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Mediterranean vegetation dynamics: modelling problems and functional types

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Abstract

Gap models have been applied to a wide range of ecosystems, mainly temperate and boreal forests, but rarely have such models been applied to Mediterranean ecosystems. In the present review we address some problems of gap models for predicting the long-term dynamics of Mediterranean ecosystems, and we suggest plant functional types suitable for modelling based on responses to disturbance. Most gap models do not take into account different life forms, interactions with fire (e.g., resprouting and stimulation of the germination), and underground structures. Long term human impact on Mediterranean ecosystems has made a significant impact on the current landscapes. That intense land use, involving long-lived slow-growing species, has had long-term consequences. It is not possible to understand Mediterranean vegetation and to validate any model without considering these factors. The lack of data for Mediterranean species may be overcome by taking into account correlations of traits and trade-offs between different functional types. A simple disturbance-based functional group system is discussed.

Abbreviations: MB = mediterranean basin; MTE = mediterranean-type ecosystems.

Introduction

Models of vegetation dynamics are useful tools to investigate the long-term consequences of different scenarios of climate (Solomon 1986; Bugman 1997), harvesting (Pausas & Austin 1997), or fire regime (Austin et al. 1997; Pausas in press). These models are especially important for studying the consequences of interval-dependent processes (in contrast to even-dependent processes; Bond & van Wilgen 1996), where the experimental approach is difficult to apply. Interval-dependent processes such as establishment, maduration and dormancy are key factors for predicting long-term consequences of alternative disturbance scenarios. One of the most important reasons for building models of vegetation dynamics is that they can help to predict when subtle changes in the environment or disturbance regime might provoke profound changes in the vegetation. Under the pressure of continuing global change, there is a need for modelling vegetation dynamics in different ecosystems and using similar techniques. Considerable effort is underway to organise and create a future dynamic global vegetation model (Steffen et al. 1996; Walker 1996).

Individual-based gap dynamic modelling is a standard technique currently used to predict vegetation patterns (Botkin et al. 1972; Shugart 1984). Gap models are based on the theory of gap-phase dynamics (Watt 1947; Shugart 1984), and they simulate stand development by modelling mechanistically the establishment, growth, and death of individual trees. Gap models have been used extensively in different ecosystems (see review by Shugart et al. 1992; Urban & Shugart 1992). In Europe they are currently applied to boreal vegetation (Prentice et al. 1993), and to the vegetation of central Europe (Kienst & Kuhn 1989; Bugmann 1997). However, no such model has been applied to the Mediterranean Basin. Malanson et al. (1992) developed a gap model for Mediterranean ecosystems in California but they did not investigate the consequences of different fire regimes, a key factor in these types of ecosystems, and only climatic scenarios were considered. The gap-model approach has also been adopted by the Global Change and Terrestrial Ecosystems team of the International Geosphere-Biosphere Programme (Steffen et al. 1994).

The objective of this paper is to review some difficulties when applying gap models to Mediterranean conditions and to emphasise research directions towards elaborating a Mediterranean vegetation dynamic model. There are several features that make Mediterranean Basin (MB) landscapes different from those of the rest of Europe, and these differences are mainly related to climate, the role of fire and the long and intense human impact. These features together with the limited knowledge of the species' biology make modelling difficult. Most current dynamic models do not consider these factors and are not able to simulate the dynamics of Mediterranean vegetation. Furthermore, information on the ecology of species in the MB has just started to become available. Note, for example, that not long ago (Keely 1989) it was considered that neither species with germination stimulated by fire, nor species with lignotubers occurred in the Mediterranean basin; however, both strategies are common. Some of the shortcomings in the knowledge of species attributes may be overcome by using the functional-type approach (Smith et al. 1993). Functional types are groups of species that share some adaptational traits for a specific function, and are an important ecological framework for describing the mechanisms underlying vegetation responses. There is considerable research underway on plant functional types and climate (Woodward & Cramer 1996). However, in some areas (e.g., Mediterranean basin, Australia), disturbance and changes in disturbance regimes may be more important than climate factors in shaping the landscape (Noble & Slayer 1978; Noble & Gitay 1996). Disturbance-based functional groups may be a powerful tool for studying long-term Mediterranean vegetation dynamics.

Below, I summarise the main points that need to be considered when understanding Mediterranean vegetation dynamics and modelling using mechanistic gap models. I also suggest a disturbance-based fuctional classification suitable for modelling vegetation dynamics. Examples are mainly given from western Mediterranean areas because this is where I have more experience. There are other common problems of most gap models that are not discussed here but have been addressed elsewhere. These common problems are mainly related to the confounding of realised niche and fundamental niche of the species (Austin 1992; Austin et al. 1997; Pacala & Hurt 1993), and the unlimited dispersal problem (Pacala & Hurt 1993).

