.1	14.9	16.6
21	529.4	523.7	68.85	68.95	9.2	7.8	1.5	1.1	0.16	0.10	0.63	0.69	2.1	2.4	11.3	10.2	10.8	14.3
26	519.85	544.8	67	70.45	9.3	6.8	1.4	0.9	0.12	0.20	0.54	0.54	1.6	1.5	15.0	14.0	8.1	9.4
28	517	517.9	66.95	67.2	8.9	9.3	1.9	1.4	0.15	0.16	0.68	0.62	2.2	2.2	9.6	8.9	13.3	13.3
29	532.05	535.85	69.95	70.65	10.3	9.3	2.2	2.0	0.10	0.10	0.99	0.77	2.5	1.8	15.0	15.0	13.2	9.6
Mean	521.0	519.7	68.0	68.0	8.8	8.3	1.7	1.4	0.13	0.16	0.68	0.64	2.2	2.1	11.4	11.4	12.6	13.7
SE	1.8	3.6	0.3	0.5	0.3	0.3	0.1	0.1	0.01	0.02	0.05	0.04	0.1	0.1	0.7	0.6	0.8	0.7
t	0.33		-0.11		1.43		2.56		-2.29		0.86		0.53		-0.23		-1.76	
P	0.746		0.912		0.180		0.027		0.043		0.410		0.610		0.822		0.106	

Average foliar nutrient contents of current-year leaves of R.officinalis 11 years after the 1994 fire in areas burnt once and twice, and *t* and *P* values of paired *t*-Student tests.

Study Site	**C (mg·g^{-1})**		**H (mg·g^{-1})**		**N (mg·g^{-1})**		**S (mg·g^{-1})**		**Fe (mg·g-1)**		**P (mg·g-1)**		**Mg (mg·g-1)**		**K (mg·g-1)**		**Ca (mg·g-1)**	
	Once-burnt	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**
3	496.3	488.8	57.6	55.6	11.9	10.8	1.3	0.7	0.09	0.12	0.54	0.71	2.0	2.4	6.1	5.1	14.8	15.7
10	500.6	497.0	57.8	56.8	9.8	8.7	0.7	0.8	0.10	0.11	0.50	0.50	2.1	1.6	6.9	7.9	10.6	10.9
11	499.0	492.9	57.9	57.8	10.2	10.0	0.3	0.9	0.12	0.13	0.50	0.39	2.7	2.2	4.0	5.2	14.8	13.3
15	488.3	491.2	56.4	56.4	9.3	10.0	0.7	1.0	0.09	0.09	0.55	0.56	2.0	2.0	5.4	4.4	14.1	14.9
16	495.9	492.5	57.2	56.4	10.5	10.1	1.0	1.2	0.10	0.08	0.59	0.62	1.5	1.2	6.1	6.8	13.4	11.1
17	500.6	491.2	59.7	55.6	10.5	10.5	0.8	0.8	0.09	0.09	0.52	0.51	1.7	1.9	4.5	5.0	16.3	15.1
18	478.0	489.3	55.9	58.3	7.4	8.6	0.9	1.1	0.08	0.12	0.48	0.46	2.7	1.8	4.3	4.4	21.1	15.7
26	494.1	490.2	57.4	56.4	9.7	9.3	0.8	0.9	0.14	0.14	0.52	0.55	2.2	1.8	6.5	6.9	13.8	14.8
29	490.1	498.7	55.7	56.6	9.4	9.3	0.6	0.7	0.09	0.06	0.52	0.45	1.9	1.4	7.2	7.6	11.2	6.7
Mean	493.6	492.4	57.3	56.6	9.8	9.7	0.8	0.9	0.10	0.10	0.52	0.53	2.1	1.8	5.7	5.9	14.5	13.1
SE	2.4	1.1	0.4	0.3	0.4	0.3	0.1	0.1	0.01	0.01	0.01	0.03	0.1	0.1	0.4	0.5	1.0	1.0
Z	-0.65		-1.12		-0.70		-1.47		-0.40		-0.07		-1.89		-1.01		-1.48	
P	0.515		0.263		0.484		0.142		0.674		0.944		0.059		0.314		0.139	

Average foliar nutrient contents of current-year leaves of P.lentiscus 11 years after the 1994 fire in areas burnt once and twice, and *Z* and *P* values of Wilcoxon rank tests.

