

THE EVOLUTIONARY SIGNIFICANCE OF FIRE IN THE MEDITERRANEAN REGION*

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Introduction

Due to the destructive combination of overgrazing and land abuse with burning, wildland fires have been regarded in the Mediterranean Region as a wholly condemnable, man-made element. This might be the reason for the few, systematic studies of fire effects and neglect of their evolutionary role in Mediterranean vegetation. In previous studies, fire has been mentioned only briefly as a destructive factor (Zohary, 1962) or in connection with man-induced regression stages, leading away from the 'maquiclimax' (Braun-Blanquet, 1925; Bharucha, 1952; Kuhnhotz-Lordat, 1939). Only in a recent, most comprehensive description of Mediterranean vegetation types, Walter (1968) has recognized fire as one of the major ecological factors which shaped the Mediterranean landscape and affected its present mosaic-like pattern of regeneration and degradation stages.

Shantz (1947) recognized that shrub communities of mediterranean climates, not only in California but also in South Africa and South Australia and in the Mediterranean Region proper, should be considered a 'fire type' or 'fire climax' because of their long subjection to recurring fires. Naveh (1967) drew attention to the striking similarity in fire response of individual plants and communities of mediterranean shrub ecosystems in California and Israel. This is manifested in both countries by rapid regeneration of the same individuals and/or by a shifts in

composition through volunteer seeds of burned mother plants. Such a process of 'autosuccession' (Hanes, 1971) is obscured, in general, by a short interlude of herbaceous plant domination (Muller et al., 1968). Naveh (1967) also pointed to the comparable role of fire in both mediterranean environments in the evolution of shrub ecosystems and in their maintenance in a rejuvenated and vigorous state, coupled with the mobilization of tied-up nutrients and the removal of heat-unstable phytotoxic, allelopathic agents. After comparing monotonous, impenetrable and completely protected maqui with burned and disturbed, but biologically much richer maqui and batha (a biblical term applied by Eig (1927) in Israel to heather-like dwarfshrub and herb associations), Naveh (1971) concluded that prescribed burning should become an indispensable tool in the ecological management of nature parks and reserves in the maqui belt for conservation of biological diversity.

LeHouerou (1973) recently discussing the effect of fire on Mediterranean vegetation also came to the conclusion that it is dominated by pyrophytes and that periodically burned forest and shrubland is more complex in composition and structure than that not burned at all or burned too frequently. Mooney & Dunn (1970) outlined the convergent evolutionary strategies of mediterranean climate-type sclerophyll shrubs and included fire as one of the major environmental stress factors. They referred, however, only to examples of fire-stimulated germination and resprouting behaviour of California plants. Such adaptive mechanisms for California 'fire types' have also been described in more detail by Sweeney (1967) and Vogl (1967).

The object of this paper is to discuss in more detail the evolutionary significance of fire behaviour by woody as well as herbaceous plants from the Mediterranean Region against the background of a long fire history.

* Nomenclature follows

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The fire history of Mediterranean ecosystems

At present, lightning causes wildfires only on 0,6–4% of the annually burned areas in the Mediterranean Region (Susmel, 1973). In Israel, lightning out of clear skies may occur on several days in April–June and cause wild-fires. In ancient times, however, even such a single lightning fire on a dry day, if not put out immediately, could catch the undisturbed, dense and highly inflammable woody and herbaceous vegetation and spread rapidly over vast areas. Such fires on wildland and pastures were already mentioned in the Bible in connection with lightning as the ‘fire of God’ in the Book of Job (1/16) and in connection with ‘the heat of the summer drought’ by the prophet Joel (1/11).

The great geographer and ecologist, Sauer (1961, p. 262) claimed that ‘mountainous areas in arid and semi-arid lands do set up dry-season turbulence with lightning discharges into inflammable plant matter. Such fires occur under conditions of low humidity and are accompanied by little or no rain . . . The capture of fire may well have come about as a discovery on food collecting, following after a natural fire. As the source of such fires I should prefer vulcanism; Italy and the eastern Mediterranean, the East African Rift Valley.’

According to Rosenan (pers. communication) such lightnings as well as volcanic eruption caused many large-scale fires in geological times, especially since the Last Interglacial desiccation, when the main Mediterranean climate patterns and vegetation types became finally established (Butzer, 1972; Horowitz, 1968).