The role of fire

Wildfires are an important feature of Mediterranean ecosystems and many species have evolved strategies that allow them to survive periodic fires (Naveh 1975). The MB ecosystems have often been compared with other Mediterranean-type ecosystems (MTE, i.e., South Africa, California, south of Australia and central Chile). However, due to the differential evolution of the floras and the fire history, some of these areas have floras that are probably better adapted to fire than the MB flora. An example is that most of the trees in Australia are able to sprout after fire from epicormic stem buds and recover the canopy in a very short period. The only European species that is able to respond to fire in a similar way is the cork-oak (*Quercus suber*; Pausas 1997), a tree species confined to some MB areas. Some strong fire adaptations found in other MTE, such a serotiny, are rare in the MB. Serotiny (=bradyspory), that is the retention of the seed in the canopy until a fire occurs (fire-induced seed dispersal), is only found in a relatively low level in some pines (e.g., *Pinus halepensis*, *P. brutia*). In contrast with some other MTE, no plants have been found to be strictly dependent on fire for completing their life cycle in the MB. Fire seems to be an important factor in the boreal and North American conifer forest, too (Johnson 1992; Payette 1992). However, no strategies to survive fire have been reported in this ecosystem, probably due to the low recurrence of fire in evolutionary time.

The MB area has a Mediterranean climate, with a hot and dry summer, and a mild winter. This makes moisture a very important limiting factor for plant growth. Total annual rainfall ranges from <300 up to 900 mm, but irregularly distributed within and between years. Predictions for climatic change due to doubling CO_2 in the MB 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, consequently, changes in fire regime.

Land abandonment also plays a major role in promoting fires. The increase in abandoned lands is changing the landscape pattern and promoting large continuous areas of uniform early-successional vegetation with the consequence of a strong increase in the annual number of fires, total surface burned and the geographical distribution of areas affected by fire (Moreno et al. 1998).

Vegetation structure

Most published gap models are applied to forest conditions (but see Coffin & Lauenroth 1990, discussed below). MTE include forests and open woodlands (mainly dominated by pines and evergreen-oaks), heathlands and dense shrublands (dominated by multiple-stemmed woody species) and open scrublands (dominated by scrubs and grasses). The occurrence of one of these vegetation types is a function of the environment but also of the disturbance regime. The structure of most current gap models cannot model ecosystems with mixed growth forms where scrublands and forest may be at different stages of succession or have different wildfire regimes. Most gap models assume the same allometric equations for different tree species, an appropriate assumption when life forms are very similar, but unacceptable in MTE. A model for MTE should be able to model the different life forms in order to study transient changes to structure and composition (due, for example, to changes in climate and land-use). The same can be said about savanna ecosystems, and for this reason Noble et al. (pers. commun.) is currently developing a new formulation of gap models able to simulate the dynamics of communities with different life forms such as savanna and open woodlands. Their approach may be promising for Mediterranean ecosystems as well.

Kellomäki & Väisänen (1991) model understorey species in boreal forests using the same algorithm as for trees. Coffin & Lauenroth (1990) have developed a gap model for grasslands with different life forms (e.g., graminoids, forbs, annuals and succulents) assuming different resource (nutrients, water) requirements for the different life forms, but with the same temperature constriction for all species. The growth model of clonal plants is assumed to be similar to the growth in forest models, but mortality is increased based on plant size. Because their different life forms are similar in aboveground height, they do not consider light competition. This assumption cannot be held in MTE where a mixture of structural forms is common.

Growth

One of the main requisites needed to apply a gap model is to know the growth rate of the species. This parameter can be estimated by growth ring analysis, or alternatively, Botkin et al. (1972) proposed a method based on the maximum size and maximum age of the species. The latter method has some implicit assumptions but may be used as a first approximation.

It is very difficult to detect growth rings in Mediterranean woody species, and when it is possible (by dying or other chemical treatment and microscopic observations), rings cannot be easily associated to years. This is due to the slow growth rates of Mediterranean species and the unseasonal growth of these species. Plants may have one or several growth periods in a year (Figure 1) depending on the weather conditions of the given year and the physiological response of the species (Mitrakos 1980; Abril 1987; Caritat et al. 1996). Furthermore, for many Mediterranean woody species, cores cannot be extracted with a standard Pressley borer because of the hardness of the wood. Measures of change in stem diameter are seldom found in the literature and usually they are made for short periods. A three-year study in a *Quercus ilex* forest (Prades, NE Spain) showed a mean stem increment of 0.27±0.07 mm/year with an increase of 66% in irrigated plots (Mayor & Rodà 1994). In the same experimental plots, Mayor et al. (1994) found a mean growth increment of 0.67 mm in a year with exceptionally high rainfall, and up to ca. 2.5 mm for N-fertilised dominant trees. A growth of up to 4.19 mm/year was observed for the same species after experimental thinning (Gracia et al. 1996), as was a growth of 4 mm/year in natural conditions but in a moister area (Montseny, Ferrés 1985). Much lower values were found in 2–3 year old saplings of the same species in drier areas (Valencia, E Spain, Vallejo 1997). These results together with the observed stop in growth during the summer that may occur in some species (Figure 1) suggest that the availability of water is a very important factor in the growth of many Mediterranean species.

