



Responses of Mediterranean Plant Species to different fire frequencies in Garraf Natural Park (Catalonia, Spain): field observations and modelling predictions.

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Received 26 June 2000; accepted in revised form 25 January 2002

Key words: *Ampelodesmos mauritanica*, Fire recurrence, Model, Resprouting, Simulation

Abstract

Dynamics of the coexisting Mediterranean species *Pinus halepensis*, *Quercus coccifera*, *Erica multiflora*, *Rosmarinus officinalis*, *Cistus albidus*, *C. salviifolius* and *Ampelodesmos mauritanica*, with contrasted life history traits have been studied under different fire scenarios, following two approaches: a) field survey in areas with three different fire histories (unburned for the last 31 years, once burned in 1982, and twice burned in 1982 and 1994), and b) simulations with different fire recurrence using the FATE vegetation model. We compared observed abundance in the field survey to simulation outputs obtained from fire scenarios that mimicked field fire histories. Substantial mismatching did not occur between field survey and simulations. Higher fire recurrences were associated with an increase in the resprouting *Ampelodesmos* grass, together with a decrease in *Pinus* abundance. Resprouting shrubs did not show contrasting changes, but trends of increase in *Quercus* and decrease in *Erica* were observed. The seeders *Rosmarinus* and *Cistus* achieved maximum abundance at intermediate fire recurrence. We also performed ten 200 year simulations of increasing fire recurrence with average times between fires of 100, 40, 20, 10, and 5 years. A scenario without fire was also simulated. High fire recurrence produces an increase in *Ampelodesmos*, a grass which is becoming dominant in the area, and a small increase in *Erica*, but *Quercus* abundance decreases and *Pinus* disappears. *Rosmarinus* and *Cistus* abundance peaks at intermediate fire frequencies. When comparing these simulations to those in which *Ampelodesmos* was excluded, we found that the absence of the grass only increased *Cistus* occurrence in the community, this effect being more important at frequent fire recurrence. The study suggests that simple models based on life history traits may be useful in interpreting plant community dynamics in Mediterranean ecosystems that are greatly influenced by differences in the fire regime.

Introduction

Vegetation dynamics in Mediterranean-type ecosystems are largely determined by the fire regime (Hanes 1977; Gill 1981; Kruger and Bigalke 1984; Trabaud 1994; Fuentes et al. 1994). Several regeneration mechanisms involved in species response to fire (i.e. germination, resprouting) may produce a fast post-fire recovery of the compositional and structural attributes of the vegetation (Hanes 1977; Pausas 1999a). Variation in fire regime related to increasing fire recur-

rence, intensity or timing (Sousa 1984; Johnson and Gutsell 1994), however, may also change vegetation (Bond et al. 1984; Pausas (1999b, 2001)). For example, fires of high intensity may increase mortality of resprouters (Lloret and López-Soria 1993; Moreno and Oechel 1993). High fire recurrence may prevent seeders from replenishing seed banks or may deplete bud banks of resprouters (Zedler et al. 1983), but might favor species that combine high resprouting ability and fast reproduction and seedling establishment after fire (Vilà et al. 2001). Furthermore, long

inter-fire periods may reduce abundance of short-lived opportunistic species whose populations increase shortly after fires, but decline over time (Trabaud and Lepart 1980; Haidinger and Keeley 1993). Therefore, the vegetation response to changes in fire regimes of Mediterranean-type ecosystems should be strongly influenced by the life-history traits of plant species.

The number, size and frequency of fires have increased in the last several decades in the northern Mediterranean Basin. Changes in fire regimes have resulted from changes in land use (Moreno et al. 1998; Pausas and Vallejo 1999) and increases in climatic fire hazard (Piñol et al. 1998a). A shift toward communities dominated by low structured, herbaceous vegetation has been proposed for the Mediterranean Basin under scenarios of high disturbance frequency (Bolòs 1962; Naveh 1974; Trabaud 1991). For example, dominance of large tussock grasses rather than shrubs has been locally reported in areas with frequent fires, and the existence of a positive feedback between fire and grass has been proposed (D'Antonio and Vitousek 1992). Frequent fires thus may promote a shift in Mediterranean-type vegetation from shrublands to savannas (Vilà and Lloret 2000). Although long-term consequences of this shift are not completely understood, a change in dominant life forms should be expected.

Models of vegetation dynamics are useful tools for investigating the long-term consequences of different scenarios involving climate (Solomon 1986; Bugmann 1996), harvesting (Pausas and Austin 1998), or fire regime (Malanson 1985; Pausas (1998, 1999b)). They are especially important for studying the consequences of interval-dependent processes (Bond and van Wilgen 1996), in which the experimental approach is difficult to apply. Interval-dependent processes such as plant establishment, maturation and dormancy are key factors for predicting long-term consequences of alternative fire scenarios.

The FATE model (Functional Attributes in Terrestrial Ecosystems; Moore and Noble (1990)) represents a good compromise between minimal data requirement and realistic description of the vegetation dynamics in fire-prone systems (Pausas 1999b). FATE is a deterministic qualitative vegetation model based on the vital attributes approach (Noble and Slatyer 1980) and on the assumption that the best way to understand the dynamics of plant communities is to know how individual plants perform in their environment.

In this study, we explored whether increasing fire recurrence in Mediterranean-type ecosystems would favour a shift from pine forests and evergreen shrublands to more grass-dominated communities. Focusing on shrubland-pine forest formations of Garraf Natural Park (Catalonia, Spain), we applied the FATE model to predict variation in the abundance of dominant species under different historical fire regimes, and we compared model results to field observations. We also ran the model under scenarios of increasing fire recurrence to evaluate long-term effects of a large, perennial grass (*Ampelodesmos mauritanica*) on community dynamics.

Material and methods

Study area

The Garraf Natural Park (Garraf hereafter) is located about 30 Km south of Barcelona (NE Spain, 41°15' N, 2°0' E). The area (almost 10,000 ha) is a karstic massif ranging from sea level to 600 m altitude. Soils are Jurassic and Cretaceous limestones and marls with a high presence of rock outcrops and abandoned terraces (old fields). We stratified the study area into 3 classes based on the fire history over the past three decades, during which we have precise, spatial record of fire occurrence. These classes were: 1) small, scattered areas that have remained unburned for at least the last 31 years (hereafter, unburned areas), 2) a 7000 ha area that was burned in July 1982 (hereafter, once-burned areas), and 3) a 4800 ha area within the 7000 ha area that was burned again in April 1994 (hereafter, twice-burned areas).

The climate is typically Mediterranean, with mild and moderately moist winters, and warm and dry summers. Mean annual rainfall at the closest climate station is 548 mm (Vilanova i la Geltrú, Barcelona), with a pronounced summer drought (around 100 mm of rainfall from June to August). Mean annual temperature is 16.7 °C. Mean maximum and minimum temperatures are reached in August (30.6 °C) and January (0.5 °C), respectively.

