2 The role of fire in European Mediterranean Ecosystems

Juli G. Pausas and V. Ramon Vallejo Centro de Estudios Ambientales del Mediterráneo (CEAM)

Abstract. Fire is an integral part of many ecosystems, including the Mediterranean ones. However, in recent decades the general trend in number of fires and surface burnt in European Mediterranean areas has increased spectacularly. This increase is due to: (a) land-use changes (rural depopulation is increasing land abandonment and consequently, fuel accumulation); and, (b) climatic warming (which is reducing fuel humidity and increasing fire risk and fire spread). The main effects of fire on soils are: loss of nutrients during burning and increased risk of erosion after burning. The latter is in fact related to the regeneration traits of the previous vegetation and to the environmental conditions. The principal regeneration traits of plants are: capacity to resprout after fire and fire-stimulation of the establishment of new individuals. These two traits give a possible combination of four functional types from the point of view of regeneration after fire, and different relative proportions of these plant types may determine the post-fire regeneration and erosion risk. Field observations in Spain show better regeneration in limestone bedrock type than in marls, and in northfacing slopes than in south-facing ones. Models of vegetation dynamics can be built from the knowledge of plant traits and may help us in predicting post-fire vegetation and long-term vegetation changes under recurrent fires.

2.1 Introduction

There are several features that make the landscapes of the European Mediterranean Basin different from those of the rest of Europe, and these differences are mainly related to the climate, the long and intense human impact, and the role of fire. The latter is, in turn, influenced by the other two. Mediterranean ecosystems of Europe have been subjected to a long-term history of human use (Wainwright 1994, Grove 1996, Margaris et al. 1996), and this has provoked older and very intense disturbance regime when compared to the other Mediterranean-climate regions in the world (Fox and Fox 1986). However, within the Mediterranean basin, differences in land-use patterns have increased during this century between Euro-Mediterranean and Afro-Asiatic-Mediterranean countries (Blondel and Aronson 1995). In the southern areas of the western Mediterranean (Maghreb), growing populations are reducing forests and shrublands by overgrazing and extending arable lands, whereas in the northern countries abandoned land is increasing at the expense of marginal agriculture (Puigdefábregas and Mendizabal 1998). These differential trends make the European Mediterranean Basin more fire prone than the southern area, as shown in the fire statistics of the last decades (Vélez 1997, Moreno et al. 1998).

2.2 Fire history

2.2.1 Statistics

Natural fires are common in many parts of the world and are an integral part of many terrestrial ecosystems. Fire has been used by man as a management tool since early times. It has been suggested that Palaeolithic people already burnt deliberately to facilitate hunting and food gathering (Stewart 1956). The first evidence of human-induced changes by fire in the Mediterranean landscape is during the Neolithic (Naveh 1975). Since then, the Mediterranean basin has seen the evolution of many cultures, some with high population densities, and most making use of fire and farming. However, from the 60s until today the general trend in number of fires and surface burnt in the European Mediterranean areas (mainly Iberian, Italic and Greek Peninsulas and surrounding islands) has increased exponentially. Fire statistics compiled for Spain from the 60s (Martínez-Ruiz 1994, Moreno et al. 1998, Piñol et al. 1998) show a clear increase in number of fires and surface burnt especially since the mid-70s (Fig. 2.1 and 2.2). From 1960 to 1973 the mean annual burnt area was about 50 kha and the annual number of fires was less than 2000. However, since 1974, the mean annual area burnt is about 215 kha, caused by a mean of 8550 annual fires, and in some of these years the area burnt was more than 400 kha, i.e. nearly 2% of the total non-arable land

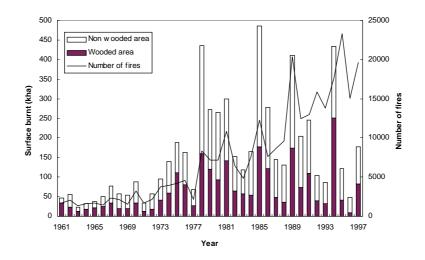


Fig. 2.1.Yearly number of fires (line), wooded surface burnt (close bars, kha) and nonwooded (e.g. shrublands) surface burnt (open bars, kha) in Spain for the period 1961 -1997. Elaborated from data of ICONA (Martínez Ruiz 1994, Vélez 1996, 1997b)

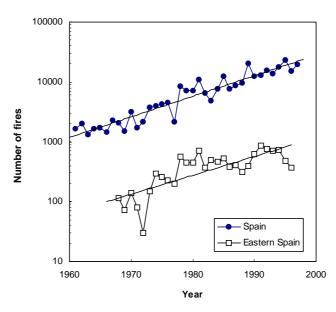


Fig. 2.2. Number of fires in the last decades for the whole Spain (black dots) and for the eastern part (Valencia region). Note the logarithmic scale of the y-axis.

4 The role of fire in European Mediterranean Ecosystems

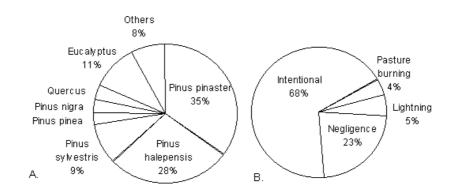


Fig. 2.3. Percentage of surface burnt by dominant species (A) and percentage of number of fires by causes of ignition (B, 38% of the fires were of unknown cause and are not considered in the figure), in Spain during the period 1974-1994. Elaborated from data in Moreno et al. (1998).

