Journal of Vegetation Science 10: 717-722, 1999
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Response of plant functional types to changes in the fire regime in Mediterranean ecosystems: A simulation approach

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Abstract. In the Mediterranean basin, the climate is predicted to be warmer and effectively drier, leading to changes in fuel conditions and fire regime. Land abandonment in the Mediterranean basin is also changing the fire regime through the increase in fuel loads. In the present study, two simulation models of vegetation dynamics were tested in order to predict changes in plant functional types due to changes in fire recurrence in eastern Spain. The two modelling approaches are the FATE-model (based on vital attributes) and the gap model BROLLA (based on the gap-phase theory). The models were arranged to simulate four functional types, based mainly on their regenerative strategies after disturbance: *Quercus* (resprouter), *Pinus* (non-resprouter with serotinous cones), *Erica* (resprouter), and *Cistus* (non-resprouter with germination stimulated by fire). The simulation results suggested a decrease in *Quercus* abundance, an increase in *Cistus* and *Erica*, and a maximum of *Pinus* at intermediate recurrence scenarios. Despite their different approaches, both models predicted a similar response to increased fire recurrence, and the results were consistent with field observations.

Keywords: Disturbance; Fire recurrence; Functional group; Gap modelling; Life form; Spain.

Introduction

Currently developed scenarios of climate change within the next century indicate that water deficit in the Mediterranean basin would increase (Houghton et al. 1996; Piñol et al. 1998). This change would lead to an increment in water stress conditions for plants, changes in fuel conditions and, consequently, changes in the fire regime. Current land-use changes (mainly abandonment) are also modifying the fire regime (Moreno et al. 1998; Pausas & Vallejo 1999). A prediction of the consequences of these human-induced changes on Mediterranean landscapes is needed, and simulation models may be appropriate tools for this task.

Functional types are groups of species that share some adaptative traits for a specific function; they are an important ecological framework for describing the mechanisms underlying vegetation responses (McIntyre et al. 1995; Lavorel et al. 1997). Much research has been undertaken on plant functional types in relation to climate (Box 1981; Woodward 1987; Woodward & Cramer 1996). At least in some areas (e.g. Mediterranean basin, Australia) disturbance and changes in the disturbance regime may be more important factors in shaping the landscape than the direct effects of climate or CO_2. Disturbance-related functional types may provide a powerful framework for studying long-term Mediterranean vegetation dynamics (Noble & Slayer 1980; Noble & Gitay 1996; Pausas 1999). In the present work, four plant functional types recognized for eastern Spain are described. I hypothesized that it would depend on the fire regime which of the different species groups would dominate.

Models of vegetation dynamics are useful tools for investigating the long-term consequences of different scenarios such as climatic (e.g. Solomon 1986; Bugmann 1996), harvesting (Pausas & Austin 1997), or fire regime (Austin et al. 1997; Pausas 1998) scenarios. These models are especially important for studying the consequences of interval-dependent processes (in contrast to event-dependent processes; Bond & 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 long-term consequences of alternative fire scenarios. There is no vegetation model that is accurate, realistic and general at the same time; rather, there is a trade-off between these three characteristics. Usually, accurate models lack generality and may be built without considering realistic processes. On the other hand, general models may have some realism but they usually lack accuracy. Models of vegetation dynamics based on the functioning of individual plants are thought to be the most suitable in order to achieve both realism and generality (Huston et al. 1988; Shugart 1984).

In the present study, two modelling approaches applied to eastern Spain ecosystems were tested and compared: the FATE model approach (Funtional Attributes in Terrestrial Ecosystems; Moore & Noble 1990) and the gap model approach (Botkin et al. 1972; Shugart 1984). FATE is based on the vital attributes approach

(Noble & Slatyer 1980), and gap models on the gap-phase dynamics (Watt 1947). Both modelling approaches are based on the assumption that the best way to understand the dynamics of plant communities is to work from a knowledge of how individual plants function in their environment (Gleason 1926). FATE is a deterministic qualitative rule-based model while gap models are stochastic, quantitative and mechanistic. The question addressed is: Can these models simulate, in a realistic way, the variations in functional-type composition and abundance due to changes in the fire regime in Mediterranean ecosystems? Are these models sensitive to changes in the fire regime? Do they produce similar and consistent results? For addressing these questions, a gap model (called BROLLA) based on several previous gap models was constructed to simulate vegetation dynamics in eastern Spain and to compare the results with the FATE model.