The earliest archeological evidence of the presence of fire in the maqui belt of the Mediterranean Region reaches back to findings of wooden ash and hearths in the final Acheullian and Levalloiso-Mousterian levels of the Mesolithic period at the Mount Carmel caves in Israel by Garrod & Bate (1937) and at the Kastritsa caves near lake Ioanina in Greece (Higgs et al., 1970).

We have no direct evidence of intentional burning by these paleolithic hunters and food gatherers. But it is reasonable to assume that, after realizing how natural fires opened the dense and unpenetrable forest and maquis thicket near their habitats and created biologically richer ecotones and successional stages, they might have used fire deliberately to facilitate hunting and food gathering and to increase edible food for man and beast by the lush regenerating trees and shrubs and invading grasses, herbs, bulb and tuber plants, typical for these burns. That fire became, thereby, the first forceful tool for ecosystem

manipulation by the Pleistocene hunter-gatherer economies has been suggested not only by Sauer (1957), but also by eminent anthropologists and archeologists such as Stewart (1957), Oakley (1961) and others, cited by Komarek (1967) who discussed this problem most comprehensively.

With increasing human populations and advanced hunting and food collecting economies, such as the Natufian cultures of the Carmel Caves, described by Garrod & Bate (1937), Garrod (1958) and Vita-Finci & Higgs (1970) the extent and intensity of burning probably increased steadily and became more and more linked with grazing by wild and semi-domesticated ungulates, such as fallow deer, gazelle, wild goat and cattle. The steady increase in Mediterranean garigue, steppe and rock dwelling rodents, relative to more mesic forest and maqui dwellers, from this period onwards has been shown in recent paleontological findings in these caves by Tchernov (1968) and indicate the gradual enlargement of drier, more exposed and rockier habitats in the vicinity. As these trends were not accompanied by over-all climatic desiccation (van Zeist, 1969; Butzer, 1972; Ucko & Dimbleby, 1969), they can be interpreted as the first, fire-induced stage of the anthropogenic biofunction which has led through various cycles of degradation and aggradation to the present Mediterranean landscape (Naveh & Dan, 1971).

Fire has played a no less active role in further phases of this anthropogenic biofunction in the pastoral and agricultural ecosystem modification and conversions, in forest and land clearing for cultivation and apparently also in the domestication of cereal crops.

As reviewed extensively by Whyte (1961) and Ucko & Dimbleby (1969), the transition zones between the semi-arid steppic Irano-Turanian and the sub-humid Mediterranean woodlands are amongst the first known centres of successful cereal and stockbreeding economies. These regions include the most fire-prone Mediterranean biomes (Naveh, 1973a), in which the progenitors of our cereals, the large grained wild barley = *Hordeum spontaneum* and the Emmer wheat = *Triticum dicoccoides*, are abundant (Zohary, 1969). The annual grasses are amongst the most prolific fire followers, and post-fire collection of seeds, as also suggested by Komarek (1967) could have been one of the first phases in their domestication. Their fire-scorched seed dispersal units with big parched kernels can easily be collected after a wildfire, and according to Harlan (1967) these primitive glumed cereals needed to be parched before they could be threshed and winnowed. Harlan & Zohary (1966) suggested that actual domestica-

tion and farming may not have taken place where these cereals were most abundant and could be collected from natural stands, but in adjacent areas. These include the maqui belt, in which the semi-sedentary Natufian cultures using flint sickles and grinding stones were located, as well as the drier Jordan Valley where the first pre-pottery neolithic settlement (Jericho) and the Jarmukian cultures have been found. The origins of domestication and cultivation in the Near East are, therefore, still very much a matter of speculation (Flannery, 1969). But K. Kenyon – the discoverer of Jericho – claimed (Kenyon, 1969, p. 331): ‘It would be quite in keeping with the trend of archaeological evidence that the first experiments in agriculture were made by the Neolithic Natufians of, for instance, the Mound Carmel caves, and the migrants to the Jordan Valley brought with them grain that had already produced mutations that made it more suitable for agriculture.’ As mentioned above, from these caves we already have the first evidence of use of fire and its possible after-effects on expansion of drier and more exposed sites. One should not discount, therefore, the importance of fire as one of the environmental and cultural triggers of cereal domestication in the fire-swept drier grasslands and in the fire-induced maqui-edges.