2.2.2 Land-use changes

In the Mediterranean basin, many centuries of severe human pressure resulting in burning, cutting and grazing on non-arable lands and clearing, terracing, cultivating, and later abandonment of arable portions, have created a strongly human-influenced landscape. The cultivation of marginal areas under increasing population pressure have been common in southern Europe since the 16th century (Roxo and Mourao 1995, Kosmas 1996). It is not possible to understand current vegetation patterns in the Mediterranean basin without taking into account past anthropogenic activities and land-uses. Human intervention has been so strong that it is still making a significant impact on current and future vegetation patterns.

The changes in fire occurrence during the last decades closely reflect the recent socio-economic changes underway in the European Mediterranean countries (Vélez 1993, Moreno et al. 1998). With industrial development, European Mediterranean countries have experienced: depopulation of rural areas, increases in agricultural mechanisation, decreases in grazing pressure and wood gathering, and increases in the urbanisation of rural areas (LeHouérou 1993). These changes in traditional land-use and lifestyles have implied the abandonment of large areas of farm-land, which has led to the recovery of vegetation (García-Ruiz et al. 1996, Roxo et al. 1996) and an increase in accumulated fuel (e.g. Rego 1992). In Southern Europe, human activity has dramatically increased fire frequency as a consequence of land abandonment and tourist pressure. Piñol and Terradas (1996) found a significant relationship between population density and fire occurrence in Mediterranean areas of the Iberian Peninsula. As a consequence of these processes, landscapes are becoming homogeneous (Moreno and Oechel 1992, Sala and Rubio 1994). In summary, land-use changes produced during the present century in southern Europe are parallel to the changes in the fire regime, from being few in number and affecting small areas, to becoming very numerous and

affecting large extensions every year. This trend is not observed in the southern Mediterranean basin where traditional land-uses remain the major socio-economic system.

2.2.3 Climate change

Although the main reason for fire increase in the last decades is probably changes in land use, climatic factors should be considered as a contributing factor. Fires tend to be concentrated in summer when temperatures are high, and air humidity and fuel moisture are low. Predictions on climate warming in the Mediterranean basin indicate an increase in air temperature and a reduction in summer rainfall (Houghton et al. 1996). Although there is uncertainty on the mean and variance of the precipitation changes, all predictions suggest a future increment in water deficit. These changes would lead to an increase in water stress conditions for plants, changes in fuel conditions and increases in fire risk, with the consequent increase in ignition probability and fire propagation. Analysis of past climate data already show some of these trends (Maheras 1988, Amanatidis et al. 1993, Piñol et al. 1998). For example, the recent analysis of meteorological data from 1910 to 1994 in the eastern Iberian Peninsula (Piñol et al. 1998) show a clear increase in temperature and potential evapotranspiration and a reduction in summer humidity. These changes are correlated to an increase in the number of fires. The climate changes that are predicted to occur in the near future as a result of releasing greenhouse gases are likely to induce increased fire risk not only in the Mediterranean area, but also in other fire-prone regions of the world (Flannigan and van Wagner 1991, Torn and Friend 1992).

2.3

Fire effects on soils

Fire effects on soils can be separated in two phases, that is, direct losses of nutrients during burning, and post-fire changes due to low vegetation cover. These two phases include different processes, and they eventually require different measures to reduce soil degradation risk.

During burning, direct nutrient losses are produced by volatilisation, mostly C, N and S, and by ash convection in the smoke column (Raison et al. 1985, Gillon and Rapp 1989, Trabaud 1994). These losses are especially relevant in high intensity fires (Little and Ohmann 1988). In addition, the vegetation and forest floor cover disappear partially or totally, and the topsoil suffers heating (Christensen 1994). These processes associated to burning operate in a time scale of seconds to weeks, the latter in the case of smouldering in small spots. The magnitude of these impacts is included in the often ambiguous term 'fire severity', which is somehow related to fire intensity, and may be defined as the residence time of a threshold temperature, e.g. 150°C (Pérez-Ramos 1997). As fire temperature is related to fuel load and spatial structure, actions to reduce fire impact during combustion are addressed to control fuel accumulation.

The burned land has lost most of the plant and forest floor cover, therefore the

6 The role of fire in European Mediterranean Ecosystems

ash layer and bare soil are exposed to water and wind erosion, and to soluble nutrients leaching from the ash layer during the post-fire period of low vegetation cover (DeBano et al. 1979, Khanna and Raison 1986). The time scale of this second phase is from fire extinction up to a few months to years depending on the vegetation recovery rate. Nutrient losses produced after fire could be higher than those produced during burning, especially when soil erosion is relevant. The greatest damage by fire is caused in those areas with a long dry season where organic horizons can be burnt, exposing, and perhaps affecting, the mineral soil (Trimble 1988). In Mediterranean regions, the frequent autumn rainstorms constitute a high erosion risk after summer wildfires. Thornes (1990) considered that a minimum of 30% projective plant cover is sufficient for protecting the soil against water erosion. The risk of post-fire soil erosion is higher the higher the time required for vegetation to reach this threshold plant cover value. In eastern Spain, critical time values varied from a few months to more than 1.5 years (Vallejo et al. in press), and these are quite dependent on the regenerative strategy of the vegetation. Post-fire soil degradation in vulnerable soils (erodible soils, steep slopes and low plant-regeneration capacity) could be mitigated by applying emergency seeding techniques (Vallejo and Alloza 1998) that aim at enhancing a protective herbaceous cover shortly after the fire. In spite of nutrient losses produced during combustion and post-fire leaching and erosion, soil fertility increases temporarily by ash incorporation in the soil and soil biological activity enhancement shortly after the fire (Walker et al. 1986, Kutiel and Naveh 1987), although a late short-term depression in nutrient availability may appear (Ferran 1996). Soil biological activity after fires requires more than 20 years for complete recovery (Prodon et al. 1987). In addition, fire may modify mycorrhizal inocula in the soil (Torres and Honrubia 1997, Tartaglini 1992) that can limit plant regeneration. Soil properties usually increase their spatial heterogeneity because of processes associated to the fire, such as patchiness in fire severity (Pérez-Ramos 1997), short-distance redistribution of ashes and top soil material after fire (Serrasolsas 1994), and the modifications in nutrient cycling produced by the different litter qualities of colonising plants (Ferran and Vallejo 1992).

