INTERNATIONAL SYMPOSIUM

FOREST FIRES: NEEDS & INNOVATIONS

VOLUME OF PROCEEDINGS

A DELFI action

18-19 November 1999
Athens, Greece

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EFFECTS OF FIRE ON VEGETATION DEMOGRAPHY

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INTRODUCTION

Mediterranean ecosystems have evolved in close relation to fire. Actually, fire has acted as an important environmental factor in all terrestrial ecosystems, with the only possible exception of those that have remained either very cold or very humid. High temperatures prevailing during summer in the mediterranean regions together with the extremely low water availability dry out the herbaceous vegetation of the understorey as well as parts of the standing woody biomass. Leaves and twigs are massively shed of plants (Arianoutsou, 1979) and these together with the dead herbaceous plants, form a quite flammable litter layer. Several mediterranean plants also produce flammable substances such as volatile oils and resins. Historical evidence of the action of fire upon the mediterranean vegetation exists for all the regions of the world having a mediterranean type climate. In the Mediterranean Basin itself there are references for fire occurrence since the end of the last glacial period.

PLANT ADAPTIVE TRAITS

Having suffered the repetitive action of fire Mediterranean plants have developed special adaptations which ensure their survival. Thus they respond to the action of fire with two basic mechanisms: vegetative regeneration (*resprouting*) of the same burned individuals and establishment of new individuals through *seed germination.*

Most shrubby species which constitute the seasonal dimorphic plant communities (phryganic) such as the thorny burnet (*Sarcopoterium spinosum*) and the Jerusalem sage (*Phlomis fruticosa*) and the communities with evergreen sclerophyllous plants (maquis), such as the kermes oak (*Quercus coccifera*), lentisc (*Pistacia lentiscus*), strawberry tree (*Arbutus unedo*), tree heath (*Erica arborea*), prickly juniper (*Juniperus oxycedrus*) are resprouters. Resprouting occurs usually at the root crown of the burned plants from dormant buds that had remained intact after fire, being protected by the soil. Resprouting is also the regeneration mechanism of the plants that possess lignotubers, such as the greek spiny spurge (*Euphorbia acanthothamnos*) or underground bulbs as many geophytes do, e.g. cyclamens (*Cyclamen* spp.), tassel hyacinth (*Muscari commosum*) etc.

The start of regeneration is timed differently in the seasonal dimorphic and in the evergreen sclerophyllous plants. Maquis species regenerate almost immediately after fire, while phryganic species wait for the first rains. This difference has been attributed to the different penetration depths of their root systems.

Leaves developing on the resprouted shoots are generally larger, richer in chlorophylls (Arianoutsou and Margaris 1981a) and have higher rates of photosynthesis (Oechel personal communication) than their equivalent on the unburned plants. It is not only the growth of the resprouting species which is higher; they also reach their reproductive maturity rather quickly, producing flowers and fruits a couple –or at most– years after resprouting.

The second adaptive mechanism that mediterranean plants possess is seedling recruitment. Seedlings emerge after the first autumn rains from seeds that were either dispersed before fire and were remaining dormant in the soil as a so called 'seed bank' or were dispersed because of the action of fire. Seeds that can be found in the soil seed bank are hard coated and they belong to the plant families of rockroses (Cistaceae) and legumes (Leguminosae). These seeds normally lie dormant in the litter or topsoil layers and are released from their dormancy by the heat which develops during a fire. On the other hand high temperatures reaching the plant canopy induce dehiscence of the cones and the subsequent dispersal of the pine (Pinaceae) seeds that were remaining intact in their structures. In every square meter of burned phryganic soil there are hundreds of seeds, which germinate after the first autumn rains and soon provide a protective shield which, along with the new resprouts, holds the soil in place. In every square meter of burned pine forest there are plenty of pine seeds which germinate after the first autumn rains. At the end of the first postfire summer these yield a mean density of pine seedlings equal to the density of trees in the site before fire.

