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A three thousand year succession of plant communities on a valley bottom in the Vosges Mountains, NE France, reconstructed from fossil pollen, plant macrofossils, and modern phytosociological communities

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Abstract Pollen and macrofossils were studied in a core from a fen at the foot of a slope in the Vosges Mountains, NE France. The present-day vegetation of little disturbed *Abies*, *Fagus*, and *Picea* forest and wetlands has been described in detail in terms of phytosociological communities using the Braun-Blanquet approach. Past ecological conditions are reconstructed in five steps: (1) The modern vegetation types are described as combinations of phytosociological species groups. (2) Micro- and macrofossils are assigned to these groups. (3) These in combination determine the past vegetation types at the site; there were simultaneously several such types in some biozones. (4) The sequence of past vegetation types is interpreted as successional pathways. (5) Past ecological conditions are inferred from these pathways. Results are: (1) The types of local forest and fen were the same around 1000 B.C. as today. (2) Rising groundwater around 650 B.C. caused a natural wet meadow to develop at the site. (3) Trees were felled near the site in the first century B.C. (Late Iron Age), facilitating the immigration of *Picea*. (4) Groundwater level rose during early Medieval times because of a wetter climate and alder carr replaced the dry-soil forest close to the site. (5) During High Medieval Times (10th–13th century) the nearby raised bog expanded over the site. (6) Forestry starting around A.D. 1750 caused nutrient-rich water to reach the site, resulting in abrupt vegetation change. (7) The creation of a forest road around A.D. 1855 (historical information) caused further nutrient

enrichment of the site. The validity of the method used depends on the assumption that past and present vegetation types are virtually identical, which is true in our study area and study period, according to all the indications that we have.

Keywords Braun-Blanquet · Pollen · Macrofossils · Succession · Phytosociological species groups

Introduction

In the approach taken by the French–Swiss school of phytosociology (Braun-Blanquet 1928, 1932, 1964), present-day vegetation is seen as being structured in phytosociological communities; and the assumption is made that this was also the case in the past (Tüxen 1974a). From the reconstruction of those past communities from the fossil record, inferences can be made about the environment of the past ecosystem, thus fulfilling one of the aims of modern Quaternary palaeoecology.

Waterlogged sediments often contain large amounts of well-preserved plant remains. In situations where the sediment is largely autochthonous, most of the fossils once lived within the basin of deposition. Autochthonous deposits such as peat have the highest potential to contain plant communities fossilised nearly in their entirety. But even the record of past peat communities is usually incomplete, because not all species are preserved, recovered, and recognised. An additional complication is that even autochthonous deposits often contain fossil plant assemblages derived from several different plant communities.

The first step in reconstructing the incompletely preserved communities is to determine the taxonomic affinities of the fossils with modern communities. A number of species identified in the fossil assemblage, through their known modern niches and the ways in which they are associated, can be used to indicate the past occurrence of particular communities; this is the so-called “application

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backwards in time of known ecological and sociological preferences of taxa" (Birks and Birks 1980, p. 231). Such species with a well-defined narrow ecological tolerance are called *indicator species* (Janssen 1967, 1986). The use of indicator species, however, has its limitations for the following reason. In modern floristic phytosociology (according to the Braun-Blanquet approach) plant communities (phytocoenoses) are defined in terms of taxonomic (qualitative) rather than quantitative composition. The type of community is determined by the presence or absence of so-called *diagnostic species* (character- and differentiating species). Presence or absence of particular fossils might therefore provide a basis for reconstructing past communities. Unfortunately, diagnostic species typically have a narrow ecological amplitude, occurring in a few communities only, this being what makes them diagnostic in syntaxonomy. Diagnostic species are therefore rare in real vegetation and may be lacking in fossil assemblages. This makes them of little use for the recognition of the syntaxonomic type of most actual plant communities. The importance of diagnostic species lies in their value as exclusive species in the syntaxonomic system; they were never meant to enable the identification of a given stand of vegetation, let alone a particular fossil plant assemblage.

Because of the wide ecological range of the more abundant (not diagnostic) plant species, most plant communities combine species from several series of syntaxa. Therefore the phytosociological position of communities is determined not from the behaviour of single plant species, but by comparing the full combination of species with that of the syntaxa described in the formal syntaxonomic system; it is the combination of species rather than a few diagnostic species that characterises the plant communities and that is used to identify them in the field (Scamoni and Passarge 1959). This method differs from the Uppsala school of vegetation science in its acceptance of the association concept in the sense of Braun-Blanquet (Malmer and Trass 1973).

We therefore attempt to identify the past vegetation types by using characteristic combinations of taxa from the total list of fossils encountered in the fossil assemblages. Special care is needed, because fossil assemblages do not fulfil the requirements of homogeneity of vegetation and completeness of species inventory as set by the modern phytosociological approach of vegetation sampling (Mueller-Dombois and Ellenberg 1974; Schaminée et al. 1995), and also the information on taxon abundance and cover is lost. The fossil assemblages are incomplete as they depend on the former input of plant remains, preservation, and taphonomic processes; however they retain their characteristic taxonomic composition, provided that a reasonable number of taxa are preserved.

One method of reconstructing past vegetation that uses the complete fossil assemblage of taxa starts with the delimitation of recurrent groups of fossils (pollen, spores, and macrofossils) in temporal sequences by way of visual arrangement of the fossils in diagrams. Each recurrent group includes fossils that are consistently found together and is interpreted as having formed a community in the past. In the studies by Rybníček and Rybníčková (1974),

Große-Brauckmann (1968, 1976), and Janssen and Birks (1994a, b), these groups generally make good ecological and phytosociological sense and can be readily related to modern vegetational analogues. Whereas Janssen and Birks (1994a) strive for some numerical delimitation of recurrent groups through quantitative methods, the other authors stress the subjective arrangement of species in appropriate groups of similar ecology and phytosociology (e.g., Große-Brauckmann 1986, p. 605). The method of recurrent groups can give detailed results only if the fossils of just one plant community are encountered in a sediment sample. Usually, however, modern wetland vegetation is a mosaic of different plant communities and this was probably also the case in previous times. Thus in sediments that contain the remains of several plant communities, the use of recurrent groups leads only to very generalised reconstructions such as alder carr, sedge swamp, wet meadow etc., as is the case in the studies cited above. Here, we propose a different, more refined approach, resulting in a syntaxonomically more detailed reconstruction.

In this paper we reconstruct past communities from fossil assemblages by using groups of plant species showing similar phytosociological behaviour today. Modern communities can be defined by the presence and absence of sociological species groups, a method first described by Scamoni and Passarge (1959). Sociological species groups are groups of species with similar phytosociological behaviour, i.e. they occur as a group in more or less the same list of plant communities and are absent in all others. Species within a group often have comparable ecological demands, but this is not necessarily so because plant communities consist of complex inter-species relationships that can cause species to grow outside their ecological optimum. Sociological species groups are therefore appropriate for an alternative description of modern plant communities. The great advantage of this approach is that all species, including the common ones, play a role in the definition of plant communities. This allows different ways of unravelling fossil plant assemblages, as was pointed out by Janssen (1967).

A prerequisite of our approach is the principle of actuality. Phytosociological species groups can only be determined in modern vegetation, whereas their application to fossil assemblages demands the assumption that the plant species involved had the same sociological behaviour throughout the time span studied. The further one goes back in time, the less likely this assumption may be, because the sociological behaviour of plants depends heavily on the species pool. As long as one deals with more or less the same flora, plants will have grown together according to the same principles as they do in modern vegetation. This can be assumed for our study area of mire and woodland in the upper montane vegetation belt of the Vosges Mountains during the last three millennia. This approach may fail in earlier periods such as the Atlantic, when the fir and beech that dominate the forests today were absent. However, according to known palaeobotanical finds mesotrophic wetland vegetation seems already to have reached its present species composition in early

Holocene times (Tüxen 1974b). The principle of actuality also requires that the environmental factors acting in the past upon the vegetation fall within the range that these factors have today. We can safely assume that this was the case in our study area, not only with factors dependent on topography (such as microclimate and soil), but also with human impact on vegetation, which ranges from absent to low even today.

