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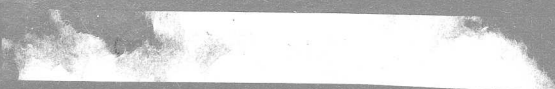
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Burkhard Frenzel (Hrsg.)

SONDERDRUCK

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Late-glacial and postglacial fluctuations of the tree limits in the Mediterranean Pyrenees: the use of pollen ratios

Guy Jalut, Didier Galop, Sandrine Aubert & Jean Marc Belet

Summary

The use of pollen ratios to estimate the fluctuations of the late-glacial and Holocene tree-limits and the timber line is discussed. An attempt is made with fossil data from some sites from the eastern part of the Pyrenees. Comparisons with the records of *Pinus* stomata indicating local occurrence of *Pinus* show a good correlation between the two complementary approaches and emphasize the value of the pollen ratio. However, in all cases, the components of the ratio have to be discussed. For reconstructing the timber line, local floristic studies are necessary so that the most appropriate pollen indicators can be chosen.

Résumé

L'intérêt du rapport entre taxons pour l'étude des variations des limites forestières et de la limite supérieure de la forêt est souligné, et une application de cette méthode à quelques sites de la moitié orientale des Pyrénées est proposée. La bonne corrélation existant entre les données provenant de la détermination des stomates de pin d'une part, et les résultats fournis par le rapport pollinique d'autre part, souligne l'intérêt de cette méthode d'étude rarement utilisée jusqu'à présent. Toutefois, le choix de chacun des termes du rapport ne peut se faire qu'avec prudence, principalement lorsqu'il s'agit d'étudier les variations de la limite supérieure de la forêt. Des études floristiques préalables sont alors nécessaires afin de déterminer quels sont les meilleurs indicateurs polliniques.

1. Introduction

Until recently, palynological studies in the Pyrenees have mostly addressed the chronology of the vegetation development, the climate history, and during the last ten years, the stages of the deglaciation. Because of these objectives, the sites were selected on account of their depth, age or position with respect to glacial features.

Late-glacial and postglacial fluctuations of the tree limits were rarely studied and generally only estimated from pollen percentages (MONTSERRAT-MARTI, 1985). Pollen concentration values were used by MONTSERRAT-MARTI (1991), and more recently the stomata of *Pinus*

have been used to indicate its local presence (REILLE, 1990, 1993; REILLE & ANDRIEU, 1993). Valuable data have also been obtained from charcoal contained in the soils that provide new information on the altitudinal range of species such as *Pinus sylvestris*, *Pinus uncinata*, *Abies alba*, *Fagus sylvatica* and *Quercus petraea*, but they unfortunately cover only the 18th, 19th and 20th centuries (BONHOTE & VERNET, 1988; DAVASSE & GALOP, 1990; BONHOTE, 1993). In no case was the pollen ratio used.

2. The pollen ratio

The use of pollen ratios for the study of tree-limits and phytogeographic boundaries was originally described by MAHER (1963) and then by COUR & DUZER (1978) respectively in California and Northern Africa and Sahara. Calculated from the percentages or the number of pollen counted for each pair of selected taxa, the pollen ratio depends only on these two taxa. In modern pollen spectra, its value expresses only the relationship between the components of the ratio. As shown by the previous authors, the changes of the ratio's value at a phytogeographic border closely correspond to changes in the vegetation cover. For this reason, the variations of the pollen ratio in fossil data can give an indication of the "apparent elevation" of the selected taxa (MAHER, 1963).

From fossil data, an estimate of the apparent change in elevation of the tree-limits can be made by comparison between the pollen ratio values in the fossil and in modern pollen spectra collected along altitudinal reference transects.

Similarly, using sites situated at present phytogeographic transitions, it is possible to elucidate the former fluctuations of the tree limits by comparison between modern and fossil values of pollen ratios. We use this approach in an attempt to study the fluctuations of the timber line and the *Pinus-Abies* and *Quercus-Abies* limits in the eastern part of the French Pyrenees.

