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Subalpine Vegetation Dynamics in the Southern French Alps during the Holocene: Evidence from Plant Imprints and Charcoal Preserved in Travertine Sequences

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Abstract

In the Aigue Agnelle Valley (Queyras, southern French Alps), between 2200 and 2300 m a.s.l., several travertine deposits are present. Some, containing leaf imprints and pine cones, have been dated back to the early Holocene. Others containing charcoal fragments and dating back to the middle Holocene have also been found. The study of the plant imprints and charcoal within these travertines allowed us to reconstruct the vegetation dynamics of this valley. During the early Holocene (9800 B.P.), *Pinus uncinata* (mountain pine) was the most common tree. It was gradually replaced by *Pinus cembra* (arrolla pine) in association with *Betula* (birch) and *Vaccinium* sp. (berry), probably as a result of climatic warming (ca. 7600 B.P.). Since ca. 5600 B.P., *Pinus cembra* seems to have regressed in correlation with the development of *Larix decidua*/*Picea abies* (larch/spruce) as a consequence of fire events related to climatic and/or anthropogenic factors.

Introduction

Up to the present time, paleobotanical data from the French Alps above 1900 a.s.l. have been provided mainly by palynological investigations (de Beaulieu, 1977; Wegmüller, 1977; David, 1995; Nakagawa et al., 2000). With the exception of data from small peat bogs, these studies have generally reported vegetation dynamics on a regional scale. However, studies based on charcoal found in soils (pedoanthracology) have demonstrated that local events such as human-induced disturbances can control fire regimes and deforestation processes (Carcaillet, 1996, 1998). These local vegetation variations are not or are imprecisely recorded by pollen analysis. Consequently, in order to understand local vegetation changes in response to climatic and/or human pressure, it is important to carry out studies based on plant remains. This high spatial-resolution approach helps to characterize with precision the vegetation dynamics and to identify significant local changes triggered by the abiotic and biotic diversities of the alpine ecosystems.

Charcoal fragments larger than 0.4 mm in diameter enclosed in soils result from local burned woody vegetation (Clark et al., 1998; Ohlson and Tryterud, 2000) and are suitable to recognize, with high spatial resolution, past vegetation cover (Talon, 1997b; Carcaillet, 1996, 1998). Nevertheless, in the Alps above 1700 m a.s.l., Carcaillet (2000, 2001) has shown that in soil, charcoal fragments are not "time-stratified" due to bioturbation phenomena. Consequently, these charcoal fragments are not appropriate to demonstrate subalpine vegetation changes through time. As a result, the study of soil charcoal fragments should be supported by the analysis of stratified plant remains, such as those enclosed in travertine sequences (Ali et al., 2003).

Travertines, or tufa, are abundant in the French Alps, particularly in the Queyras Massif (Brotto, 1983, 1986). They result both from physiochemical mechanisms in relation to the saturation of bicarbonate in water and from biological processes. Homeostatic conditions such as a regular flow of rivers and streams, few perturbations (both climatic and anthropogenic), and a good development of vegetation induce optimal travertinization, i.e., formation of homogeneous travertine facies containing plant imprints (Ali et al., 2003). Climatic changes and/or human activities (deforestation, slash-and-burn agriculture) may

disturb the deposition of carbonates, favoring an increase of detrital deposits generally rich in charcoal fragments (Magnin et al., 1991).

Imprints of plant remains enclosed in travertine facies result from materials transported by wind and/or water (rivers/streams) before the deposit and fossilization. The transportation distance depends on many factors, such as weight, shape, and dimension (Ferguson, 1985). These plant remains are more or less well preserved, but they always record the composition of the local vegetation (Ferguson, 1985; Spicer, 1987).