Location and description of the site

The study site is a valley-bottom peat bog (48°02.9'N, 6°57.1'E; elevation 945 m a.s.l.) in the central Vosges Mountains, a 120 km long mountain range stretching NNE–SSW in northeastern France (Fig. 1). The central Vosges reach altitudes of around 1200 m, culminating in the Hohneck at 1362 m a.s.l. The valley of concern is the Grande Basse, a 2.5 km long and 900 m wide former glacier cirque situated about 5 km west of the Hohneck in the municipality of La Bresse. The lowest part of the valley bottom lies at 900 m a.s.l. and its steep slopes reach to about 1100 m, even to 1180 m on the north-facing slope. The last glaciation has left a complex pattern of glacial and periglacial features such as boulder fields, kame terraces, and kame ridges, which make the valley almost inaccessible. The kame ridges hamper the discharge of water and, in combination with a precipitation of around 2000 mm/year, have given rise to a complex mosaic of wetlands including mires, carrs, peat bogs, and wooded mires. This has further reduced the accessibility, eventually leading to the preservation of several nowadays very rare near-natural ecosystems. The vegetation types surrounding the study site are shown in Fig. 2. The valley was first opened up in A.D. 1855, when a gravel road was built that passes the study site at a distance of ca. 55 m.



Fig. 1 A star indicates the location of the study site Grande Basse in the Vosges Mountains, France

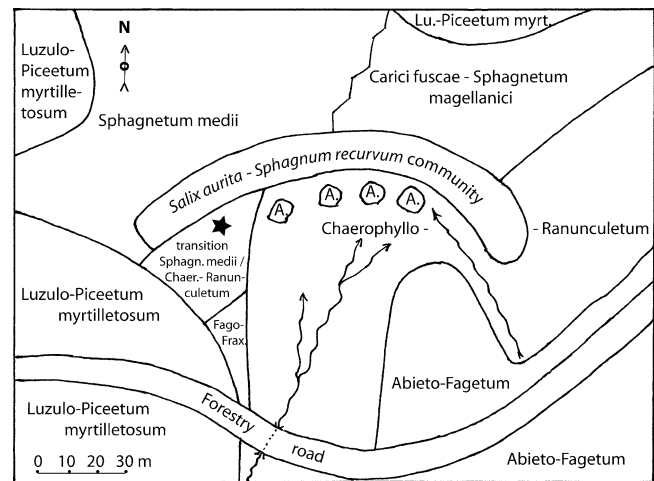


Fig. 2 Sketch map of vegetation surrounding the coring site, made in July 2005. Vegetation types are according to Table 2. The star indicates the study site; the vegetation at site is transitional between *Sphagnetum medii* and *Chaerophyllo-Ranunculetum*. A, *Alnus glutinosa*, small group of trees

The present vegetation of the valley is near-natural forest and mires. A diverse geology and the complex geomorphology enabled the development of a rich variety of plant communities. From a biogeographical view this valley is famous for having one of the few indigenous locations of spruce (*Picea abies*) in the Vosges (Kalis 1984b).

The area belongs to the upper montane vegetation belt. Fir (*Abies alba*) dominates the montane vegetation belt and reaches its upper limit at about 1000 m a.s.l., above which the woodland is dominated by beech (*Fagus sylvatica*) and sycamore (*Acer pseudoplatanus*). Spruce forests are restricted to a few steep north-facing slopes around 1050 m a.s.l. (plant communities belonging to *Luzulo-Piceetum*) and along the margins of peat bogs (*Mastigobryo-Piceetum*). The bedrock has a distinct impact on the plant cover. The eastern part of the valley has poor oligotrophic soils on acid granite, with coniferous forests (*Luzulo-Fagetum* and *Luzulo-Piceetum*). The western part (where the study site is) has basic granite rich in easily weathering minerals and fertile mesotrophic soils with species-rich deciduous woodland (*Aceri-Fraxinetum*, *Fago-Fraxinetum*, and *Ulmo-Aceretum*). Also on the wetlands the whole range from highly oligotrophic raised-bog communities to almost eutrophic megaforb (tall herb) communities is present, depending on the origin of the surface water. The relevant plant communities will be presented in more detail below.

Methods

Pollen analysis

Overlapping sediment cores were taken in the field using an Eijkelkamp gouge (diameter 6 cm) and subsampled in the laboratory for pollen analysis with a small corer of a known volume (0.3 cm³). The pollen samples were

chemically treated to extract the pollen following Fægri and Iversen (1989). The residue was mounted in silicone oil and analysed for pollen and spores. Analysis was carried out using a Leica Laborlux S microscope at magnifications from 312.5 to 787.5. Whole slides were counted.

Pollen and spore identification was made to the lowest taxonomic level using the following keys: Fægri and Iversen (1989), Punt et al. (1976–1995), and Moore et al. (1991), as well as the reference collection of the Laboratory of Archaeobotany of Frankfurt University and of the Institute of Plant Sciences of the University of Bern. The pollen types are named, and partly re-named, after plants common in the region of study, here the Vosges Mountains. The identity of the re-named pollen types is given in the caption to Fig. 3. All pollen and spore percentages are calculated on the basis of a pollen sum (100% by definition) of trees, shrubs, and herbs growing on dry soil (shown in Fig. 3A); excluded from this sum are pollen and spores of wetland and aquatic taxa (shown in Fig. 3 parts 2 and 3).

Macrofossil analysis

Macrofossil analysis was carried out on the same core as the pollen analysis. The subsample volume was 25.5 ± 3.6 ml. The samples were washed over a 0.2 mm sieve and the residue searched for plant remains. Identification of plant macrofossils was made by comparison with mod-

ern reference material and the identification keys of Berggren (1969, 1981), Anderberg (1994), and Körber-Grohne (1964, 1991). The macrofossils are depicted in the diagrams either as counts per subsample, or as presence/absence.

Radiocarbon dating

Four samples were radiocarbon dated (Table 1). The age–depth relationship was established by linear interpolation between calibrated radiocarbon dates.

Establishment of the phytosociological species groups

The vegetation of the municipality of La Bresse, in which the study area Grande Basse lies, has been the object of phytosociological studies by a research team from the University of Utrecht (Janssen and Punt 1998). These studies were carried out before the region was opened up for skiing tourism. This has resulted in three dissertations (De Valk 1981; Kalis 1984a; Bick 1985), several publications (Daniels et al. 1987; Janssen 1986; Janssen and Braber 1987; Kalis 1984b, 1985), and many research reports. The vegetation of the Grande Basse is extensively described in van Reenen (1979), Kalis (1984a), and Bick (1985). Similar studies of woodland vegetation in La Bresse are