2.1 Selection of the pollen ratio

When a tree limit of interest concerns essentially two arboreal taxa, the selection of each component of the pollen ratio seems evident (e.g. *Pinus-Abies* or *Abies-Quercus*). However, difficulties arise when studying the timber line. Due to the dominance of *Pinus uncinata* in the Pyrenean subalpine zone, *Pinus* is a normal component of the ratio. Poaceae, abundant above the tree limit, can be a possible second component. However, in many cases, Poaceae species, particularly *Nardus stricta*, colonize the surface of the sites. Their pollen production is a dominant component of the local pollen rain and may lead us to infer an extension of alpine meadows when we have only a local presence of wet communities. In this case the *Pinus/Poaceae* ratio is not useful. However, in others cases, it can be used

when the sites are open water colonized by aquatic species or when the terrestrial associations have a very limited extent and are not dominated by Poaceae.

In many cases, the development of heaths may be an argument to use the Ericaceae pollen. Unfortunately, the number of Ericaceae pollen grains is frequently low and their curve is rarely continuous. The same applies to Apiaceae or the various types of Compositae considered separately.

From our field observations and for the selected examples concerning the timber line, we have considered as valuable two pollen ratios: the *Pinus*/Poaceae ratio within the limits described above and the *Pinus*/Compositae ratio. Except during the Late-glacial and the beginning of the Postglacial period, the Compositae are poorly represented in the pollen diagrams and their curves are frequently discontinuous. Thus, we have combined all the pollen grains of this family. Some species may grow in mire communities (e.g. *Cirsium palustre*, *Crepis paludosa*, *Willemetia stipitata*), but their pollen is usually infrequent while the others are good indicators of open terrestrial areas.

From the previous discussion it is clear that we cannot use the same pollen ratio in all cases. The study of the timber-line fluctuations requires preliminary investigations to determine which plants characterize the forest-heath-meadow ecotones and consequently what the pollen or pollen assemblages are that characterize the transition and the adjacent ecosystems. The use of only one pollen ratio is probably not sufficient to estimate the changes in altitude of the timber line and of the other tree-limits, and it is necessary to use several combinations.

Such investigations are in process in the French Pyrenees. In this paper, due to the lack of modern and fossil pollen spectra collected along transects, we have only estimated with respect to present the periods of possible divergence or similarity in the position of some selected limits.

2.2 Counting error and representation of the results

The ratios have been calculated using percentages of each considered taxon (e.g. A/B). To estimate the precision of the percentages and consequently that of the ratio A/B, the confidence limit of each percentage has been calculated using the Mosimann equation (MOSIMANN, 1965 in MAHER, 1972; BIRKS & GORDON, 1985). When the pollen sum was not available (e.g. Gourg Nègre; REILLE, 1990), we have estimated the confidence limits on a constant low pollen sum of 100 pollen grains in order to take into account the greatest values.

The larger values (L A and L B) and the smaller values (S A and S B) of the confident limits have been used to calculate two pollen ratios for each sample: S A/L B and L A/S B.

The variations of these two ratios are represented by two curves. In the modern pollen ratio, the interval between the two curves is considered as the reference datum from which the fluctuations of the limit in the past are estimated. In the figures, the present datum is represented by the two parallel vertical lines. At the right and the left, the values of the ratio indicate movements of the tree limit (e.g. Fig. 5 levels 180 to 60), but their quantification is impossible. Similarities with the present are supposed when the two curves of the ratio are situated between the parallel vertical lines (e.g. Fig 7, levels 100 to 30) or near these lines (e.g. Fig. 5, levels 400 to 250). When the two curves overlap the value of the reference datum (e.g. Fig. 4, levels 350 to 175) no conclusion is possible.

In the figures, the values of the pollen ratios are plotted logarithmically against depth.

3. Fluctuation of the timber line

Three sites have been selected: Gourg Nègre (REILLE, 1990), Ruisseau de Laurenti (JALUT, 1974; JALUT & VERNET, 1989), Freychinède (JALUT et al., 1982) (Fig. 1).