Charcoal fragments collected in detrital levels result from local fire events. Their deposition in travertine sequences is a consequence of erosion processes occurring after fire perturbations on the slopes. Small charcoal fragments (<0.4 mm in diameter) can be airborne over several kilometers, as shown by previous works (Wein et al., 1987; Clark, 1988; Clark et al., 1998; Thinon, 1992; Ohlson and Tryterud, 2000). Therefore, they are not suitable to demonstrate local fire events. Charcoal collected in the travertine formations of the Queyras Valley is generally larger than 5 mm in diameter, suggesting that the burned areas were situated close by.

Our study based on the analysis of plant imprints and charcoal fragments enclosed in travertine deposits aims to demonstrate that these calcareous formations, abundant in the French Alps and containing time-stratified local plant remains, are important to characterize at a local or microregional scale the organization of subalpine woody vegetations and to discuss vegetation responses to climatic fluctuations and fire perturbations.

Study Area and Site Description

The travertines studied are located on the southern slope of the Aigue Agnelle Valley (Fig. 1). Two formations have been distinguished: the Tioures 1 formation (2200 m a.s.l.), enclosing cone and leaf imprints, and the Devez formation (2300 m a.s.l.), containing charcoal remains.

The Queyras massif is subdivided in two different geographic substratums. At the west side of the massif, the substratum is mainly constituted by limestone, while at the east side, corresponding to our study area, schist is dominant. These schist are rich in calcium

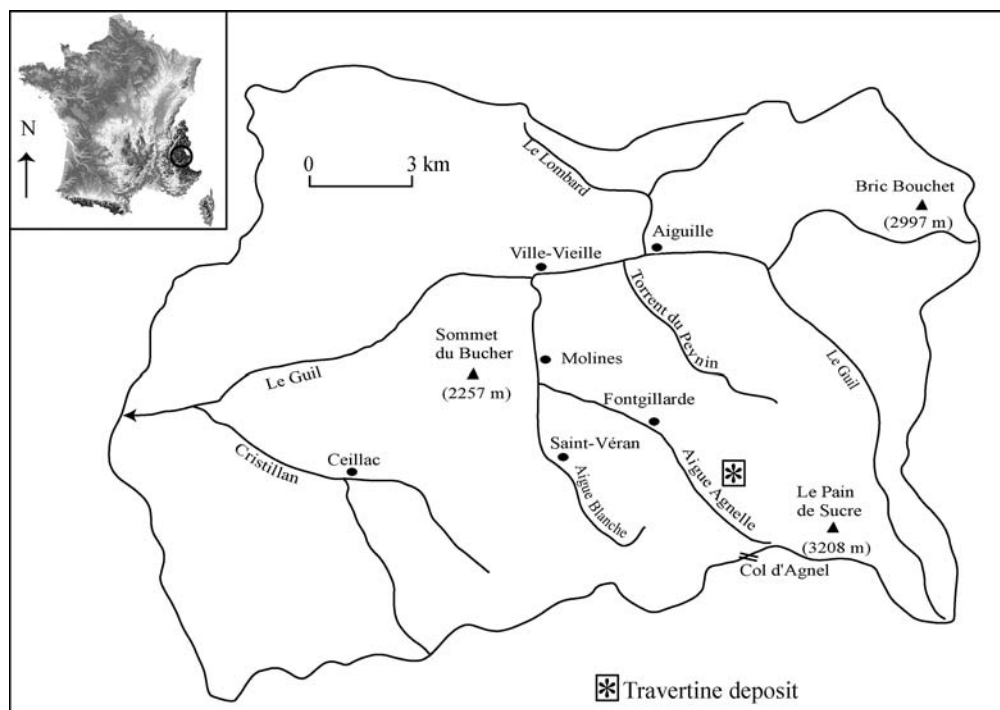


FIGURE 1. Location of site and travertine formations.

bicarbonate, which favors the formation of travertine deposits (Ballandras, 1997).