Usually seedlings appear in large numbers; however, after the first dry season a self thinning occurs, which is mainly due to the drought effect (Arianoutsou and Margaris, 1981a; Papavassiliou and Arianoutsou, 1997; Daskalakou and Thanos, 1997; Skourou and Arianoutsou, 1998). The seedlings of the shrubs have a very rapid growth. Soon the young saplings flower and produce seeds, which are dispersed on the site enriching the soil seed bank.

POST-FIRE SUCCESSION

Plant succession after fire in Mediterranean plant communities consists largely of the regeneration and development through the respective life cycle of the species that were present before fire (Arianoutsou, 1998). It is a process of *autosuccession* in which the burned stand, although initially appearing to be different from the pre-burned one, retains its floristic identity in time (Arianoutsou, 1979; 1998; Trabaud, 1994, Kazanis and Arianoutsou, 1996; Kazanis and Arianoutsou, 1998). During the first years after fire a remarkable abundance of herbaceous species (mostly annuals) is observed in the burned sites, something which does not occur in the unburned ones. Among this herbaceous flora legume species are predominant together with the composites. This prolific appearance of herbaceous plants may be attributed to many reasons one of which would be the promotion of their seed germination by increased temperature regimes prevailing during and immediately after the fire (such as the legumes) or by other factors (e.g. nitrogenous compounds, fluctuating temperatures, changes in the light quality). As succession proceeds and the canopy closes the herbaceous vegetation is either restricted to small openings, or remain dormant in the soil in the form of seeds waiting for the next fire to come. Establishment of previous communities is a rapid process. As burned communities age they return to a state similar to that of the unburned system, with vegetation structure becoming more and more complex, while plant biomass shifts increasingly shifting from herbaceous to woody components. Highlights of post-fire succession in Mediterranean plant communities are shown in Table 1.

almost all recent studies there is an agreement that the development of the vegetation after fire follows the *initial floristic composition model* described by Egler (1954) or the *inhibition model* described by Conell and Slatyer (1977): all prefire species are present immediately after fire, even if later the relative abundance or frequency of individuals changes. In other words, there is no real succession, or floristic relays, or different communities on the same site, as is the main characteristic of the secondary succession, but an autosuccession process leading to a recovery of the prefire communities (Trabaud, 1994; Kazanis and Arianoutsou, 1998; Arianoutsou and Ne'eman, 2000).

Table 1. Highlights of post-fire succession in Mediterranean plant communities

	Communities with seasonal dimorphic plants (phrygana)	Evergreen sclerophyllous shrublands (maquis)	Pine forests
Annuals and short-live ephemerals	Abundant	Abundant	Abundant
Geophytes	Many	Many	Many
Herbaceous perennials	Many (mostly grasses)	Many (mostly grasses)	Many (mostly grasses)
Regeneration mode of dominant woody species	Sprouting / seeding	Sprouting	Sprouting / seeding
Timing of plant recruitment	Immediately after fire	Immediately after fire	In the 1st post-fire rainy season
Fire stimulated seed germination	Yes	Not in shrubs	Yes
Development of canopy cover	100% in less than 10 years	100% in less than 5 years	100% in more than 10 years
Diversity trends	Initially increases – decreases with community maturity	Initially increases – decreases with community maturity	Initially increases – decreases with community maturity

PLANT DEMOGRAPHY

Recovery of plant species that regenerate vegetatively is a rather straight forward process which depends on the meteorological conditions prevailing on the site, the productivity of the site (available nutrients in the soil), competition between recovering plants and external factors such as grazing. Populations of these species generally consist of one age cohort, that of the initially regenerated plants. The situation is different with the seeding species, as their recovery is strongly dependent on the specific life histories of the plants, that is whether they are short living plants, such as the annual herbaceous legumes, or relatively short living plants, such as the rockroses or long living plants, such as the pines.

From the few demographic studies in post-fire communities it is shown that a decrease in seedling density of seeding shrubs occurs in the 1st post-fire year (Naveh, 1974; Papanastasis, 1977; Arianoutsou and Margaris, 1981b; Kazanis and Arianoutsou, in preparation; Skourou and Arianoutsou, unpublished data). No evidence of remarkable seed germination exists so far for these woody species during the second post-fire year. On the contrary, several herbaceous legumes exhibit massive seed germination during the second and even the third post-fire year (Papavassiliou and Arianoutsou, in Arianoutsou and Ne'eman, 2000).