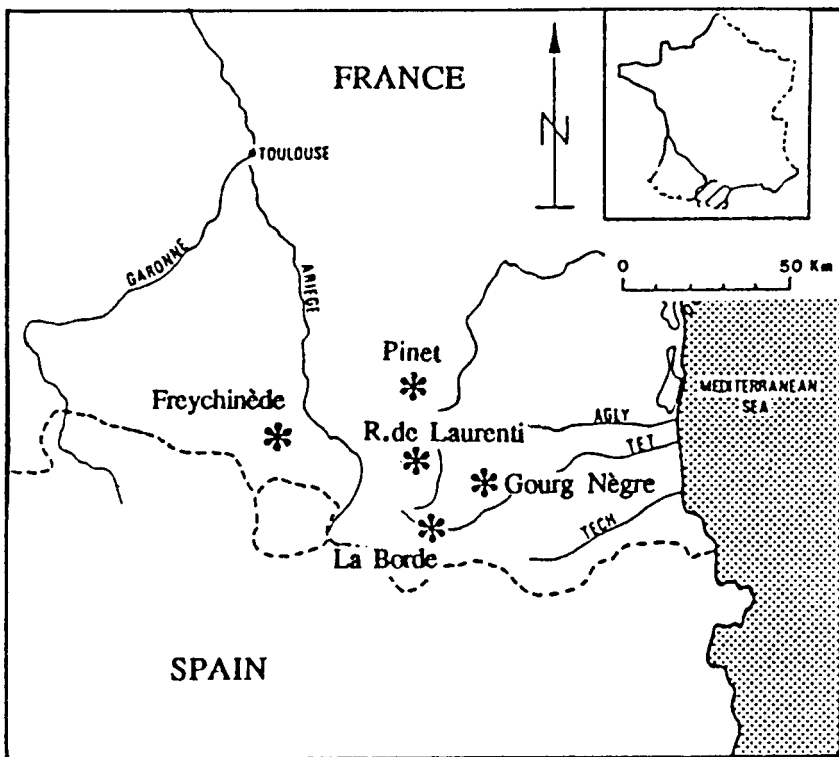


Fig. 1 Location of the sites

3.1 Gourg Nègre, alt. 2082 m

The site is situated in the south-eastern part of Massif de Madrès, in the Mediterranean climate area. During the two last millenia, and particularly during the two last centuries, this area has experienced intensive human impact. This was responsible for the extinction of the fir forest, the expansion of pastures and the presence of large areas covered, according to the aspect, by *Rhododendron ferrugineum* or *Cytisus purgans* (JALUT, 1974). At present, the *Pinus uncinata* forest can reach about 2280 m. The site of Gourg Nègre is situated in a zone of contact between heath and forest. Because the site is a lake, Poaceae are restricted to the terrestrial zone, thus making it practical to use the *Pinus*/Poaceae ratio here (Fig. 2).

In Figure 2, the low pollen sum available is responsible for the large standard deviation. Despite this drawback, one can see that the first situation possibly similar to present occurred near level 120 (Allerød, according to REILLE, 1990). However, this hypothesis is not supported by the presence of plant macrofossils, namely stomata of *Pinus*. The following period (110) is contemporaneous with the Younger Dryas. It is only near level 90, between 9890 ± 380 and 9400 ± 220 yr B.P. (only uncalibrated dates are used) that the pollen ratio is again comparable to the present but in this case stomata of *Pinus* are present, which reinforces the hypothesis of the presence of the timber line near the altitude of the site from this period onwards. This does not exclude the possibility of a higher timber line during the Holocene or a possible presence of scattered stands of pine during the Allerød. As REILLE (1990) emphasizes for the sites of La Borde and Balcère, stomata can be absent in the sediment despite a probable local presence of the trees near the coring site, very close to the edge of the lake.