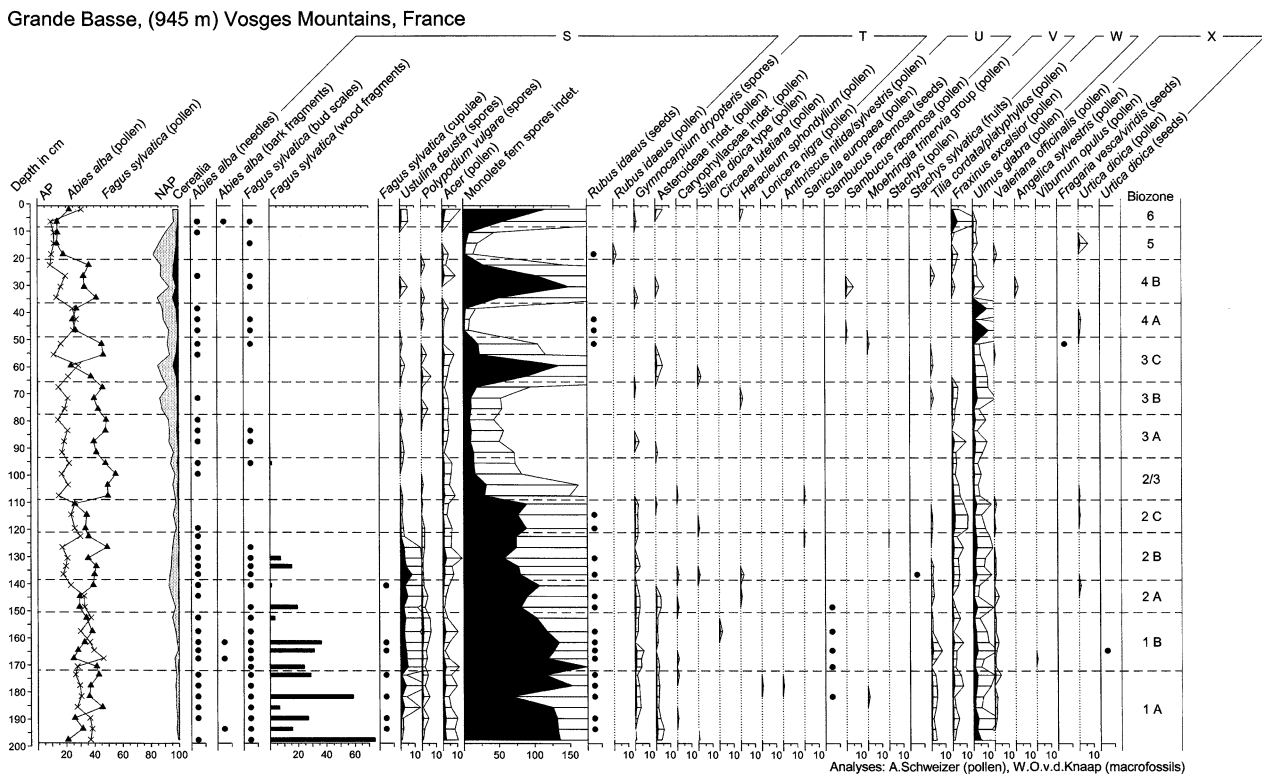


Fig. 3 Pollen and macrofossil diagram for the Grande Basse. Microfossils (pollen and spores) are drawn as black silhouettes, with 5-times exaggeration in white and depth bars at sample levels and dotted baseline; macrofossils are drawn as histograms (numbers

or dots (presence), with solid baseline. Pollen types renamed from Punt et al. (1976–1995) are: *Ranunculus aconitifolius* group (*Ranunculus sceleratus* group), *Stellaria alsine* group (*Cerastium fontanum* group), and *Stellaria nemorum* group (*Cerastium cerastioides* group)

by Jager (1976), Scheepstra (1978), and De Valk (1981). These studies give a comprehensive view of the modern plant communities of the Grande Basse. The delimitation of the sociological species groups used in the evaluation of the fossil plant assemblages has been made on the basis of those descriptions. Plant nomenclature follows Oberdorfer (1994).

Results

Pollen and macrofossil data

The pollen and macrofossil data are shown in Fig. 3.

Recent vegetation

Recent vegetation communities are listed in Table 2.

Phytosociological species groups

In Table 3, 97 vascular plant taxa belonging to 21 phytosociological species groups are ordered on the basis of absence/presence and dominance in the 26 vegetation types (Table 2) relevant for the study area. Five among the 97

fossil taxa encountered (pollen and/or macrofossils) are not listed for any of these vegetation types (*Carex ovalis*, *Prunella vulgaris*, *Rhinanthus spec.*, *Rumex acetosella*, and *Stellaria media ssp. neglecta*), but the species do grow in the study area today, mostly not in closed forest but on forest tracks and along roadsides. Most of these were found as macrofossils at a depth of 51 cm (biozone 3C). Some of the fossils could not be assigned to species, which is regrettable notably for Poaceae and *Carex* because these include many relevant species. The assignment of plant species to phytosociological species groups is uncertain for some other pollen types (Asteraceae subfam. Cichorioideae). The plant communities are sufficiently well separated by the fossils, even though species not encountered as fossils are omitted. Additional information on the species groups is given below.

- Group D: *Carex limosa* (and *Scheuchzeria palustris*; not found as a fossil) characterises bog hollows.
- Group E: *Drosera rotundifolia* and *Carex pauciflora* (the latter not identified as a fossil) characterise raised bogs.
- Group F: All species were found as fossils.
- Group G: Characterised by Cyperaceae pollen; relevant species in the vegetation are mainly *Eriophorum vaginatum*, *Carex rostrata*, and *Carex fusca*.
- Group H: *Vaccinium myrtillus*, *V. uliginosum*, and *V. vitis-idaea* (all represented by *Vaccinium* pollen) have their

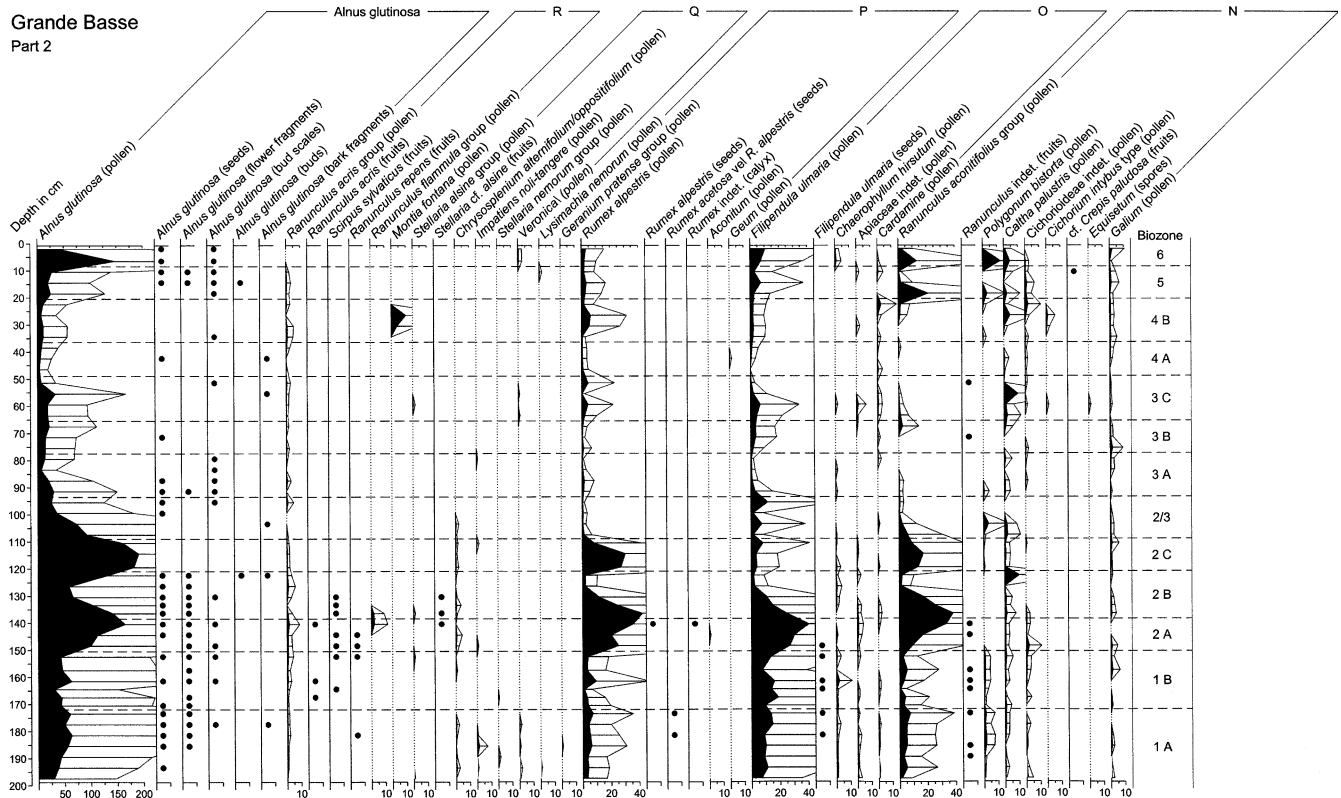


Fig. 3 Continued.