It is very difficult, if not impossible, to know the life span of some of the woody species in MB ecosystems, especially the ones that are able to sprout, making the Botkin's method difficult to apply. For ex-

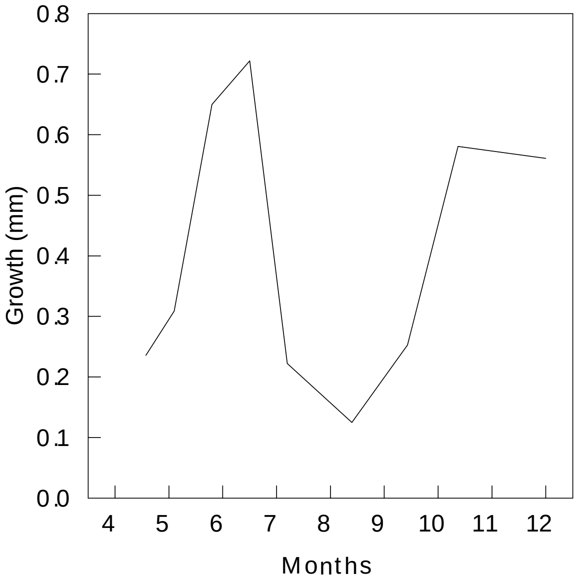

Figure 1. Growth pattern of *Quercus coccifera* during 1986 in Garraf mountains (Barcelona). Data are mean diameter increment at the base of the stem of 3 plants. Note the existence of two growth peaks (spring and autumn) and the similarity of this pattern with the typical precipitation pattern of the Mediterranean climate. Elaborated from data of Abril (1987).

ample, the root system of *Q. ilex* (one of the main tree species in the MB) may be hundreds or thousands of years old, and a simple guess may have a very large error. Most of the *Q. ilex* trees may have existed before the Little Ice Age, implying that the establishment of individuals in a site may not be related to current climatic conditions, and models based on the current species distribution may be inappropriate. The same can be said for *Q. coccifera,* the dominant species of garrigues, and for other resprouting species. It is also very difficult to know the number of years it takes a clonal grass to reach its full-size, and little information is available in the literature.

A new approach to model growth, based on the pipe theory rather than on maximum growth and size, is being developed (e.g., FORSKA model by Prentice et al. 1993). Although this method is more realistic and physiologically-based, the lack of physiological data and the difficulty in recognising sapwood and heartwood in Mediterranean species make this approach rather difficult. Few physiological studies on native Mediterranean species have been undertaken, provably because of the low comercial value.

Resprouting

A large number of MB species are able to resprout after disturbance. Many Mediterranean forests (e.g., some *Q. ilex* forests) are composed of multiple-stemmed trees (coppices) resulting from fire or logging (e.g., Retana et al. 1992), with the underground structures being much older than the aboveground structures. This needs to be considered when modelling the vegetation dynamics. Strasser et al. (1996) and Pausas (1997) provide empirical models for trees that resprout from stem buds (*Eucalytpus* and *Quercus suber*, respectively). Both examples suggest an increase in resprouting capacity with increasing plant size, but the inverse has also been found in a *Banksia* species in Australia (Burrows 1985). No such model is yet available for MB species with basal resprouting capacity (including most MB woody species), but experimental studies suggest that the size of underground structures may be positively related to resprouting vigour at least for *Arbutus unedo* (Vilà et al. 1994). Hence, we can hypothesise that resprouting vigour may be positively related to underground biomass (Auld 1990; Vilà et al. 1994) which, in turn, is related to starch source and bud-bank (Canadell et al. 1991; Canadell & Zedler 1995; Canadell & López-Soria 1998). However, resprouting capacity could also decrease with senescence, as has been shown for *Calluna vulgaris* (Giningham 1972) and *Bacharis pilularis* (Hobbs & Mooney 1985).