Throughout the following phases of intensive agricultural and pastoral land use and especially from the Bronze and Iron Age until the Hellenistic and Roman period, the wide occurrence of fire is well documented in the Bible, the Talmud, and Hellenistic and Roman literature. Burning was a common practice for clearing of forest, wood and shrubland, for pastoral use and cultivation as well as for cleaning of thistles and stubbles in fields, and out of revenge and sheer carelessness. A. Derman & Z. Naveh (unpubl., cited in Naveh, 1973b) have listed 28 references of fire and vegetation from the Old Testament and Liacos (1973) has cited many Greek and Roman sources which show how common natural and man-made fires were in those days. According to LeHouérou (1973) there is also evidence of ancient burning of forests and maquis for pasture improvement in Southern France. This practice was used by herdsmen in all Mediterranean countries throughout history (Semple, 1931; Shantz, 1947). Vivid descriptions of such ‘Brandkulturen’ are provided by Anderlind (1886) in the last century and more recently by Rickli (1942).

At present the human and livestock pressure in many Mediterranean countries, especially in the Levant, has become so severe that little grass fuel and dense woody vegetation has been left for wildfires. Nevertheless, Le

Houérou (1973) estimated that each year close to 200 000 ha of Mediterranean forest and shrublands are burned annually; and the causes of these wildfires have not changed much since biblical times.

The adaptation of mediterranean plants to fire

Typical Mediterranean ‘fire bioclimates’ (Naveh, 1973b) are characterized by long, hot and dry summer seasons with maximum average daily temperatures around 30 °C, average relative air humidities of 50–60% and frequent heat waves of ‘sharav’ (Winstanley, 1972) or ‘sirocco’ (western Mediterranean) in the beginning and the end of the dry season, when temperatures rise above 40 °C and relative humidities can drop below 30 %.

Under these circumstances the chances for the highly inflammable Mediterranean woody and herbaceous vegetation canopies to escape the high temperatures of wild fires are slim. As has been shown above, this vegetation has been exposed to recurring fires for such a long period, that only species and biotypes adapted by post-fire regeneration from underground or fire tolerant parts survived. These adaptations can be understood in a cybernetic context as homeostatic feedback control responses to changes in the plant-environment system, induced by the fire. In these, the information of the catastrophic fire event and its ecological after-effects is partly transformed or re-coded, by survival and increased frequency of genes contributing to fire tolerance, whilst genes contributing to vulnerability to fire are deleted. According to the Law of Requisite Variety (Ross-Ashby, 1956) those genotypes in which this information feedback was large enough to permit endurance or evasion of fire had the best chances of survival.

Positive feedback responses are those which help in overcoming the fire hazard and its after-effects by increased physiological activity. This is chiefly expressed by vegetative, fire-stimulated resprouting and-or fire-stimulated seed germination and post-fire flower and seed production. Examples of these from representatives of the major ecological plant groups in the Mediterranean Region from fire-prone upland ecosystems are shown in Table 1.

As negative feedback responses, on the other hand, can be regarded all those defence mechanisms which enable the avoidance of the fire hazard, either by direct fire tolerance of seeds or plant organs or by their reduced physiological activity during critical fire periods. Our present knowledge