Methods

Models

FATE (Moore & Noble 1990) is a general model of vegetation dynamics which is based on the functioning of individual plants in a stand. It was designed to predict vegetation dynamics at a qualitative level and from simple parameters. The model is deterministic and simulates cohorts of plants that pass through a series of four discrete stages: propagules, seedlings, immature and mature plants. The model runs at annual time steps, and the output are qualitative descriptions of the vegetation (abundance is measured on a scale of absent, low, medium, and high). A detailed description of the model is given by Moore & Noble (1990).

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; Urban & Shugart 1992; Shugart & Smith 1996) 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 1998), that simulates the establishment, growth, and death of individual plants in a 200-m^2 plot and at annual time-steps in a similar manner to other gap models.

BROLLA is a simplified gap model that aims at capturing the main features for modelling the dynamics of Mediterranean vegetation. Establishment is simulated in a similar manner to the Australian gap models (Shugart & Noble 1981; Pausas et al. 1997), that is, considering that seed germination may be triggered by fire in species with hard-coated seed (e.g. Troumbis & Trabaud 1986; Roy & Sonie 1992). This is different from most gap models where a constant and unlimited seed source is assumed. Growth is simulated by the Botkin et al. (1972) method, but using Moore's (1989) growth equation. Light response is simulated as in most gap models (Botkin et al. 1972; Shugart 1984), and drought response is also included in a simple way similar to the light response and following Coffin & Lauenroth (1990); that is, species of different structural form (trees, shrubs, herbs) were assumed to have different vertical root distribution in the soil profile, and a drought tolerance value (intolerant, intermediate, tolerant) was assigned to each functional type. Climatic variability was simulated by assuming that 20% of the years (chosen randomly, i.e. on average once every five years) are dry years. In these years, the water availability in the soil profile is assumed to be lower, and different life forms (having different root distribution) are differently affected (i.e. plants with shallow roots are more affected than plants with deep roots). Furthermore, in dry years, the growth for drought-intolerant species is more reduced than that of tolerant species.

Thus the model simulates, in a simple manner, two drought strategies (*sensu* Levitt 1972): drought tolerance (physiological strategy) and drought avoidance (by a deep root system). The fire module is very simple; when a fire occurs it is assumed to burn the whole simulated patch. Then, all non-resprouting species die, while resprouting species may resprout from basal or stem buds depending on the species (Pausas 1997). Resprouting failure is also considered. Thus, BROLLA has different plant mortality causes:
(1) stress-mortality (mortality due to slow growth);
(2) age-dependent mortality;
(3) fire-mortality (non-sprouting species after fire); and
(4) resprouting failure (i.e., when individuals of a resprouting species fail to resprout). Temperature and soil nutrients were not included in the model.

Both FATE and BROLLA are non-spatially explicit models, that is, they do not take into account either the spatial position of plants or the spatial position of the simulated patch. However, in these models, an important spatial process such as seed dispersal may be simulated in a simple manner by increasing the local establishment (i.e., simulating the arrival of seeds from the surroundings). Although the models remain non-spatially explicit, this procedure allows us to test the influence of external seed sources for post-fire dynamics.

Table 1. Main life history traits for the four functional types used in the simulations.

	Quercus	*Erica*	*Cistus*	*Pinus*
Life form	Tree	Shrub	Shrub	Tree
Maturation time (yr)	15	5	2	12
Life span (yr)	1000	50	15	125
Able to resprout?				
immature phase	Most	Most	No	No
mature phase	All	All	No	No
Establishment stimulated by fire?	No	No	Yes	Yes
Seed dormancy?	No	No	Yes	No
Life span of dormant seed pool (yr)			20	
Drought tolerance	Low	Med	High	High
Shade tolerance	High	Low	Low	Low

Simulations

In the present study, FATE and BROLLA were arranged to simulate the dynamics of four functional types found in eastern Spain (Table 1). These functional types are given genus names which represent the functional types in eastern Spain in a realistic way:
Quercus (broad-leaved evergreen resprouter);
Pinus (non-resprouter needle-leaved with serotinous cones);
Erica (heath, ericoid-leaved resprouter); and
Cistus (broad-leaved non-resprouter with germination stimulated by fire).

