

DIVERSITY AND STABILITY IN GARRIGUE ECOSYSTEMS AFTER FIRE*

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Introduction

By its frequent recurrence fire is an important factor for the dynamics of plant communities in the French mediterranean region. Up to now it was considered to create series of more and more degraded successive stages (Braun-Blanquet 1936, Kuhnholz-Lordat 1938, 1958, Kornas 1958, effect of fire was studied by Le Houerou (1974, 1977) and as due to fire action. But, the processes by which vegetation is recovering after fire were not tackled precisely: the authors only compared different associations.

Elsewhere in the Mediterranean Basin, the ecological of fire was studied by Le Houerou (1974, 1977) and Naveh (1974a), 1974b, 1975, 1977). However, they did not analyse exactly the vegetation succession in the course of time after the fire.

In California, vegetation succession after fire was intensively studied in the chaparral (Sampson 1944, Stone & Juhren 1951, Horton & Kraebel 1955, Sweeney 1956, 1967, Biswell 1963, Patric & Hanes 1964; Hanes & Jones 1967, Hanes 1971, Vogl & Schorr 1972). According to these authors, chaparral is well adapted to withstand recurring fires. Hanes (1971) mentioned 'autosuccession' of chaparral; he considered chaparral as a stable plant community for thousands of years.

The present contribution deals with the following problems: The determination of species development in burnt areas is rather unknown: some species settle after the fire, others were pre-existent and are developing considerably as soon as competition lessens by the help of fire. In fact, what is the antagonism between the species

of the communities which existed before fire and the foreign species which settle afterwards? Which will finally occupy the burnt area?

Moreover, does fire make the flora more common or richer? Do communities get more dynamical, i. e. is a secondary succession involved, or does fire lead towards a new equilibrium? Are the phenomena the same for all communities? In short, our aim is to know if fire is, or is not, a factor of diversity and stability in garrigue ecosystems.

Method, device and kind of observations

The 'direct method' (Pavillard 1935), or diachronic method, based on permanent plots was chosen to observe the vegetation recovery in a burnt area; This method allows to follow relatively small both floristic and structural changes.

Our study deals mainly with the first years following fire (10–11 yr); they are of primary importance for the establishment of vegetation.

The 47 studied plots are located in formly burnt areas in Bas-Languedoc, representing the most frequently encountered communities in this area.

- dense *Quercus ilex* coppices, where the tree cover was over 50 % three years after fire;
- open *Quercus ilex* coppices, where the tree cover was always below 50 % during the observation period
- dense *Quercus coccifera* garrigues where the cover was over 90 % three years after fire;
- open *Quercus coccifera* garrigues, where the cover was always below 90 %;
- *Pinus halepensis* woodlands;
- *Rosmarinus officinalis* garrigues

Nomenclature: P. Fournier (1966) Les quatre flores de France.

- *Brachypodium ramosum* swards
- *Brachypodium phoenicoides* swards

The observation plots were chosen with the help of the 'Service d'Incendie et de Secours du département de l'Hérault', which authorized us to examine all fire reports since 1962. Thus we could draw a map of the burnt areas in the county and date all recorded wildfires.

After a reconnaissance of the burnt areas, the study plots were selected according to the apparent homogeneity of the stands.

Each observation plot consists of a permanent 20 m. long line (Levy & Madden 1933, Long 1957, 1958, Daget & Poissonet 1971). Reference posts are cemented into the ground. Observations are done every 10 cm. Presence and number of hits per species are noted.

In addition to these observations, a floristic survey of species present in a 100 m² plot (in. e. in a 2.5 m wide strip at either side of the line) is done. Only the results dealing with these floristic lists are taken into account in this paper.

During the first five years which followed burning the observations were carried out every year in spring. Afterwards, the vegetation was observed only every two years, since the stands appeared to stabilize.

Development of floristic composition

The main problem is how the different species of a plant community establish after a fire has totally destroyed the above-ground part of the vegetation. We considered three important points:

- the development of floristic richness,
- the relative stabilization of floristic enrichment,
- the spatial changes in floristic composition.