Study Site	**C (mg·g^{-1})**		**H (mg·g^{-1})**		**N (mg·g^{-1})**		**S (mg·g^{-1})**		**Fe (mg·g-1)**		**P (mg·g-1)**		**Mg (mg·g-1)**		**K (mg·g-1)**		**Ca (mg·g-1)**	
	Once-burnt	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**
3	477.9	476.2	57.4	59.2	10.3	11.7	0.6	1.3	0.22	0.27	0.57	0.86	1.4	1.6	4.8	4.5	9.1	14.1
9	477.7	478.6	57.6	58.7	8.6	8.1	1.1	1.0	0.14	0.14	0.83	0.57	1.5	1.6	5.3	4.1	12.9	9.5
15	480.0	478.5	60.2	59.1	9.1	9.8	0.8	0.9	0.13	0.13	0.58	0.53	2.3	2.3	3.7	4.2	8.8	8.6
21	478.4	475.3	59.7	58.3	10.7	10.1	1.4	1.1	0.21	0.15	0.54	0.66	1.9	1.4	3.8	5.0	7.2	9.1
28	472.8	478.4	57.8	59.6	8.6	9.3	0.0	1.2	0.12	0.16	0.45	0.56	1.4	2.1	3.8	3.2	7.7	7.5
Mean	477.3	477.4	58.5	59.0	9.4	9.8	0.8	1.1	0.16	0.17	0.59	0.64	1.7	1.8	4.3	4.2	9.1	9.8
SE	1.2	0.7	0.6	0.2	0.4	0.6	0.2	0.1	0.02	0.03	0.06	0.06	0.2	0.2	0.3	0.3	1.0	1.1
Z	-0.41		-0.81		-1.21		-0.81		0.00		-0.67		-0.73		-0.27		-0.14	
P	0.686		0.419		0.225		0.419		>0.9990		0.500		0.465		0.787		0.893	

Average foliar nutrient contents of current-year leaves of Q.ilex 11 years after the 1994 fire in areas burnt once and twice, and *Z* and *P* values of Wilcoxon rank tests.

Appendix 5

Leaf Nutrient Contents of P.halepensis

Study Site	**C (mg·g^{-1})**		**H (mg·g^{-1})**		**N (mg · g^{-1})**		**S (mg·g^{-1})**		**Fe (mg·g^{-1})**		**P (mg·g^{-1})**		**Mg (mg·g^{-1})**		**K (mg·g^{-1})**		**Ca (mg·g^{-1})**	
	Once-burnt	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**	**Once-burnt**	**Twice-burnt**
3	496.0	484.9	63.4	63.9	10.9	9.9	1.0	0.4	0.14	0.10	0.69	0.91	2.2	1.9	3.2	4.3	9.7	7.5
10	494.7	498.1	63.4	64.5	9.9	10.2	1.0	1.1	0.21	0.14	0.60	0.85	1.8	2.5	2.7	3.3	5.6	8.4
11	490.2	500.8	63.0	65.0	7.6	9.2	0.8	0.5	0.17	0.16	0.53	0.53	2.1	2.1	2.6	2.9	7.1	6.1
16	482.9	487.7	62.7	61.7	8.9	8.6	0.6	1.1	0.13	0.09	0.94	0.91	1.6	1.2	4.7	4.9	6.5	5.7
21	487.1	485.0	63.8	62.0	10.4	9.5	0.5	0.8	0.10	0.11	0.76	0.90	2.0	1.8	3.2	3.9	5.6	5.0
26	486.0	487.9	62.3	63.1	9.8	9.2	0.6	0.8	0.20	0.18	0.92	0.84	1.3	1.6	5.4	5.2	5.2	6.3
29	500.1	497.8	63.4	63.4	8.3	9.5	1.2	0.9	0.09	0.11	0.64	0.59	2.0	1.8	4.2	3.6	7.2	6.7
Mean	491.0	491.7	63.1	63.3	9.4	9.4	0.8	0.8	0.15	0.13	0.73	0.79	1.9	1.8	3.7	4.0	6.7	6.5
SE	2.3	2.6	0.2	0.5	0.5	0.2	0.1	0.1	0.02	0.01	0.06	0.06	0.1	0.1	0.4	0.3	0.6	0.4
Z	-0.34		-0.52		-0.09		-0.17		-1.52		-0.94		-0.21		-1.35		-0.34	
P	0.735		0.600		0.933		0.866		0.128		0.345		0.834		0.176		0.735	

Average foliar nutrient contents of current-year leaves of P.halepensis 11 years after the 1994 fire in areas burnt once and twice, and *Z* and *P* values of Wilcoxon rank tests.