TABLE 1. POSITIVE FEEDBACK RESPONSES OF POST-FIRE REGENERATION OF SOME COMMON MEDITERRANEAN PLANTS

Ecological groups and plant species	Regeneration Veget. Reprod.	
<u>Phanerophytes</u>		
Quercus coccifera, Q. calliprinos, Q. ithaburensis	+) ¹	-
Pistacia lentiscus, P. terebinthus, P. palaestina, P. atlantica	+	-
Phyllirea media, Olea europea, Rhamnus alaternus, R. palaestina	+	-
Ceratonia siliqua, Laurus nobilis, Styrax officinalis, Myrtus communis	+	-
Tetraclinis articulata, Juniperus phoenicia	+) ²	-
Arbutus unedo, A. andrachne, Spartium junceum	+	+
Calycotome villosa)* Erica arborea, E. multiflora	+	+
Pinus halepensis)*, P. brutia, P. pinea	-	+
<u>Chamaephytes</u>		
Sacropoterium spinosa)*, Rosmarinus officinalis, Helianthemum tuberaria	+) ³	+
Thymus capitatus, Satureja thymbra, Teucrium spp., Phlomis lynchnitis	+	+
Salvia triloba, Salvia spp. & many other Labiatae	+	+
Cistus villosus)*, C. salvifolius)*	+	+
Cistus monspeliensis, Cistus spp.	-	+
<u>Climbers</u>		
Aristolochia parvifolia, A. spp., Asparagus aphyllus, Asparagus acutefolius, A. spp.	+) ⁴	
Smilax aspera, Tamus communis	+	
Clematis, cirrhosa, Rubia tenuifolia, R. spp.	+	
<u>Geophytes, Hemicryptophytes, Perennial herbs</u>		
Ophris, spp., Orchis spp., Asphodelus microcarpus, A. spp.	+	+
Iris spp., Allium spp., Narcissus tazetta, Cyclamen persicum and many other geophytes	+	+
Eryngium falcatum, Dorycnemum suffruticosum, Echinops spp.	+	+
Carlina involucreta, Cephalaria leucantha, Ononis spp.	+	+
Sanguisorbia minor, Galina corruadaefolium & many others Perennial herbs	+	+
<u>Perennial grasses</u>		
Oryzopsis miliacea)*, O. caerulescens)*, Stipa bromoides)*	+	+
Brachypodium ramosum, B. pinnatum, Festuca arundinacea	+	+
Arrhenatherum elatus, Phalaris tuberosa, Bromus syriacus	+	+
Dactylis glomerata, Hordeum bulbosum)*, Poa bulbosa,	+	+
Hyparrhenia hirta)*, Andropogon distachius)*	+	+
<u>Therophytes</u>		
Avena sterilis)*, A. spp., Stipa tortillis)*, Bromus spp.	-	+
Aegilops spp. and many other annual grasses	-	+
Lotus peregrinus)*, Psoralea bituminosa, Trifolium spp.		+
Medicago polymorpha)* M. spp. and many other legumes		+
Anthemis spp. Crepis spp., Senecio spp., Sonchus spp.	+	-
Scabiosa spp.	+	-
Erodium spp., Geranium spp., Cephalaria joppica)*	+	-
Anagallis coerulea)*, Lagoecia communis & many other annual plants	+	-

)¹ = resprouting from underground stumps and root crowns and adventive roots (suckers)

)² = resprouting from underground stumps and root crowns, no suckers

)³ = resprouting from root crowns

)⁴ = resprouting from roots and underground bulbs or corms, tubers and other regeneration buds.

)* pronounced post-fire germination observed in field experiments in Israel.

is far too limited to give a detailed account of all these fire adaptations in different plants and their genetical, physiological and morphological mode of action. For this purpose much more extensive field and laboratory work is necessary than the studies now carried out in this region and summarized in the Tall Timber Fire Ecology Conference at Tallahassee, Florida in March 1973, by Le Houerou, Liacos, Naveh and Trabaut.

Le Houerou (1973), reviewing the effect of fire on Mediterranean vegetation types, distinguished between active and passive pyrophytes. This classification is closely related to dominance of positive or negative fire feed-back responses. Trabaud (1973) studying the response of garigue plants in South France to different frequencies and timings of fire, has graded these plants according to post-fire regeneration capacities to frequent burning. In evaluating these results it should be kept in mind that only dense and well developed maqui and garigue stands, which have recovered 5 years and more after the fire, are highly inflammable. We can, therefore, assume that those fire frequencies which had greatest evolutionary significance for these woody plants are probably not greater than once in 5-10 years.

As can be seen in Table 1, most sclerophyll trees and shrubs, as well as climbers, rely solely on vegetative regeneration and are therefore *obligatory root resprouters*. On the other hand, all chamaephytes, as well as herbaceous perennial plants are *facultative root resprouters*. They may resprout vegetatively but also regenerate by fire-stimulated seed germination and growth, and most of them produce seeds from resprouting plants already in the first year after the fire and from (volunteering' seedlings (from seeds already in the soil at the time of fire) in the second year (Naveh, 1960, 1973a).

Mediterranean conifers, like *Pinus halepensis* and *P. brutia* do not resprout at all, but rely solely on post-fire seed germination from cones that burst open from the heat of the fire. They are, therefore, *obligatory seed regenerators* and fire apparently provides the only opportunity for their natural regeneration under a dense maqui understory (Walter, 1968; Naveh, 1973a).

Fire regeneration behaviour is closely linked with response to season and water availability. The obligatory root resprouters are sclerophyllous, mostly evergreen, *drought-enduring* and summer-active trees and shrubs.