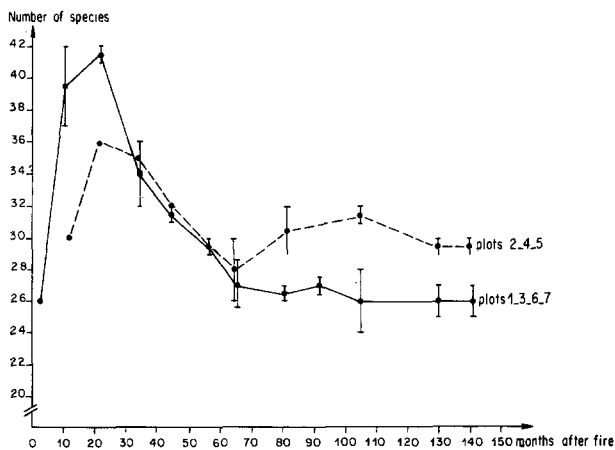


Fig. 1. Floristic richness of dense *Quercus ilex* coppices.

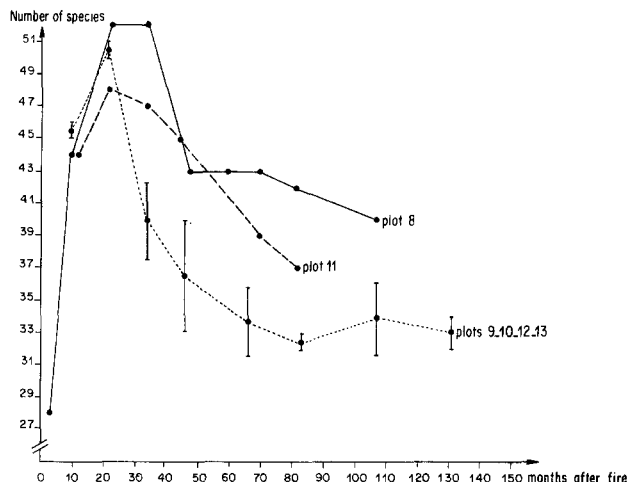


Fig. 2. Floristic richness of open *Quercus ilex* coppices.

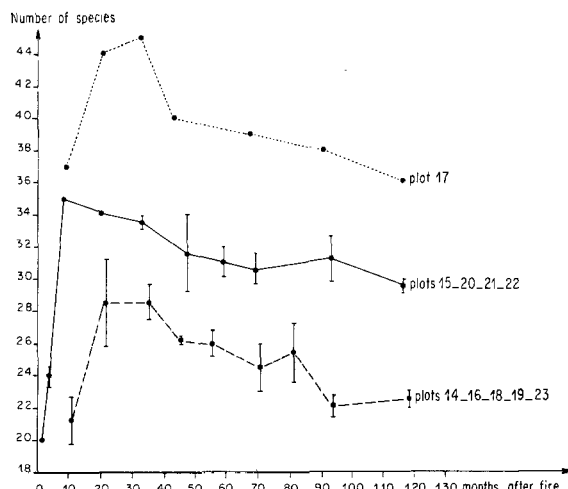


Fig. 3. Floristic richness of dense *Quercus coccifera* garrigues.

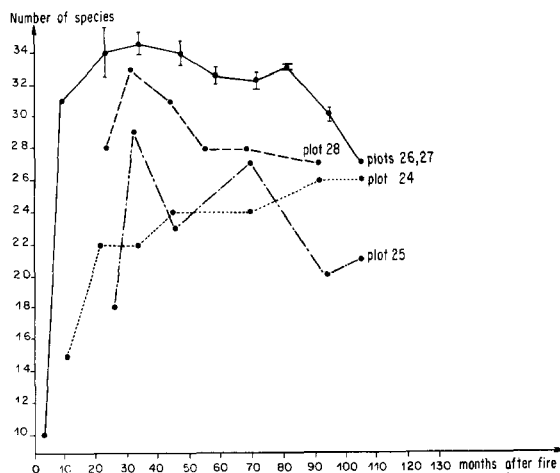


Fig. 4. Floristic richness of open *Quercus coccifera* garrigues.