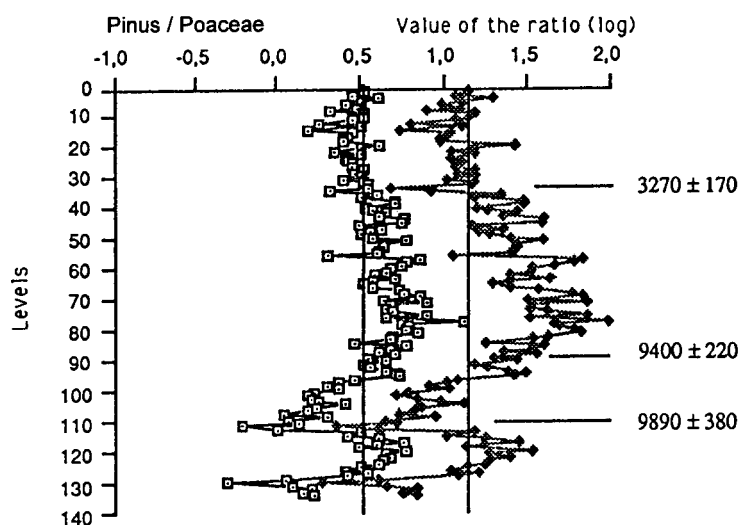


Fig. 2 Fluctuation of the timber line at Gourg Nègre (alt. 2082 m), south-eastern slope of Massif de Madrès, basin of Têt, Mediterranean Pyrenees

Between levels 90 and 60 the increasing trend in the pollen ratio could suggest a change in the position of the limit. However, the curves overlap with the vertical parallel lines, allowing no conclusion to be drawn. In such cases, the changes in the values of the pollen ratio are not informative. They could indicate only, from 3270 yr B.P. upwards, a position of the timber line more or less comparable to the present. Information can only be found in the pollen diagram. From level 55, the beginning of human impact is recorded and characterized by the first presence of *Cerealia* type and the occurrence of *Plantago lanceolata* pollen. Development of pastures (regular presence of *Chenopodiaceae* and increasing values of *Cichorioideae*) is indicated at approximately 3270 ± 170 yr B.P. The regular decrease of the *Abies* percentages particularly from about 3000 yr B.P., then more strongly near 920 ± 100 yr B.P. (JALUT, 1974) emphasises the importance of the deforestations responsible for its present scarcity. In the light of its past percentages on the one hand, and by comparison with its history in other valleys (see below) and its present altitudinal distribution on the other hand, it can be assumed that during its maximum (5000-4500 yr B.P.; JALUT, 1974), its upper limit in this part of the Madrès massif was probably close to the altitude of the lake.

3.2 Ruisseau de Laurenti, alt. 1860 m

The site is situated about 50 m above the present limit between the fir and *Pinus uncinata* forests. In this area, the development of pastures and later also the presence of mines and forges were responsible for the destruction of the natural forests. *Rhododendron ferrugineum*, *Cytisus purgans*, *Betula pendula* and *Populus tremula* are the best indicators of this intense human impact.

The site is covered by Poaceae, so we have used the *Pinus*/Compositae ratio (Fig. 3). The first period during which the pollen ratio is comparable with the present corresponds to the Bølling-Allerød phase and the second to the beginning of the postglacial period. As observed at Gourg Nègre, stomata of *Pinus* found by REILLE (1990) are only present from the beginning of the postglacial period. In this case, their presence is in a good agreement with the course of the pollen ratio, indicating that the timber line was probably situated near or above the altitude of the site. In a site at lower elevation in the same area, near Ruisseau de Laurenti (La Restanque, 1620 m, Fig. 1; REILLE & ANDRIEU, 1993), the first stomata are found during the Allerød. They are absent during the Younger Dryas, and then again observed from the beginning of the Postglacial.

As indicated by the course of the pollen ratio and the pollen diagram (JALUT, 1974; JALUT & VERNET, 1989; REILLE, 1990) the optimum development of the forest occurred between 8230 ± 180 and 6080 ± 140 yr B.P. (JALUT, 1974). A situation possibly similar to the present may have occurred at 4800 ± 130 yr B.P. Due to the presence of mines and the use of charcoal, the timber line was lower than the site during the historical period (level 25).