But the facultative root resprouters are typically *drought-evaders* adapting to the dry summers by more restricted physiological activity and especially by reduction of their transpiration surface (Orshan, 1972). They com-

mence resprouting only after the first winter rains. Obligatory resprouters, in contrast, since they rely on deep and well-branched root systems, can begin to resprout by the middle of the summer immediately after the fire and continue intensive growth at least through the first and second summer to regain their former, dominant position after a few years' time. As long as their young suckers and shoots are soft and lush and their leaves are not yet lignified and thorny, they are browsed heavily by herbivores. Thus, as stated by Mooney & Dunn (1970), postfire grazing pressure has acted as an additional powerful selective agent, favoring those species and biotypes which very soon developed hard, thorny or distasteful leaves and twigs, but also those with highest vegetative regeneration capacities to overcome defoliation stresses or both fire and grazing. We may also assume that this re-coding of information from fire and grazing has preadapted them to further defoliation catastrophes from cutting and coppicing.

As outstanding examples of successful evolutionary strategies for maximization of over-all survival three sclerophyllous small trees can be used – the West Mediterranean Kermes oak = *Quercus coccifera* and its East Mediterranean vicariad = *Q. calliprinos*, and *Pistacia lentiscus*. The first, dominating burned garigue on an eroded rendzina near Montpellier, South France, produced 374 g/m² above ground biomass in the first year after the fire and 874 g/m² in the sixth year (Specht, 1969). The second, in a mixed garigue on dark rendzina in the Western Galilee, in Israel, regained its pre-burn height of 2,5 meter in the second summer and gained, together with other obligatory resprouters 60% of the ground cover in the second summer and 80% in the third summer after the burn (Naveh, 1960, 1973b). In the East Mediterranean zone, *Pistacia lentiscus* is the most tenacious evergreen shrub, resistant to drought, fire, grazing, and cutting, and remaining as the last wood survivor in degraded maquis and woodlands (Naveh & Dan, 1973). By resprouting vigorously, not only from extensive deep and laterally branched and rock penetrating roots, but also by rooting from rapidly spreading, prostrate and very leafy twigs, it very soon forms a dense and compact shrub canopy with high soil and water conserving features. (Figure 1). Its small, sclerophyllous leaves are highly resinous and very soon become distasteful (Naveh, 1960). In this way its potentials are maximized – moisture and nutrient extraction, energy and water trapping and photosynthetic activity, carbohydrate reserve storage, hydro-ecological efficiency, and post-defoliation recuperative powers.

In most facultative root resprouters, positive feedback of fire-stimulated vegetative and reproductive regeneration is coupled with morphological and physiological plasticity and aggressiveness in invasion and establishment of newly-opened, fire-denuded but mineral-rich habitats. Thus fire has favoured not only the tenacious maqui dominants, but also the evolution of opportunistic and potentially fast-growing subordinate species – dwarfshrubs, hemicryptophytes, perennial grasses, geophytes, and therophytes – that remain for years as suppressed relics near tree and shrub edges, rock outcrops and shallow soil patches, until their next fire-induced upsurge (Naveh, 1960, 1973a).

All woody facultative root resprouters are low unpalatable thorny or aromatic chamaephytes, like *Sarcopoterium spinosum*, *Cistus*, *Salvia* and *Erica* spp. and many others. Under heavy postfire grazing pressure they have best changes of survival and can create monotonous and



Fig. 1. Fire-, drought- and grazing tolerant Mediterranean plant community in the Western Galilee, Israel. In the background *Ceratonia siliqua* and *Quercus calliprinos* trees, in the center *Pistacia lentiscus* shrubs and in the front *Sarcopoterium spinosum* dwarfshrubs with tall flowerstalks of *Hordeum bulbosum* and flowering annual plants.

even-aged batha stands (LeHouerou, 1973). Amongst the most successful herbaceous fire followers and ecotone colonizers in not too heavily grazed maquis and garigue are xeromorphic, shade tolerant and mostly calciphil perennial bunchgrasses. Thus *Brachypodium ramosum* has shown the highest 'post-fire regeneration index' (Trabaud, 1973) and dominates frequently burned, moderately grazed garigue in South France (LeHouerou, 1973). Its East Mediterranean, ecological counterpart is *Oryzopsis miliacea*, which excelled in vegetative and reproductive regeneration and forage production after maqui and garigue burns in Israel (Naveh, 1960). Increased germination in this grass, after heating the seeds up to 90 °C, has been shown by Meiri (1959). It has also been widely used as a reseeded pasture grass-'Smilo'-after chaparral burn in California and has naturalized itself well in these conditions as a prolific fire follower (Love & Jones, 1952). These grasses have adapted themselves to the fluctuating radiation, moisture and nutrient regimes of edge habitats by a remarkable hydro- and pheno-ecological plasticity in growth rhythm and habit and in timing of regeneration from basal buds, as well as by a unique shrub-like 'whole shoot regeneration' capacity from intercalary meristem and axillary buds along the charred or dormant culm (Naveh, 1960).