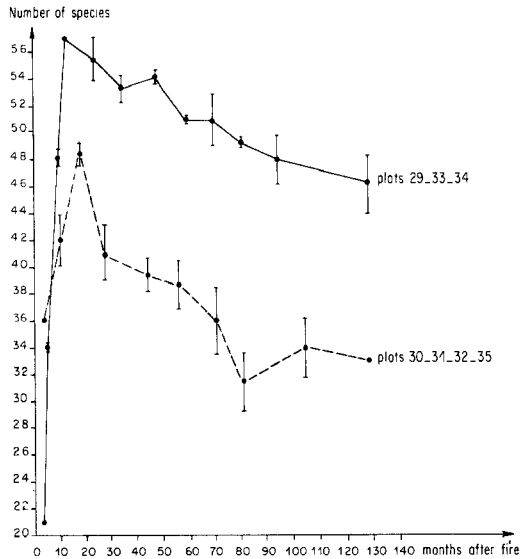


Fig. 5. Floristic richness of *Pinus halepensis* woodlands.

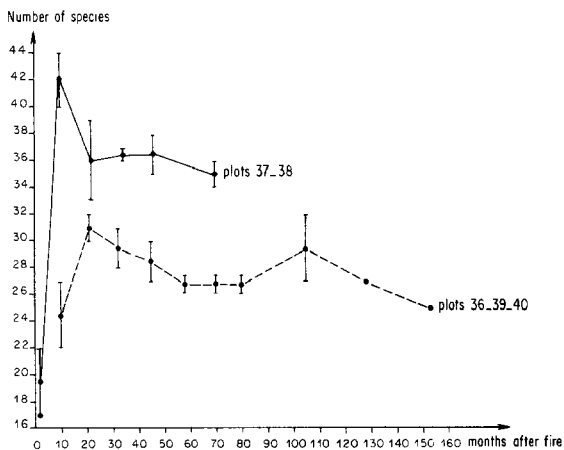


Fig. 6. Floristic richness of *Rosmarinus officinalis* garrigues.

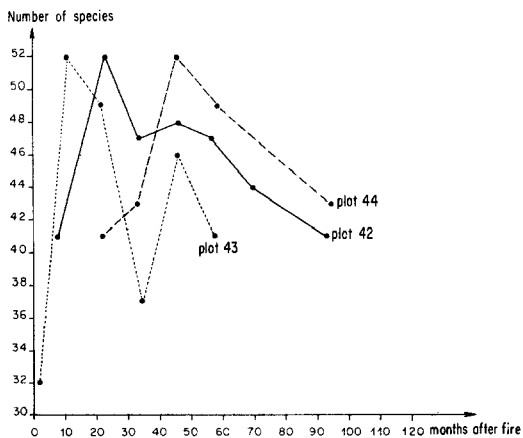


Fig. 7. Floristic richness of *Brachypodium ramosum* swards.

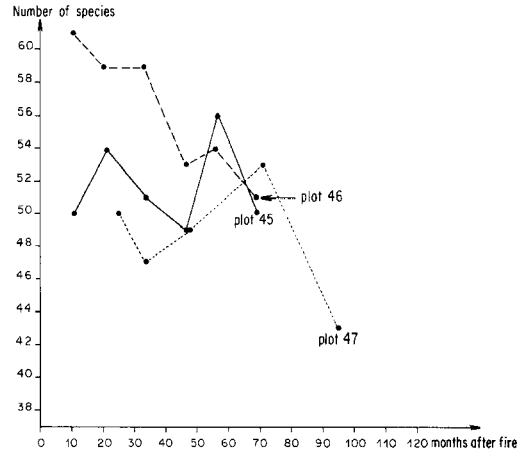


Fig. 8. Floristic richness of *Brachypodium phoenicoïdes* swards.

Development of floristic richness

The floristic richness corresponds to the number of taxa encountered in plots at each time of observation.

During the years which follow fire, the development of floristic richness follows a general model. Immediately after a fire, the ground is entirely bare; then species appear progressively. Floristic richness of the communities is low during the first twelve months. It grows gradually to reach a maximum between the 10th and 40th month. Then, the floristic richness diminishes. Finally, a relative stabilization does appear from the 60th month onwards.