The juvenile phase for most of the woody seeding species, such as the rockroses, lasts for only two years, that is they reach maturity and consequently reproductive age quite soon. Skourou and Arianoutsou (unpublished data) have found that there is a secondary seedling recruitment in these species which coincides with the maximum of the initial population decline, approximately 15 years after fire.

Pinus halepensis (Aleppo pine) and *Pinus brutia* (East Mediterranean pine) are the most important Mediterranean pines forming a canopy seed bank. This seed bank is composed of bradychorous (serotinous) cones and their enclosed seeds. Serotiny is impressively obvious in the newly formed cones on the young pine treelets of Aleppo pine although their seeds exhibit normal germinability (Thanos et al., 1998). The juvenile phase of the tree seeders, the Mediterranean pines last longer than in the shrubs. It has been found by Thanos et al. (1998) that the juvenile phase lasts for 4 years in Aleppo pine forest, while it is slightly longer in the East Mediterranean pine. However, at the population level this characteristic is very much affected by the conditions prevailing on the site (meteorological and soil). Based on personal observations on a series of sites forming a post-fire chronosequence of *Pinus halepensis* forests, it is after the 15th – 20th year that a pine population is at reproductive maturity.

THE FIRE REGIME

For the long term survival of the plants it is essential to know not only their adaptive traits towards a 'normally' occurring fire event, but also how they are affected by the fire regime, i.e. frequency, intensity, season, spatial extent. In this contribution we will examine in detail fire frequency, fire intensity and fire spatial extent as in the Mediterranean region wildfires occur only in summer. On the other hand, arson also occurs in summer. Spatial extent of a fire may be important, as it will define the possibilities of propagule dispersal from unburned areas, susceptibility to grazing etc.

Fire Frequency

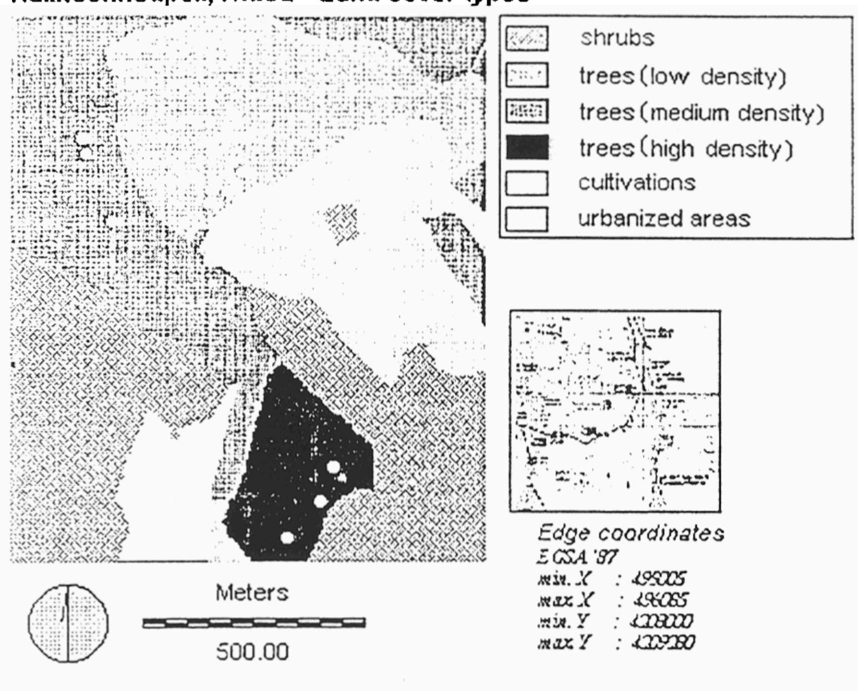
All fires in the mediterranean regions of the world burn areas that have also been burned in the past. Consequently, the vegetation is really a mosaic of fire histories, with some parts having had more fires than others, over a given period of time.