The vegetation is dominated by evergreen, sclerophyllous shrublands 1.5 m high and open *Pinus halepensis* forests (Bolòs 1962). One main source of variability in vegetation is land use history, especially abandoned terraces and uncultivated slopes that tend to correspond to deeper and stony soils, respectively. A second source is a coastal to inland gradient that

determines climatic variation; moister conditions occur inland, where higher altitudes enhance rainfall. Given the large extension of two fires (in 1982 and 1994), the different land use histories and the climatic gradient are well represented in all three types of fire histories (Riera and Castell 1997).

Through many centuries, grazing by domestic livestock, mainly sheep and goats, has been important in all the area comprising Garraf. Cores from ancient lakes have provided charcoal dated to the Middle Ages, which has been attributed to burning of woodlands to increase pastures (Riera-Mora and Esteban-Amat 1994). However, agricultural practices have not been historically intensive in the area because of the dominance of stony soils with superficial limestone bedrocks. Since the end of the 18th century and during the 19th, vineyard expansion increased (Ferrer 1998), but in the 1890's phyloxera arrived in Garraf (Giralt 1990) leading to the abandonment of most of these areas, which have not been re-cultivated. These areas have been colonized by shrublands and *Pinus halepensis* forests. This type of ecosystem, with a long history of human influence, is dominant in the Mediterranean Basin, where pristine, natural woodlands are the exception (Naveh 1974).

Field survey

An extensive survey was conducted in Garraf from January to March 1996. This survey occurred 31 years at least since the last fire in the unburned area, 14 years after the last fire in the once-burned area, and two years after the most recent fire in the twice-burned area. We randomly selected a subset of 92 quadrats from a 500 × 500 m grid map covering the park. We chose 30 quadrats in the unburned and the twice burned areas, and 32 quadrats in the once burned areas. Within each quadrat we established one 10 × 10 m stand. Within each fire history area, stand site selection was stratified to balance the different combinations of aspect (north or south), topographical location (steep or flat areas), and soil type (presence of rock outcrops in more or less 30% of the total soil surface). Vegetation cover of perennial species in each stand was estimated by the point intercept sampling procedure. We recorded the presence of the species every 0.5 m along the four sides of the stand quadrat and in a 10 m transect located in the middle of the stand. Thus, in each stand 94 points were used to estimate cover of perennial species. Annuals were not included because their relative cover is low in this

type of woodlands (Folch 1981). This procedure is appropriate to quantify the plant cover of dominant species, six of which were selected for this study (see below). Comparisons between the three types of fire history were performed by one-factor ANOVA and the Fisher's PLSD test was used for post-hoc pairwise comparisons (SuperAnova procedure, Abacus Concepts (1989)). Data on cover percentage of each species were $\ln(x+1)$ transformed before analysis to normalise residuals.

Model and species description

All simulations were performed using the FATE model (Moore and Noble 1990). FATE is a general model of vegetation dynamics, which is based on the performance of individual plants in a stand. It predicts vegetation dynamics at a qualitative level and from simple parameters describing life history traits; these include maturation time, lifespan, resprouting and germination ability after fire, seed ability to colonize a new site (hereafter, seed arrival), seed dormancy, and shade tolerance (Table 1). The model is deterministic and simulates cohorts of plants that pass through a series of discrete stages: seeds, seedlings, immature and mature (adult) plants. The model is not spatially explicit, but species interactions are included in the model by considering groups of coexisting species. Then the model estimates the performance of the different species from the response of the different stages to decreasing light levels caused by the presence of neighbours. The model runs at annual time steps, and the outputs are qualitative descriptions of the abundance of each stage, measured on a scale of absent, low, medium, and high. Fire events, and the respective post-fire vegetation recovery may be included stochastically or at given times, allowing the simulation of different fire recurrences. Fire intensity is not considered by the model. A detailed description of the model is given by Moore and Noble (1990).

The model was set to simulate a community composed of six native species. These species typically grow along the Mediterranean coast of NE Spain (Bolòs 1962), and are representative of the different life-history types occurring in these communities. *Ampelodesmos mauritanica* (hereafter *Ampelodesmos*) is a perennial, large resprouting tussock grass. This species is distributed through the Mediterranean Basin from Spain to Western Greece, and from Eastern Morocco to Tunisia. In the NE Iberian Peninsula, it occurs in only two areas: in Garraf, and around

Table 1. Qualitative life history-traits of the six Mediterranean species considered in the FATE model. Data were obtained from direct field observations in the study area and from the literature (Cucó 1987; Lloret and López-Soria 1993; Papió 1994; Salvador and Lloret 1995; Lloret 1998; Habrouk et al. 1999; Vilà and Lloret 2000). (All, Most, Half, Few, None: qualitative description of the proportion of individuals)

	<i>Ampelodesmos</i>	<i>Pinus</i>	<i>Quercus</i>	<i>Erica</i>	<i>Rosmarinus</i>	<i>Cistus</i>
Time to first reproduction (yrs)	5	10	10	7	4	3
Lifespan (yrs)	25	120	250	40	25	15
Fraction of individuals able to resprout	All	None	All	Most	None	None
Seeds killed by fire	All	Few	All	Most	Half	None
Seed arrival	Yes	Yes	No	Yes	Yes	Yes
Seed innate dormancy (yrs)	No	Yes (5)	No	No	No	Yes (15)
Fraction of seeds with dormancy broken by fire	None	All	None	None	None	Most
Germination under shade	Medium	Very low	Low	Low	Low	Very low
Survival under shade	Low	Low	Medium	Very low	Low	Very low

Tarragona, about 100 km southwest of Barcelona (ORCA 1985). In both areas wildfires have been common in the last decades. The causes of the absence of this species in the other sites along the coast is yet unknown. In Garraf, *Ampelodesmos* may attain local dominance, with increasing populations in areas that have been more frequently burned (Vilà et al. 2001). *Pinus halepensis* (hereafter *Pinus*) is a non-resprouter needle-leaved evergreen pine with serotinous cones; *Quercus coccifera* (hereafter *Quercus*) is a broadleaved evergreen resprouter shrub. *Erica multiflora* (hereafter *Erica*) is a ericoid-leaved resprouter shrub; *Rosmarinus officinalis* (hereafter, *Rosmarinus*) is a narrow-leaved evergreen non-resprouter shrub. Finally, *Cistus spp.*, including two species that were pooled (*Cistus salvifolius* and *C. albidus*, hereafter *Cistus*), are broadleaved non-resprouter shrubs. The main species attributes considered in the model are given in Table 1. Time of first reproduction and lifespan are approximate, and have been obtained from regular visits to burned and unburned areas, and from published information (Cucó 1987). Ability to resprout has been obtained from descriptions of other authors (Cucó 1987; Papió 1994), from our own visits to burned areas, and in the case of *Erica* from experimental burnings (Lloret and López-Soria 1993). Fire effects on seeds have been obtained from heating experiments (Salvador and Lloret 1995; Habrouk et al. 1999; Vilà et al. 2001) and field observations (Lloret 1998). Dispersal ability is used in FATE to estimate the rate of seed input from outside the simulated stand. We assumed it to be similar (wide dispersal) for all species except *Quercus*; its recruitment from seeds is very low in the area as a consequence of acorn predation by rodents and the short time of

seed viability (Lloret, pers. obs.). Seed dormancy, and shade effect on germination and survival have been estimated from field observations and published information (Papió 1994; Lloret 1998).