Table 1 AMS radiocarbon dates from the Grande Basse. OXCAL 3.5 with INTCAL98 calibration data set was used for calibration^a

Lab. code	Depth (cm)	Material dated	$\delta^{13}\text{C}$ (‰)	^{14}C age (B.P.)	Cal age (1 σ -range)
Erl-4242	67.5	<i>Sphagnum</i> stems	-29.11	880 ± 55	A.D. 1040–1220
Erl-4311	127.5	<i>Picea</i> needles	-28.78	1994 ± 54	50 B.C.–A.D. 80
Erl-4243	135.5	<i>Urtica</i> seeds	-28.85	1981 ± 57	50 B.C.–A.D. 80
Erl-4244	197.5	<i>Fagus</i> branch	-29.66	2845 ± 64	1130–910 B.C.

^aLaboratory No.: Erl, Physikalisches Institut der Universität Erlangen–Nürnberg, Erlangen

optimum here; also important are *Avenella flexuosa* (Poaceae pollen) and *Galium hircynicum* (*Galium* type pollen).

Group I: *Lycopodium annotinum*, *Huperzia selago*, and *Blechnum spicant* characterise the transition from *Picea* wooded mire to *Picea* forest on oligotrophic mineral soil.

Group J: Relevant species are mainly *Molinia coerulea*, *Avenella flexuosa*, *Agrostis canina*, and to a lesser degree *Deschampsia caespitosa* and *Festuca altissima*.

Group K: Also belonging here are *Carex nigra* (Cyperaceae pollen) and *Molinia coerulea* (Poaceae pollen); *Potentilla palustris* and *P. erecta* (*Potentilla* pollen) have their optimum here.

Group L: Also *Dactylorhiza maculata*, not found as a fossil.

Group M: *Salix aurita* (*Salix* pollen) occurs at the edges of minerotrophic fens, together with *Agrostis canina* and *Deschampsia caespitosa* (Poaceae pollen), and *Juncus effusus* (not found as a fossil).

Group N: Fossil *Galium* type pollen represents mainly *Galium palustre*; fossil *Equisetum* spores represent mainly *E. sylvaticum*; fossil Asteraceae subfam. Cichorioideae pollen represents *Crepis paludosa*.

Group O: *Myosotis sylvatica* (not found as a fossil) grows along streams; fossil *Sinapis* type pollen represents *Cardamine pratensis* and *C. amara*.

Group P: Fossil *Geranium* pollen represents *Geranium sylvaticum* and *G. robertianum*; fossil *Geum* type pollen represents *Geum urbanum* and *G. rivale*; fossil *Epilobium* pollen represents mainly *E. alpestre*, *E. montanum*, and *E. palustre*.

Group Q: Fossil *Chrysosplenium* type pollen represents *C. oppositifolium* and *C. alternifolium*; fossil *Cerastium fontanum* type pollen represents mainly *Stellaria nemorum* and *S. alsine*.

Group R: Fossil *Ranunculus acris*-group pollen represents *R. acris* and *R. repens*.

Group S: Fossil *Rubus* pollen represents *R. idaeus* and *R. fruticosus*; belonging also to this group are *Prenanthes*

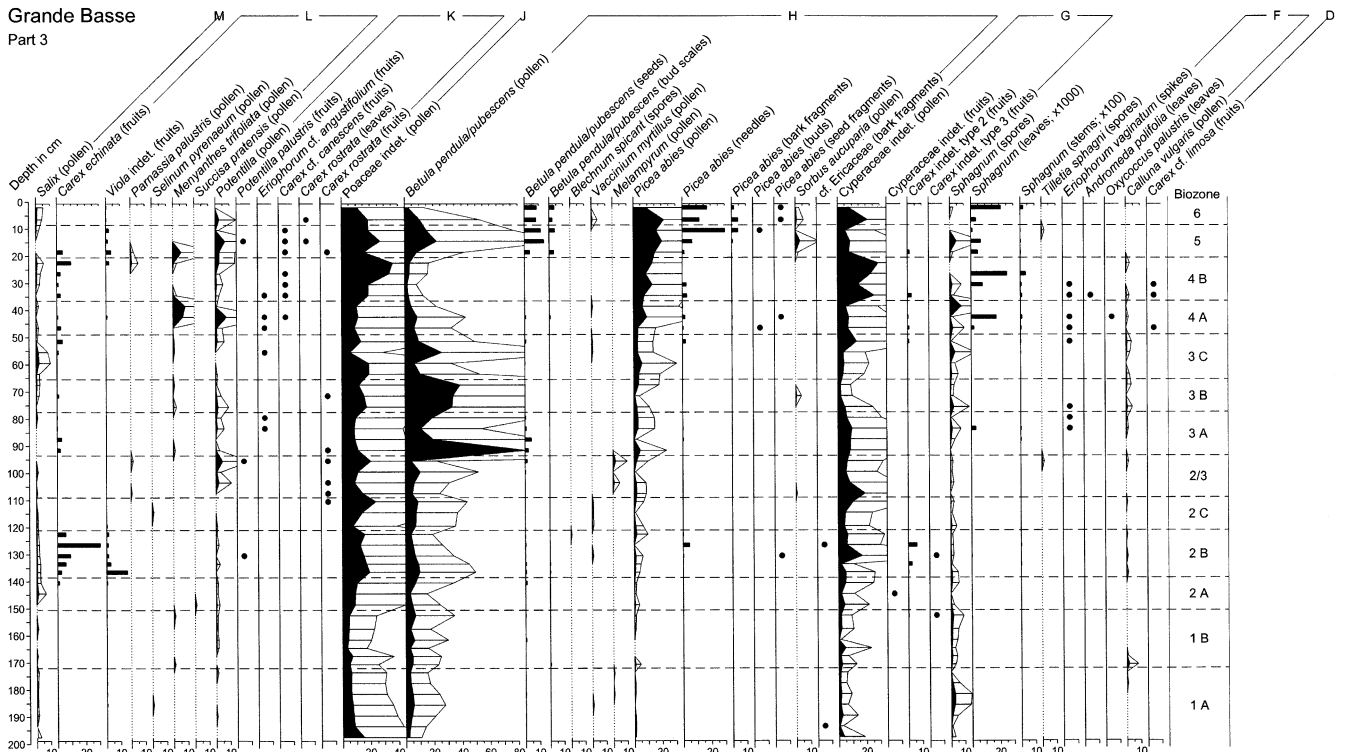


Fig. 3 Continued.