In Tabor oak = *Quercus ithaburensis*, the main tree of sub-mediterranean open woodlands with a dense, summer-dry herbaceous understorey, the thick, fire-resistant bark is an efficient defence mechanism for fire survival, because here the fire temperatures are not so high as in dense, woody maqui stands. At the same time, however, Tabor oak is an efficient obligatory root-resprouter. The annual plants that dominate the herbaceous canopy of these woodlands, as well as those of open Mediterranean and semi-arid Steppe grasslands which are even more fire-prone and may burn year after year if not grazed too heavily (Naveh, 1973a), are most successful fire-followers. Naturally, in these therophytes responses to fire, as well as to many other stress factors, are centred around reproductive and growth behaviour. Thus early and prolific seed production, early seed shedding, and distribution by efficient dispersal mechanisms are characteristic for most therophytes (Zohary, 1962). Seed dormancy and polymorphism – found especially in legumes – also increase the changes for at least part of the seed crop to escape fire and environmental rigor. Of special value in this respect is *trypanocarpus* – the capacity of disseminules of annual and perennial grasses and some other abundant species like *Erodium*, to 'drill' themselves into the soil with the aid of hygroscopic

awns, callous tips, and other torsion mechanisms. But there are apparently also specific fire feedback responses related directly to the high fire temperatures, such as heat tolerance. This has been proved for various successful Mediterranean grass invaders of California, such as *Bromus mollis* and *B. rigidus*, *Elymus caput-medusa*, and others (Sampson, 1944; McKell et al., 1962). In the Tabor-Oak woodland in Israel, the dominant *Avena sterilis* not only retained viability after heating the seeds for half an hour up to 125 °C but even gave increased germination after temperatures up to 105 °C. After a hot grass fire when surface temperatures reached 350 °C for several seconds and 51 °C in 1 cm soil depth, *Avena* seeds with charred awn tips which had already buried their caryopsis vertically in the upper soil surface, germinated in the following winter. In our recent burning studies (A. Naveh & Z. Naveh, 1973 unpub.), 20% of more or less charred *Avena sterilis* seedlings protected by a dense grass mulch layer emerged.

Stipa tortilis, the dominant annual grass of the semi-arid and fire-prone steppe grasslands of the Upper Jordan Valley, is one of the most rapid seed buriers because of its small seeds. In the last dry winter only those seeds which were covered with 1–2 cm soil emerged both in the burned and unburned plots (Z. Naveh, S. Shalom & Z. Zaith, 1973 unpub.). These buried seeds could not only escape the high surface fire temperatures, but also germinate under more favourable moisture and temperature regimes and probably also escape grazing and seed-collecting animals. In these grasslands, perennial grasses and geophytes also demonstrated most successful strategies for maximization of over-all drought, fire, and grazing survival potentials. Thus *Hordeum bulbosum* and *Poa bulbosum* combine all the above described reproductive adaptations of the annual grasses with vegetative post-fire resprouting from underground bulbs. Geophytes like *Asphodelus microcarpus*, which are completely unpalatable, resist even the greatest fire and grazing pressure and dominate the most degraded stages of these grasslands and bathas (Walter, 1968; Naveh & Dan, 1971).

Of special interest are prolific perennial grass fire-followers of tropical origin like *Hypperhenia hirta*, abundant on rocky and sunny slopes in open maqui and batha, as well as in frequently burned mediterranean and semi-arid grasslands. The capacity of these grasses to regenerate from the intercalary meristems of charred culms and basal buds, even in the middle of the summer in arid habitats (Naveh, 1960, 1973a), might be a relic of their rhythm of growth and post-fire regeneration in tropical savannas.