Naveh (1975) provides a list of species with resprouting ability. However, we have detected some discrepancies with our observations. He suggests that *Juniperus phoenicea* and *Rosmarinus officinalis* are able to resprout after fire; however, we have never seen these species resprouting in eastern Spain (Carreira et al. 1992; Papió 1994, pers. obs.). *Calluna vulgaris* is considered a resprouting species, but it failed to resprout in an experimental burn in northern Portugal (Rego et al. 1991). Are these differences related to fire intensity only? Does the resprouting ability depend on environmental factors for some species? or does it depend on the provenance of the species?

The capacity of many species to resprout determines that some of the demographic processes described in temperate forest ecosystems which occur at the individual or population level (e.g. competition and self-thinning), are more complex in MTE. Species with basal resprouting capacity may have processes working at the population, individual (genet) and sprout (ramet) level. For example, Vilà & Terradas

(1995) showed that the recruitment of new sprouts which accompanied sprout mortality in *Erica multiflora* masked the self-thinning trajectory. They also suggested that competition among sprouts is modified by competition among genets.

Recruitment

Most gap models assume the same recruitment rate for all species, and all years. Only models for Australian forests (Shugart & Noble 1981, Pausas et al. 1997) have the recruitment process modified when a fire occurs. In fire-prone ecosystems the assumption of continuous and equal recruitment is unjustified because of the presence of species with fire-stimulated recruitment. Different recruitment processes may be stimulated by fire (Keeley 1991, 1995), with germination being the most important one. Seeds of some species have innate (primary) dormancy and they require a fire-related stimulus to germinate (refractory seeds; Keeley 1991). Fire may also stimulate flowering or dispersal. Some species may have seed population heterogeneity in relation to coat hardness, so that any heat conditions produced by fire induce the germination of a certain seed fraction. Therefore, in a simulation work, after a fire, fire-stimulated recruiters must increase their chance to recruit with respect to species whose recruitment is not affected by fire (Shugart & Noble 1981). More data is needed on MB species in order to quantify and model this process accurately.

Examples of MB species with germination stimulated by fire include a large number of leguminous species (e.g. *Ulex parviflorus*, *Hippocrepis unisiliquosa, Scorpiurus muricatus, Spartium junceum, Anthyllis cytisoides, A. hermanniae, Calicotome villosa*, etc.; Doussi & Thanos 1994) and most *Cistaceae* species (e.g., *Cistus sp. pl., Fumana sp. pl., Tuberaria sp. pl., Halimium sp. pl.;* Thanos et al. 1992). However, the way these species are stimulated by fire is complex, and depend on different factors, mainly temperature. For instance, the germination of some species is stimulated by fire due to high temperature, but when the temperature is very high the germination may be low again. The degree of stimulation (i.e., the proportion of seeds stimulated) is also different for different plants. Heterogeneous seed banks have been observed at least in some *Cistus* species (Thanos & Georghiou 1988). Charred wood (e.g., Keeley 1995) and smoke (e.g., Brown et al. 1993; Keeley & Fotheringham 1998) have also shown to stimulate germination in some plants, mainly in Mediterranean areas others than the MB (where such experiments have been rarely conducted).

The cones of *Pinus halepensis* and *P. brutia* have some degree of serotiny, and their recruitment is also stimulated by fire because of increased seed dispersal rather than germination stimulation. In contrast with some MTE, no plants have been found to be strictly dependent on fire for completing their life cycle in the MB. Most resprouting species do not have their recruitment stimulated by fire (e.g., *Quercus, Rhamnus*), although some species are able to resprout and, at the same time, have their recruitment stimulated by fire (e.g., *Thymus vulgaris, Anthyllis cytisoides, Dorycnium pentaphyllum*).

Underground structures

Most published gap models do not model underground structures. Underground structures may be very important in MTE because of the low water availability (below-ground competition), and because of the ability to resprout after disturbance. Some MB species have underground structures such as lignotubers, burls, root crowns or root stocks that may be involved in the capacity to resprout (bud-bank) and for the accumulation of starch (see above).

The gap model for temperate grassland communities (Coffin & Lauenroth 1990) considers underground competition by substituting the vertical effect of light (in forest models) by the vertical effect of resource use in the soil, without modelling mechanistically the underground system. For MTE, both above- and below-ground competition should be considered. Experimental studies in different Mediterranean heathlands (*brolles*) of NE Spain show different results: above-ground competition is more important than below-ground competition in *Erica arborea* communities (Canadell 1995), and the opposite is true in *Erica multiflora* heathland (Vilà 1997). It is reasonable to suppose that, just after a fire, below-ground competition may be more important than above-ground competition, but later, light competition may play an important role. Light needs to be considered when predicting long-term vegetation dynamics and transient changes between different life forms.