Simulation scenarios

The first step in the application of vegetation dynamics models was to compare the predictions of the model behaviour to field observations. Therefore, a first set of scenarios utilized the observed fire recurrence patterns for the three fire history areas in Garraf. The second set of simulations aimed to predict possible long-term responses to changes in fire recurrence.

The first set of the three scenarios used a period of 31 years, starting at 1965. Before this date, we do not have reliable information on fire distribution in the area. This period mimicked the three types of fire history identified in the field survey. Thus, the three scenarios were: a) no-fire (hereafter, unburned scenario), b) a fire 17 years after the setup (hereafter, once-burned), c) a fire 17 years after the initiation and a second fire 12 years later (hereafter, twice-burned). We do not know the real initial abundances for the different species. Therefore, we assumed a community with the same abundance of the different species. The default condition used in the model, which considered several coexisting species, was low levels of adults for each species. This condition may influence simulation results, for example, by underestimating the real abundance of long-lived species, such as trees. After a single run, the model output and the field survey were compared by contrasting the qualitative output for each species with the respective percentile

distribution of percent cover, after $\ln(x+1)$ transformation.

The second set of scenarios considered periods of 200 years, in which the probability of a fire in a given year was 0.01, 0.025, 0.05, 0.1, and 0.2. These scenarios simulated fire regimes with average time between fire (fire return) equivalent to 100, 40, 20, 10, and 5 years, respectively (hereafter F100, F40, F20, F10 and F5). Piñol et al. (1998b) have estimated that fire return intervals in the region range approximately from 25 to 130 years, though higher recurrence at a single site is also common (Trabaud et al. 1993). Given that in the absence of fire the model output is always the same, a single simulation of a scenario without fires was also performed. For all species, ten simulations for each fire scenario were obtained. In these simulations, fire occurred stochastically following the respective probabilities (see above). Then, we calculated the mean percentage of years during the 200 year period in which each species and stage were present. As in the first set of scenarios, initial abundances in all simulations were equal, low levels of adults of each species.

For each species pairwise comparisons between fire scenarios (F100, F40, F20, F10, and F5) were performed by post-hoc Fisher's PLSD tests, after one-factor ANOVA in which the main factor was the fire scenario. In this analysis, the dependent variable was the number of years along the 200 year simulation period in which adult plants (including low, medium and high abundances) were present. This estimation avoided the specific effect of the last fire, which affected final abundances. Visual screenings of the outputs along the 200 years simulations did not show great discrepancies between the final abundance and the pattern of abundance along the 200 year period. For our purpose (comparisons between scenarios), the percentage of years of the different abundance classes was considered a good summary of this abundance pattern. Successful establishment in the community was considered to occur when the mature (adult) stage was obtained. Comparisons between each fire scenario and the no-fire scenario were performed for the same variable by two-tailed t-tests for significant differences between a population mean (10 simulations for each fire scenario) and a constant (1 simulation for the no-fire scenario).

Simulations of fire scenarios and no fire scenario using the same set of species, excluding *Ampelodesmos*, were used to compare changes in presence or absence of this grass on the community. We analyzed

the results of these simulations using a two-factor ANOVA in which the main factors were fire scenario and the presence of *Ampelodesmos* in the simulation. As in the previous analysis, the dependent variable was the number of years during the 200 year period in which adult plants were present.

Results

Field observations

Cover of *Ampelodesmos* was more than 1.5 times as high in the twice burned areas than in the once burned areas and more than twice that in the unburned areas; these cover values were significantly different (Table 2). The post-fire *Ampelodesmos* cover increase has been related to the pronounced ability of this species to resprout and to recruit after fire (Vilà et al. 2001). The plant cover of *Quercus* was also twice as high in burned areas than in the unburned areas, being the values of once and twice burned areas nearly identical. *Pinus* cover in once burned areas was nearly tenfold lower than in unburned areas, while *Erica* and *Rosmarinus* did not show significant differences between unburned and once burned areas. Plant cover of *Pinus*, *Erica*, *Rosmarinus*, and *Cistus* was lower in the twice burned area, although this trend was not significant in the case of the seeding *Cistus*. The short time since the last fire in the twice burned area, explain the low cover values of the small resprouter *Erica* and the seeders *Pinus*, *Rosmarinus* and *Cistus*.

Comparisons between field observations and short-term simulations

The observed *Ampelodesmos* increase, *Pinus* decrease, and the lack of change in *Erica* with increasing fire recurrence were all predicted by the single run model which simulated the respective fire histories (Figure 1). However, the observed increase of *Quercus* abundance is not well predicted by the model, which indicated outputs with little variation in this species in the three fire history scenarios. This discrepancy may result from competitive effects of *Pinus* trees on *Quercus coccifera* shrubs in the understorey of old-unburned forests, an effect which is not well developed in the model.

The model also predicts a decrease in *Rosmarinus* abundance following fires. Such decreases were ob-

Table 2. Mean (+ SE) percent cover of each of the six species in the field survey. F and p values were obtained from one-factor ANOVA comparing percent cover in different fire regimes, after $\ln(x+1)$ transformation of data (see Figure 1 for percentile distribution). Values followed by different letters indicate significant differences ($P < 0.05$) between stands with different fire history obtained from Fisher pairwise tests.

	Unburned	Once-burned	Twice-burned	F _{2,89}	p
<i>Ampelodesmos</i>	15.6 (3.5) a	22.9 (4.0) b	35.8 (3.3) c	11.01	0.0001
<i>Pinus</i>	42.1 (5.3) a	5.9 (1.9) b	0.5 (0.2) c	77.06	0.0001
<i>Quercus</i>	11.6 (3.0) a	23.8 (4.1) b	23.9 (3.4) b	4.93	0.0093
<i>Erica</i>	7.7 (2.0) a	4.3 (1.0) ab	1.6 (0.4) b	4.15	0.0188
<i>Rosmarinus</i>	6.6 (1.4) a	9.8 (2.1) a	0.6 (0.2) b	15.34	0.0001
<i>Cistus</i>	1.1 (0.9) a	0.8 (0.4) a	0.4 (0.2) a	0.22	0.8045

served in the field only in the twice-burned areas. *Rosmarinus* has high growth of seedlings after fire (Lloret 1998), which may not be considered sufficiently in the model. Finally, the increase of *Cistus* observed in burned areas is also predicted by the model, despite low abundances in the field surveys.

