PRODUCERS AND THE FIRE CYCLE IN A PHRYGANIC ECOSYSTEM

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1. INTRODUCTION

The severe summer drought combined with high temperatures leads to a high frequency of fires in mediterranean-type ecosystems. The relation of this climatic type with fire has been long ago noted (Griesebach, 1872). Shantz (1947) refers to the mediterranean-type ecosystems of California as "fire-type" or "fire-climax". The numerous adaptations of plants dominating mediterranean-type ecosystems indicate that fire has been a strong selective force and that these systems can be considered as "fire-induced" or "fire-adapted" (Jepson, 1930; Naveh, 1973; Biswell, 1974).

According to Mutch (1970) ecosystems subject to frequent fires over evolutionary time have developed characteristics, which make them extremely flammable. This point of view is reinforced by the fact that these ecosystems have developed adaptations which result in their surviving fire and further periodic fires of about every 15 years or so, appear necessary to maintain their maximum diversity and productivity' without frequent fires, fuels would accumulate in high quantities, and then fires would lead to large changes in ecosystem structure (Biswell, 1974).

According to Naveh (1975) adaptations to fire can be considered as an homeostatic feedback control. Positive feedback responses are those which result in overcoming the after-effects of fire by increased physiological activity. This is chiefly expressed by vegetative resprouting, fire-stimulated seed germination and post-fire flower and seed production. Negative feedback responses can be regarded as all those mechanisms which enable the avoidance of the fire hazard, either by direct tolerance of seeds or plant organs, or by their reduced physiological activity during critical fire periods.

Le Houerou (1973) reviewing the effect of fire on mediterranean vegetation types, classified them as either active or passive pyrophytes according to their positive or negative feedback responses. Phrygana species (plants of the arid mediterranean-climate regions of Greece) seem to be active pyrophytes. They have developed, in the course of evolution, several features that make them very flammable. Their leaves are small, hairy and have thin cuticles. They have slender shoots with fine loosely arranged twigs, while most of the dead shoots remain on the mature plants. On the other hand, the dead leaves which fall at the base of the plants during the summer period provide a substrate for quick spreading fires. Two major types of plant regeneration can be distinguished: obligatory resprouters (mainly maquis), which regenerate vegetatively from undisturbed underground buds and facultative resprouters (mainly phrygana) which in addition can regenerate by seeds. Vegetative regeneration in obligate resprouters begins almost immediately after fire, but is delayed in facultative ones until the first rains. This difference has been attributed to the different depths reached by the root systems of the two plant groups (Naveh, 1975).

Fires are very frequent in the phrygana communities. This study reports on part of multifaceted eco-physiological study designed to provide information about Greek phryganic ecosystems and especially fire's effect on them.

2. SITE DESCRIPTION

A phryganic ecosystem located at Mount Hymettus, near Athens University Campus was studied. It was burnt accidentally in July 1976 (Fig. 1).

3. METHODS

Throughout a two years period, burnt and control sites were frequent surveyed. Seedlings of woody plants dominating the ecosystem were counted in ten $1m^2$ plots randomly selected in the burnt site.

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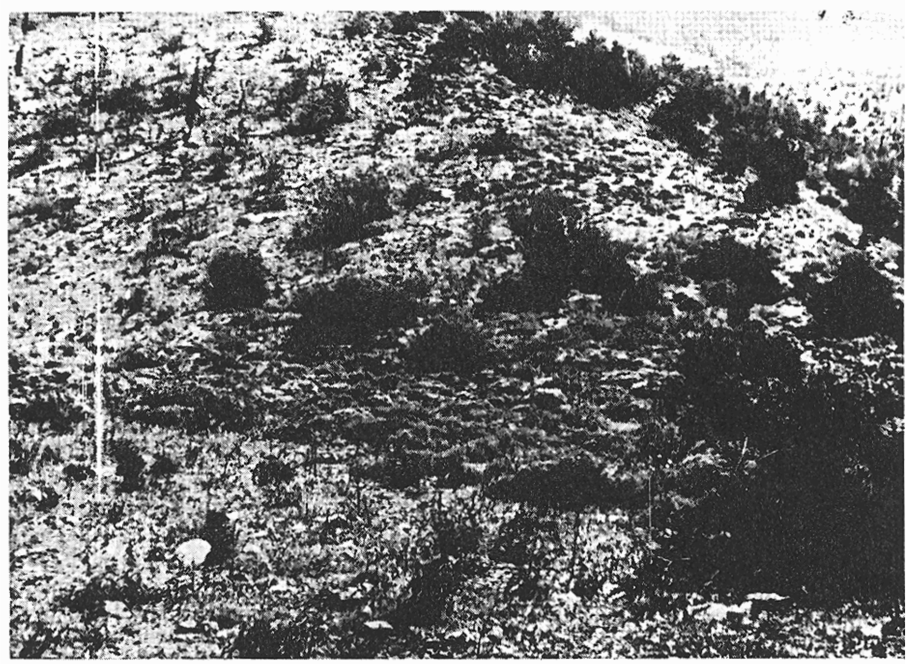