Table 2 Plant communities described in the Vosges Mountains relevant to the fossil communities

No.	Plant community	Based on relevées in:
1	Caricetum limosae typicum	Bick (1985)
2	Sphagnetum medii typicum, typical variant	Bick (1985)
3	Sphagnetum medii cladonietosum arbusculae	van Reenen (1979); Bick (1985)
4	Sphagnetum medii typicum, inops variant	Bick (1985)
5	Sphagnetum medii typicum, <i>Dicranum affine</i> variant	Bick (1985)
6	Carici fuscae–Sphagnetum magellanici inops, typical variant	Bick (1985)
7	Pino–Sphagnetum, treeless facies	van Reenen (1979)
8	Pino–Sphagnetum, treeless facies	Bick (1985)
9	Initial stage of Mastigobryeto–Piceetum	van Reenen (1979)
10	Pino–Sphagnetum piceetosum	Kalis (1984a); Bick (1985)
11	Luzulo–Piceetum myrtilletosum	Kalis (1984a)
12	Mastigobryeto–Piceetum betuletosum	Kalis (1984a)
13	<i>Betula–Sphagnum recurvum</i> community	Bick (1985)
14	Caricetum fuscae agrostietosum caninae, <i>Potentilla palustris</i> variant	Bick (1985)
15	Caricetum fuscae agrostietosum caninae, inops variant	Bick (1985)
16	<i>Salix aurita–Sphagnum recurvum</i> community with <i>Vaccinium myrtillus</i>	Bick (1985)
17	<i>Salix aurita–Sphagnum recurvum</i> community with <i>S. squarrosus</i>	Bick (1985)
18	<i>Salix aurita–Sphagnum recurvum</i> community	van Reenen (1979)
19	Salicetum auritae	Jager (1976)
20	Chaerophyllo–Ranunculetum	Scheepstra (1978)
21	Chaerophyllo–Ranunculetum	De Valk (1981)
22	Scirpetum sylvatici	Oberdorfer (1993)
23	Chrysosplenietum oppositifolii	Jager (1976)
24	Abieto–Fagetum rumicetosum	Kalis (1984a)
25	Fago–Fraxinetum (Abieto–Fagetum impatientetosum)	Kalis (1984a)
26	Stellario–Alnetum	De Valk (1981)

purpurea (Asteraceae subfam. Cichorioideae pollen), *Oxalis acetosella*, and *Paris quadrifolia* (the last two not found as fossils); fossil *Acer* type pollen represents mainly *Acer pseudoplatanus*.

Group T: Fossil Asteraceae subfam. Asteroideae pollen represents *Solidago virgaurea*, *Adenostyles alliariae*, and *Senecio nemorensis*. Fossil *Lamium* type pollen includes here only *Lamiastrum galeobdolon*. Also, *Festuca sylvatica* is represented by Poaceae pollen, and *Hieracium murorum* by Asteraceae subfam. Cichorioideae pollen; *Myosotis sylvatica* was not encountered as a fossil.

Group U: All species were also found as fossils.

Group V: Also belonging here are *Carex sylvatica*, represented by Cyperaceae pollen [Group G], *Geranium robertianum* by *Geranium* pollen [Group P], and *Viola reichenbachiana*, which was not found as a fossil. Fossil *Stachys* type pollen includes *Stachys sylvatica*, *Ajuga reptans*, and *Galeopsis tetrahit*.

Group W: All species were also found as fossils.

Group X: All species were also found as fossils.

Past vegetation communities

The left hand part of Fig. 4 shows the characterisation of the phytosociological communities occurring today in the broad surroundings of the study site (Table 2), by combi-

nations of phytosociological species groups (Table 3). The right hand part of Fig. 4 shows the occurrence of the species groups as fossils in the biozones delimited in the pollen and macrofossil diagram (Fig. 3). This forms the basis for the reconstruction of past phytosociological communities for each biozone by means of fossils, as shown in detail in Fig. 5. Arrows in Fig. 5 indicate the potential successional pathways between the reconstructed past phytosociological communities.

Interpretation

Biozone 1A. Tree pollen over 98% indicates a completely forested landscape; *Polypodium vulgare* (an epiphyte on old deciduous trees) and *Ustilina deusta* (a fungus having its optimum on the bark of old *Fagus* trees) indicate an undisturbed state. Macrofossils of *Fagus* and *Abies* indicate that the reconstructed Abieto–Fagetum grew at the coring site. The 1–2% *Acer* pollen is sufficient to indicate local presence of *Acer pseudoplatanus* and/or *A. platanoides*. Ferns dominated the forest undergrowth, as today on similar N-exposed slopes. The rather low pollen values of *Fraxinus excelsior*, *Ulmus glabra*, and *Tilia* (group W) indicate the presence of these trees, not in the immediate locality but in the surroundings, probably in Ulmo–Aceretum ravine-forest that still occurs today higher on the slope. *Quercus*,

Table 3 Present-day phytosociological communities on the valley bottom and the lower slopes of the Grande Basse, Vosges Mountains, France^a

Phytosoc. community → ↓ Plant taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	
Raised bog																											
D <i>Carex limosa</i>		V1-2																									
E <i>Drosera rotundifolia</i>	II	V1	II	III	III	II								R	I												
Raised and intermediate bog																											
F <i>Andromeda polifolia</i>	II	V1	V1	IV1	V1	III	V1	III	I																		
<i>Eriophorum vaginatum</i>	II	V1-2	V1-2	V1-2	V2	V2	V2	V+	III1	II		I	II	II	III+	r											
<i>Oxycoccus palustris</i>	II	V1-2	V1	V1-2	IV	V1	V2	V1	III+	V1		r	II	II													
<i>Calluna vulgaris</i>		V2	V3	V1-2	V3	IV	V2	V2	II	V2		II	r														
<i>Empetrum nigrum</i>			r	I		I	I	I	II	III1																	
G Cyperaceae indet.	V1-2	V1-2	V1-2	V1-2	V2	V2	V2	V+	III1	II		I	IV	V2	V1	III	III		1	IV1		V			III+	1	
Mire forest																											
H <i>Vaccinium myrtillus</i> type		I	II	I	r	R	V1	V3	V2	V3	V2	V3	V			V1	I	I					III				
<i>Betula pubescens</i> (as tree)							IV+			V2		IV	V3			V3	III3										
<i>Melampyrum pratense</i>				I		r		IV1		II	I																
<i>Picea abies</i> (as tree)										V2	V1	V3	I			I									I	II	
<i>Sorbus aucuparia</i>										II	III	II	II			III	III								I	IV+	3
<i>Listera cordata</i>										I		r															
<i>Pinus sylvestris</i>										III																	
I <i>Lycopodium annotinum</i>												III															
<i>Blechnum spicant</i>												III															
<i>Huperzia selago</i>												III															
Mire forest and fen																											
J Poaceae indet.					I	V1-2	I	III	V2	IV1	V1	IV1	V2	V1	V1	V2	V2				IV+	V			V	IV+	4
Fen																											
K <i>Carex rostrata</i>	II			I		II							III2	V2	V1	III	III		1	IV1	IV						
<i>Potentilla</i> type				r	r	V+							V+	V2	V1	IV	III	III1	I	II	I						2
<i>Potentilla palustris</i>													I	V2	II	IV	III	III1									
<i>Viola palustris</i>													III	V1	IV2	III2	V2	V1		II							
<i>Carex canescens</i>	I												III	III			r										
<i>Eriophorum angustifolium</i>	II			I	I	II								II	II												
L <i>Carex echinata</i>														III	IV+	III	II										
<i>Menyanthes trifoliata</i>						r							r	III	I	III3											
<i>Selinum pyrenaicum</i>														III	IV+												
<i>Parnassia palustris</i>														r	r	r											
<i>Succisa pratensis</i>														r		III					II	I	I				
M <i>Salix aurita</i>													II			V3	V4	IV	2								
Riverine megaforbs (tall herbs)																											
N <i>Polygonum bistorta</i>													III	I	r	III	V2	V2	1	V+	III	V		I			3
<i>Caltha palustris</i>														I		III	V1	V1	1	V+	IV	IV	I				
<i>Crepis paludosa</i>														I	r		III	IV+	2	IV+		I	I		II		1
<i>Ranunculus aconitifolius</i>													II			r	IV1	V+	2	III2					r		2
<i>Equisetum</i> type								I						II		II	I	V1	1	IV+	II	II					
Rubiaceae										III			II	I		I	IV+	III1	2	IV+	IV			V	V1		1
Cichorioideae indet.														I	r		III	IV+	2	IV+	III	I	I	IV	V1		3
O <i>Chaerophyllum hirsutum</i>																r	IV+	1	V2	V		IV2					3
<i>Filipendula ulmaria</i>																I		2	V2	IV	II	II					2
<i>Sinapis</i> type																III		1	V1	IV	V	III	II	III			2
P <i>Rumex alpestris</i>																		2	IV+	IV		I	V	IV+			
<i>Lysimachia nemorum</i>																II		1	IV2	III			III	V+			
<i>Primula elatior</i>																				III+	II	II			III+		4
<i>Geranium</i> type																			1	V+	V	I		III	IV+		4
<i>Epilobium</i> indet.														I			II		1	II	III			III	III+		3
<i>Aconitum napellus</i>																			1		I			I	I		1
<i>Geum</i> type																				1	III					I	3
Stream vegetation																											
Q <i>Impatiens noli-tangere</i>																r			2	I			V3	V	V2		3
<i>Chrysosplenium</i> type																			2	II	I		V3	II	II		
<i>Cerastium fontanum</i> type																			2	I	II		IV2	III	V1		3
<i>Stellaria nemorum</i>																			2	I	I		IV2	III	V1		3
<i>Veronica montana</i>																				I			II		IV+		
<i>Stellaria alsine</i>																				r							1