Discussion and conclusions

Although natural fires are at present of minor importance in the Mediterranean Region, this was not the case in earlier times when lightning and volcanic eruptions could have caused sweeping fires over large areas. As Axelrod (1958) has shown in California, fires also played an important role together with drought in post-Glacial evolution of Mediterranean plants, communities and ecosystems. But in addition they apparently also served as an environmental stimulant for cultural evolution.

The paleontological records in this region are still too fragmentary to provide a basis for all our assumptions. But the palynological evidences of the abundance of fire-tolerant sclerophyll and fire-dependent conifer trees 60–80,000 years ago, and of the presence of wood ash in the caves of the Palestinian Neanderthal man 60–40,000 years ago give strong support to them. Up to now only in north-west Europe, under much more favourable conditions for paleo-ecological research, have charcoal horizons given proof of large-scale and apparently deliberate burning of pine forests by Upper Paleolithic hunters (Butzer, 1972). In this region too, because of the preoccupation with climatically determined organic and cultural evolution, too little attention has been paid to the impact of primitive man on his habitat by burning and hunting. In the Mediterranean region the cold winters and dry summers of the Upper Pleistocene and early Holocene apparently created conditions which were no less favourable for the use of fire for heating and creating forest thicket openings than in Europe. Here also the collection of big, parched grain kernels after fire may have been a first step toward dry-land farming and grain domestication during the late Mesolithic period, more than 10,000 years ago. From early historical times onward, the wide occurrence of fire on Mediterranean wildlands is well documented in the Bible and later sources. Most of the earlier causes, such as burning of forest and shrubland for pasture improvement apparently prevailed throughout history until the present.

We may, therefore, accept the role of fire as a long-term and important stress factor and selective force in Mediterranean ecosystems. Fire operated first as an independent climatical and geological external stress, and later as part of the multivariate anthropogenic biofunction, in which man became the dominant controlling ecosystem factor (Naveh & Dan, 1971). As Mooney & Dunn (1970) have shown so clearly, fire has also been a selective force in other mediterranean biomes and is closely interwoven with other environmental stress factors that brought about

convergence in form and function. A more thorough, comparative study of the effect of fire on structure and function of mediterranean-type climate plants and communities would be desirable in order to define more closely this convergence in respect to fire behaviour.

From our study in the Mediterranean Region it is apparent that fire response is closely linked with the ecological status of the plant within the community and the coenocline, its ecological requirements for germination, ecesis and competition. As Anderson (1956) has shown in California, fire-induced ecotones and disturbed shrub openings can provide ideal opportunities for further speciation, hybridisation and genotype recombination. They created not only favourable conditions for light-demanding dwarfshrubs and herbs but also facilitated the invasion of more xeric elements from adjacent, drier regions, including weedy and aggressive annual grasses, amongst these the progenitors of our cereal grains. It is of interest to note that the most successful invaders of California foothills from the Mediterranean Region are some of these annual grass fire-followers, such as *Bromus*, *Avena* and also *Erodium*, which were also pre-adapted to pastoral and agricultural disturbances, and were introduced to California by the Spaniards (Naveh, 1967).

The evolution of natural plant communities has recently been discussed by Whittaker & Woodwell (1972). Many centuries of severe human and livestock pressure, resulting in indiscriminate burning, cutting and grazing on non-arable wildlands and in bushclearing, terracing, cultivating, and later-on abandoning and neglecting of arable portions (Naveh & Dan, 1971), have induced so many retrogressive stages from the pristine climax and have distorted this evolutionary process so much, that its reconstruction has become very difficult. This has caused some quasi-stable vegetation stages to be confused with climax communities, rather than regarded as vegetation types that prevail under specific combinations of environmental conditions and particular regimes of human disturbance or protection (Naveh, 1971). Any attempt at reconstruction of the true climax communities should take into account the fact that fire has been an integral part of their evolutionary process, affecting their composition, structure, productivity, and nutrient circulation from their earliest stages of evolution.