High fire frequency affecting nutrient-poor ecosystems strongly increases the risk of soil fertility depletion and desertification. In semiarid shrublands of southeastern Spain, Carreira et al. (1996) found a sharp depletion of soil available nutrients, especially extractable inorganic phosphorus, associated to a linear increase in the fire frequency along a successional chronosequence. In addition, C accumulation in the soil could be limited by N losses during fire in ecosystems affected by high fire frequency (Menaut et al. 1993, Vitousek and Howarth 1991). In spite of the short-term nutrient losses produced by severe wildfires, and that model predictions indicate that regular burning may result in a decline of forest productivity (O'Connell 1989), few evidences have been found so far of long-term decreases in soil productivity because of fire. Recently, Ferran et al (1998) found that 3.5 years after the fire, *Quercus coccifera* garrigues accumulated less biomass in stands affected by recurrent fires (up to 3 fires in 16 years) as compared to those affected by only one.

2.4 Post-fire regeneration of vegetation

The effects of fire on vegetation are very complex, not only because of the great complexity of Mediterranean ecosystems and the interactions with land-uses, but also because of the different responses to different type of fires and fire regimes (i.e., different intensities, seasonalities, recurrences and extent of the fire). At the landscape level, post-fire regeneration would depend mainly on the initial vegetation, that is, plant traits of the initial species occurring on the site, and on-site environmental factors (climatic and terrain parameters).

2.4.1

Plant traits

There are two main plant traits conditioning the regeneration pattern: a) the capacity to resprout after fire (resprouter species), and b) the stimulation of the recruitment by fire (seeder or recruiter species). We consider fire-stimulated species to be those in which fire stimulates or facilitates the recruitment process (seed dispersal, germination, flowering, etc.) by some physical or chemical mechanism (e.g. heat, smoke). Species that increase after fire because there is more light/space available (opportunistic species) are not considered fire-stimulated by fire or not, in four possible combinations (Pausas 1999): resprouters without recruitment stimulated by fire (R+S-), resprouters with recruitment stimulated by fire (R-S+, obligate seeders) and non-resprouters without recruitment stimulated by fire (R-S-).

These functional types have different demographic patterns and responses to repeated wildfires (for details see Pausas 1999). Resprouting species always maintain some biomass alive (often below-ground biomass) and recover quickly from fire. A typical example is the *Ouercus coccifera* (kermes oak, the dominant species of the garrigues), a vigorous resprouter shrub with rhizomes that quickly recover from fire. Trabaud (1991) experimentally burnt this species every two year for 19 years and it kept resprouting. Ferran et al. (1998) have demonstrated the loss of some growth capacity in this species after recurrent fires. This loss can be due to the depletion of carbohydrates and nutrients stored in the below-ground system. Other Quercus species have demonstrated their high resprouting capacity from basal buds (e.g., Q. ilex). An interesting case is Quercus suber (cork-oak) which is able to resprout from stem buds (Pausas 1997) thanks to protection by a thick bark (cork). It is the only European tree species that resprouts from stem buds, as do most Australian Eucalyptus (Gill 1981, Strasser et al. 1996), and it produces a quick regeneration of the landscape after fire. This feature together with its economic importance make this species a good candidate for reforestation programs in fire-prone areas.

The recovery of non-resprouting species is slower and depends on the fire interval, the age of maturity (to produce seeds for regeneration) and seed longevity, and resistance to fire. Species with fire-stimulated recruitment show a peak-phase soon after a fire, and then they decrease due to their low competition ability. Different recruitment processes may be stimulated by fire, with germination being the most important. Seeds of some species have innate (primary) dormancy and require a fire-related stimulus to germinate (refractory seeds). Fire may also stimulate flowering or dispersal. Examples of species with fire-stimulated germination are most of the *Cistaceae* and *Papilonaceae* (legumes) species (e.g. Thanos et al. 1992, Arianoutsou and Thanos 1996). Furthermore, it has been postulated that post-fire vegetation may be rich in legume species because their capacity to fix nitrogen may alleviate nutrient losses caused by fire. However, while some studies seem to supports this hypothesis (e.g., in the Greek phryganas, Arianoutsou and Thanos 1996), others do not (in French and Iberian garrigues, Trabaud 1992, Pausas et al, in review).

Another adaptation to fire is the serotiny (=bradyspory), that is, the retention of the seed in the canopy until a fire occurs (fire-induced seed dispersal). This fire stimulation system is frequent in other Mediterranean type ecosystems (South Africa, Australia) but in the Mediterranean basin it is only found in a relatively low level in a few species such as the Mediterranean pines (e.g., *Pinus halepensis, P. brutia*). In these pines the recruitment is stimulated by fire because of increased seed dispersal rather than germination stimulation. In contrast with some other Mediterranean type ecosystems (such as South Africa, Australia), in the Mediterranean Basin no plants have been found to be strictly dependent on fire for completing their life cycle.

There are some species which posses both the capacity to resprout after fire and to have their recruitment stimulated by fire (e.g. *Thymus vulgaris, Anthyllis cytisoides, Dorycnium pentaphyllum*). However, in these cases both factors are usually developed in a lesser degree (i.e. lower resprouting capacity and lower stimulation of the recruitment) than for resprouting (non stimulated recruitment) species and obligate seeders.