FIGURE 1. Aspect of the burned and unburned site

At the same study site the total aboveground vegetation was cropped monthly by means of 10 randomly-spaced 1m line intercepts. Ground litter (all dead organic material on the ground down to the surface of the mineral soil) was also collected from the same plots. The samples were oven-dried and weighed. From these data total and relative percentage biomass as well as litter present were calculated. Measurements were also taken of the heights of the dominant woody plants. In addition their leaf size and chlorophyll content were determined.

4. RESULTS AND DISCUSSION

Seed germination after fire in the phryganic ecosystem is very characteristic in the case of Cistus spp. (Arianoutsou-Faraggitaki, Margaris in press). Under normal conditions, germination occuring in autumn is about 10 to 20 seedlings per square meter, while after fire it rises dramatically to 300-400 seedlings per square meter (Fig. 2). Similar data are noted by Papanastasis (1977) for Cistus salvifolius and Cistus monspeliensis, as well as for other regions (Le Houerou, 1973; Naveh, 1974). Cistus species have been considered by all these investigators as obligatory seed regenerators (Naveh, 1975; Papanastasis, 1977; Arianoutsou-Faraggitaki, Margaris, in press).

Most of the dominant phryganic species are facultative resprouters. Forty-five days after fire the burned plants of Sarcopoterium spinosum produce new leaves from their root crowns. One month later Euphorbia acanthothamnos and Phlomis fruticosa develop resprouts in the same way. The new leaves of these resprouts are soft, large and with intense green colour (Fig 3).

Even though the resprouting begins in a period in which all the leaves of the unburnt plants are small (summer leaves, Margaris, Papadogianni, 1978) the new leaves of the resprouted species are larger. This difference in leaf size exists during almost all the first post-fire year (Fig. 4).