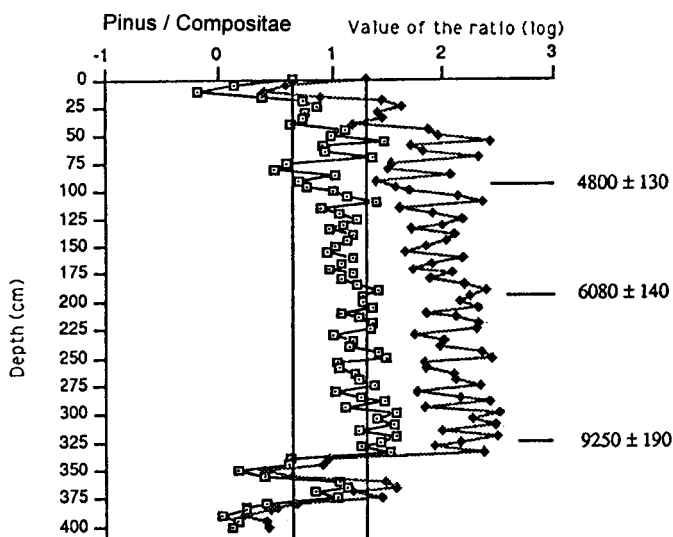


Fig. 3 Fluctuation of the timber line at Ruisseau de Laurenti (alt. 1860 m), upper basin of Aude, Mediterranean Pyrenees

3.3 Freychinède, alt. 1350 m

This former lake is situated near the local upper limit of the oak forest (*Quercus petraea*). It is partly surrounded by a beech forest with scattered stands of fir on the slope to the south. Most of the *Pinus uncinata* forest was destroyed during the Middle Ages and the 18th century, and it is now very reduced. Heaths with *Calluna* or *Pteridium aquilinum* cover the slopes of the Massif des Trois Seigneurs to the north (JALUT et al., 1982).

As the frequency of grasses is low, except on wet *Nardus stricta* meadows remote from the coring site, we have used the *Pinus*/Poaceae ratio.

Figure 4 first shows a situation comparable to the present near level 377-380, dated to $11,200 \pm 250$ yr B.P. (Allerød) (JALUT et al., 1982). During the same period, in another coring very close to the first one, stomata of *Pinus* are present (REILLE, 1993; REILLE & ANDRIEU, 1993). With respect to the present distribution of pine in the vicinity, it can be assumed that during this period an open pine forest may have been present at the altitude of the site and probably above. The probable change in the vegetation cover which is recorded could be interpreted either as the result of a closer presence of pine or as the increasing density of the pine forest. At the same time, a general increase in the pollen concentration is recorded (JALUT et al., 1982) (Fig. 4), affecting most of the pollen types. However it is difficult to say if it is or is not correlated with a significant change in the sedimentation processes frequently responsible for such modifications.