The present-day climate is characterized by a minimum of precipitation during the summer (mean July: 50 mm) and a maximum during the autumn (mean October: 100 mm). The mean temperature for the coldest month (February) is -3°C , and that of the warmest month (July) is 13°C . Climatic data are provided by the weather station at St-Véran (2125 m a.s.l.) (Fig. 1). Distinct vegetation characterizes the two valley slopes. The northern slope is covered by sparse, shrubby vegetation, including *Rhododendron ferrugineum*, *Vaccinium uliginosum*, *Juniperus communis*, and stands of *Larix decidua*, the only tree identified. The southern slope is characterized by a grassland, totally devoid of woody vegetation (Fig. 2).

TABLE 1

U/Th and ^{14}C dates (calibrated and noncalibrated) of travertine levels studied

Formations, profiles, and levels	Materials	Dating methods	^{14}C or U/Th age ^a (years B.P.)	Calibrated age ^b (years BP)	Sample code
Tioures	Calcite	U/Th	9800 + 100/-200	no calibrated	C-6644
Devez 3 (L. II)	Charcoal	^{14}C	7605 + 135/-140	8663-8146	A-11799
Devez 5A (L. III)	Charcoal	^{14}C	5655 ± 70	6570-6299	A-11800
Devez 6 (L. II)	Charcoal	^{14}C	2915 ± 70	3264-2868	A-11930
Devez 5B (L. IV)	Charcoal	^{14}C	1785 ± 75	1871-1538	A-11801

^a Conventional radiocarbon (radiometric) years B.P.

^b Calibrated according to Calib. 4.2 program (Stuiver et al., 1998).

TIOURES 1 FORMATION

The Tioures 1 formation (Fig. 2) shows several features of diagenesis such as stalagmites and stalactites and is totally disconnected from present-day stream sources. Its position on the slope indicates that landslide events occurred after the travertinization process. This formation is constituted by homogenous travertine facies, testifying to stable environmental conditions such as regular river flow, few perturbations, and good development of the vegetation during travertinization. Th/U dating indicates that this travertine was deposited during the early Holocene, around 9800 B.P. (Table 1).

DEVÉZ FORMATION

We studied four travertine profiles in the Devez formation (Dev 3, Dev 5A, Dev 5B, and Dev 6) (Fig. 3). These travertine sequences were formed on a substratum of schist and altered moraine. Each profile presents travertine or chalky facies and detrital levels with charcoal fragments. ^{14}C dating of charcoal fragments preserved in the different detrital levels (Dev 3 L. II, Dev 5A L. III, Dev 5B L. IV, and Dev 6 L.II) show that these travertine sequences were deposited between ca. 7600 and 1700 B.P. (Table 1).

Materials and Methods

IMPRINTS

Big travertine blocks were extracted during field sampling, with the help of hammer and chisel. These blocks were then reduced to smaller pieces to facilitate transport to the laboratory. Imprints that were fragmented during the extraction were consolidated with an adhesive solution.

In the laboratory, plant imprints were carefully extricated from the blocks with the help of dentist's needles and drawn afterward using a stereomicroscope ($\times 12$, $\times 25$, $\times 50$) coupled with a "camera lucida." Taxonomic identifications were based on the observation of morpho-