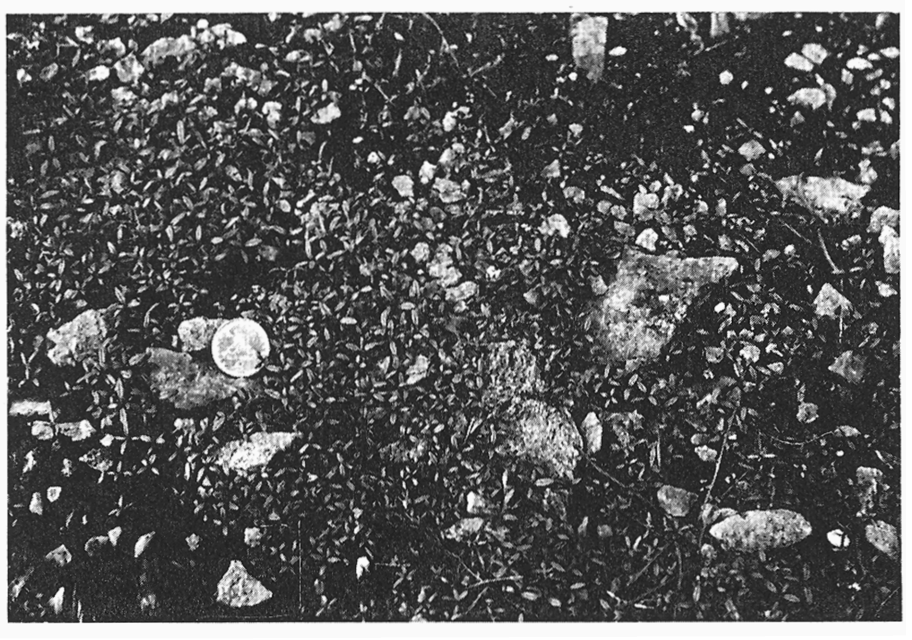

FIGURE 2. Cistus spp seedlings in the burned site

FIGURE 3. Comparison between Phlomis fruticosa resprouted and unburned plants

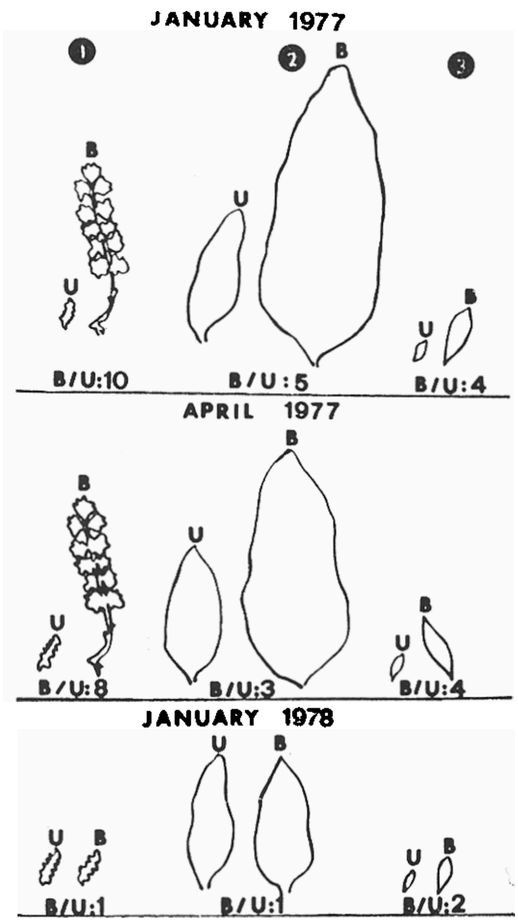

FIGURE 4. Comparison between resprouted and unburnt plant leaf sizes in S. spinosum, P. fruticosa and E. acanthothamnos

In a period of nine months after the fire the resprouts reach a level of maturity so that they have gradually developed the characteristics of seasonal dimorphism (new, smaller leaves, spiny formations, woody shoots) and are thus adapted for the unfavourable drought conditions of the summer (Fig. 5).

During the first post-fire year, E. acanthothamnos and S. spinosum form flowers and fruits, while P. fruticosa flourishes the second post-fire year, a fact that in normal conditions does not happen until the forth or fifth year (Fig. 6)

Phenological differences between resprouted and unburnt plants during the second post-fire year are not great. The leaves of the resprouted are still larger, but smaller than those of the previous year. The resprouting woody species of P. fruticosa, E. acanthothamnos and S. spinosum attain almost their original height by the end of the study period (Fig. 7).

Naveh (1973) indicates that S. spinosum reaches 40 cm high within two years after fire, while Papanastasis (1977) stated that phrygana sprouts, in general, attain one third of their original height by the end of the first growing season. Parsons (1976) found that Adenostoma fasciculatum (chamise chaparral of California) was about 40-60 cm tall 4 years after fire. Papanastasis (1977) notes that, in general, phrygana plants produce seeds by the second season after fire.

Unfortunately, there are no data available regarding plant phenology after fire in mediterranean-type ecosystems. Data on the midwestern American grasslands (Kucera, Ehrenreich, 1962; Hadley, Kieckhefer, 1960) refers to a significant acceleration in the life cycle of the dominant species, which was attributed to such factors as: 1) litter removal, 2) earlier growth of species as a result of the higher soil temperature after burning, 3) greater quantities of available nutrients and 4) greater radiation.

Probably, the same processes would also operate in the phryganic ecosystem. As mentioned above, mediterranean-type ecosystems are fire-induced and fire-adapted. So, they possess an endogenous rhythm which determines their numerous adaptations but with a general feature: the quick response to environmental conditions, especially fire. Otherwise, all those characteristics would have ceased acting as adaptations. The new leaves of the resprouting plants are not only larger, but richer in chlorophyll than normal. No doubt, photosynthesis is also significantly increased (Table 1).