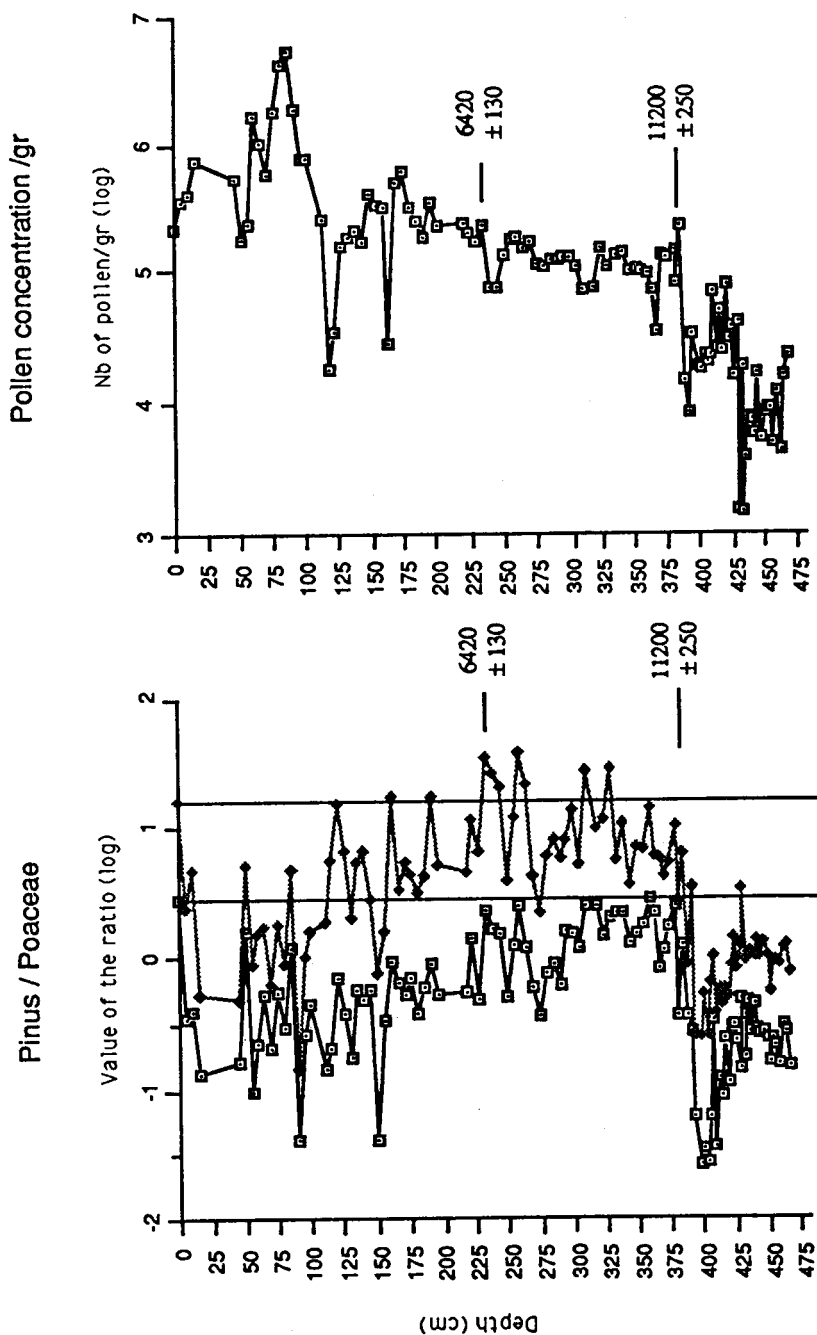


Fig. 4 Fluctuation of the timber line at Freychinède (alt. 1350 m), basin of Ariège. Comparison between the variations of the pollen ratio and the pollen concentration (pollen/gram)

From these three examples, we can see that there is a good correspondence between the pollen ratio data and the presence of *Pinus* stomata. For the considered area, it can be assumed that the timber line reached 2000 m a.s.l. and probably more, at the beginning of the Postglacial, possibly between 9890 ± 380 and 9400 ± 200 yr B.P. In the area of Ruisseau de Laurenti, the highest limit of the pine forest was probably near 1860 m around 9250 ± 190 yr B.P. Taking the standard error of the dates into account, we may consider the two events to be more or less contemporaneous. Lower, at Freychinède, in a part of Ariège experiencing more oceanic climate, the timber line was probably at 1350 m during the Allerød. This agrees with the estimates of REILLE & ANDRIEU (1993).

4. Fluctuation of the *Pinus-Abies* limit

The three selected sites are situated in the Mediterranean Pyrenees. In all three cases we have used the *Pinus/Abies* ratio.

4.1 La Borde, alt. 1650 m

In the high valley of the Têt, this former glacial lake is situated at the lower limit of a fir forest on the right bank of the river Têt, facing north between about 1650 and 1950 m. The fir forest is surrounded by a *Pinus uncinata* forest (JALUT, 1974).

In Fig. 5 the relatively large interval of the surface sample as well as of the oldest levels are due to the small amount of *Abies* pollen in the samples studied. This could be partly due to the distance between the coring site and the fir forest. One can see that the situation was possibly similar to the present from the beginning of the curve up to level 250. During this phase it can be assumed that *Abies* was present in the area but not abundant. Then, from level 180, *Abies* takes a larger place in the landscape and it was probable at that time it spread not only up to its present upper limit, but also in zones of medium altitude covered today by *Pinus uncinata* forest, below its present lower limit. As everywhere it began to retreat around 4000 yr B.P. In the Mediterranean Pyrenees, particularly in the high valleys of the Têt and the Aude (Capcir), it was replaced by *Pinus uncinata* (JALUT, 1984).