The generally higher number of species during the first three years can be ascribed to the opening of the vegetation cover created by fire, to the disappearance of litter and to the richness in nutrients of the layer of the upper soil (cf. Biswell 1974, Harper 1977). Some species may come from outside the communities; they will disappear again as the stands get older.

To compare the communities, floristic richness can be measured by:

- the maximal richness at any time during the observations
- the richness at the time of the last observation (at the end of the 10th or 12th year).

Floristic richness appears to be linked with the type of community (Table 1 and Figs 1–8). So, *Brachypodium phoenicoïdes* swards do possess the highest floristic richness, followed by *Pinus halepensis* woodlands and *Brachypodium ramosum* swards; whereas *Quercus coccifera* garrigues present the lowest numbers of species.

Floristic richness is high and does not differ much from that of the more mature communities (Bharucha 1932, J. Braun-Blanquet 1935, 1936, G. Braun-Blanquet

Table 1. Comparison of floristic richness between the different studied communities.

| | Extreme values of maximal richness | Extreme values of last observation | Classification | Extreme values of floristic richness of corresponding associations | Extreme values of the similarity coefficient between our lists and those of the corresponding associations |
|--|------------------------------------|------------------------------------|----------------|--|--|
| dense <i>Quercus ilex</i> coppices | 36 and 42 | 25 and 30 | 6 | 19 and 30 J. BRAUN-BLANQUET (1936) | 0.08 and 0.47 |
| open <i>Quercus ilex</i> coppices | 48 and 54 | 32 and 40 | 4 | - | 0.07 and 0.42 |
| dense <i>Quercus coccifera</i> garrigues | 21 and 45 | 22 and 36 | 7 | 12 and 33 J. BRAUN-BLANQUET (1935) | 0.16 and 0.60 |
| open <i>Quercus coccifera</i> garrigues | 26 and 35 | 21 and 30 | 8 | - | 0.12 and 0.60 |
| <i>Pinus halepensis</i> woodlands | 42 and 57 | 32 and 51 | 2 | 26 G. BRAUN-BLANQUET (1936) | |
| <i>Rosmarinus officinalis</i> garrigues | 30 and 44 | 25 and 39 | 5 | 35 G. BRAUN-BLANQUET (1936) | |
| <i>Brachypodium ramosum</i> swards | 52 | 41 and 43 | 3 | 38 and 62 BHARUCHA (1932) | 0.10 and 0.62 |
| <i>Brachypodium phoenicoïdes</i> swards | 53 and 61 | 43 and 51 | 1 | 32 and 67 SOROCEANU (1936) | 0.04 and 0.28 |

these authors all used 100 m² plots. Jaccard's similarity coefficient was used to improve the floristic comparison (Table 1).

Limits of the model

The general model seems to be quite representative for *Quercus ilex* coppices and *Pinus halepensis* woodlands, and most of the *Quercus coccifera* and *Rosmarinus garrigues*. The development of floristic richness of *Brachypodium ramosum* or *B. phoenicoïdes* swards tends to deviate. This could be explained by the proportion of annuals and short-lived low perennials encountered in those communities (Bharucha 1932, Soroceanu 1936, Braun-Blanquet et al. 1952). As a matter of fact, when only phanerophytes and chamaephytes are considered, the development curves for floristic richness follow a very simply and broadly distributed model: the number of species increases regularly during the first three years, then tends to stabilize.

Although in all the studied communities, annuals are relatively frequent during the first two or three years, it is only in *Brachypodium ramosum* and *Brachypodium phoenicoïdes* swards that they continue to play an important part. Probably their germination is related to factors

we cannot control (amount of viable seeds in the soil type of weather, comings and goings of flocks of sheep).

Another irregularity of the model is due to the time elapsed between the fire date and the date of the first observation. It seems to be difficult to find all the species present in a rather dense vegetation at this first observation.