Table 3 Continued.

Phytosoc. community→ ↓Plant taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	
Wood club-rush meadow (named after <i>Scirpus sylvaticus</i>)																											
R	<i>Scirpus sylvaticus</i>																										
	<i>Valeriana dioica</i>															r		r					V				
	<i>Ranunculus acris</i> group																						V				1
	<i>Ranunculus repens</i>																						III				1
	<i>Ranunculus acris</i>																						V				
	<i>Ranunculus flammula</i>																						II				
	<i>Lychnis flos-cuculi</i>																				II		V				
Beech–fir mixed forest (<i>Fagus–Abies</i>)																											
S	<i>Abies alba</i> (as tree)									r	V2	V2	III				I					I			III	V2	
	<i>Fagus sylvatica</i>										V+						r	I	I				IV3	V	V2	2	
	<i>Dryopteris dilatata</i>										V+	II	II				II	I			r			V	V1		
	<i>Athyrium filix-femina</i>										III	r	II			r	IV+		I	II	I			V	V2	4	
	<i>Rubus idaeus</i> type										III					r	II	IV+					V	IV+	3		
	<i>Rubus idaeus</i>										III					r	II	IV+					V	IV+	2		
	<i>Acer</i> type										II						IV	I	II	III		II	V	V1	3		
Mesotrophic forest																											
T	<i>Dryopteris filix-mas</i>															II								V	V1	3	
	Asteroidae indet.										I		r				r							V	V1	3	
	<i>Silene dioica</i>																				I	II		III	V+	3	
	<i>Gymnocarpium dryopteris</i>																							III	V1		
	<i>Lonicera nigra</i>										II													II	IV+		
	<i>Heracleum sphondylium</i>																							III	I	2	
	<i>Scrophularia nodosa</i>																							II	I		
Ravine forest (Schluchtwald)																											
U	<i>Ribes alpina</i>																								II		
	<i>Sanicula europea</i>																								II		
	<i>Anthriscus nitida</i>																								II		
	<i>Sambucus racemosa</i>																							I	I		
	<i>Circaea intermedia</i>																								I		
Forest																											
V	<i>Anemone nemorosa</i>												r			r	I								III+	2	
	<i>Moehringia trinervia</i>																								I	4	
	<i>Phyteuma nigrum</i>																								II	3	
	<i>Stachys sylvatica</i>																								III+		
	<i>Stachys</i> type																						III		III+	3	
Riverine forest																											
W	<i>Fraxinus excelsior</i>																								III+	3	
	<i>Ulmus glabra</i>																								I	I	3
	<i>Tilia platyphyllos</i>																								II		3
	<i>Alnus glutinosa</i>															I					II						2
Montane forest																											
X	<i>Corylus avellana</i>																										4
	<i>Quercus robur</i>																										3
	<i>Urtica dioica</i>																				r			II			3
	<i>Angelica sylvestris</i>																										4
	<i>Valeriana officinalis</i>																										2
	<i>Fragaria vesca</i>																										2
	<i>Mercurialis perennis</i>																										1
	<i>Viburnum opulus</i>																										1

^aThe phytosociological communities 1–26 are listed in Table 2. Species groups are coded D–X; species not encountered as fossils are omitted. Headers of species groups give the general vegetation types in which the groups occur. Plant nomenclature follows Oberdorfer (1994). Some species are lumped together according to their pollen morphology. Roman numerals I–V and + and r indicate species frequency in present-day vegetation types; the following Arabic numerals (1, 1–2, 2, 3) are abundance/dominance according to the scale of Braun-Blanquet (1964) and Mueller-Dombois and Ellenberg (1974); 1–4 in type 26 are presence classes

Pinus sylvestris, and *Carpinus betulus* are absent from the nearby surroundings today and, judging by the pollen values being lower than at present, were also absent in the past. *Picea abies* was absent. Fossils of group Q (normally found in Chrysosplenietum oppositifolii, typical of areas with springs) suggest a spring-type forest community. The reconstructed Abieto–Fagetum impatientetosum Oberdorfer 1957 (= Fago–Fraxinetum *sensu* Bartsch 1940) grows today at some hundreds of

metres distance at the foot of steep N-exposed slopes on nutrient- and base-rich soils that depend on base-rich bedrock, base-rich upwelling groundwater, and a highly sheltered position (Kalis 1984a, p. 145). Local occurrence of spring water (up-welling groundwater) would also explain the presence of the reconstructed Chaerophyllo–Ranunculetum aconitifolii Oberdorfer 1952 (groups N, O, and P), which is a spring-mire vegetation type on permanently percolated, base-rich,

Fig. 4 *Left:* The occurrence of present-day phytosociological species groups (P.S.G.) D–X (Y-axis; Table 3) in present-day phytosociological communities 1–26 (X-axis; Table 2) in the broad surroundings of the study site. *Right:* The (mostly incomplete) occurrence of the same phytosociological species groups (Y-axis) as fossils in the biozones (X-axis; Fig. 2). *Black field*, strongly represented; *gray*, incompletely represented; *p*, minor representation; *white*, absent