2.4.2 Environmental conditions

Environmental conditions affect both fire behaviour and vegetation response, and the differential effect on each of these factors is difficult to separate from field observations. Several samplings in the eastern Iberian Peninsula have been undertaken to test the effect of different environmental (terrain and climate) parameters on regeneration (Vallejo 1997, Pausas et al., in review).

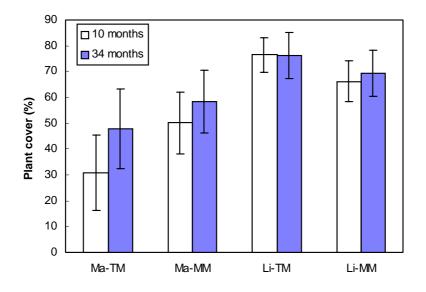


Fig. 2.4. Plant cover (%) 10 and 34 months after fire in four environmental conditions: two bedrock types (Ma: marls, Li: limestones) and two bioclimatic regions (TM: thermo-Mediterranean and MM: meso-Mediterranean). Vertical lines are standard deviations. Elaborated from data in Pausas et al. (in review).

Two main bioclimatic zones from the point of view of temperature and two main bedrock types are found in the eastern Iberian Peninsula (Valencia region): the thermo-Mediterranean zone right next to the coast with a mean annual temperature between 17-19°C (vegetative period = whole year) and the meso-Mediterranean zone, a bit inland with a mean annual temperature between 13-17°C (vegetative period = 9 - 11 months). The two main bedrock types are: limestone, that is, calcareous hard rocks producing very shallow and decarbonated brown-red soils with abundant outcrops and cracks, and marls which produce deeper and highly carbonated soils but without cracks. The combination of these factors (bioclimatic region x bedrock type) gives four distinctive environmental conditions. Several sites were selected in each of these environments after the 1991 fires, and the vegetation covers were analysed 10 and 34 months after the fire (Vallejo 1997, Pausas et al. in review, Fig. 2.4). Results clearly show the influence of bedrock type, while difference in climatic region were less evident: plant recovery was significatively lower on marls in both samplings (10 and 34 moths after fire). Ten months after fire the mean plant cover was over 71% on limestone bedrock type, and ca. 40% on marls. At that time two highly resprouting species (both having rhizomes), Quercus coccifera (kermes oak) and Brachypodium retusum (a perennial grass) covered ca. 30 and 46% on limestone and 7 and 24% on marls.

The effect of facing slope on post-fire recovery was studied after the 1994 large fire in the meso-Mediterranean bioclimatic zone under limestone bedrock of the

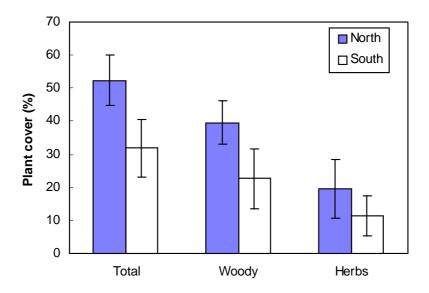


Fig. 2.5. Vegetation cover (%) for total and for two species groups (woody species and herbaceous species), on different facing slopes, one year after the 1994 fire on limestone bedrock type and under meso-Mediterranean bioclimates in Eastern Iberian Peninsula. Vertical lines are standard deviations. Elaborated from data in Pausas et al. (in review).

eastern Iberian Peninsula. A year after the fire, on the average, vegetation covered 42% of the soil, and the cover was significantly greater on the north slopes (52.4%) than on the south ones (32%, Fig. 2.5). This recovery was mainly due to the resprouting species *Quercus coccifera* and *Brachypodium retusum*, and to the obligate seeders *Ulex parviflorus*, *Helianthenum marifolium* and *Cistus albidus*.

The regeneration of *Pinus halepensis* has also shown some relation with environmental conditions. This species tends to regenerate better at low altitude (Fig. 2.6), at low/middle position on the hillside and on moderate slopes or flat areas (Tsitsoni 1997). Furthermore, other parameters have been found to be important in the regeneration of this species, such as the thickness of the ash layer after fire, which reduces the germination rate of *Pinus halepensis* and *Cistus* species (Ne'eman et al. 1993). The regeneration of this important forest species depends on fire recurrence, that is, if the fire free period is shorter than the age to reach maturity, the species would be locally eliminated.

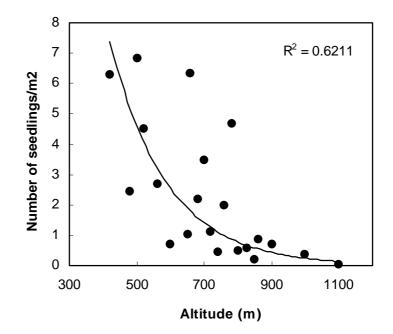


Fig. 2.6. Mean number of pine (*Pinus halepensis*) seedlings per m^2 under burnt adults along an altitude gradient. Elaborated from data in Pausas et al. (in review).

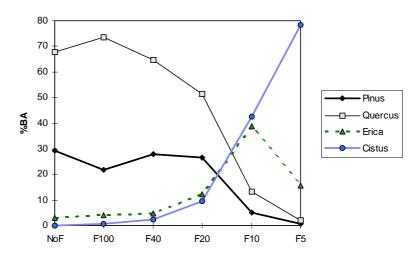


Fig. 2.7. Summary of the BROLLA simulation results for 6 scenarios with four species groups (named *Quercus, Pinus, Cistus, Erica*). No fire (NF) and fire every 100 (F100), 40 (F40), 20 (F20), 10 (F10), and 5 (F5) years. The y-axis represents the mean percent basal area of 10 replicated simulations for 500 years. From Pausas (in press).