Stabilization of the floristic enrichment

The curves of the development of floristic richness are similar to those which are observed when an unbalanced biological system returns to a metastable state. The stabilization can be described through – the change in fugacity pattern of species, and – the emergence of the 'terminal' community (defined by the last observation)

Fugacity: proposal for an index

A species is called fugacious when it does not remain on the plot all along the period of observations. The fugacity of any species is measured by the number of observations in which it is missing. A fugacity index for the floristic ensemble of a plot should correspond to the mean value of the fugacities of the species present on the plot at a given time.

The fugacity index can be considered as a measure of floristic stability of a plot: if the index is high, the community has not reached a stable state, if it equals zero, the community is floristically stable. The fugacity index IF can be computed with the following formula:

$$IF = (F_{max} - \bar{F}_i) / F_{max}$$

Maximal frequency (F_{max}) equals the number of observations done on the same plot.

Mean frequency (\bar{F}_i) corresponds to the mean number of observations which possess the species present in the observation i .

The fugacity index can vary between 0 and $(F_{max} - 1) / F_{max}$. It is minimal if all species at one observation are present in the whole series analyzed on the same plot. The community is then said to be in floristical equilibrium. It is maximal if all species observed at observation i are only present at this time. In our study, the fugacity index is not very high; it rarely exceeds 0.25.

The fugacity index is low immediately after the fire and remains low during the first year (Figs. 9–16). The species which are the first to appear on the plot do remain thereafter. Most often, they are species which have strong stumps or rhizomes to withstand fire. Fugacity reaches its maximal value during the second and third year after a fire when floristic richness is at its maximum. Therefore, the richness of the intermediate stages proceeds clearly from species which temporarily add to the community richness and disappear later on. Most often these species are adventitious therophytes. Then the fugacity index decreases progressively to stabilize around 0.10 towards the 8th year after the fire.

Communities which present the highest fugacity during

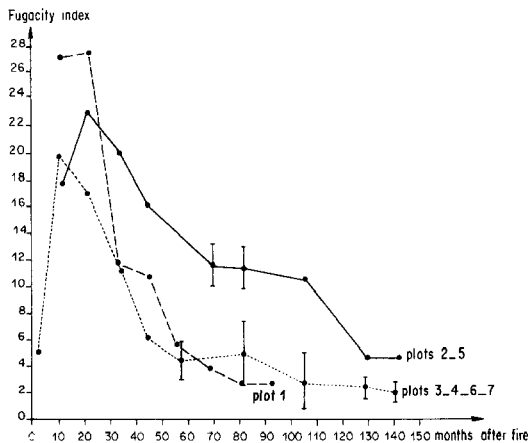


Fig. 9. Development of the fugacity index ($\times 100$): dense *Quercus ilex* coppices.

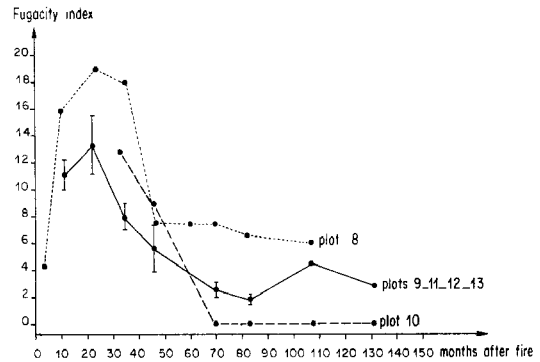


Fig. 10. Development of the fugacity index ($\times 100$): open *Quercus ilex* coppices

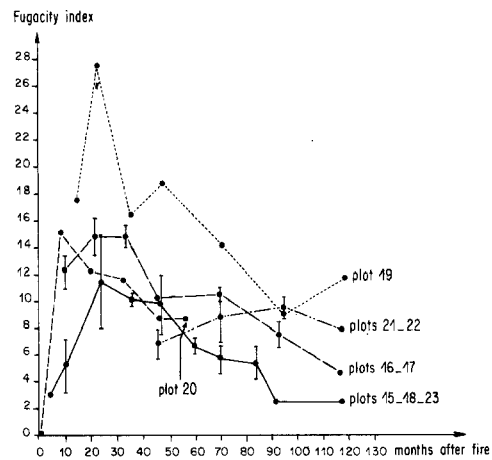


Fig. 11. Development of the fugacity index ($\times 100$): dense *Quercus coccifera* garrigues.