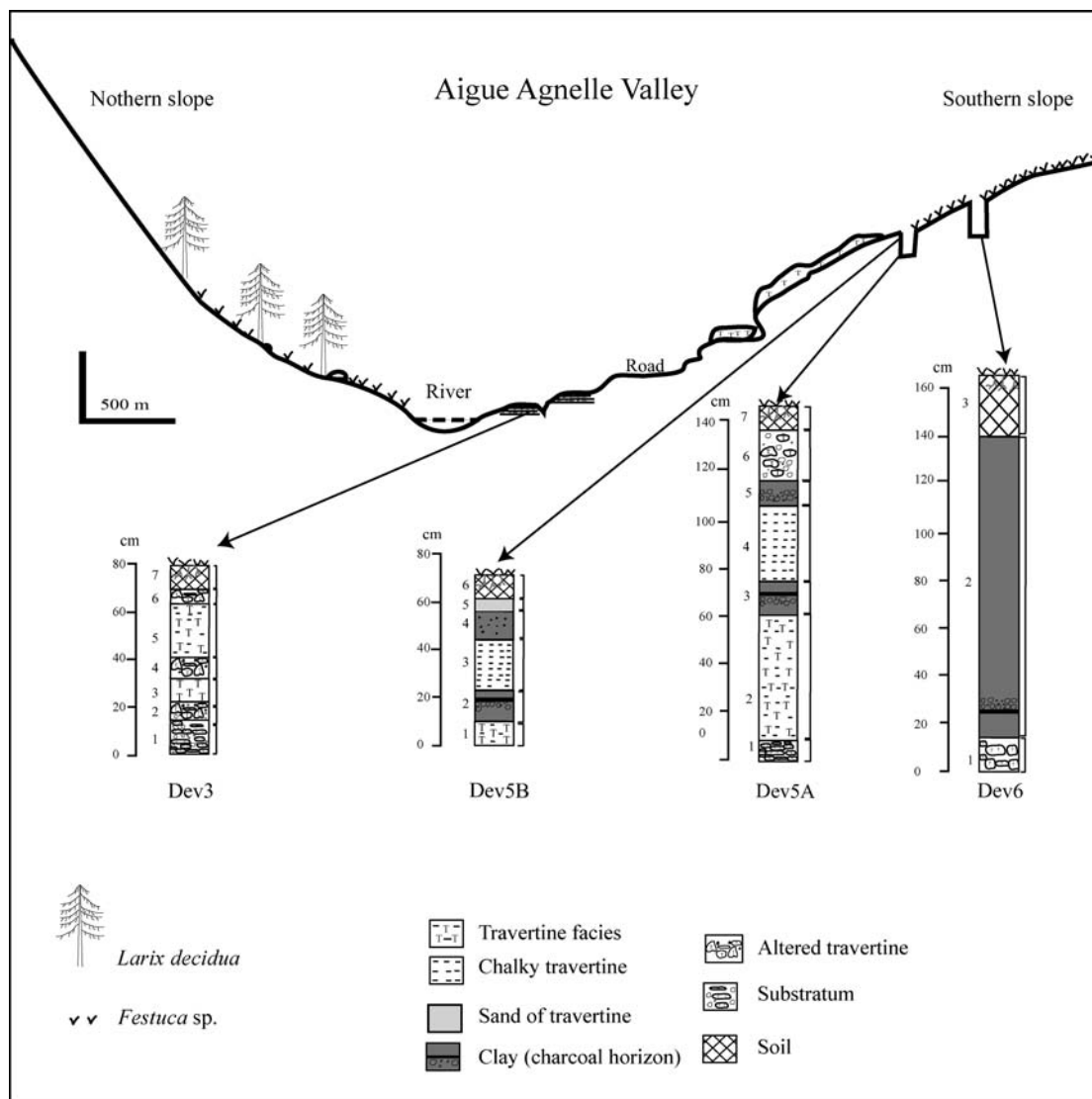


FIGURE 2. Schematic representation of Deveze travertine sequences.

logical characters of leaves and cones (shape, type of margin, and venation) and compared with specimens from the leaf and cone collection of the Centre de Bio-archéologie et d'Ecologie (CNRS, Université de Montpellier II) and data from morphological atlases (Cronquist, 1981; Rameau et al., 1989; Blamey and Grey-Wilson, 1991). Generally, the morphological features preserved in macrofossil specimens allow specific identifications, which are particularly important in recognizing vegetation diversity.

Frequently, the fragmentation of the imprints during the extraction prevents interpretation based on relative frequencies of taxa identified (combined quantitative and qualitative approach). Therefore, only a qualitative approach (presence of taxa) is used here. However, in certain travertine formations, the abundance of fossil remains overcomes fragmentation impairments, and a diachronic quantitative assessment of the vegetation on stratigraphic sequences can be achieved, as previous studies have shown (e.g., Ali et al., 2003).