2.4.3 Prediction of long-term effects

The long-term consequences of disturbances on landscapes are difficult to predict on the basis of field observations only. Models of vegetation dynamics are useful tools for investigating the long-term consequences of different scenarios such as climatic (Solomon 1986, Bugmann 1997), harvesting (Pausas and Austin 1997), fire regime (Pausas 1998) or land-use scenarios. These models are especially important for studying the consequences of interval-dependent processes (in contrast to event-dependent processes; Bond and van Wilgen 1996), where the experimental approach is difficult to apply. Interval-dependent processes such as establishment, maturation and dormancy are key factors for predicting the long-term consequences of alternative fire scenarios on Mediterranean landscapes.

Modelling vegetation dynamics in fire-prone ecosystems requires two steps (Pausas 1998). The first is to produce descriptive (often statistical, e.g. Strasser et al. 1996, Pausas 1997) models based on field observations after wildfire or experimental fire. These models are a simplified description of the response of vegetation to disturbance events (fires). The second step is to introduce ecological knowledge of how plants function and descriptive models from field observations into a mechanistic simulation model. This simulation model allows us to simulate long-term vegetation dynamics, and to test alternative scenarios or management options.

The most standard modelling technique currently used to predict vegetation dynamics is the gap model approach (individual-based gap dynamic modelling approach, Botkin et al. 1972, Shugart 1984) which simulates stand development by modelling mechanistically the establishment, growth, and death of individual plants. We have developed a simple gap model, called BROLLA (Pausas, in press), that simulates the establishment, growth, and death of individual plants in a 200 m² plot and at annual time-steps. BROLLA aims at capturing the main features for modelling the dynamics of Mediterranean vegetation. It is based on other gap models (Botkin et al. 1972, Shugart 1984, Coffin and Lauenroth 1990, Pausas et al. 1997) and includes 4 species groups (plant functional types) growing in the north-eastern Iberian Peninsula: *Quercus* (tree, broad-leaved evergreen resprouter; e.g. O. ilex), Pinus (tree, needle-leaved non-resprouter with serotinous cones; e.g. P. halepensis), Erica (heath, ericoid-leaved resprouter; e.g. E. multiflora), and *Cistus* (shrub, broad-leaved non-resprouter with germination stimulated by fire; e.g. C. albidus). Six fire scenarios were simulated for a 500 year period (mnemonic names in brackets): no fire (NF) and fire every 100 (F100), 40 (F40), 20 (F20), 10 (F10) and 5 (F5) years. The objective of these fire scenarios was to create a fire recurrence gradient to study the behaviour of the functional types with changes in fire recurrence. In the presented model runs, it is assumed that the simulated patch is within a large fire, that is, there is no external source of seeds from surroundings.

The BROLLA model predicted changes in the relative abundance of the different species with changes in the fire recurrence in NE Iberian Peninsula (Fig. 2.7). *Quercus* showed a progressive decrease in relative abundance, from ca. 70% (NF)

to less than 5% (F5) of the total basal area. *Pinus* had its maximum relative abundance (30%) at low and intermediate fire recurrences (NF-F20). *Erica* and especially *Cistus* increased with increased fire recurrence (F10 and F5).

Without fire, BROLLA predict a forest dominated by Quercus (oak forest), with some *Pinus* and a very low presence or total absence of *Erica* and *Cistus*. With high fire recurrence (F5), the model predict a community (shrublands) dominated by Erica and Cistus, with very low abundance or absence of Quercus and Pinus (immatures only). At intermediate fire recurrences, the predicted community is dominated by Quercus with Pinus (mixed forest) depending on the fire recurrence. These results are roughly as expected for eastern Spain (Terradas 1987, Ferran 1996), that is, mature oak (e.g. Q. ilex) forest in areas with low fire recurrence, pine/oak woodlands (e.g., P. halepensis) in areas with higher fire recurrence, and shrublands (e.g. Erica multiflora and Cistus sp. pl.) in the highest fire recurrence areas. Similar patterns of increasing shrublands and decreasing *Quercus* communities due to increasing fire recurrence are found in other Mediterranean basin systems (e.g., Trabaud and Galtié 1996). In a successional study using a chronosequence in the NE Iberian Peninsula (Ferran 1996), Quercus ilex, Pinus halepensis, and Cistus salviifolius followed a similar pattern to the one simulated here, although Erica species were less abundant. That is, Quercus was abundant in the mature stands (23 and 35 years since last fire), while Cistus was very abundant in the young ones (2 years since fire). Pinus was low in abundance or absent in all the chronosequence, and absent in the young stands. A Quercus coccifera garrigue in eastern Spain (Ferran et al. 1998) showed a significant decrease in Quercus biomass from a plot unburned at least for the last 18 years to similar garrigues burnt once, twice, and three times in that period; the cover of *Cistus* species (biomass was not sampled) showed an opposite trend. Model results are consistent with these trends although accurate comparisons are not possible. It is very difficult, if not impossible, to verify accurately these types of models because of the difficulty in obtaining reliable fire history information at the patch level; and because of the spatial variability in the response. Current vegetation is a mosaic of different patches, with different fire histories and different site (e.g. soil, microclimate) characteristics.

The land-use history may interfere with the dynamic pattern described here. Cultivation requires the uprooting of resprouters, and although land abandonment permit new plant colonisation, this is often difficult for many sclerophyllous resprouter species because of their low dispersal capacity and/or their requirement of an animal vector for dispersal (zoochory) which may not be available in degraded lands (Alcántara et al. 1997). In addition, germination rates and seedling survival are often low for these species in degraded drylands, as is the case of *Quercus rotundifolia* (Laguna and Reyna 1990, Pausas 1999).