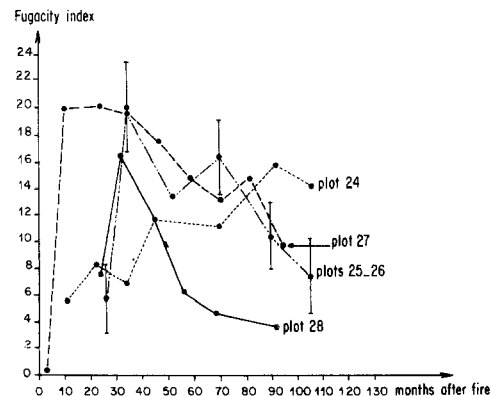


Fig. 12. Development of the fugacity index ($\times 100$): open *Quercus coccifera* garrigues.

the first three years after fire are the dense *Quercus ilex* coppices, *Pinus halepensis* woodlands and *Rosmarinus garrigues*. Whereas those which have the less fugacious species during the same period are dense or open *Quercus coccifera* garrigues and open *Quercus ilex* coppices. This is not surprising for the *Quercus coccifera* garrigues where the vegetation rapidly closes up and prevents any species outside the community to enter.

Emergence of the 'terminal' community

The emergence of the terminal community is determined by the moments the species of the community present at the last observation appeared during the total period of observation. An 'emergence index' can be calculated as the percentage of the species encountered at one observation, which are also found in the terminal community.

Most of the species which belong to the terminal community appear very quickly: one year after the fire 70 % of the plots already possess more than 75 % of the species which are still present at the time of the last observation (Fig. 17), after two years more than 80 % and in five years almost 100 %. The return towards a metastable state, is thus very quick. It follows that there is no real secondary succession, in the sense that species, or communities, do not follow each other on the same plot, after the disturbance of fire.

This phenomenon can be interpreted as an example of resilience as defined by Holling (1973) and Boesch (1974). Although for many authors the notion of resilience is not very different from that of stability, the latter one is lacking precision (Lewontin 1969, Margalef 1969, Holling 1973, Boesch 1974, Golley 1974, Goodman 1974, Orians 1974).

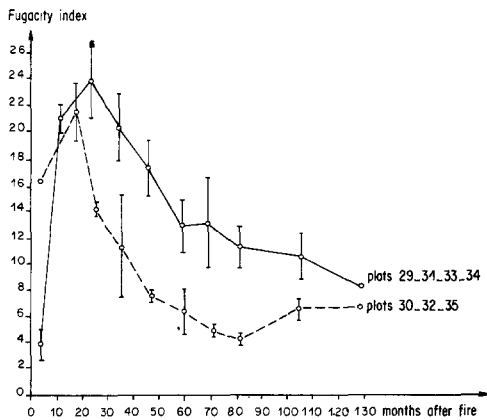


Fig. 13. Development of the fugacity index ($\times 100$): *Pinus halepensis* woodlands.

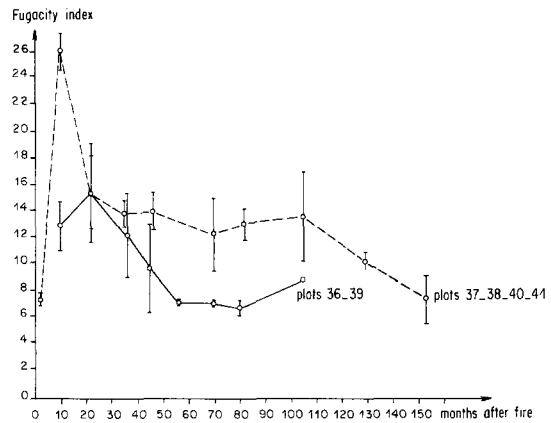


Fig. 14. Development of the fugacity index ($\times 100$): *Rosmarinus officinalis* garrigues.