The herbaceous vegetation which usually grows among the woody phryganic species are also adapted to recurrent fires. Many workers have noted the scarcity of herbs in mature mediterranean-type ecosystems (Sampson, 1944; Went et al., 1952; Horton, Kraebel, 1955; McPherson, Muller, 1967, 1969; Chou, Muller,

FIGURE 5. Seasonal dimorphism on P. fruticosa leaves (summer and winter leaves)

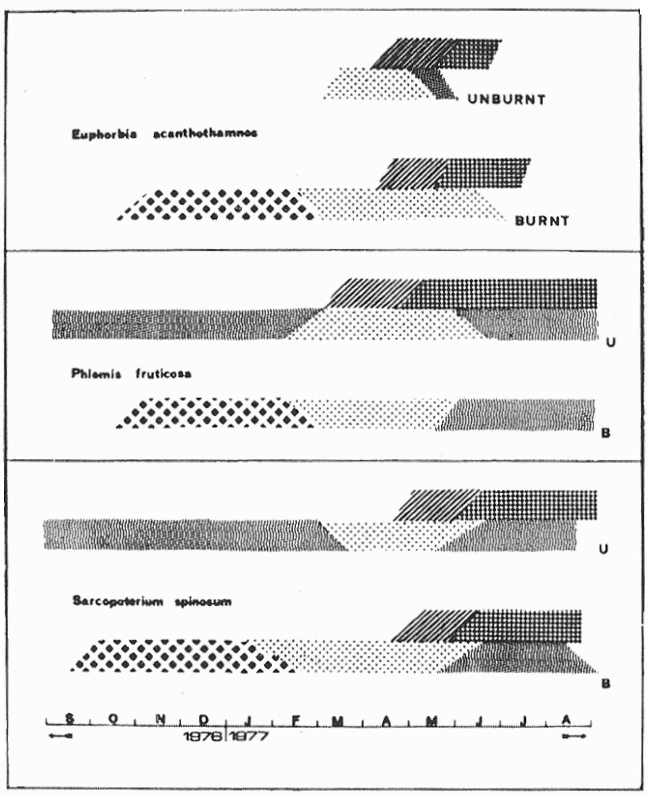

FIGURE 6. Phenological stages of the resprouting species during the first post-fire year

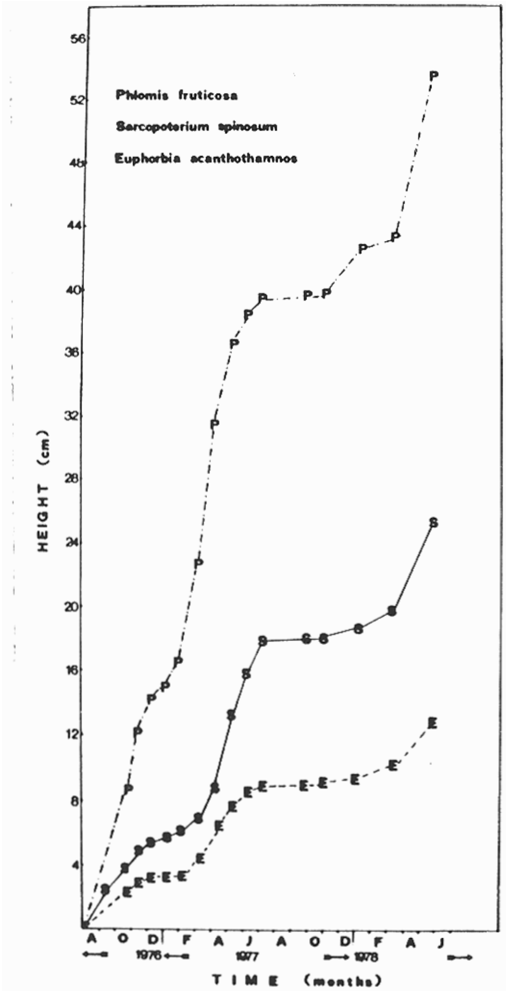

FIGURE 7. Growth in height of the resprouting species, during the study period

TABLE 1. Total chlorophyll content

	Total chlorophyll ($mg.g^{-1}$ leaf dry weight)		
	Phlomis fruticosa	Sarcopoterium spinosum	Euphorbia acanthothamnos
JANUARY 1977			
Unburnt plants	2.0	2.3	4.7
Burnt plants	3.5	5.7	5.4
Increase %	70	150	17
APRIL 1977			
Unburnt plants	2.4	2.2	4.9
Burnt plants	4.6	5.0	5.2
Increase %	90	128	7
JANUARY 1978			
Unburnt plants	4.0	3.6	6.3
Burnt plants	3.2	4.4	8.6
Increase %	-18	17	36