CHARCOAL REMAINS

The amount of sediment sampled in the field depended on the abundance of the visible charcoal fragments. When clear charcoal horizons were observed, we considered 10 L of sediment to be

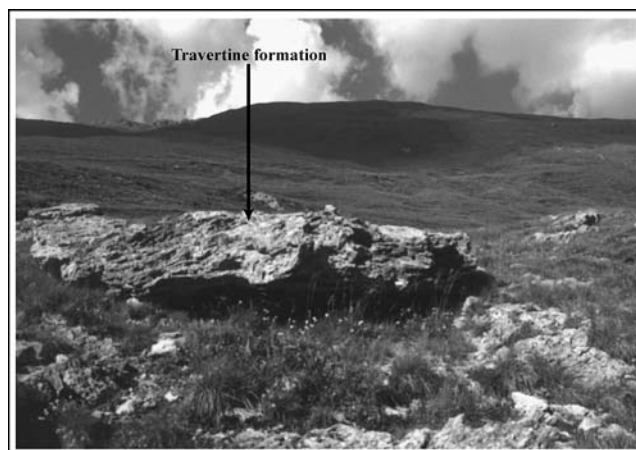


FIGURE 3. View of the summit of the Tioures travertine, where plant remains were collected.

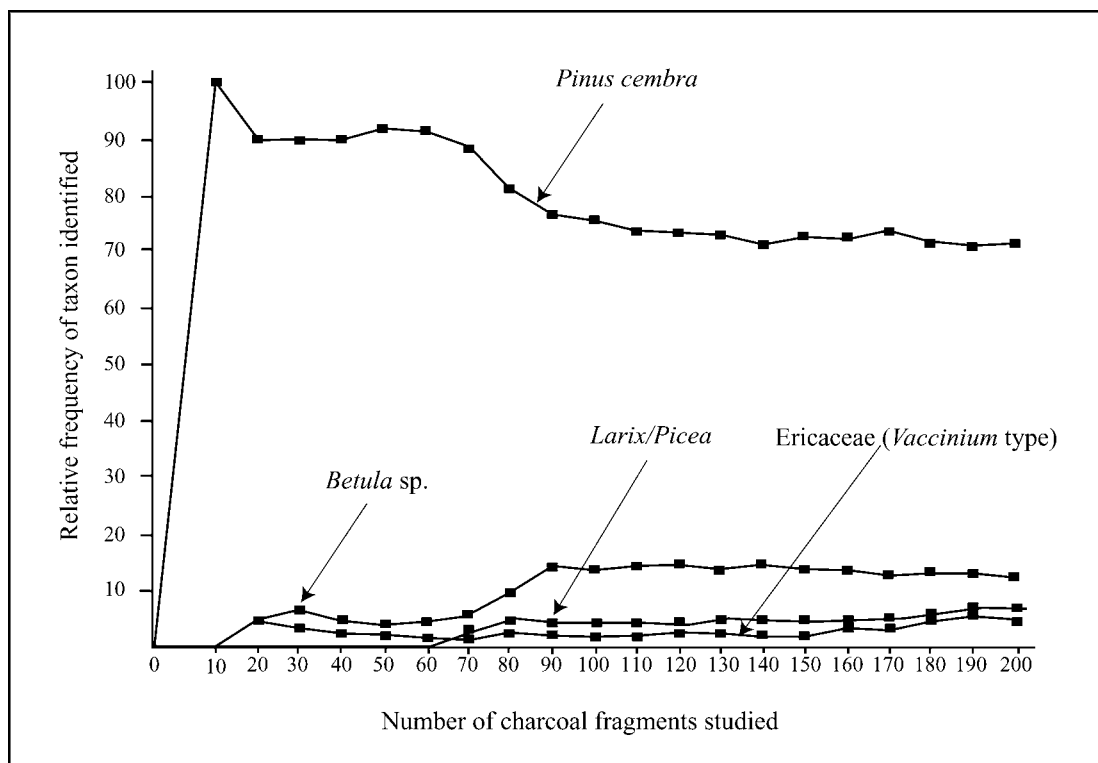


FIGURE 4. (a) Detrital deposit in the torrential basin of Aigue Agnelle valley during the Holocene period (Ballandras, 1997). (b) Devez travertine profiles. Profile 6 is not illustrated because it represents no morphosedimentary interest. (c) Forested dynamics of the southern slope as shown by charcoal analysis, based on frequencies of taxa identified from Devez formations.

sufficient. In the absence of clear signs of charcoal fragments, we collected 30 L of sediment.