Plants that are killed by fire and reproduce through seed germination rely on this seed germination in order to persist at the specific location. For these plants, there must be sufficient time between successive fires for the seedlings to mature and produce seeds and hence add seeds to the seed bank. This time will vary between species (see above), from species that flower within the 1st year after fire (such as the herbaceous legumes), to species that flower within 1-2 years after fire (such as the rockroses) to those that may take 6-8 years to reach maturity (the pines). If another fire occurs before these plants have matured, dramatic changes in the vegetation composition and physiognomy might occur. Plate 1 provides a typical example of the latter case in a region of Mt. Penteli, which has suffered the experience of repeated fires. The risk of having dramatic changes in the vegetation physiognomy and form is extremely high in that part of the region that has been burned three times in intervals less than 10 years. This is because treelets of Allepo pine, which was the dominant tree on the site, did not have adequate time to reach maturity and produce seeds which would ensure the subsequent recovery of the pine population.

Fire Intensity

Fire intensity is expressed as the amount of heat released during its passage. This is due to several factors among which the most important ones are the amount of the fuel, the moisture of the fuel, its distribution etc. Plants experience fire intensity through the amount of the heat released and the duration of the heating. Intense fires usually kill the stems of the resprouters, but it seems that their regeneration is not generally affected, as it is relied upon the available carbohydrates of the underground parts, being protected by the soil. Seeds lying in the soil seed banks seem also not to be negatively influenced by intense fires. On the contrary, there are several references in the literature about heat induced seed germination after fire (Arianoutsou and Margaris, 1981b; Thanos and Georgiou, 1988; Keeley, 1991).

Kallitechnoupoli, Attica - Land cover types



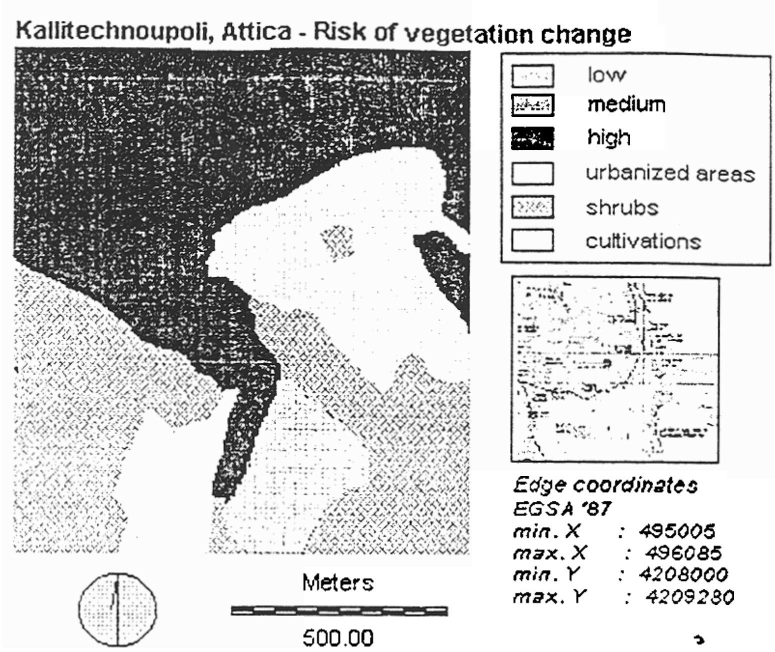


Plate 1. Maps of Kallitechnoupoli region in Mt. Penteli, Attica, Greece. Upper part: Vegetation map of the area. Lower part: Risk of vegetation type change due to repeated fires. The criterion used for the estimation of the risk was density of *Pinus halepensis* seedlings.

PREDICTING VEGETATION DYNAMICS

Mediterranean ecosystems have been under the influence of man for thousands of years. However, it is only after the Second World War that this influence had a profound impact. On the other hand, environmental awareness is steadily increasing and the demand for a rational management of ecological systems appears strong. To this end, models designed to predict vegetation changes in response to environmental changes (disturbances, land use changes, climate changes..) are useful tools. One of the most recent and promising approaches is the use of plant functional types as suitable for modelling based on responses to disturbance, such as fire and grazing (Pausas, 1999; Lavorel et al., 1997). These models can predict the possible population dynamic trends for the 4 functional types that can be distinguished in the Mediterranean plants (Figure 1 and Table 2).