It is difficult to estimate quantitatively the underground structures (i.e., biomass, length, shape) because of the sampling problems involved. Examples of root/shoot ratios for MB species (Table 1) suggest higher values than for other ecosystems such as (compiled by Cannell 1982) coniferous forests (0.26±0.03, $n = 70$), deciduous forests (0.25±0.02, $n = 31$) and tropical forests (0.31±0.05, $n = 34$). The root/shoot biomass ratio should be studied when above-ground biomass has reached a steady state with the roots, and that may be difficult in areas with low growth rates and high disturbance frequency (fire and coppicing for firewood or charcoal production). This value changes also for different environmental conditions (Canadell & Rodà 1991, Table 1), and increasing atmospheric CO_2 concentration may increase the R/S ratio (Hilbert & Reynolds 1991). Equilibrium models of resource allocation developed for grasses (Davidson 1969) are difficult to apply to Mediterranean woody species due to the presence of large structural and storage organs (lignotubers, burls, etc.). More data is needed for MB species before generalisations can be made.

Post-disturbance conditions

Post-fire weather conditions may be a critical parameter for the regeneration of vegetation after fire, not only because of temperature and moisture conditions for germination and resprouting, but also because of possible soil erosion. Torrential precipitation at the end of summer or during autumn in burnt areas may cause loss of soil and seeds and transform a potentially vegetated area into a quasi-desert area without almost any possibility of natural recovery. This desertification process is common in the southern part of the MB and needs to be considered when modelling the dynamics of MTE at the landscape level (Thornes et al. 1996).

Soil parameters

Most gap models estimate water availability from soil depth and texture (or water holding capacity). Different soils developed over different bedrock types seem to be a significant parameter for the occurrence and survival of plant species in eastern Spain (Vallejo 1997). These differences are mainly due to the structure of the soil rather than to different nutrient availability or different water holding capacity. In eastern Spain, two main bedrock types producing basic soils appear to be common (Vallejo 1997): marls and hard limestone. The former develop unfissured soils while the latter develop shallower but fissured soils. Species with a deep root system adapted to take water from the depth (such as evergreen *Quercus* species) show preference for the latter (Table 2). Rambal (1984) observed water uptake by *Quercus coccifera* at 470 cm of soil depth in a limestone bedrock with a very shallow soil mantle. Recovery after fire is quicker in the shallower but fissured soil than in the deeper unfissured soil (Table 2). Mean soil depth and water holding capacity may not be good parameters to estimate water availability in large areas of the MB, and the presence of fissures and cracks (a difficult parameter to sample) may be a more important factor. This is also related to the importance of underground structures in MTE.

Anthropogenic factors and land use changes

The origin of man may be in the African savannas, but he soon moved to the MB (Carbonell et al. 1995; Stringer & McKie 1996). 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 in the Mediterranean landscape is during the Neolithic (Naveh 1975). Since then, many cultures have evolved in the MB, some of them with a high population density, making use of fire and farming since early history. Many centuries of severe human pressure resulting in burning, cutting and grazing on non-arable lands and clearing, terracing, cultivating, and later abandoning on arable portions, have created a strongly human-influenced landscape in most of the MB. It is not possible to understand current vegetation patterns in the MB 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. In fact, the effect of climate change on Mediterranean vegetation is difficult to illustrate because of the overwhelming impact of human activities on those areas. Three main scenarios of land abandonment are currently observed in Mediterranean landscapes which are the consequences of recent socio-economic changes: (a) areas with a previous land use of wood production (forests), that have been repetitively overexploited and burned, and currently appear as shrubland dominated by resprouter species; (b) areas with a previous land use of farming (often terraced) that have been abandoned, and currently are dominated by seeder species and maintained by recurrent fires. These areas are seldom invaded by resprouter species; they would need a long fire-free period (not occurring in dry Mediterranean areas) to

Table 1. Root:shoot biomass ratio (R/S) observed in some European Mediterranean species. Single numbers of R/S are average values or single values; two numbers are the range of average values at different sites.

Species	Locality	R/S	Observations
Quercus ilex	Montseny, NE Spain	0.45	xeric sites, single-stemmed forest (1)
	Montseny, NE Spain	0.37	mesic sites, single-stemmed forest (1)
	Montseny, NE Spain	1.20	mesic sites, single-stemmed forest (1)
	Prades, NE Spain	0.85	multi-stemmed forest (2)
	Prades, NE Spain	1.25	multi-stemmed forest (3)
	near Rome, Italy	0.27	(4)
Q.i. ssp. *ballota*	Alacant-València, E Spain	1.4–2.9	3–4 years old saplings (5)
Quercus coccifera	Alacant-València, E Spain	1.1–1.7	3–4 years old saplings (5)
	Montpellier, S France	2.0	(7)
	Montpellier, S France	4.8	(8)
Arbutus unedo	Corredor, NE Spain	0.5	(6)
Erica arborea	Corredor, NE Spain	0.3–0.4	(6)
Pistacia lentiscus	Alacant-València, E Spain	0.7–0.9	3–4 years old saplings (5)
Pinus halepensis	Alacant, SE Spain	0.3–0.4	3–4 years old saplings (5)
Phlomis fruticosa & *Euphorbia acanthothamnos*	Greece	1.48	community dominated by these 2 species (9)