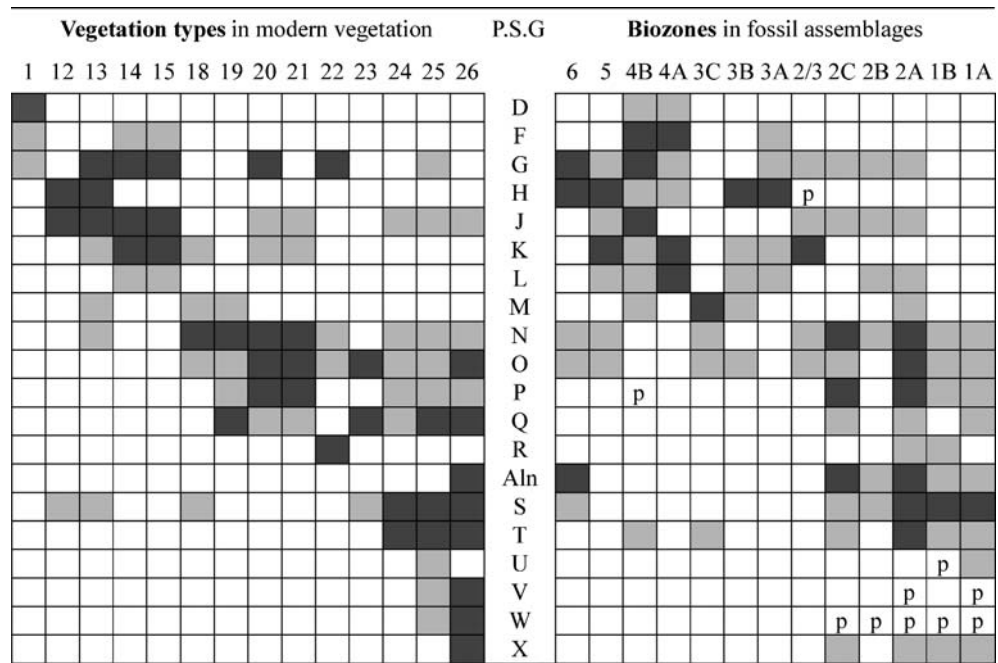


Fig. 5 Reconstructed fossil plant communities; biozones are shown in the pollen and macrofossil diagram (Fig. 3). Ages B.C./A.D. are of boundaries between biozones. Fossil groups are phytosociological species groups (listed in Table 3) of pollen and macrofossils encountered in the biozones (Fig. 4). Combinations of groups characterise the phytosociological communities listed. *Arrows* indicate inferred succession pathways between plant-sociological communities (listed in Table 2); *horizontal lines* indicate a supposed break in the natural succession

Bio-zone	B.C./A.D. (approx.)	Fossil groups	Past phytosociological communities
6	A.D. 1850	HS+GNO	Chaerophyllo–Ranunculetum with <i>Alnus</i>
5	A.D. 1750	GHJKL+GNO	<i>Betula–Sphagnum recurvum</i> community
4B	A.D. 1600	GJKL+DFG	Caricetum fuscae agrostietosum
4A	A.D. 1400	GKL+DFG	Caricetum fuscae agrostietosum, <i>Potentilla palustris</i> variant
3C	A.D. 1250	MNOS	Impoverished Salicetum auritae
3AB	A.D. 750	GHJK	<i>Betula–Sphagnum recurvum</i> community
2/3	A.D. 450	GJK+NO	Impoverished Chaerophyllo–Ranunculetum
2C	A.D. 250	ST+NOPQ	Chaerophyllo–Ranunculetum with <i>Alnus</i> fringe
2B	100 B.C.	S+GJL	Caricetum fuscae agrostietosum caninae, Inops variant
2A	250 B.C.	ST+R+NOPQSTVWX	Scirpetum sylvatici
1B	650 B.C.	ST+R+NOP	Abieto–Fagetum
1A	1000 B.C.	STQU+NOP	Abieto–Fagetum impatientetosum

humic gley soils (Oberdorfer 1993), indicating that the spring water was emerging as an incipient stream. *Alnus glutinosa* was locally present in this vegetation type, as today, but not forming alder carr.

Biozone 1B. The near-disappearance of group Q indicates that the Abieto–Fagetum impatientetosum was no longer strictly local, though *Sambucus racemosa* seeds indicate that it was still close. Fossils of group R indicate the development of Scirpetum sylvatici,

which requires a forest opening, nutrient- and base-rich soil, and semi-stagnant groundwater up to the surface; it is therefore likely that the forest opening had come into being due to the local death of trees. Chaerophyllo–Ranunculetum vegetation continued on wet places where groundwater could move horizontally.

Biozone 2A. Large changes in the proportions of macrofossils (*Abies* and ferns declining, *Alnus glutinosa*,

Rumex alpestris, *Filipendula ulmaria*, and *Ranunculus aconitifolius* increasing markedly) indicate better light conditions allowing more vigorous flowering, suggesting that the forest edge retreated from the study site. Also the area of the treeless *Scirpetum sylvatici* increased (group R and Cyperaceae), which indicates that the site became water-logged. An explanation for the disappearance of trees and the resulting water-logging is human impact. Although the study area is relatively inaccessible, human impact is a plausible explanation, as the southern part of the adjacent Chajoux valley (5 km distant) was intensively cultivated with fields and grasslands in this period (Late Iron Age) (Janssen and Braber 1987). The Chaerophyllo–Ranunculetum of the preceding biozone developed into an upper-montane variant of Stellario–Alnetum rich in *Ranunculus aconitifolius* and *Rumex alpestris* (De Valk 1981). Although today this is usually gallery forest along mountain streams inundated in spring, it also occurs rarely on water-logged slopes, as here in the past. De Valk (1981) described this vegetation type for the eastern Vosges, and it is known to occur below 800 m in the western Vosges, so its former presence here at 940 m altitude in the western Vosges is remarkable.

Biozone 2B. Re-advance of the forest edge to the study site is indicated by increased Abieto–Fagetum and the disappearance of Stellario–Alnetum and *Scirpetum sylvatici*. The freshly developing Caricetum fuscae agrostietosum caninae Inops-variant is a fen community on peaty soil with permanently up-welling spring water and inundation during spring. Today it is mainly found where the forest has been clear-felled, where springs initiate renewed peat formation (Bick 1985), thus strengthening the interpretation of Late Iron Age human impact as the cause of the forest opening in biozone 2A.

The early *Picea abies* needles in this biozone are of particular biogeographic interest. The indigenous as opposed to introduced status of this tree in the Vosges Mountains has long been under discussion. Kalis (1984b) showed pollen-analytically that the tree grew in the valley of the present study (Grande Basse) at least since early Medieval times. The present finding of two needles directly AMS ¹⁴C dated to 1994 ± 54 yrs B.P. (Early Roman Age) confirms the validity of the pollen-analytical method used and even indicates an immigration date of half a millennium earlier.

The habitat preferences of *Picea* are relevant in deciding where the tree may first have obtained foothold. According to Kalis (1984b), the majority of natural *Picea* trees today (i.e. not descended from introduced trees in the area; natural and introduced *Picea abies* can be distinguished in the Vosges Mountains by growth form) are underdeveloped and grow on the most acid, nutrient-poor soils and on raised bogs, whereas small numbers of well-developed natural spruce trees grow in Abieto–Fagetum. In the north-western Alps and the Jura Mountains, *Picea* is considered a pioneer in exploited forests, where it can establish eas-

ily. Forest exploitation is thought to have caused its rapid Holocene expansion (Markgraf 1970). This was also most probably the case in our study area as the Abieto–Fagetum forests exploited by man in the Late Iron Age (biozone 2A) must have been a very suitable habitat for *Picea* to gain a foothold in the Vosges. However the local forest stabilised after this phase of human impact and competition with *Abies* prevented any further spread of spruce. Spruce growth became limited to habitats with hardly any competition from other tree species, namely on raised bogs and extremely acid soils on poor granite where natural *Picea* still grows today.

Biozone 2C. A renewed retreat of the forest edge from the site is shown by the lack of *Fagus* and *Abies* macrofossils, the decline of *Ustulina deusta* spores, and increases of *Rumex alpestris*, *Ranunculus aconitifolius*, and *Alnus glutinosa* pollen. The absence of *Alnus glutinosa* macrofossils indicates that the local Chaerophyllo–Ranunculetum wetland was too wet for the species and it grew at some distance, at the edge of the wetland.