If we compare the six species through their respective FATE results, field and model observations match well in the unburned scenario, except for the predicted medium value of *Pinus*. In the once-burned scenario, the most important discrepancy is found in *Pinus* and *Rosmarinus*. These species are predicted by the model to be absent, but they were present in the field survey. In the twice-burned scenario, the qualitative output of the model is medium abundance for *Cistus* and *Erica*, but the mean cover percentage of these species in the field was only 0.4 and 1.6, respectively. In the case of *Ampelodesmos*, the predicted model output is medium abundance, while field survey obtained a mean cover of 35.8% for this species in twice burned areas. The large grass *Ampelodesmos* is able to achieve high values of plant cover only two years after fire, while the seeder *Cistus* and the small resprouter *Erica* need more time. We believe that this discrepancy may arise because the model does not consider plant growth rates.

Long-term simulations

The six types of long-term simulations produced a gradient of fire return intervals from an absence of fire during a 200 year period to 5-year fire returns (Table 3). Figure 2 shows the different trends for each species.

All species were predicted to show significant changes in abundances with different annual probabilities of fire (Table 4). *Ampelodesmos* abundance,

expressed as the number of years in the 200 year simulation period with presence of adults, was predicted to increase with annual probabilities of fire < 0.05 . *Pinus* abundance was predicted to peak at low to intermediate annual probabilities of fire. Adults of this species were predicted to decrease in the F10 scenario and almost disappear in the F5 scenario. *Quercus* was predicted to have the highest abundance values in the absence of fire or at the F100 scenario, decreasing at the higher annual probabilities of fire. The long lifespan of this species and its ability to establish in the shrubland understorey could explain this dominance at long fire return times. *Erica* abundance was predicted to be low in the no fire and in the F100 scenario, with a maximum abundance at the F10 and F5 scenarios. *Rosmarinus* is predicted by simulations to be more abundant at the F100, F40 and F20 scenarios, significantly decreasing at the higher annual probabilities of fire recurrence. *Cistus* is predicted to have the lowest abundance values, with a peak at intermediate annual probabilities of fire (F10 and F20 scenarios).

Under a scenario without fire, the model predicts a community dominated by the resprouter shrub *Quercus* and a mixture of seeders (*Rosmarinus*, *Pinus*) and resprouters with shorter life span (*Erica*, *Ampelodesmos*). Low annual probability of fire (F100) does not change this pattern very much, except for an increase of *Pinus*, which reaches a maximum at about annual probability of fire of 0.025 (F40), as a consequence of its long lifespan and its ability to establish in open sites after the death of shrubs. However, high annual probability of fire is predicted to cause important changes in the vegetation: *Pinus* tends to disappear, while the resprouting, perennial grass *Ampelodesmos* becomes dominant. *Quercus* cover also decreases probably because the short time between fires does

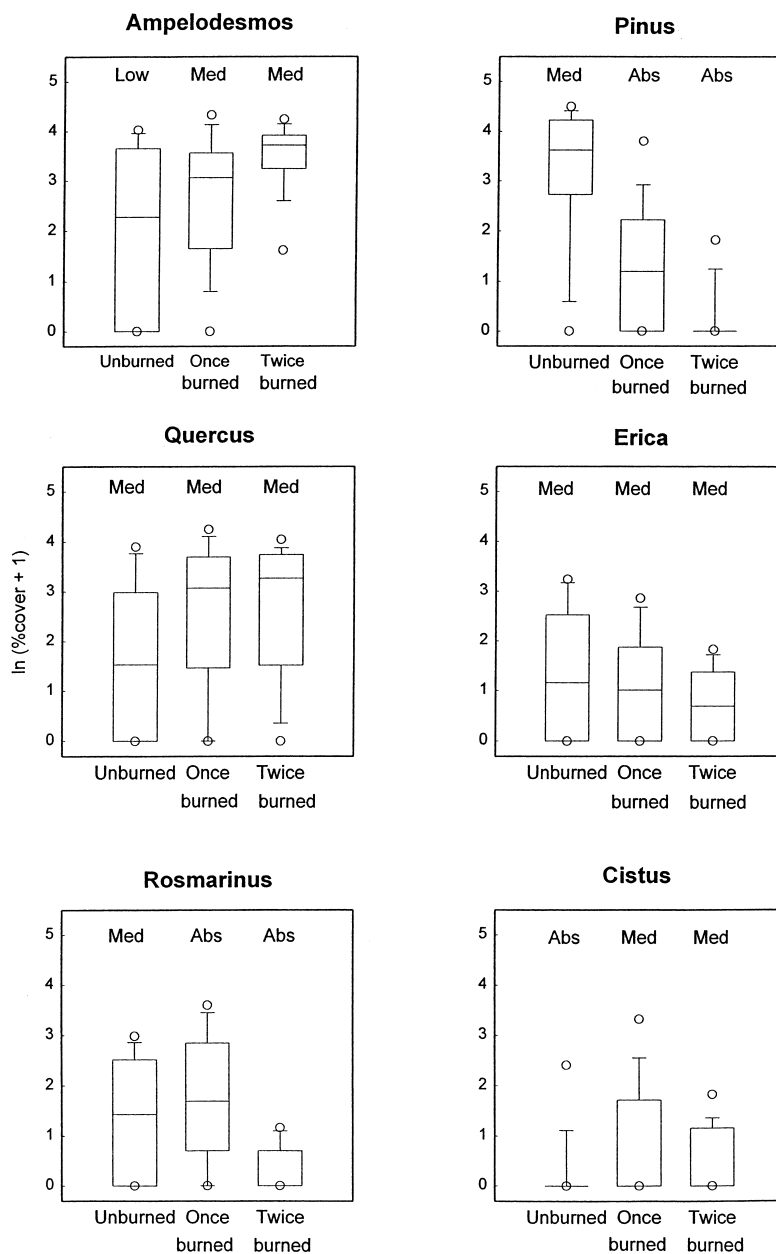


Figure 1. Percentile distribution of the observed cover abundance (%) after $\ln(x+1)$ transformation of each species in the areas with different fire history: unburned for at least the last twenty years (unburned areas), burned in July 1982 (once burned areas), and burned in July 1982 and again in April 1994 (twice burned areas). The bottom and the top of each box represent 25% and 75% of the data, the middle line represents the median value of the data (50%), the bars represent 10% and 90% of the data, and the open circles 5% and 95%, respectively (see Table 2 for mean and SE values). Simulation outputs for each scenario are written at the top of each box: Abs = absent (or presence of seeds only), Low = low abundance, Med = medium abundance.

not allow this long-lived species to reach high values of plant cover. As a consequence of the loss of dominance of *Quercus*, another species such as *Erica* would be favoured. The seeder *Cistus* shows a peak at intermediate annual probabilities of fire, when the

time between fires is long enough to ensure reproduction.

When we compare the outputs of simulations with and without *Ampelodesmos*, we conclude that the presence or absence of this grass in the community

Table 3. Mean, standard deviation, minimum and maximum (n = 10), of the mean fire return intervals obtained in each 200 year simulation period under the different fires scenarios.