References: (1) Canadell & Rodà (1991); (2) Lledó et al. (1992); (3) López et al. (1996) and Gracia et al. (1997); (4) Bruno et al. (1976); (5) Vallejo (1997); (6) Canadell & Zedler (1995); (7) Rapp & Lossaint (1981); (8) Kummerow et al. (1990); (9) Margaris (1976).

be invaded by resprouting shrubs; and (c) old fields with invasion by resprouter species (occurring in moist Mediterranean areas). The previous land uses together with climate and fire interactions have led to different vegetation patterns, and the recognition of these patterns is essential to understand and predict vegetation changes in Mediterranean landscapes. Below, I give a few concrete examples which show the importance of anthropogenic factors in structuring current MB landscapes.

Deforestation has long been occurring in the MB, mainly clearing for farming, and forests have disappeared in large areas, with few trees remaining at the sides of properties. In eastern Spain, after abandoning cultivation, *Quercus ilex* (holm oak) trees may appear at the side of properties because of the resprouting of old underground structures, but germination and recruitment of new individuals are seldom observed (Vallejo, pers. commun.). Forest recovery seems to be impossible if reforestation planning is not undertaken (Vallejo 1997). This contrasts with other Mediterranean regions, like California, where resprouters have high dispersability and continuous seedling establishment (Keeley 1986). It seems that some species in the MB require a rare event for establishment to occur, but once this has occurred, the resulting cohorts persist for a long time with high resilience (high demographic inertia *sensus* Westoby et al. 1989).

Quercus coccifera (kermes oak) is a common evergreen shrub occurring in the MB (e.g., North Africa, Spain, south of France, Greece) with a very high resprouting capacity (Malanson & Trabaud 1988; Trabaud 1990). However, large areas of eastern Spain (e.g., Vall de la Gallinera), where climatic and edaphic conditions suit this species' requirements well, are almost free of it. These areas have been intensively used (cleared, terraced and cultivated) for a long time. This intense land-use may be related to the near absence of this species in the area. This land-use contrasts with the use of *Q. coccifera* in other parts of Spain and in southern France, where it has been preserved and its growth stimulated for dye production (kerm). Differences in the present occurrence of *Q. coccifera* cannot be explained by current environmental factors and natural disturbance only; anthropogenic factors (i.e., previous land-uses) are also needed.

The tussock grass *Stipa tenacissima* is another common and native species in south-eastern Spain. It was planted long ago in some non-arable lands (i.e., south facing dry and stony areas), and harvested for making shoes and farm tools (Cavanilles 1795; Barber et al. 1997). All these crops were abandoned many

Table 2. Soil depth (cm) and mean cover values (%) of two evergreen *Quercus* species (*Q. ilex* ssp. *ballota* = *Q. ilex* ssp. *rotundifolia*) one and three years after fire in the València area (E Spain) on two different bedrock types (marls and hard limestone) and with similar climatic conditions. Cover values are the mean of ten transects. Standard deviations are in brackets. Data from Vallejo (1996).

	Marls		Hard limestone	
Soil depth (cm)	32 (16)		26 (14)	
Fissures and cracks	No		Yes	
Time since fire (yr)	1	3	1	3
Cover (%)				
Quercus coccifera	7.0	9.8	34.1	42.3
Q. ilex ssp. *ballota*	< 1.0	< 1.0	7.0	11.0
Total plant cover	50.1 (12.0)	58.9 (12.1)	66.3 (8.1)	70.2 (8.6)

years ago, but because of the high resilience of this species once it is established, the current distribution may not be related to the original distribution. It is very difficult, if possible, to distinguish the original distribution of this species from the current distribution.

Land abandonment in temperate systems may have short-term consequences, and, after some years of succession, the field may be restored to natural vegetation. Something similar may have occurred in moist Mediterranean areas, such as parts of France. However, in dry Mediterranean areas, land uses that involve slow-growing highly-resilient species have long-term consequences. Land use needs to be considered not only to predict future vegetation distribution, but also to predict and understand current vegetation patterns.