Biozone 2/3 transition. Water-logging was the probable cause of the local disappearance of forest (Abieto–Fagetum). Impoverishment of the Chaerophyllo–Ranunculetum and appearance of fen plants (group K) indicate acidification and decrease of nutrients. This suggests a shift in origin of the surface water from the nutrient-rich slopes south of the site to the raised bog northeast of the site. This shift was related to the accumulation of peat on this raised bog since the beginning of the Subatlantic estimated by Kalis (1984a) as 12.3 cm per 100 years on average and the resulting lateral expansion of the bog. An additional factor might have been increased precipitation during this early-Medieval time, which is also apparent from other proxy data (Schmidt and Gruhle 2003).

Biozone 3 A ± B. In the reconstructed *Betula–Sphagnum recurvum* fen community, Cyperaceae declined and *Betula* increased, indicating overgrowth by fen-birches (*Betula pubescens* ssp. *carpatica* Koch). Bick (1985) describes two alternative habitats for this community, minerotrophic fens below which the mineral subsoil provides sufficient nutrients to the groundwater to enable the growth of fen-birches, or along streams through the fen providing the relevant nutrients. The latter is more likely here, as a continuation of the stream-accompanying vegetation that was reconstructed for the underlying biozones.

Biozone 3C. 2% pollen of *Salix* (a poor pollen disperser) is sufficient to assume the local presence of willows. The fern that was so abundant is most probably *Athyrium filix-femina* that is at home in the reconstructed *Salicetum auritae*. The development to *Salicetum auritae* indicates a somewhat stronger contribution of nutrients in surface water, which is possibly related to a shift in the course of the stream.

Biozone 4A. The *Potentilla palustris* variant of the Caricetum fuscae reconstructed here develops today, ac-

ording to Bick (1985), as secondary peat growth in stagnant parts of streams. An expansion of raised bog that is also reconstructed for this biozone is the likely cause of stagnation of the stream at the study site and the subsequent development of this community. The local development of *Caricetum fuscae* was therefore natural in this biozone, in contrast to the human cause assumed in biozone 2B (in which it concerned the *Inops* variant). The increased number of *Picea* macrofossils and increased spruce pollen reflect the presence of spruce trees on the approaching bog.

Biozone 4B. The reconstructed *Caricetum limosae* indicates bog-hollows, which must have developed directly from the *Caricetum fuscae* in the stagnant stream of the underlying biozone. This amazingly rapid acidification indicates that the laterally expanding raised bog had encroached on the site.

Biozone 5. Here we observe a break in the development, as follows. The reconstructed *Betula-Sphagnum recurvum* community is, as far as can be judged, identical to the present one described by Bick (1985). This, and even more so the reconstructed *Chaerophyllo-Ranunculetum*, indicate an abrupt transition from extremely nutrient-poor to nutrient-rich surface water. It is clear that the nutrient-rich stream coming down the slope S of the site again ran through the site, as it does today, but we are unable to explain this in terms of any undisturbed development. The cause must have been man, who intensified forestry on this slope around A.D. 1750 and thus altered the hydrology and the exact courses of the streams. Although the plant communities in this part of the forest can be considered natural in their composition, their spatial distribution has been modified.

Biozone 6. The reconstructed *Chaerophyllo-Ranunculetum* with *Alnus glutinosa* is the vegetation present at the site today. The rapid expansion of *Alnus glutinosa* indicates further nutrient-enrichment of the surface water, suggesting further changes in hydrology. The latter must be related to the building of the first road through the valley in A.D. 1855 (Mer 1917) that runs along the slope above the site at a distance of about 55 m (Fig. 1). The water formerly running down from the slope S of the site over a broad front now passes under the road through pipes at a few places only, including the stream that passes the site today. This stream is therefore increased in discharge and brings much erosional material, building up a small alluvial fan between the road and the site. The limit of raised-bog vegetation is today about 20 m NW of the site.

Discussion

Two different methods are encountered in the literature to exploit the rich palaeoecological potential of the plant micro- and macro-fossils preserved in water-logged sedi-

ments. One method searches for recurrent groups of fossils and then infers their ecological indication by analogy with present-day vegetation. This method does not take into account the possibility that not one but various different vegetation types contributed to a fossil assemblage, and therefore in the best case leads to very generalised reconstructions of past vegetation (on the level of e.g. alliance, such as *Alnion*), or else to the reconstruction of the wrong or even non-existent vegetation types. The other method is used mainly in archaeobotany and exploits Ellenberg's ecological indicator values (Ellenberg et al. 1992) for the individual species encountered as fossils, these values being then averaged to estimate the former ecological conditions (pH, trophic state, humidity, etc.) on the site. This method, like the preceding one, ignores the possibility of multiple vegetation types contributing to the fossil assemblage, which may lead to the reconstruction of ecological conditions of non-existent habitats. In addition, it ignores the fact that only a (mostly small) selection of the plant species that grew in the past can be retrieved as fossils, whereas Ellenberg et al. (1992) explicitly state that the calculation of ecological conditions from ecological indicator values is only valid for complete plant communities. Therefore, an assemblage of fossils that happens not to be representative in ecological terms will result in an erroneous reconstruction of ecological conditions. The method used in this paper endeavours to solve these problems by grouping the fossil assemblage into phytosociological species groups, which form the basis of the reconstruction of (potentially) multiple vegetation types from each fossil assemblage. The validity of the method depends heavily on the principle of actuality: it works only if the assumption is correct that the vegetation types reconstructed for the past occur today somewhere in the study area with virtually the same species composition. This assumption is correct for our study area according to all the indications that we have. The method requires a thorough knowledge of present-day phytosociological communities including the less common ones. This knowledge is available for our study area.

In summary, our method works as follows. (1) The micro- and macro-fossils encountered are assigned to phytosociological species groups determined from the present-day vegetation of the area. (2) Relying on the principle of actuality, it is assumed that the phytosociological species groups represented by fossils in an assemblage (i.e., a biozone) were growing in the past vegetation in their entirety, including the species not encountered as fossils. (3) Combinations of the reconstructed phytosociological species groups are used to infer the former presence of one or several phytosociological communities during the period represented by the fossil assemblage. (It should be noted here that the use of phytosociological species groups in identifying present-day phytosociological communities is an accepted alternative to the use of diagnostic species; see Schaminée et al. 1995). (4) The present-day ecological requirements of the reconstructed past phytosociological communities are used to infer past vegetation-successional pathways and the evolution of past ecological conditions. With this method we recon-

structed the following environmental history of our study area:

1. The forest type growing at the site about 1000 B.C. is the same as that growing on the nearby slopes today, and the local stream-accompanying vegetation was the same as it is today.
2. At about 650 B.C. a rising groundwater table had caused a natural wet meadow at the site.
3. In the first century B.C., a period of dense habitation in nearby valleys (Late Iron Age), trees were felled in the close surroundings of the site. This short-lived phase of minor disturbance of the forest facilitated the immigration of *Picea*, which became established when the forest recovered in the subsequent Roman Era.
4. Groundwater level increased markedly during early Medieval Times, probably due to a cooler and wetter climate, and carr typical of wet oligotrophic soils replaced forest typical of drier nutrient-rich soils.
5. During High Medieval Times (10th–13th century) the nearby raised bog expanded laterally over the site.
6. Around A.D. 1750 forest exploitation started, disturbing the hydrology and causing nutrient-rich water to pass over the site. The vegetation changed abruptly.
7. Around A.D. 1855 a forest road was constructed (historical information) running 55 m from the site on the slope above, causing the stream to pass across the site resulting in a nutrient-rich stream-side vegetation. This is the situation today.

Some important aspects of the reconstruction of the past environment depend completely on the reconstruction of past phytosociological communities and their successional pathways. These are the minor human disturbance of the local forest in the Late Iron Age, the impact of climate on the local vegetation in early Medieval Times, the start of forestry around A.D. 1750, and the impact of road building in A.D. 1855 on the local hydrology.

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