Scenario name	Annual fire probability	Fire-return interval (years)			
		Mean	SD	Min	Max
No Fire	0				
F100	0.010	145.8	58.9	66.7	—*
F40	0.025	40.2	22.3	25.0	100.0
F20	0.050	23.9	8.4	14.3	40.0
F10	0.100	10.0	2.1	5.7	13.3
F5	0.200	5.5	0.6	4.5	6.3

* No fire during 200 years

does not significantly change the results for most of the species considered, even with increasing annual probability of fire. The absence of *Ampelodesmos* is associated with a significant increase of the adult presence in *Cistus* simulations (Figure 3). This change was particularly important at high annual probabilities of fire (F20, F10 and F5 scenarios). All other four species simulations did not change significantly by the *Ampelodesmos* presence. Fire and Fire \times *Ampelodesmos* interaction had a non significant effect on species abundance (Table 3).

Discussion

Field observations

The field survey revealed differences in community structure that were related to fire history. Life-history traits may explain the variability of species abundance in relation to fire recurrence. The post-fire resprouting ability of perennial grasses has been broadly studied in grasslands (Vogl 1974; Silva et al. 1991; Gitay et al. 1992; Masters et al. 1992), but this has been less considered in Mediterranean-type ecosystems, in spite of their local abundance, and their relevance in fire-related processes (Bond and van Wilgen 1996). Although *Pinus halepensis* has been reported to regenerate well after fire (Trabaud 2000), success may be diminished by frequent fires that limit seed storage (Thanos and Daskalidou 2000), by the presence of shading neighbours (Espelta 1996), such as the resprouting *Quercus*, and by the existence of shallow, stony soils in Garraf (Riera and Castell 1997). Lower values of *Quercus* in unburned areas may be related to its limited ability to colonize unburned, old fields.

In addition to fire recurrence, event-dependent processes, such as fire season or climatic conditions after fire, are important in determining vegetation recovery after fire (Bond et al. 1984; Le Maitre 1988; Trabaud 1991). In our case, fall and spring rainfall ensured post-fire germination and resprouting in 1982 and 1994, respectively. Fire season may particularly influence the ability of the seed bank to restore populations (van Wilgen et al. 1992). In 1982, the fire was in the summer, when the seed bank had been recently filled. In 1994 the fire was in the spring when there was a reduced seed bank of *Pinus* and *Rosmarinus* (*Cistus* has a more permanent seed bank). Data on *Rosmarinus* indicate, however that the levels of germination in 1995 were similar to the observed before the fire (Lloret 1998). *Pinus* regeneration may have been more influenced by the season of this fire.

The fire histories considered in our study include the number of fire events in the last two decades and time since last fire. The unburned and once burned areas are likely to be comparable because of fast recovery of the structure and composition of Mediterranean-type communities after disturbance (Keeley 1986; Malanson and Trabaud 1987). Comparisons including the more recently burned areas (two years old) should be considered with caution because the time since the last fire was short. For instance, seeder species, such as *Pinus*, *Rosmarinus* or *Cistus* are likely to show low abundances in twice-burned areas because of this effect.

Comparisons between field observations and short-term simulations

Given the large variation in the field data the model predicts qualitative changes in abundances of species. There are several reasons for the inaccuracies of some

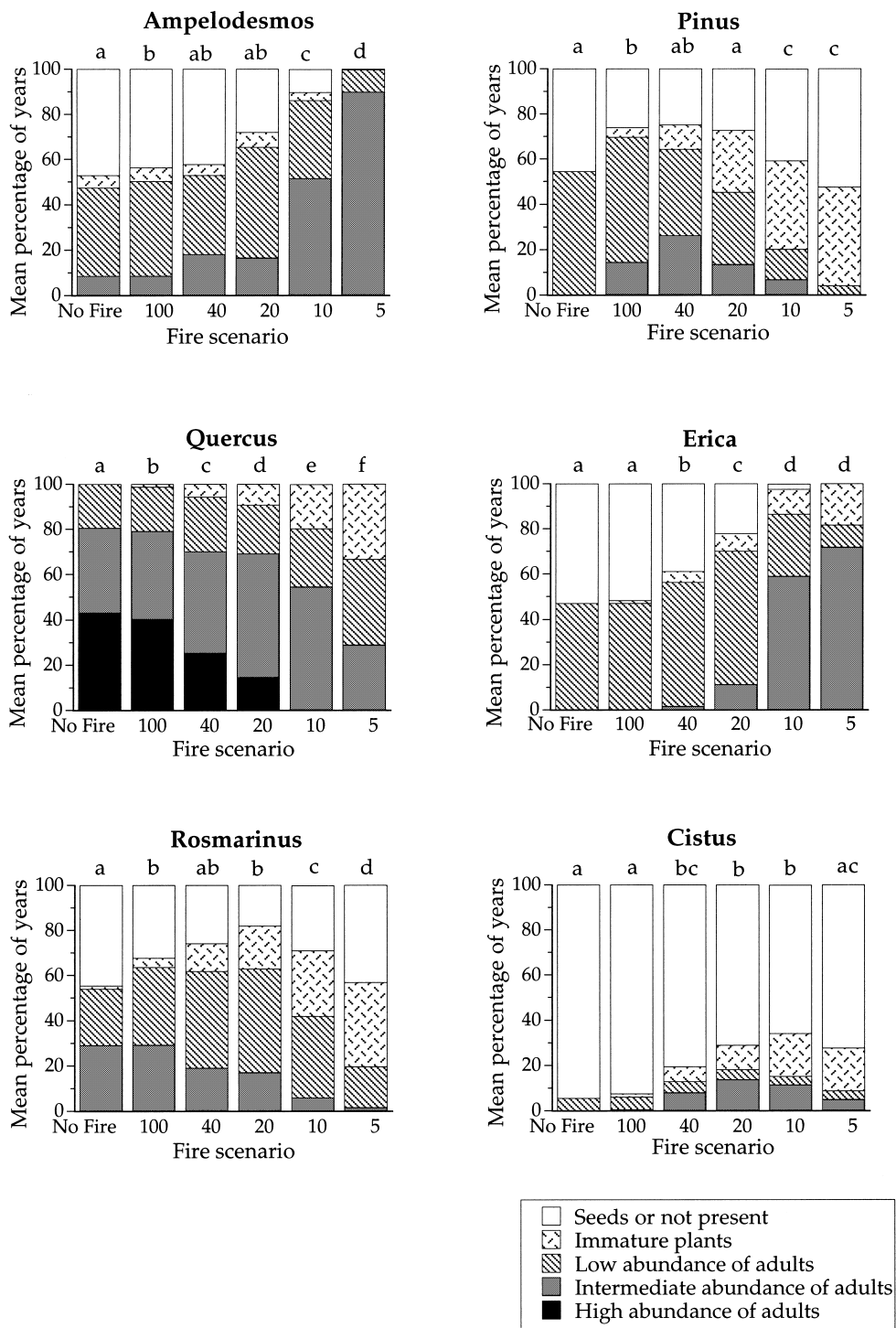


Figure 2. Abundance of five stages of six species predicted for each of six fire scenarios described in Table 3. Abundance was estimated as the mean percentage of years of the 200 year simulation period in which each of five stages was present. (Bars with different letters at the top indicate significant differences in presence of adults (Low, intermediate and high abundance) between scenarios ($P < 0.05$, Fisher's PLSD test after ANOVA, except for comparisons between fire and no fire scenarios, in which two-tailed t-tests were used).