Vegetation dynamic models provide us some insights into the fate of vegetation with changes in fire recurrence, and can be used to test alternative management scenarios. However, further work is needed before we can obtain reliable models for global change predictions. The main research needed includes: the extension to spatially explicit gap models (including realistic dispersion processes), realistic environmental (especially temperature) response of the species, knowledge of key species attributes, and the inclusion of below-ground competition. Research on these topics would improve our ability to produce more accurate simulation models.

2.5 Concluding remark

Large forest fires have spread at an unprecedented rate in southern Europe during the last decades, after dramatic changes in land use and population distribution between urban and rural areas. Similar trends could be predicted for northern African countries in the future. The challenging questions now are to what extent the present fire regime can be modified through suppression and prevention policies, and what might be the consequences for ecosystems and landscape structure and dynamics. To get some insight into these questions, ground-based observations should be coupled with remote sensing techniques in order to provide the knowledge basis for modelling various management scenarios at the appropriate scale.

Acknowledgements. This research was supported by the government of Valencia (*Generalitat Valenciana*) and by the Spanish government (*Ministerio de Educación y Ciencia*).

2.6. References

- Alcántara JM, Rey PJ, Valera F, Sánchez AM, Gutiérrez JE (1997) Habitat alteration and plant intra-specific competition for seed dispersers. An example with *Olea europaea* var. *sylvestris*. Oikos 79: 291-300
- Amanatidis GT, Paliatsos AG, Repapis CC, Bartzis JG (1993) Decreasing precipitation trend in the Marathon area, Greece. Int J Clim 13: 191-201
- Arianoutsou M, Thanos CA (1996) Legumes in the fire-prone Mediterranean regions: an example from Greece. Int J Wildland Fire 6: 77-82
- Blondel J, Aronson J (1995) Biodiversity and ecosystem function in the Mediterranean
 Basin: Human and non-human determinants. In: Davis GW & Richardson DM (eds)
 Mediterranean-type Ecosystems: The function of Biodiversity. Springer-Verlag,
 Berlin, pp. 43-119
- Bond WJ, van Wilgen BW (1996) Fire and Plants. Chapman & Hall, London
- Botkin DB, Janak JF, Wallis JR (1972) Some ecological consequences of a computer model of forest growth. J Ecol 60: 849-872

Bugmann HKM (1997) Sensitivity of forests in the European Alps to future climatic

change. Clim Res 8: 35-44.

 Carreira JA, Arevalo JR, Niell FX (1996) Soil degradation and nutrient availability in fireprone Mediterranean shrublands of southeastern Spain. Arid Soil Res Rehab 10: 53-64
 Coffin DP, Lauenroth WK (1990) A gap dynamics simulation-model of succession in a

semiarid grassland. Ecol Modelling 49: 229-266

Christensen NL (1994) The effects of fire on physical and chemical properties of soils in

Mediterranean-climate shrublands. In: Moreno JM, Oechel WC (eds) The role of fire

in Mediterranean-type Ecosystems. Springer-Verlag, New York, pp. 79-95

DeBano LF, Eberlein GE, Dunn PH (1979) Effects of burning on Chaparral soils: I. Soil nitrogen. Soil Sci Soc Am J 43: 504-509.

Ferran A (1996) La fertilitat dels sòls forestals en la regeneració després del foc de diferents ecosistemes mediterranis. PhD thesis Universitat de Barcelona, Barcelona

Ferran A, Vallejo VR (1992) Litter dynamics in post-fire successional forests of *Quercus ilex*. Vegetatio 99-100: 239-246

Ferran A, Delitti W, Vallejo VR (1998) Effects of different fire recurrences in Quercus

coccifera communities of the Valencia region. Proceedings of the III International

Conference on Forest Fire Research, Vol. 2, pp. 1555-1569. Coimbra, 16-20 November 1998

Flannigan MD, van Wagner CE (1991) Climate change and wildfire in Canada. Can J For Res 21: 66-72

Fox BJ, Fox MD (1986) Resilience of animal and plant communities to human disturbance.In: Dell B, Hopkins AJM, Lamont BB (eds) Resilience in Mediterranean-type

Ecosystems. Dr. W. Junk Publishers, pp. 39-64

García-Ruiz JM, Lasanta, T, Ruiz-Flano P, Ortigosa L, White S, González C, Martí C

(1996) Land-use changes and sustainable development in mountain areas: A case study in the Spanish Pyrenees. Landscape Ecol 11: 267-277

Gill AM (1981) Adaptative responses of Australian vascular plant species to fire. In: Gill AM, Groves RH, Noble RI (eds) Fire and the Australian Biota. Australian Academy of Sciences, Canberra, pp. 243–272

Gillon D, Rapp M (1989) Nutrient losses during a winter low-intensity prescribed fire in a Mediterranean forest. Plant Soil 120: 69-77

Grove AT (1996) The historical context: Before 1850. In: Brandt CJ, Thornes J (eds) Mediterranean desertification and land use. J. Wiley & Sons, Chichester, pp. 13-28

Houghton JT, Meiro Filho LG, Callander BA, Kattenburg A, Maskell K (eds) (1996)

Climate Change 1995. The Second Assessment Report of the IPCC. Cambridge University Press, Cambridge