Species that are not able to resprout and are not stimulated by fire are always in low abundance in the study area and are not included in the modelling exercise. FATE was originally designed to simulate the dynamics of functional types, while gap models are often used at species level. However, the structure of gap models is very appropriate for simulating the dynamics of functional types (Bugmann 1996; Shugart & Smith 1996), and in this sense it is used here.

Six fire scenarios × two dispersal scenarios (i.e. 12 scenarios in total) were simulated for a 500-yr period using each of the two models. Fire scenarios were (mnemonic names added): No fire: NF and fire every 100 yr: (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. Dispersal scenarios were: (1) considering seed dispersal from surrounding vegetation (i.e. simulating a patch within a vegetated area), and (2) without considering the possibility of seed dispersal from the surroundings (isolated patch). Because of the stochastic nature of BROLLA (like other gap models), each simulation was replicated 10 times and the results averaged.

Results

FATE predicts a constant 100 % occurrence of *Quercus* in all fire recurrence scenarios, and an increase in the occurrence of other functional types along the fire recurrence gradient (Fig. 1). However, the abundance of these species groups follows a different pattern.

The abundance of *Quercus* decreases with increasing fire recurrence, from ca. 60 % of the years that mature trees occur at intermediate abundance in the NF-scenario, to ca. 20 % of the years at low abundance (plus ca. 80 % of the years in which immature plants occur) in F5. The abundance of *Pinus* clearly increases with the presence of fire (see NF *vs.* F100), but decreases later on with increased fire recurrence. With scenarios F10 and F5, only immature *Pinus* individuals are present. Propagules (pine nuts) are always available for germination. The presence and the abundance of *Cistus* increases with fire, from almost absent in the NF-scenario to ca. 95 % of occurrence and with ca. 70 % intermediate abundance in the F10-scenario. A slight decrease seems to occur at F5. Propagules (seeds in the soil bank) of *Cistus* are always present in all scenarios. *Erica* presents low occurrence (10 - 15 %) at low fire recurrence levels (NF, F100, F40);

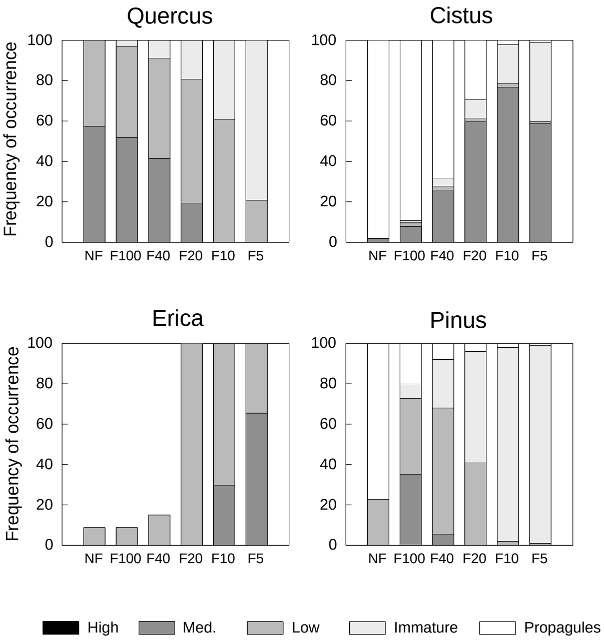

Fig. 1. Results obtained with FATE for six simulation scenarios with four functional PFTs: *Quercus*, *Pinus*, *Cistus*, *Erica*. X-axis: NF: no fire; F100: fire every 100 yr; F40: fire every 40 yr; F20: fire every 20 yr; F10: fire every 10 yr; F5: fire every 5 yr. Different patterns are different abundance classes (high, intermediate or low) of mature plants, or the presence of immature plants and propagules. Y-axis: frequency of occurrence in a 500-yr simulation.