Table 4. Results of the ANOVA performed for each species in which the dependent variable was the number of years in the 200 year simulations ($n = 10$) with adults present. Five fire scenarios (simulations with annual probabilities of 0.01, 0.025, 0.05, 0.1 and 0.2) and the presence or absence of *Ampelodesmos* were the main effects.

	Fire scenarios (F)			<i>Ampelodesmos</i> (A)			F × A			Error	
	df	MS	F	df	MS	F	df	MS	F	df	MS
<i>Pinus</i>	4	52139.8	23.61**	1	5431.7	2.46 ns	4	1375	0.62 ns	90	22.1
<i>Quercus</i>	4	14283.8	410.02**	1	53.3	1.53 ns	4	77.9	2.34 ns	90	34.8
<i>Erica</i>	4	19571.2	35.34**	1	1.4	0.01 ns	4	187.9	0.34 ns	90	553.7
<i>Rosmarinus</i>	4	26890.6	64.22**	1	510.8	1.22 ns	4	329.3	0.79 ns	90	418.7
<i>Cistus</i>	4	3580.4	14.01**	1	5882.9	23.00**	4	916.6	3.58**	90	255.8

ns: not significant, **: $p < 0.001$

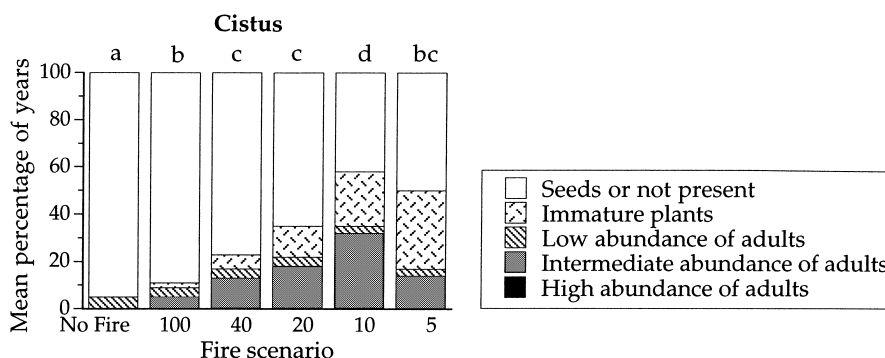


Figure 3. *Cistus* abundance in the different fire scenarios without *Ampelodesmos*. *Cistus* abundance was estimated as the mean percentage of years of the 200 year simulation period in which each of five stages was present. Bars with different letters at the top indicate significant differences between scenarios ($P < 0.05$, Fisher's PLSD test after ANOVA, except for comparisons between fire and no fire scenarios, in which two-tailed t-tests were used).

predictions. First, community history cannot be exactly reproduced by the model. For example, the presence of large pine stumps suggests quite a long period without extensive fires before 1982. The presence of the slow growing shrub *Juniperus phoenicea* in unburned areas also suggests a relatively long period without fire (Riera and Castell 1997). In the simulated scenarios, the initial conditions are considered to be the same (low abundance of adults) for all scenarios, but we do not know the real abundance of each species three decades ago. In unburned areas, higher abundances of *Pinus* in the field than in the model outputs may be explained by this inaccuracy: *Pinus* could have been more abundant at the beginning of the considered period in these areas (Riera and Castell 1997).

Second, the FATE model is not spatially explicit and does not consider environmental heterogeneity resulting from historical processes, including fire and date of agricultural abandonment. Since the model only produces a single qualitative estimation of plant abundance, the comparison between the distribution

of species abundance in the surveyed plots and the model output allows only roughly estimate the adjustment of the model to the field variability.

Finally, discrepancies may also be due to species interactions or population processes which are not considered with enough detail by FATE. Despite these inconsistencies, the pattern emerging from both approaches shows that fire is associated with an increase of the resprouting *Ampelodesmos* grass together with a decrease of pine forested areas. Resprouting shrubs do not show a significant shift, but a trend of *Quercus* to increase and of *Erica* to decrease is observed from field observations. For the seeder species, the *Rosmarinus* decrease with fire and the *Cistus* increase in burned areas are predicted by the model.

Long-term simulations

Long term simulations allow prediction of possible vegetation responses to different fire regimes. When annual probability of fire increases, a dominance of resprouters, and particularly *Ampelodesmos* arises.

Seeder species peak at intermediate fire recurrences. This peak seems dependent on the species lifespan. The long lived resprouter *Quercus* is dominant when fires become rare. The adjustment of life-history strategies to fire recurrence is important for understanding Mediterranean-type communities. For example, fire-persister species have been found to be prevalent over seeder, fire-recruiter species in Californian chaparral that remained unburned for as much as a century (Keeley 1992). In contrast, seeder Proteaceae from South Africa need a narrow window of fire intervals for survival (van Wilgen et al. 1992).

Ampelodesmos removal experiments performed in shrublands of Garraf suggest that this large grass does not competitively suppress other resprouting shrubs or seedlings of seeder species (Vilà and Lloret 2000). Although the dynamics of the community seem more influenced by the fire regime than by the direct effect of this grass, a positive feedback between fire and *Ampelodesmos* abundance may occur (D'Antonio and Vitousek 1992): fire recurrence may increase in *Ampelodesmos* dominated communities because this grass increases fine fuel loads (Vilà et al. 2001). The model suggests that *Cistus* may become more frequent in the community if *Ampelodesmos* is not present. This trend increases at higher annual probability of fire. Therefore, under high annual probability of fire, the success of this seeder, short-lived shrub, which has often been considered to be favored by fire (Trabaud 1987), would be mitigated by the existence of the fast growing, resprouter grass *Ampelodesmos*.

The effect of fire intensity, extent and season on post-fire regeneration has been widely explored (Whelan 1995). Fire recurrence has been less studied, probably because of difficulties in obtaining field data. The importance of a shift in fire recurrence in some ecosystems is a matter of concern for land managers and policy makers (Lavorel et al. 1998). In spite of the recognized ability of Mediterranean-type vegetation to maintain its composition after a fire (Trabaud 1994), this study shows that high annual probability of fire may change the relative abundance of species with different life history traits. Zedler et al. (1983) showed how short intervals between fires produced a shift from shrub to grass vegetation in the Mediterranean California. Similarly, Naveh (1999) has shown how the combined effect of recurrent fires and heavy grazing pressure may lead to degraded scrublands after the depletion of the herbaceous seed bank. The current wide spectrum of life history types

found in Mediterranean-type ecosystems provides the basis for alternative vegetation pathways under different disturbance regimes. Models based on life history traits are appropriate tools for testing the consequences of alternative disturbance scenarios on changes in vegetation structure.