1972; Christensen, Muller, 1975). After fire, however, such areas are often carpeted with annual and perennial herbaceous species rarely seen in the undisturbed sites. The seeds of many of these herb species lie dormant in the soil beneath the shrubs from one fire to the next. The numbers of seedlings are highest in the first and second years following fire (Naveh, 1974). Germination is restricted and the herb population gradually diminishes as the shrub cover increase. The temporal dominance of herbs and their subsequent decline in our study site is shown in Figure 8.

In the phryganic ecosystem, typical examples of post-fire herbs are Andropogon hirtus, Asphodelus microcarpus, many species of Cyclamen, Allium, Ornithogallum, Arisarum vulgare, Crocus nudifolius and the Papilionaceae, especially Trifolium spp., Lathyrus aphaca, Medicago spp., Lotus spp., Vicia spp., etc. The presence of the latter has been correlated with nitrogen replenishment after fire in the site, since as much as 96% of site nitrogen can be lost in the smoke of a fire (Arianoutsou-Faraggitaki, Margaris, in press). Probably the abundance of herbs in burnt areas may be related to one or more of the following causes: 1) removal of the shrub cover and litter, 2) inactivation of phytotoxic materials produced by the shrubs, 3) more available nutrients in the soil, 4) decreased competition with the shrubs, for a short at least period (Sweeney, 1967; Muller et al., 1968 etc).

On April 1975 the relative percentages of P. fruticosa, E. acanthothamnos, S. spinosum and Cistus spp., in the total aboveground biomass were 33%, 24%, 13% and 8% respectively, while that of the other woody plants and herbs (Helianthemum sp., Thymus capitatus, Asparagus aphyllous) was 22% (Margaris, 1976).

After fire and in the same growth season (April 1977) the situation was quite different: the relative percentages of P. fruticosa, E. acanthothamnos, S. spinosum and Cistus spp., were 5%, 3%, 3% and 5% respec-