Table 2. Relation between different life history traits and the four functional types distinguished in the Mediterranean vegetation in relation to the regenerative response after fire (after Pausas, 1999).

Life history traits	Functional types			
Resprouting ability	Yes (high)	Yes (moderate)	No	No
Fire stimulated recruitment	No	Yes	Yes	No
Life Span	Long	Long/intermediate	Short	Short
Growth rate	Low	Intermediate	High	High/interm.

ıspersal units	Big, fleshy or acorns, non refractory	Small, light, refractory	Small, light, hard, refractory	Small, light, non refractory
Number of dispersal units	Few	Intermediate	Many	Many
Dispersal agent	Animals	Variable	Wind	Wind
Seed bank	No	Variable	Yes (soil or canopy)	Variable?
Seed viability	Short	Short/variable	Long	Short
Seedling establishment	Low	Intermediate	High	High
Susceptibility to disturbance	Low	Intermediate	High	High
Examples	*Quercus ilex* *Q. coccifera* *Arbutus unedo* *Pistacia lentiscus* *Phyllirea* spp.	*Anthyllis cytisoides* *Bituminaria bituminosa* *Genista scorpius* *Piptatherum*	*Cistus* spp. *P. halepensis* *P. brutia* *Ulex parviflorus*	*Taraxacum* spp. *Chenopodium* *Juniperus phoenicea*

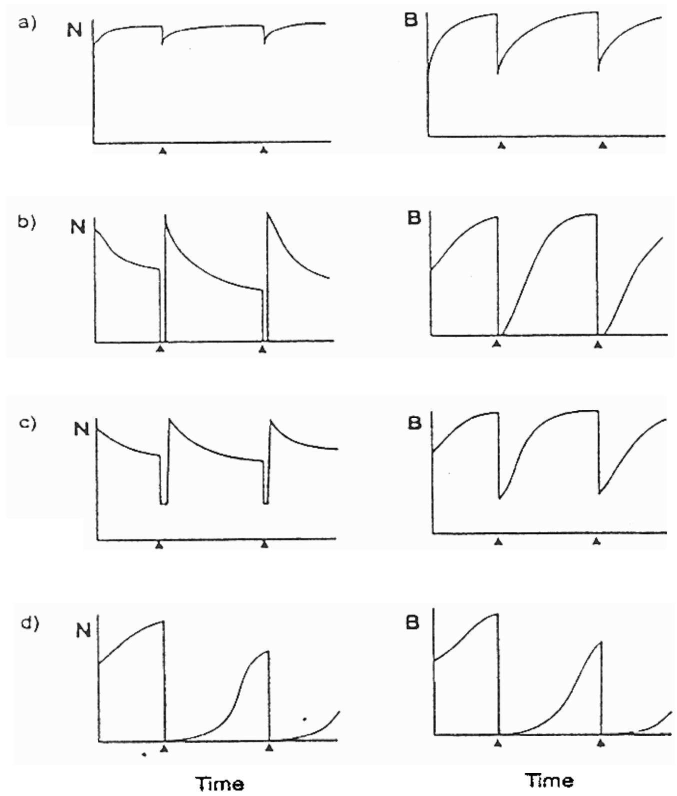


Figure 1. Possible population dynamics for the 4 functional types. (N: population size, B: Biomass-including below ground). Arrows indicate fires. (a): resprouting species, (b): non-resprouting but seed germinating species, (c): resprouting species with seed germination stimulated by fire, (d): non-resprouting species with recruitment non- stimulated by fire (after Pausas, 1999).

CONCLUSIONS

Long term exposure of Mediterranean ecosystems to fire has induced specific adaptations towards this environmental factor. Increasing human impact upon these systems is creating a significant impact upon the current Mediterranean landscape. It is not possible to manage Mediterranean landscapes and their vegetation without considering the characters of the plants flourishing there. A most promising tool in this direction is the use of prediction models for vegetation dynamics based on plant functional types.

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