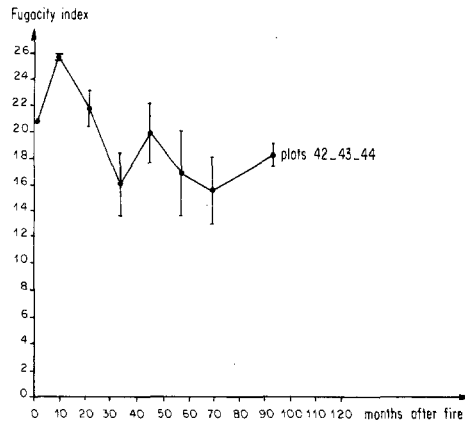


Fig. 15. Development of the fugacity index ($\times 100$): *Brachypodium ramosum* swards.

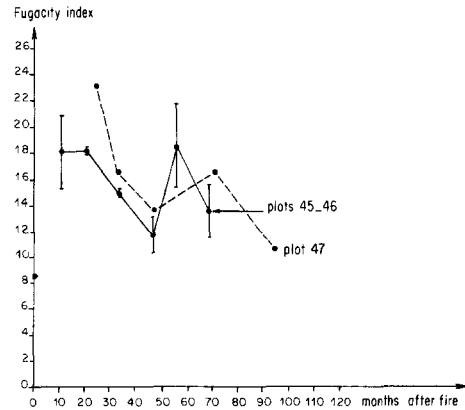


Fig. 16. Development of the fugacity index ($\times 100$): *Brachypodium phoenicoides* swards.

Spatial variation in floristic composition of communities

The return of the floristic composition towards a meta-stable state after fire is a general phenomenon in all communities studied. This state seems very similar to the one which existed before the fire, as appears from the comparison with similar associations already described in literature (Table 1).

A comparison by means of Jaccard's coefficient, between the 'terminal' lists of each of the plots and those of the corresponding associations described by Braun-Blanquet (*Cocciferetum*, 1935, *Quercetum ilicis*, 1937) allows the following conclusions

- 1) Our *Quercus coccifera* garrigues, are very similar to the *Cocciferetum* of Braun-Blanquet. This result is not surprising, because Braun-Blanquet described this association in the same area and as a post-fire stage.
- 2) Our *Quercus ilex* coppices are in general rather different from the *Quercetum ilicis*. The explanation may be:
 - We studied only the burnt areas, whereas Braun-Blanquet sampled a wide range of stands,
 - Recently burnt oak woodlands can be floristically different from older stands. After ten years some stands have evolved again towards a *Quercetum ilicis*.

Would fire lead to identical communities with a common flora on large areas? Apparently the floristic composition of each plot keeps its original character. An indirect way to verify this assertion is to compute the matrix of the Jaccard's similarity coefficients between the observations done in the different plots. The plots characterized by the same dominant species cluster together. Hence we studied the three submatrices determined by the dominance of *Quercus ilex*, *Q. coccifera*, and *Pinus halepensis* + *Rosmarinus officinalis* respectively.

A classification using the simple linkage algorithm was carried out for each of the three groups

To improve the analysis, we computed the compactness and disjunction coefficient (Dunn 1974) for each plot in comparison with the other plots. This coefficient equals the ratio of the lowest similarity value between the lists of plot and the highest similarity between any list of this plot and a list from another plot:

$$\text{diam } [A] = \min S(i, j) \quad i \text{ and } j \in A$$

$$\text{Sim } [A, B] = \max S(i, j) \quad i \in A, j \in B$$

$$\forall B \neq A$$

The compactness and disjunction coefficient follows from:

$$CD_A = \frac{\text{diam } A}{\text{Sim } A, B}$$

a value higher than 1 indicates that the group of lists of a plot is compact and well separated from the other groups.

The coefficient was computed in two ways: with, and without, consideration of the first list, when the first observation was done less than one year after a fire.

Most plots appear to form well separated entities. The coefficient of disjunction can reach values up to 2.

Mostly the lower values of the disjunction coefficient were recorded either during the first year or during the second and third year after a fire. In the first case this effect is due to the floristic poorness, and in the second case to the great number of present species. This effect would have been less pronounced if a coefficient would have been used in which species richness would be less important.