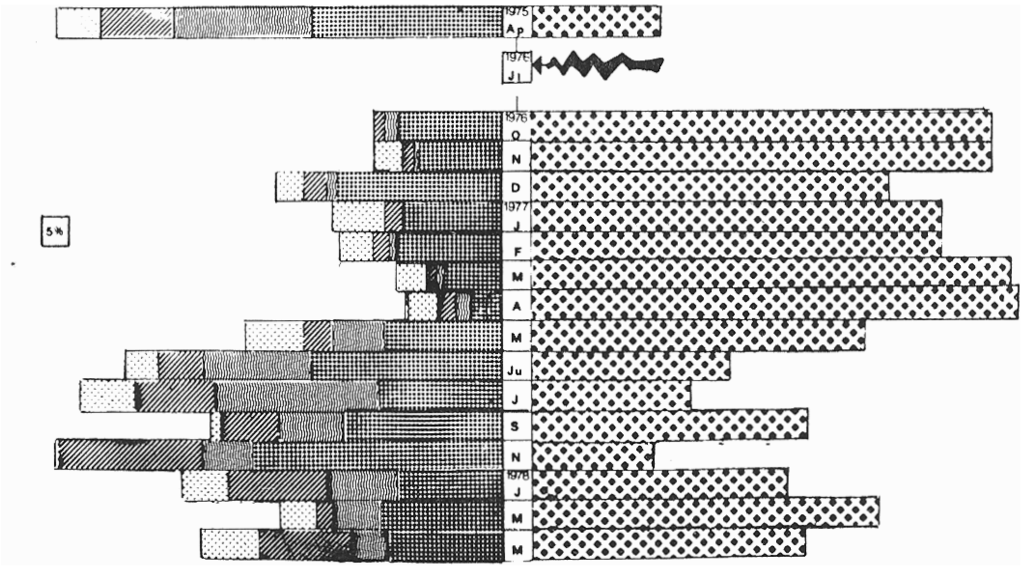

FIGURE 8. Relative biomass percentages

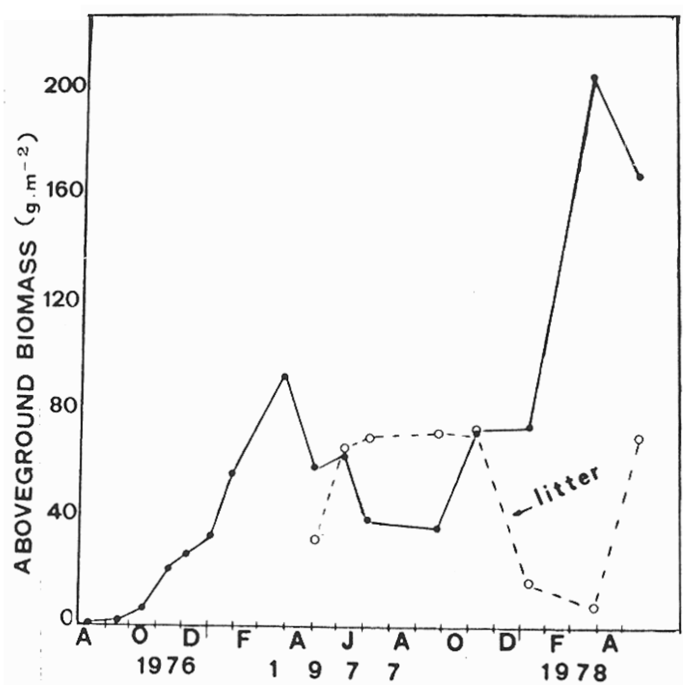

FIGURE 9. Total aboveground plant biomass measured during the study period.

tively, while for all the rest (mainly herbs) together, was 83%. It is therefore, quite obvious how the growth of the herbaceous vegetation increased. This situation lasts for the autumn and winter months till early spring. By the end of spring and the beginning of the summer the herbs dry out. The following growing season the situation is not the same but is still different from the prefire one. The secondary succession is not a series of plant substitutions but rather a gradual increase in dominance of perennial species which were found in the stand before fire. This prosess has been formed autosuccession (Hanes, 1971).

The changes in total plant biomass with time are plotted in Figure 9. Biomass production on April 1977 was 8% of the prefire production (1,111 $g.m^{-2}$, Margaris, 1976) while the following year (April, 1978) it was 19%, which means that an increase of 55% in biomass production took place. At the end of the study period the total biomass was about 200 $g.m^{-2}$.

Papanastasis (1976) found that standing biomass in a Phlomis fruticosa community was 3,000 $kg.ha^{-1}$; on the other hand, in S. spinosum community it was 1,200 $kg.ha^{-1}$ in the second and 2,800 $kg.ha^{-1}$ in the third year after fire.

Sampson (1944) found that at the end of the first growing period Adenostoma fasciculatum resprouts were 173.5 $g.m^{-2}$. Within 8 years it became 1,279 $g.m^{-2}$, growing at a mean rate of 110 $g.m^{-2}.year^{-1}$, recovering 40% of the original productivity. Long et al. (1967) and Specht (1969) noted that in the first 10 post-fire years of autosuccession the annual productivity of sclerophylls in France, California and W. Australia was 150$g.m^{-2}$.

Considering the above data and noting that from the first to the second year the biomass increase in the phryganic ecosystem was about 100 $g.m^{-2}$ we can assume that within 5-10 years full reconstitution would take place.

5. CONCLUSIONS

Fire, either natural or man caused, has been part of the Greek environment for thousands of years (Liakos, 1973). Phryganic ecosystems are adapted to fire and depend on them for their continued mainferance. As Papanastasis stated (1976) Phlomis fruticosa and Sarcopoterium spinosum plants would not live longer than 20-30 years unless they were burned and hence revitalized.

Our results are in agreement with those found in analogous mediterranean ecosystems of the world (Italy, Spain, Israel, Chile, Australia, S. Africa and USA): The lack of water in combination with the high summer temperatures lead to fire in the phrygana. This ecosystem type covers quickly by resprouting and/or activation of seed germination. This rapid recovery is probably in part due to the high photosynthesis rate of young leaves of resprouts.

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