Whittaker & Woodwell's (1972) suggestion that alternative evolutionary responses to the effects of fire as influenced by climate, soil, topography and fire frequency have been responsible for the creation of grasslands, shrublands, and woodlands in semi-arid climates seems

also to be relevant for this region. In the drier regions, the restricted winter rainfall and long summer drought, coupled with great fire hazard, has favoured the domination of short-seasoned, drought and fire avoiding therophytes as well as perennial grasses, hemicryptophytes and geophytes with similar growth rhythms and ecological requirements. Higher rainfall and better soil-and-rock moisture regimes, less frequent but more intensive fires, have probably favoured the dominance of drought tolerant, sclerophyll obligatory resprouting phanerophytes but have also opened niches for drought and fire avoiding facultative resprouting dwarfshrubs and herbaceous understorey. Somewhere along this moisture and fire ecocline, the dwarfshrub-dominated batha communities can be found. It should also be assumed that in these ecosystems before the effects of many, the grazing pressure of herbivores, without being destructive, was sufficiently severe to act as an additional selective and evolutionary force through adaptive feedback responses. As stated by Whittaker (1970) it may have induced – amongst other effects – the development of secondary chemical substances as biochemical defences of plants against grazing. At the same time, some of these secondary chemical substances, such as etheric oils, may have increased the inflammability of these woody plants under suitable meteorological conditions. They may also have caused the accumulation of allelopathic, germination-inhibiting agents in the litter and soil, as indicated by reseeded trials in the litter and duff after removal of the dense maqui and garigue canopy (Naveh, 1960). These ‘kolines’ are apparently destroyed by the high fire temperatures that convert the litter and upper humus layer into a favourable seedbed.

Thus we can reach the conclusion that fire has contributed not only to biological diversity of genotypes, but also to that of Mediterranean communities, their composition, structure, and niche differentiation. This is also true for grazing. Both, therefore, can no longer be regarded as extrinsic ‘disturbance’ factors of recent origin, but are integral parts of Mediterranean ecosystems and their evolution; and they should be studied as such.

Summary

Fire has played a decisive role in Post-Glacial biological and cultural evolution in the Mediterranean Region. Its evolutionary impact on plants has been manifested by feedback responses, in which the fire and its after-effects selected plants for physiological and other mechanisms that

enable direct fire tolerance or permit avoidance followed by vegetative and reproductive regeneration.

The dominant, sclerophyll, drought-tolerant phanerophytes of the maqui are obligatory rootsprouters, whereas the subordinate, drought-evading chamaephytes, as well as herbaceous perennials, are both vegetative and reproductive regenerators and are well adapted to new, fire-denuded habitats. Annual and perennial grass fire-followers are also able to escape high surface fire temperatures with the aid of torsion devices on seeds. Evolutionary strategies to overcome fire are closely interwoven with those against other environmental stresses such as drought and grazing. These combinations of stresses have brought about convergence in plant form and function in mediterranean climates.

Fire has thus been important in the evolution of more xeric grasslands and woodlands and more mesic maqui and shrubland communities. Contrary to the present view of fire as simply destructive, both fire and grazing have favored genetical as well as ecological diversity. They should be studied as integral components of Mediterranean ecosystems and their evolution.

Résumé*

Il est admis que le feu a joué un rôle décisif dans l'évolution biologique et culturelle de l'époque postglaciaire dans la région méditerranéenne. Son impact sur l'évolution des plantes s'est manifesté par des réponses de ‘rétroaction’ (feedback). Dans celles-ci, les effets de l'élément feu et de ses répercussions ont effectué une sélection des plantes pour certaines activités physiologiques et autres mécanismes, ce qui entraîne une tolérance directe au feu ou une protection et une régénération par voie végétative et reproductrice.

Les phanérophytes dominants du maquis, sclérophylles, tolérants à la sécheresse, présentent obligatoirement des rejets de souche, alors que les chaméphytes dominés fuyant la sécheresse aussi bien que les plantes herbacées vivaces se multiplient à la fois par voie végétative et reproductrice, et sont bien adaptés aux nouvelles habitats dénudés par les feux. Les herbes annuelles et vivaces qui suivent le passage des feux sont aussi capables d'échapper aux températures élevées des feux grâce à des mécanismes de torsion, ou des graines. Les tendances évolutives pour surmonter l'effet du feu sont étroitement liées à celles

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d'autres 'contraintes' (stresses) de l'environnement comme la sécheresse et la pression du pâturage. Certaines combinaisons des contraintes ont entraîné une convergence de forme et de fonction.

Le feu a donc joué un rôle important dans l'évolution des pelouses plus xériques, des forêts, des maquis plus mésiques et des communautés d'arbustes. Contrairement au point de vue actuel sur le rôle destructeur du brûlage, le feu et le pâturage ont favorisé la diversité génétique aussi bien qu'écologique. Ils devraient être étudiés comme des composantes intégrantes des écosystèmes de Méditerranée et de leur évolution.

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