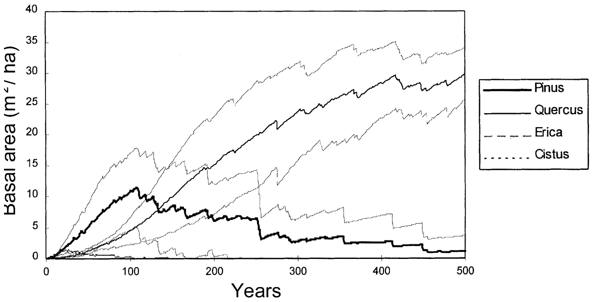

Fig. 2. Average results of 10 BROLLA-simulations without fire, showing mean basal area (m^2/ha) through 500-yr simulations for the four functional types. For *Quercus* and *Pinus*, standard deviation is indicated with a thin line. Note that without disturbance, *Quercus* and *Pinus* are the dominant species while *Erica* and *Cistus* are almost absent.

however, its occurrence and abundance increase at higher fire recurrence (F20, F10, F5).

Without disturbance, BROLLA predicts a first, short period dominated by *Pinus*, followed by a quasi-stable period of *Quercus* forest (Fig. 2). The model predicts a decrease in total biomass along the fire recurrence gradient, from 128 (±39) t/ha in NF-scenario to 3.5 (±1.1) t/ha in the F5-scenario. The relative abundance of the different species also changes with the changes in fire recurrence (Fig. 3). When dispersal is included in the simulations (Fig. 3a), *Quercus* shows a progressive decrease in relative abundance, from ca. 80 % (NF) to ca. 5 % (F5) of the total basal area. *Pinus* has its maximum relative abundance at intermediate fire recurrences, but it occurs at all fire regimes. *Erica* and *Cistus* increase up to ca. 30 % of the total basal area with increased fire recurrence (F5). However, some differences related mainly to *Pinus* and *Cistus* are observed when dispersal is not considered (Fig. 3b). With dispersal, *Pinus* was always present and with abundance greater than 20 %, while without dispersal, high fire recurrence (F5) reduces the species to near absence. In contrast, *Cistus* is very abundant (up to 80 %) in the highest recurrence scenarios (F5). Similar differences between dispersal scenarios were observed when FATE was used without dispersal (not shown).

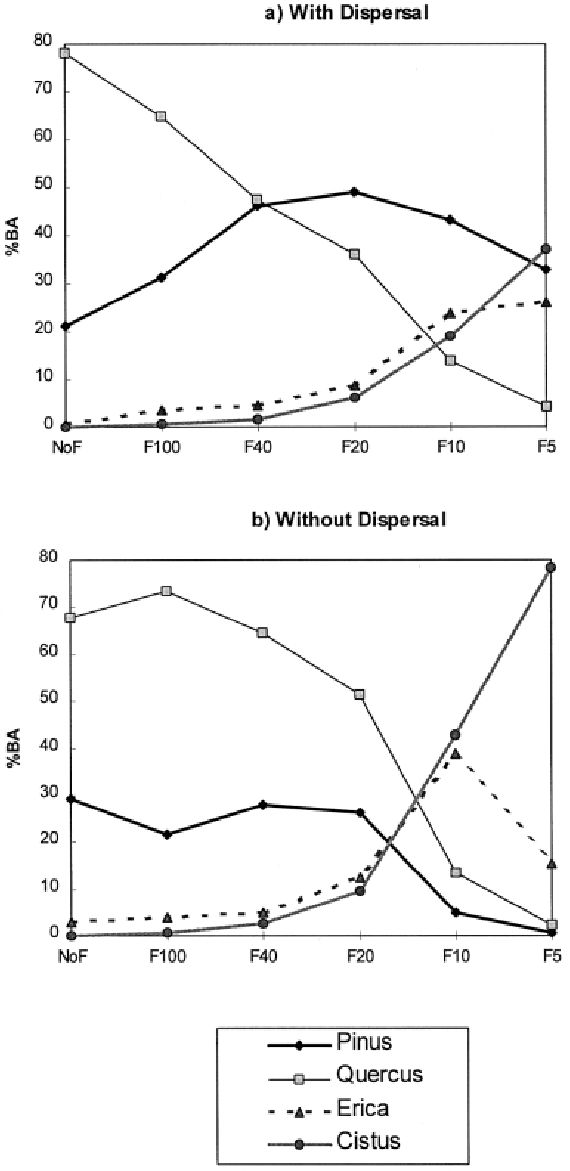

Fig. 3. Summary of the BROLLA-simulation results for 12 scenarios with the four functional types *Quercus*, *Pinus*, *Cistus* and *Erica*. NF, F100, F40, F20, F10 and F5 as in Fig. 1. **a.** The six scenarios above assume dispersal from surrounding vegetation; **b.** the six scenarios below assume no possible dispersal (i.e. isolated patches). The Y-axis represents the mean percent basal area of 10 replicated simulations for 500 yr.