- Kailidis DS (1992) Forest fires in Greece. In: Proceedings of the International Seminar on Forest Prevention, Land Use and People. Greek Ministry of Agriculture, Athens, pp. 27-40
- Khanna PK, Raison RJ (1986) Effects of fire intensity on solution chemistry of surface soil under Eucaliptus pauciflora forest. Aust J Soil Res 24: 423-434
- Kosmas CS (1996) Impacts of desertification and agriculture. International Conference on Mediterranean Desertification. Research Results and Policy Implications. Crete-Hellas.
- Kutiel P, Naveh Z (1987) The effect of fire on nutrients in a pine forest soil. Plant Soil 104: 269-274
- Laguna E, Reyna S (1990) Diferencias entre los óptimos natural y forestal de las

vegetaciones valencianas y alternativas futuras de gestión. Ecología, Fuera de Serie 1: 321-330

- Le Houérou H.N (1993) Land degradation in Mediterranean Europe: can agroforestry be a part of the solution? A prospective review. Agrofor Sys 21: 43-61
- Little SN, Ohmann JL (1988) Estimating nitrogen lost from forest floor during prescribed fires in Douglas-Fir Western Hemlock clearcuts. Forest Sci 34 : 152-164

Maheras P (1988). Changes in precipitation conditions in the western Mediterranean over the last century. J Clim 8: 179-189

Margaris NS, Koutsidou E, Giourga Ch (1996) Changes in traditional Mediterranean landuse systems. In: Brandt CJ, Thornes J (eds) Mediterranean desertification and land use. J. Wiley & Sons, Chichester, pp.29-42

Martínez-Ruiz E (1994) El problema de los incendios forestales en España, análisis de los últimos cincuenta años, previsones de cara al siglo XXI. Rev For Española 11: 40-54.

Menaut JC, Abbadie L, Vitousek PM (1993) Nutrient and organic matter dynamics in Tropical ecosystems. In: Crutzen PJ, Goldammer JG (eds) Fire in the Environment. The Ecological, Atmospheric, and Climatic Importance of Vegetation Fires. Environmental Sciences Research Report ES 13, John Wiley & Sons Ltd, Chichester, pp. 215-231

Moreno JM (ed) (1998) Large Fires. Backhuys Publishers, Leiden, The Netherlands

Moreno JM, Oechel WC (eds) (1994) The Role of Fire in Mediterranean-Type Ecosystems. Springer-Verlag, Ecological Studies 107, New York

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

Naveh Z (1975) The evolutionary significance of fire in the Mediterranean region. Vegetatio 29: 199-208 Ne'eman G, Meir I, Ne'eman R (1993) The effect of ash on the germination and early

growth of shoots and roots of Pinus, Cistus and annuals. Seed Sci Techn 21: 339-349

- O'Connell AM (1989) Nutrient accumulation in and release from the litter layer of karri (*Eucaliptus diversicolor*) forests of Southwestern Australia. For Ecol Manage 26: 95-111
- Pausas JG (1997) Resprouting of cork-oak (*Quercus suber* L.) after fire in NE Spain. J Veg Sci 8: 703-706
- Pausas JG (1998) Modelling fire-prone vegetation dynamics. In: Trabaud L (ed) Fire Management and Landscape Ecology. Internat. Ass. Wildland Fire, Washington, pp. 327-334
- Pausas JG (1999) Mediterranean vegetation dynamics: modelling problems and functional types. Plant Ecol. 140: 27-39
- Pausas J.G. (in press) The response of plant functional types to changes in the fire regime in Mediterranean ecosystems. A simulation approach. J Veg Sci. 10: 717-723
- Pausas JG, Austin MP (1998) Potential impact of harvesting for the long-term conservation of arboreal marsupials. Landscape Ecol 13: 103-109
- Pausas JG, Austin MP, Noble IR (1997) A forest simulation model for predicting eucalypt dynamics and habitat quality for arboreal marsupials. Ecol Applications 7: 921-933
- Pausas JG, et al. (in review) Post-fire regeneration patterns in Eastern Iberian Peninsula.

Pérez-Ramos B (1997) Factores que controlan la variabilidad espacial de la respuesta de la

vegetación al fuego en la sierra de Gredos: Usos del territorio e intensidad del fuego.

Ph D. thesis Universidad Complutense de Madrid, Madrid

- Piñol J, Terradas J (1996) Els incendis forestals al litoral mediterrani catalano-valencià en el període 1968-1995. Butlletí del Centre d'Estudis Selvatans 4:69-96
- Piñol J, Terradas J, Lloret F (1998) Climatic warming hazard, and wildfire occurrence in coastal eastern Spain. Clim Change 38: 345-357
- Prodon R, Fons R, Athias-Binche F (1987) The impact of fire on animal communities in Mediterranean area, In: Trabaud L (ed) The role of fire in ecological systems. SPB Acad Publ, The Hague, pp.121-157

Puigdefábregas J, Mendizabal T (1998) Perspectives on desertification: western

Mediterranean. J Arid Envir. 39: 209-224

- Raison RJ, Khanna PK, Woods PV (1985) Mechanisms of element transfer to the atmosphere during vegetation fires. Can J For Res 15: 132-140
- Rego FC (1992) Land use changes and wildfires. In: Teller A, Mathy P, Jeffers JNR (eds)

Response of forest fires to environmental change. Elsevier, London, pp. 367-373

Roxo MJ, Mourao JM (1995) Land degradation in south interior Alentejo-Mértola. Historical background of human impact by agriculture. Proceedings of the Conference on Erosion and Land Degradation in the Mediterranean, 475 pp. Aveiro