Acknowledgements

We thank I. Noble for providing the FATE model and P.H. Zedler, D. Goldberg, B. Platt and two anonymous reviewers for their useful comments. We also thank the field assistance provided by several Biology and Environmental Science students from the Universitat Autònoma de Barcelona, and particularly by C. Casanovas, I. Gimeno, U. Gamper, A. Ballés, and C. Vilà. Thanks are also due to the Servei de Parcs (Diputació de Barcelona) for providing support in the research performed in the Garraf Natural Park. This study has been funded by the EC project LUCIFER (NV4-CT96-0320), and by the Spanish Government (CICYT postdoc contract to JGP, and AGF-97-0533 project). CEAM is supported by Generalitat Valenciana and BANCAIXA.

References

- Abacus Concepts 1989. Superanova. User's guide for MacIntosh. 5th edn. Abacus Concepts, Berkeley.
- Bolòs O. 1962. El Paisaje Vegetal Barcelonés. Universitat de Barcelona, Barcelona.
- Bolòs O., Vigo J., Masalles R.M. and Ninot J.M. 1990. Flora Manual dels Països Catalans. Pòrtic, Barcelona.
- Bond W.J. and van Wilgen B.W. 1996. Fire and Plants. Chapman and Hall, London.
- Bond W.J., Vlok J. and Viviers M. 1984. Variation in seedling recruitment of Cape Proteaceae after fire. *J. Ecol.* 72: 209–221.
- Bugmann H.K.M. 1996. Functional types of trees in temperate and boreal forests: classification and testing. *J. Veg. Sci.* 7: 359–370.
- Cucó M.L. 1987. Mecanismes de regeneració. In: Terradas J. (ed.), Ecosistemes Terrestres. La Resposta Als Incendis i a D'altres Pertorbacions. Diputació de Barcelona, Barcelona, pp. 45–62.
- D'Antonio C.M. and Vitousek P.M. 1992. Biological invasions by exotic grasses, the grass-fire cycle, and global change. *Ann. Rev. Ecol. Syst.* 23: 63–87.
- Espelta J. 1996. La regeneració de boscos d'alzina (*Quercus ilex* L.) i pi blanc (*Pinus halepensis* Mill.): Estudi experimental de la resposta de les plàntules a la intensitat de llum i a la disponibilitat d'aigua. PhD Dissertation, Universitat Autònoma Barcelona, Bellaterra, Spain.

- Ferrer L. 1998. Expansió agrícola en el segle XVIII. In: Mestre J. and Hurtado V. (eds), *Atlas d' Història de Catalunya*. 62th edn., Barcelona, pp. 172–173.
- Folch R. 1981. La Vegetació dels Països Catalans. Ketres, Barcelona.
- Fuentes E.R., Segura A.M. and Holmgren M. 1994. Are the responses of matorral shrubs different from those in an ecosystem with reputed fire history? In: Moreno J.M. and Oechel W.C. (eds), *The Role of Fire in Mediterranean-Type Ecosystems*. Springer-Verlag, New York.
- Gill A.M. 1981. Coping with fire. In: Pate J.S. and McComb A.J. (eds), *The Biology of Australian Plants*. University Western Australia Press, pp. 65–87.
- Gitay H., Lee W.G., Allen R.B. and Wilson J.B. 1992. Recovery of *Chionochloa rigida* tussocks from fires in South Island, New Zealand. *J. Environmental Management* 35: 249–259.
- Giralt E. 1990. L'agricultura. In: *Història Econòmica de la Catalunya Contemporània, Població i Agricultura*. Vol. 2. Enciclopèdia Catalana, Barcelona, pp. 121–309.
- Haidinger T.L. and Keeley J.E. 1993. Role of high fire frequency in destruction of mixed chaparral. *Madroño* 40: 141–147.
- Hanes T. 1977. California chaparral. In: Barbour M.G. and Major J. (eds), *Terrestrial Vegetation of California*. Wiley, New York, pp. 417–470.
- Habrouk A., Retana J. and Espelta J.M. 1999. Role of heat tolerance and cone protection of seeds in the response of three pine species to wildfires. *Plant Ecology* 145: 91–99.
- Johnson E.A. and Gutsell S.L. 1994. Fire frequency models, methods and interpretations. *Adv. Ecol. Res.* 28: 239–287.
- Keeley J.E. 1986. Resilience of Mediterranean shrub communities to fires. In: Dell B., Hopkins A.J.M. and Lamont B.B. (eds), *Resilience in Mediterranean-type Ecosystems*. Dr W. Junk Publishers, Dordrecht, The Netherlands, pp. 95–112.
- Keeley J.E. 1992. Recruitment of seedlings and vegetative sprouts in unburned chaparral. *Ecology* 73: 1194–1208.
- Kruger F.J. and Bigalke R.C. 1984. Fire in fynbos. In: Booysen P.V. and Tainton N.M. (eds), *Ecological Effects of Fire in South African Ecosystems*. Springer, Berlin, pp. 69–114.
- Lavorel S., Canadell J., Rambal S. and Terradas J. 1998. Mediterranean terrestrial ecosystems: research priorities on global change effects. *Global Ecology and Biogeography Letters* 7: 157–166.
- Le Maitre D.C. 1988. Effects of season of burn on the regeneration of two Proteaceae with soil-stored seed. *S. Afr. J. Bot.* 54: 575–580.
- Lloret F. and López-Soria L. 1993. Resprouting of *Erica multiflora* after experimental fire treatments. *J. Veg. Sci.* 4: 367–374.
- Lloret F. 1998. Fire, canopy cover and seedling dynamics in Mediterranean shrublands of Northeastern Spain. *J. Veg. Sci.* 9: 417–430.
- Lloret F. and López-Soria L. 1993. Resprouting of *Erica multiflora* after experimental fire treatments. *J. Veg. Sci.* 4: 367–374.
- Malanson G.P. 1985. Simulation of competition between alternative shrub life history strategies through recurrent fires. *Ecol. Model.* 27: 271.
- Malanson G.P. and Trabaud L. 1987. Ordination analysis of components of resilience of *Quercus coccifera* garrigue. *Ecology* 68: 463–472.
- Masters R.A., Vogel K.P. and Mitchell R.B. 1992. Response of Central Plains tallgrass prairies to fire, fertilizer, and atrazine. *J. Range Management* 45: 291–29.
- Moore A.D. and Noble I.R. 1990. An individualistic model of vegetation stand dynamics. *J. Environ. Manage.* 31: 61–81.
- Moreno J.M. and Oechel W.C. 1993. Demography of *Adenostoma fasciculatum* in southern California chaparral. *Oecologia* 90: 50–60.
- Moreno J.M., Vázquez A. and Vélez R. 1998. Recent history of forest fires in Spain. In: Moreno J.M. (ed.), *Large Forest Fires*. Backhuys Publishers, Leiden, The Netherlands, pp. 159–185.
- Naveh Z. 1974. Effects of fire in the Mediterranean Region. In: Kozłowski T.T. and Ahlgren C.E. (eds), *Fire and Ecosystems*. Academic Press, New York, pp. 401–434.
- Naveh Z. 1999. The role of fire as an evolutionary and ecological factor on the landscapes and vegetation of Mt. Carmel. *J. Mediterranean Ecology* 1: 11–26.
- Noble I.R. and Slatyer R.O. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbance. *Vegetatio* 43: 5–21.
- ORCA 1985. *Atlas Corològic de la Flora Vascular dels Països Catalans*. Vol. I. Institut d'Estudis Catalans, Barcelona.
- Papió C. 1994. *Ecologia del foc i regeneració en garrigues i pinedes mediterrànies*. Institut d'Estudis Catalans, Barcelona.
- Pausas J.G. 1998. Modelling fire-prone vegetation dynamics. In: Trabaud L. (ed.), *Fire Management and Landscape Ecology*. Int. Ass. Wildland Fire, Fairfield, WA, USA, pp. 327–334.
- Pausas J.G. 1999a. Mediterranean vegetation dynamics: modelling problems and functional types. *Plant Ecology* 140: 27–39.
- Pausas J.G. 1999b. The response of plant functional types to changes in fire regime in Mediterranean ecosystems. A simulation approach. *J. Veg. Sci.* 10: 717–722.
- Pausas J.G. 2001. Resprouting vs seeding—a Mediterranean perspective. *Oikos* 94: 193–194.
- Pausas J.G. and Austin M.P. 1998. Potential impact of harvesting for the long-term conservation of arboreal marsupials. *Landscape Ecology* 13: 103–109.
- Pausas J.G. and Vallejo R.V. 1999. The role of fire in European Mediterranean ecosystems. In: Chuvieco E. (ed.), *Remote Sensing of Large Wildfires in the European Mediterranean Basin*. Springer-Verlag, Berlin, pp. 3–16.
- Piñol J., Terradas J. and Lloret F. 1998a. Climate warming, wild-fire hazard, and wildfire occurrence in coastal eastern Spain. *Climatic Change* 38: 345–357.
- Piñol J., Terradas J. and Lloret F. 1998b. Risk factors in wildfires along the Mediterranean coast of the Iberian peninsula. In: Trabaud L. (ed.), *Fire Management and Landscape Ecology*. Int. Ass. Wildland Fire, Fairfield, WA, USA, pp. 297–303.
- Riera-Mora S. and Esteban-Amat A. 1994. Vegetation history and human activity during the last 6000 years on the central Catalan coast (northeastern Iberian Peninsula). *Veget. Hist. Archaeobot.* 3: 7–23.
- Riera J. and Castell C. 1997. Efectes dels incendis forestals recurrents sobre la distribució de dues espècies del Parc Natural del Garraf: el pi blanc (*Pinus halepensis*) i la savina (*Juniperus phoenicea*). *Butlletí Institució Catalana Història Natural* 65: 105–116.
- Solomon A.M. 1986. Transient response of forest to CO₂-induced climate change: simulation modeling experiments in eastern North America. *Oecologia* 68: 567–579.
- Salvador R. and Lloret F. 1995. Germinación en el laboratorio de varias especies arbustivas mediterráneas: efecto de la temperatura. *Orsis* 10: 25–34.