4.2 Ruisseau de Laurenti, alt. 1860 m

As previously described, the site is situated about 50 m above the upper limit of the fir forest. Figure 6 shows that between levels 280 and 200, the upper limit of *Abies* was near the altitude of the site. From level 180-160 to level 45, the two curves of the pollen ratio and the general tendency of the pollen percentages (JALUT, 1974) show a consistent development of *Abies*. With respect to its present upper limit in the Mediterranean Pyrenees and Ariège, it can be assumed that during this period the upper limit of *Abies* was situated around 2000 m a.s.l. This expansion phase was followed by a period of human impact becoming very strong between levels 45 and 25 and responsible for the lowering of the *Abies* upper limit.

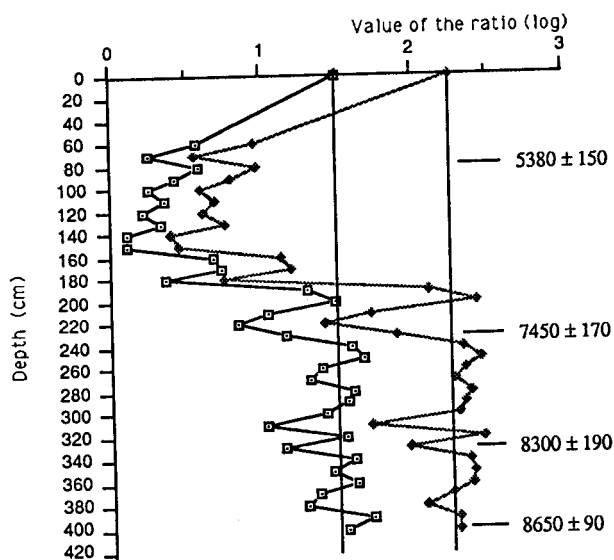


Fig. 5 Fluctuation of the *Pinus-Abies* limit at La Borde (alt. 1650 m), high valley of Têt, Mediterranean Pyrenees

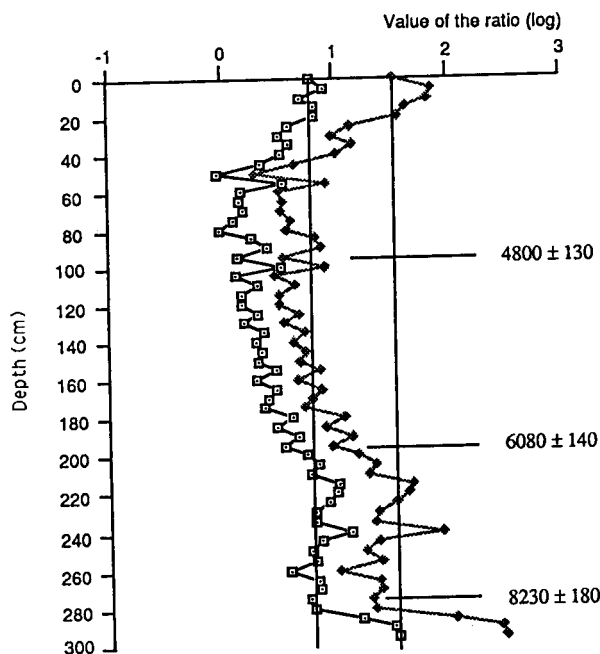


Fig. 6 Fluctuation of the *Pinus-Abies* limit at Ruisseau de Laurenti (alt. 1860 m), upper basin of Aude, Mediterranean Pyrenees