Functional types

We have pointed out some of the problems for modelling Mediterranean vegetation dynamics. However, some patterns have also been detected in relation to the close ecological and evolutionary relationships among different functional types (Tables 3 and 4). These functional types have different demographic patterns and responses to repeated wildfires (Figure 2). Resprouting species (Figures 2a, c) always maintain some biomass alive (often below-ground biomass) and recover quickly from fire. The recovery of non-resprouting species (Figures 2b, d) is slower and depends on the fire interval and the age of maturity. Species with fire-stimulated recruitment (Figures 2b, c) show a peak-phase soon after a fire, and then they decrease due to their low competition ability. 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 (heat, smoke, etc.). Species that increase after fire because there is more light/space available are not considered fire-stimulated species. Without experimental studies it may be difficult to associate an increase in recruitment with the fire. These four functional types may be subdivided as well by taking other parameters into account (for other classifications see Gill 1981), such as position of the seed bank (soil/canopy), position of resprouting buds (basal/stem), life form (woody/herbaceous) and dispersal vectors (animal/wind).

These four functional types (Table 3, Figure 2) have different response and sensitivity to the different disturbance types. A hypothesis to be tested is that communities dominated by resprouting species are more resilient under high fire recurrence than communities dominated by non-resprouting species, but the latter may be more resilient under climate change because of the higher reproduction rates and better dispersal mechanisms. An example of this effect is the *Quercus ilex* and *Q. coccifera*. They survive and resprout properly after fire, but they have very low (almost absent) seed germination and establishment in warm/dry areas. Furthermore, mutualist relationships (e.g., disperal by animals) appear to be more frequent in resprouting species than in reseeders, and the differential response to climatic change of the interacting species may break the relationship (Bond 1995). Testing the effect of initial vegetation composition (i.e., dominance of different functional types) on the sensitivity of vegetation to changes in climate

Table 3. Relation between different life history traits and the four functional types in relation to the regenerative response after fire. The four functional types are defined by the combination of the first two life-history traits (in bold). See Figure 2 for the general trend of their dynamics.

Life-history traits	Functional types			
Resprouting ability	**yes** (high)	**yes** (intermed.)	**no**	**no**
Fire-stimulated recruitment	**no**	**yes**	**yes**	**no**
Life span	long	long/intermed	short	short
Growth rate	low	interm.	high	high/interm.
Root system	deep	intermed.	intermed/shallow	shallow
Root/shoot biomass ratio	large	large/interm.	low	low
Type of dispersal units	big, fleshy or acorns, nonrefractory	small, light,	small, light, hard, refractory	small, light, nonrefractory
Number of dispersal units	few	intermed.	many	many
Dispersal vector	animals	variable	wind	wind
Seed bank	no	variable	yes (soil or canopy)	variable?
Seed life span	short	short/variable	long	short
Seedling establishment	low	intermediate	high	high
Leaf mass/area ratio	high	variable	low	low
Shade tolerance	high	low	low	low
Drought tolerance	low	high	high	variable
Susceptibility to disturbance	low	intermediate	high	high
Susceptibility to climate change	high	intermediate	low	low
Fire-related mortality	low	low/intermed.	high	high
Examples	*Quercus ilex* *Q. coccifera* *Q. calliprinos* *Arbutus unedo* *Rhamnus sp.pl.* *Phyllirea sp. pl.* *Pistacia lentiscus* *Brachypodium retusum*	*Thymus vulgaris* *Anthyllis cytisoides* *Psoralea bituminosa* *Genista scorpius* *Doricnium pentaphyllum* *Oryzopsis miliacea*	*Cistus sp. pl.* *Pinus halepensis* *P. brutia* *Ulex parviflorus*	*Taraxacum sp. pl.* *Galactites tomentosa,* *Conyza sp. pl.* *Chenopodium album* *Juniperus phoenicea*

and fire regime is a challenge in the Mediterranean ecosystems.

There may be a trade-off between resprouting ability and seed production: resprouting-non-recruiters (first column Table 3) and non-resprouting-recruiters (third column) represent the extremes in a gradient of regenerative strategies *versus* fire, the facultative type (resprouting-recruiters) being intermediate. The fourth type, non-resprouting-non-recruiters, would represent the absence of any strategy to cope with fire. This trade-off, together with other well known trade-offs in plant communities (Orians & Solbrig 1977; Smith & Huston 1989), could be a good base for a simple dynamic model. This type of approach has been taken by Noble & Slatyer (1980).

Noble & Slatyer (1980) seek to predict the dynamics of a community under recurrent disturbance by classifying the species into 13 types with similar dynamic behaviour, based on the possible outcomes rather than the mechanisms producing these outcomes (see also Noble & Gitay 1996). Their approach has been modified and coupled with a model simulator (Fate, Functional Attributes in Terrestrial Ecosystems) and has been shown to be successful in predicting the dynamics of different functional groups in Australia (Moore & Noble 1990, 1993). They take into

Table 4. Approximate relation between the four functional types in Table 3 and Figure 2 and other functional type groups found in the literature. Rows without reference are names widely used in the literature; species groups in brackets refer to part of the group.