- Silva J.F., Raventos J., Caswell H. and Trevisan M.C. 1991. Population response to fire in a tropical savanna grass, *Andropogon semiberbis*: a matrix model approach. *J. Ecology* 79: 345–356.
- Sousa W.P. 1984. The role of disturbance in natural communities. *Ann. Rev. Ecol. Syst.* 15: 353–391.
- Thanos C.A. and Daskalidou E.N. 2000. Reproduction in *Pinus halepensis* and *P. brutia*. In: Ne'eman G. and Trabaud L. (eds), *Ecology, Biogeography and Management of Pinus halepensis and Pinus brutia Forest Ecosystems in the Mediterranean Basin*. Backhuys, Leiden, The Netherlands, pp. 79–90.
- Trabaud L. 1987. Fire and survival traits of plants. In: Trabaud L. (ed.), *The Role of Fire in Ecological Systems*. SPB Academic Publishing, The Hague, pp. 65–89.
- Trabaud L. 1991. Fire regimes and phytomass growth dynamics in a *Quercus coccifera* garrigue. *J. Veg. Sci* 2: 307–314.
- Trabaud L. 1994. Postfire plant community dynamics in the Mediterranean Basin. In: Moreno J.M. and Oechel W.C. (eds), *The Role of Fire in Mediterranean-type Ecosystems*. Springer-Verlag, New York, pp. 1–15.
- Trabaud L. 2000. Post-fire regeneration of *Pinus halepensis* forests in the West Mediterranean. In: Ne'eman G. and Trabaud L. (eds), *Ecology, Biogeography and Management of Pinus halepensis and Pinus brutia Forest Ecosystems in the Mediterranean Basin*. Backhuys, Leiden, The Netherlands, pp. 257–268.
- Trabaud L. and Lepart J. 1980. Diversity and stability in garrigue ecosystems after fire. *Vegetatio* 43: 49–57.
- Trabaud L., Christensen N.L. and Gill A.M. 1993. Historical Biogeography of Fire in Temperate and Mediterranean ecosystems. In: Crutzen P.J. and Goldammer J.G. (eds), *The Ecological, Atmospheric, and Climatic Importance of Vegetation Fires*. John Wiley & Sons, New York, pp. 277–295.
- van Wilgen B.W., Bond W.J. and Richardson D.M. 1992. Ecosystem management. In: Cowling R. (ed.), *The Ecology of Fynbos. Nutrients, Fire and Diversity*. Oxford University Press, Cape Town, South Africa, pp. 345–371.
- Vilà M. and Lloret F. 2000. Woody species tolerance to the expanding perennial tussock-grass *Ampelodesmos mauritanica* after fire. *J. Veg. Sci.* 11: 597–606.
- Vilà M., Lloret F., Ogheri E. and Terradas J. 2001. Positive fire-grass feedback in Mediterranean basin shrublands. *Forest Ecol. Manage.* 147: 3–14.
- Vogl R.J. 1974. Effects of fire on grasslands. In: Koslowski T.T. and Ahlgren C.E. (eds), *Fire and Ecosystems*. Academic Press, New York, pp. 139–194.
- Whelan R.J. 1995. *The Ecology of Fire*. Cambridge University Press, Cambridge.
- Zedler P.H., Gautier C.R., and McMaster G.S. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. *Ecology* 64: 809–818.