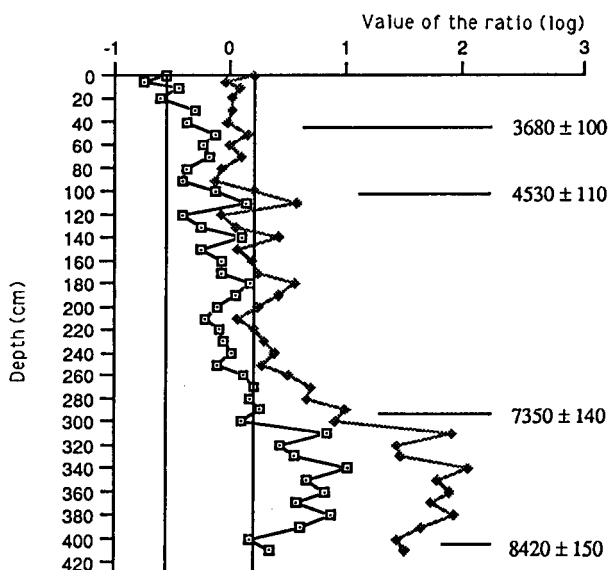


Fig. 7 Fluctuation of the *Quercus-Abies* limit at Pinet (alt. 880 m), basin of Aude, Mediterranean Pyrenees

5. Fluctuation of the *Quercus-Abies* limit

5.1 Pinet, alt. 880 m

The peat bog of Pinet is situated at the transition between the oak forest (*Quercus pubescens*) and the fir forest (JALUT, 1974). *Fagus* is present but more rare. *Abies* is favoured by climate, but also from the 18th century (FRUHAUF, 1980), for economic reasons. As a consequence, beech was systematically reduced and fir is now the dominant tree. Using the *Quercus/Abies* ratio (Fig. 7) one can see that it is only from level 100 upwards (near 4530 yr B.P.), that *Abies* seems to have a local abundance similar to the present.

Along a transect from Ruisseau de Laurenti to Pinet, it can be assumed that the upper limit of *Abies* was near 1860 m about 6500-6000 yr B.P. (Laurenti) and probably near 2000 m in the same valley at 4800-4000 yr B.P. This expansion towards high altitudes was also contemporaneous with a development in lower areas where *Abies* seems to expand around 4500 yr B.P. (Pinet, at 800 m).

In the first study of the high valley of the Têt (La Borde; JALUT, 1974) the first occurrences of *Abies* were recorded before 8300±190 yr B.P. In a new study its first occurrence and the beginning of the continuous pollen curve are dated respectively to 8650±90 and 8270±130 yr B.P. (JALUT et al., 1996). From Figure 7 and the pollen diagrams it can be assumed that between these dates and 7450±170-7780±130 yr B.P. (JALUT, 1974; JALUT et al., 1996)

Abies was probably sparse in the area. Then from 7800-7500 yr B.P. it began to expand and probably grew in areas lower than 1660 m, now covered with *Pinus uncinata*. Its maximum is dated 5240 ± 100 yr B.P. (JALUT et al., 1996)

6. Conclusions

From these examples and the comparisons with plant macrofossil studies (stomata of *Pinus*), we see that the pollen ratio can be a good tool for estimating the position of the timberline and the tree limits from fossil data. But it is necessary to use suitable pollen ratios, and as discussed above, to carry out additional investigations to quantify the changes of the limits. If the determination of stomata of *Pinus* allows the presence of this tree to be concluded, the examples of La Borde and Balcère cited by REILLE (1990), very favourable for the presence of stomata but where stomata are absent, illustrate the limitations of such conclusions. It is probable that local processes of sedimentation and preservation of stomata can influence the results of such investigations, and consequently reduce the possibilities of interpretations. For these reasons and due to the good concordance between pollen ratios, plant macrofossils and phytogeographic characteristics (MAHER, 1963; COUR & DUZER, 1978), it can be assumed that during the Lateglacial, for the considered sites, the values of the pollen ratio similar to the present and without stomata may also indicate periods during which scattered stands of *Pinus* existed, as observed in many present ecotones. New investigations in progress should give answers to this assumption. In parallel and to improve the pollen approach, particularly the choice of the pollen ratios to be used, floristic studies have to be carried out to identify the plant and pollen characteristics of the limits under investigation, and of their neighbouring ecosystems.

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