- Roxo MJ, Cortesao Casimiro P, Soeiro de Brito R (1996) Inner Lower Alentejo field site: Cereal cropping, soil degradation and desertification. In: Brandt CJ, Thornes J (eds) Mediterranean desertification and land use. J Wiley & Sons, Chichester, pp.111-135
- Sala M, Rubio JL (eds) (1994) Soil erosion and degradation as a consequence of forest fires. Geforma Ediciones, Logroño
- Serrasolsas I (1994) Fertilitat de sòls forestals afectats pel foc: dinàmica del nitrogen i del fòsfor., Ph.D. Thesis, Universitat de Barcelona
- Shugart HH (1984) A Theory of Forest Dynamics. Springer-Verlag, NY.
- Solomon AM (1986) Transient response of forest to CO₂-induced climate change:
 - simulation modeling experiments in eastern North America. Oecologia 68: 567-579
- Stewart OC (1956) Fire as a first great force employed by man. In: Thomas WI (ed) Man's role in changing the face of the earth. University of Chicago, pp 115-133
- Strasser MJ, Pausas JG, Noble IR (1996) Modelling the response of eucalypts to fire in the Brindabella Range, ACT. Aust J Ecol 21: 341-344
- Tartaglini N (1992) Post-fire succession and mycorrhizae in two mediterranean communities. In: Trabaud L, Prodon R (eds) Fire in Mediterranean Ecosystems, CEC Ecosystem Res Rep 5, Brussels, pp. 395-402

Terradas J (ed) (1987) Ecosistemes terrestres. La resposta als incendis i a altres

perturbacions. Quaderns d'Ecologia Aplicada, 10. Diputació de Barcelona. Barcelona. pp. 201

- Thanos CA, Georghiou K, Kadis CC, Pantazi C (1992) Cistaceae: A plant family with hard seeds. Israel J Bot 41: 251-263
- Thornes J (1990) The interaction of erosion and vegetation dynamics in land degradation: spatial outcomes. In: Thornes J (ed) Vegetation and Erosion. Wiley, New York, pp. 41-54
- Torn MS, Fried JS (1992) Predicting the impacts of global warming on wildland fire. Clim Change 21: 257-274
- Torres P, Honrubia M (1997) Changes and effects of a natural fire on ectomycorrhizal
 - inoculum potential of soil in a Pinus halepensis forest. For Ecol Manage 96: 189-196

Trabaud L (1991) Fire regimes and phytomass growth dynamics in a *Quercus coccifera* garrigue. J Veg Sci 2: 307-314.

Trabaud L (1992) Influence du régime des feux sur les modifications à court terme et la

stabilité à long terme de la flore d'une garrigue de *Quercus coccifera*. Rev Ecol (Terre Vie) 47: 209-230

- Trabaud L (1994) The effect of fire on nutrient losses and cycling in a *Quercus coccifera* garrigue (southern France). Oecologia 99: 379-386
- Trabaud L, Campant C (1991) Difficulté de recolonisation naturelle du Pin de Salzmann *Pinus nigra* Arn. ssp. *salzmannii* (Dunal) Franco après incendie. Biol Cons 58: 329-343

- Trabaud L, Galtié JF (1996) Effects of fire frequency on plant communities and landscape pattern in the massif des Aspres (southern France). Landscape Ecol 11: 215-224
- Trimble SW (1988) The impact of organisms on overall erosion rates within catchments in temperate regions. In: Viles HA (ed) Biogeomorphology. Blackwell, Oxford, pp. 83-142
- Tsitsoni T (1997) Conditions determining natural regeneration after wildfires in the *Pinus halepensis* (Miller, 1768) forests of Kassandra Peninsula (North Greece). For Ecol Manage 92: 199-208
- Vallejo VR (ed) (1997) La restauración de la cubierta vegetal en la Comunidad Valenciana. Fundación CEAM, València
- Vallejo VR, Alloza JA (1998) The restoration of burned lands: The case of eastern Spain. In: Moreno JM (ed) Large forest fires, Backhuys Publ, Leiden, pp. 91-108
- Vallejo VR, Bautista S, Cortina J (in press) Restoration for soil protection after disturbances. In: Trabaud L (ed) Life and environment in Mediterranean biological systems, Computational Mechanics Publ, Southampton
- Vázquez A, Moreno JM (1995) Patterns of fire occurrence across a climatic gradient and its relationship to meteorological variables in Spain. In: Moreno JM, Oechel WC (eds) Global Change and Mediterrenean-Type Ecosystems, Springer, NY, pp 408-434
- Vélez R (1993) High intensity forest fires in the Mediterranean Basin: Natural and socioeconomic causes. Disaster Management 5: 16-20
- Vélez R (1996) Bilan des feux de forêt en Espagne en 1995 / En Espagne, pas de nouvelles, bonnes nouvelles. Forêt Méditerranéenne 17: 17-18 and 323
- Vélez R (1997a) Recent history of fires in Mediterranean area. In: Balabanis P, Eftichidis G, Fantechi R (eds) Forest fire risk and management, Proceedings of the European School of Climatology and Natural Hazards course. European Commission, Brussels, pp. 15-26
- Vélez R (1997b) Les feux de forêt en Espagne en 1997. Forêt Méditerranéenne 18: 348
- Viegas DX (1998) Weather fuel status and fire occurrence: predicting large fires. In:
 - Moreno JM (ed) Large Fires. Backhuys Publishers, Leiden, The Netherlands, pp. 31-48
- Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the sea: how can it occur. Biogeochemistry 13: 87-115
- Walker J, Raison RJ, Khanna PK (1986) Fire. In: Russell JS, Isbell, JS (eds.) Australian soils. Univ Queensland Press, Australia, pp. 185-216
- Wainwright J (1994) Anthropogenic factors in the degradation of semi-arid lands: a
 - prehistoric case study in Southern France. In: Millington AC, Pye K (eds)

Environmental changes in drylands: biogeographical and geomorphological perspectives. J. Wiley & Sons, London, pp. 427-441