Discussion and Conclusions

The large demographic inertia and resilience of evergreen *Quercus* species (Trabaud 1990) led to a constant presence of this functional type independent of the fire regime, emphasizing the importance of the initial conditions for the regeneration of burnt vegetation. Experimental treatments have shown that *Quercus coccifera* (kermes oak) and *Quercus ilex* (holm oak) survive and resprout vigorously after fire (Trabaud 1990) and after intense and recurrent clipping (Tsiouvasa 1988; Retana et al. 1992). *Quercus suber* (cork oak) is probably one of the best adapted species to fire because of its ability to resprout from stem buds, thus producing a quick recovery of the canopy (Pausas 1997).

Pinus and *Cistus* were always present in the simulation results at least in the form of propagules (Fig. 1 and Fig. 3a), because of the dispersal capacity and the seed bank of these species. However, when dispersal was not considered (Fig. 3b), *Pinus* was eliminated at high fire recurrence (F5), because it was not able to produce seeds during the inter-fire period. In this case *Cistus* was abundant due to the long life span of the seeds in the soil bank (ca. 20 yr) and the short maturation time (ca. 2 yr; Roy & Sonié 1992). The importance of dispersal suggests the importance of the spatial scale when simulating vegetation dynamics in fire-prone ecosystems (Malanson 1996; Malanson & Armstrong 1996). For this reason, these types of models are currently being implemented in a grid-based framework to simulate whole landscape dynamics (e.g. Urban et al. 1991; Noble & Gitay 1996).

Although FATE and BROLLA are based on two different modelling approaches, they predict similar responses to increased fire recurrence. Without fire, both models predict a forest dominated by *Quercus* with some *Pinus* and very low presence or total absence of *Cistus* and *Erica*. With high fire recurrence, both models predict a community (shrublands) dominated by *Erica* and *Cistus*, with some *Quercus* and with abundant immature (saplings) *Pinus* (if dispersal is considered, i.e. a non-isolated patch). At intermediate fire recurrences, the predicted community is dominated by *Pinus* and/or *Quercus* (pine woodland/mix forest) depending on the fire recurrence. These results are roughly as expected for eastern Spain (Terradas 1987), 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* spp.) 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 & Galtié 1996). The precise species (rather than functional types) would depend on environmental parameters such as climate and soil type. It is very difficult, if not impossible, to accurately verify these types of models because of the difficulty in obtaining reliable fire history information at the patch level. A recent attempt in a *Quercus coccifera* garrigue in Eastern Spain (Delitti et al. 1998) showed a significant decrease in *Quercus* biomass from a plot unburned at least for the last 18 yr to similar garrigues burned once, twice and three times in that period; the cover of *Cistus* functional type (biomass was not sampled) showed an opposite trend. No sites with a longer fire history or with other functional types were found in that study. Model results are consistent with these trends although accurate comparisons are difficult. The predicted biomass for the NF-scenario is within the interval observed in evergreen *Quercus* forests in eastern Spain (e.g. 113 t/ha in Prades, 160 t/ha in Montseny et al. 1992). Beyond the accuracy of model predictions, the simulation results suggest a clear change in vegetation structure with changes in the fire regime that are consistent with field observations and expert knowledge. The fact that two different models provide similar outputs reinforces the confidence in these models (validation by comparison between models; Rykiel 1996).

Both the FATE approach and the gap dynamics approach seem to be able to simulate realistically the dynamics of Mediterranean fire-prone vegetation communities. The selection of one of these approaches would depend on the data available and the question addressed. Current gap models are more flexible for modifications and adaptations to different problems, perhaps because of the structure of the model (more mechanistic and intuitive), but also because the source code and algorithms of gap models are widely available to the research community (e.g. Shugart 1984). The functional group approach allows an easy simulation of different geographical areas; however, more accurate and realistic models for Mediterranean vegetation may be elaborated when more data on plant traits and environmental responses are known.

Acknowledgements. This work was supported by the Spanish government (CICYT) with help from the LUCIFER EC project. I thank I.R. Noble for making the FATE-model available and for his comments on functional-type dynamics.

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Received 9 December 1997;
Revision received 17 July 1998;
Accepted 9 February 1999.