In most cases, differences in floristic composition

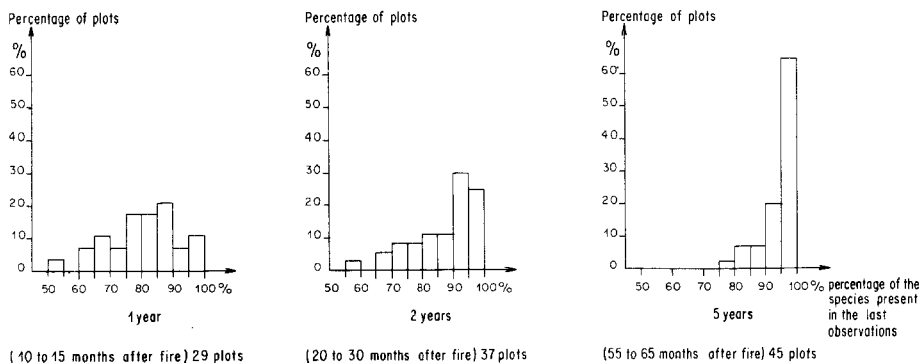


Fig. 17. Relative importance of species present in the terminal communities, measured 1,2 and 5 yr after fire.

between plots remain distinctly greater than differences between the lists of one and the same plot. Thus, fire does not appear to modify the floristic diversity of the landscape. At least for the period of observation and the local conditions in Bas-Languedoc, there is no convergence towards a common floristic composition of burnt areas.

Conclusions

The post-fire development of the floristic composition is very different from that of re-vegetation of bare soil or after abandonment of old fields (Bournerias 1959, Bazzaz 1968, 1975, Mellinger & McNaughton 1975, Guillerm 1978). The opening of the vegetation does allow adventitious species to come in, but these are rapidly eliminated after the return of community species which were present before the fire. During the period of study there is no succession in the sense of substitution of a community by another one, but only a progressive return of previously present species with the temporary superposition of some adventitious species. However, it must be noticed that we have only an inaccurate knowledge of the previous state (only based on burnt snags that remain in place). Among the species which disappeared, some could have played an important role in vegetation dynamics.

Concerning the floristic composition of plots, fire seems to be a rather superficial phenomenon. The return towards a metastable state occurs very quickly and the floristic diversity of the landscape does not seem to be affected.

The *Quercus coccifera* garrigue, a community mainly considered as pyrophytic, is no more stabilized or less diversified than the other communities.

This result can be generalized for entire phytocenoses encountered in Bas-Languedoc, which correspond to different stages of plant succession. Here, our results are similar to those obtained by American scientists about the Californian chaparral which succeeds itself (Sampson 1944, Horton & Kraebel 1955, Hanes 1971).

The rapid return towards the community existing before fire may be due to the fact that all vegetation of Bas-Languedoc has been influenced by fire for a long time; the maturity levels of communities are low, and species have developed adaptative strategies with regard to fire. Differences existing between communities arise partly from the history of the plots which support them, and

this history is clearly influenced by man's activity, i. e. the use of the land for agriculture, forestry or grazing.

Summary

Vegetation dynamics after fire was studied in six communities in Bas-Languedoc (Southern France). 47 plots were observed by means of a permanent transect for ten years.

In the first part, we describe floristic richness, species fugacity and the way by which, the 'terminal' community (as defined by the last observation) appears. The dynamics of all these communities follows a simple and general model: floristic richness reaches its maximum during the first two years after a fire, then decreases and becomes stable. Fugacity follows a similar model, whereas the mergence of the 'terminal' community is rapid: one year after fire 70% of the plots have already acquired 75% of the species of the 'terminal' community. There is no succession (in the general sense of the word), but a progressive reappearance of the species belonging to the original community.

In the second part, we study floristic similarities between our plots and corresponding associations as described in literature. It appears that after a fire the floristic diversity of the landscape remains high; while the communities rapidly reach a relative maturity.

In the study area fire seems to be a rather superficial phenomenon; it does not lead to an important modification of the community dynamics, because probably the most frequent species in Bas-Languedoc developed adaptations to withstand fire.

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