Reference	Resprouting ability			
	yes	yes	no	no
	Fire-stimulated recruitment			
	no	yes	yes	no
	resprouter fire-resistent fire-tolerant	resprouter fire-resistent fire-tolerant	non-resprouter fire-sensitive fire-intolerant	non-resprouter fire-sensitive fire-intolerant
Le Houerou (1973)	passive pyrophites		active pyrophites	non- pyrophites
Naveh (1975)	obligatory root resprouter	facultative root resprouter	obligatory seed regenerators	–
	resprouters	facultative	seeders	seeders
Gill (1981)	Sprouting	Sprouting	fire-ephemerals	annuals/ pauciennials
Keeley (1991)	fire-persister or fire-resister	fire-recruiter	fire-recuiter	–
Keeley (1991)	non-refractory seed syndrome	refractory seed syndrome	syndrome seed syndrome	–
Trabaud (1992)	fire-indifferent spp.	fire-disadvantaged/ (fire-favored) spp.	(fire-favored spp.)	alien settlers/ occasionals
Keeley (1995)	disturbance-free recruiter	disturbance-dependent recruiter	disturbance-dependent recruiter	disturbance-dependent recruiter

account the fire response of both juvenile and mature plants, maturation age, light response (shade tolerance) and dispersal ability. However, this model could be improved to account for some of the parameters discussed above, such as soil parameters, underground competition and the water response. A model based on gap models and Fate, and included in a spatial framework would be a promising tool for testing alternative management strategies in Mediterrenean ecosystems. Smith & Huston (1989) and Bugmann (1996) used gap models with the functional type approach for testing vegetation patterns along environmental gradients. This approach is suggeted for predicting the response of the vegetation to climate change at large scale (Bugmann 1996); however, for Mediterranean ecosystems, a disturbance (e.g., fire) responses needs to be incorporated.

Conclusion

Gap models have been applied to a wide range of ecosystems, but mainly temperate and boreal forest ecosystems. However, there is no gap model that can be appropriately used for Mediterranean conditions. Any model for MB ecosystem dynamics should take into account different life forms (trees, shrubs, scrubs, grasses), resprouting ability, fire-germination interactions, underground structures and post-fire conditions. Anthropogenic factors are essential before validating any model in the field. Current trends in modelling include more physiological-based approaches, however, the lack of data for Mediterranean species and the importance of disturbance processes may require other approaches, such as the one based on functional groups. The link between disturbance-based and climate-based functional groups is a promising research area for predicting future landscapes.

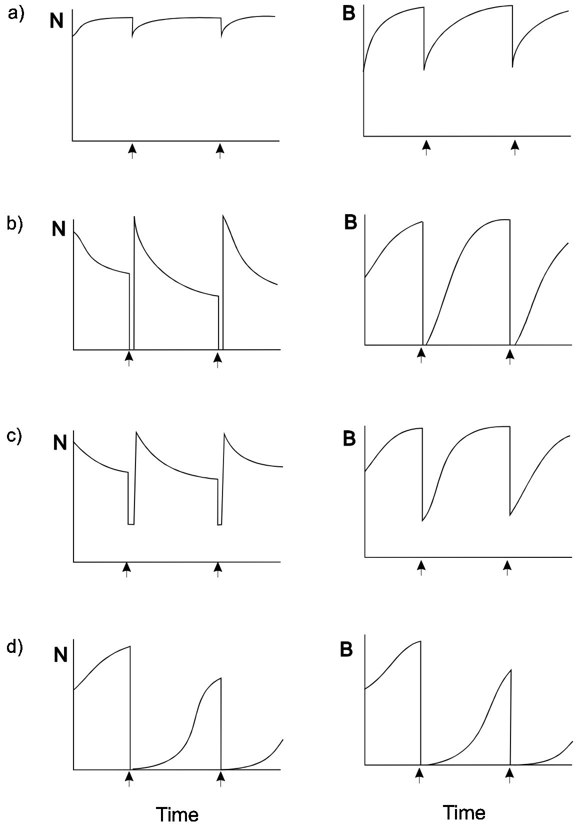

Figure 2. Possible population dynamic trends for different functional types (N: population size; B: biomass of the population, including below-ground biomass but not seed biomass). Maximum N and B are scaled for each functional type. Arrows indicate fires. (a) resprouting species; (b) species unable to resprout after fire but with recruitment stimulated by fire (disturbance-dependent recruitment); (c) resprouting species with the recruitment stimulated by fire and (d) non-resprouters with recruitment not-stimulated by fire

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