Water sieving was used to recover the charcoal fragments from sediments in the laboratory. The coarse-fraction and large charcoal fragments were recovered with a 5-mm mesh, while a 2-mm mesh recovered smaller material. Charcoal collected was identified using a reflected-light microscope ($\times 200$, $\times 500$, $\times 1000$) and based on published descriptions of wood anatomy (Greguss, 1955, 1959; Jacquot, 1955; Jacquot et al. 1973; Schweingruber, 1990) and on comparison with a modern charred-wood reference collection of the Centre de Bio-archéologie et d'Ecologie (CNRS, Université de Montpellier II).

The curve illustrating the variation in relative frequency of the different taxa during identification shows that the frequencies stabilize approximately 100 fragments studied (Fig. 4). The dominant species are more rapidly recognized. Moreover, the different charcoal assemblages analyzed present an ecological coherence reflecting plant formations present in the environment today. These data supported our approach based on quantitative (frequencies of taxa identified) analysis of the charcoal assemblages collected, in order to characterize burned plant communities.

Results

Variations in frequencies of taxa from analysis of charcoal assemblages (Table 2) and plant imprints identified in Tioures 1 travertine reveal the existence of at least four phases in the evolution of the local vegetation.

Phase 1: cones and needles attributed to *Pinus uncinata* were very abundant in the Tioures 1 formation (9800 B.P.), indicating that this species might have been the most common tree during this period. Leaf imprints of several willow species (*Salix cinerea*, *Salix* sp. 1, *Salix* sp. 2), *Betula* cf. *pubescens*, and *Populus tremula* were also identified. We

were confronted with morphologic difficulties concerning the distinction of the three different species of *Salix*. The identification of *Salix cinerea* presented no problem, but the other two species remain undetermined. Neither matches species growing at present in the area (*Salix caprea*, *Salix daphnoides*, *Salix hastata*, *Salix pentandra*, *Salix purpurea*, and *Salix triandra*).

Phase 2: charcoal fragments of the Dev 3 L. II dated ca. 7600 B.P. reveal the development of a pine formation dominated by *Pinus cembra*. The understory would be composed in part of *Vaccinium* sp. *Betula* sp. was probably the major arboreal angiosperm of this formation.

Phase 3: during this period (ca. 5600 B.P.), the charcoal assemblage (Dev 5A L. III) reported the regression of *Pinus cembra* in correlation with the development of *Larix decidua* and/or *Picea abies*. Concerning this last taxon, it is impossible to clearly distinguish these two genera on the basis of traditional anatomical features when working with small charcoal specimens. According to some authors (Bartholin, 1979; Schweingruber, 1990; Anagnost et al., 1994; Talon, 1997a; Marguerie et al., 2000), discrimination between modern *Larix* and *Picea* wood may be achieved based on the observation of bordered pits from ray tracheid. Nevertheless, this feature must be observed repeatedly in several cross-sections of the same specimen in order to obtain a reliable statistical estimate. The size of most of our charcoal fragments did not enable us to carry out such observations. However, paleobiogeographical (Ravazzi, 2002) and phytosociological (Ozenda, 1985, 1994, 2002) data concerning *Picea abies* and *Larix decidua* argue for the hypothesis that charcoal fragments identified as *Larix/Picea* actually belong to *Larix decidua*.

Phase 4: *Larix/Picea* dominated the vegetation record of the Aigue Agnelle Valley. At ca. 2900 and 1700 B.P., the charcoal assemblages (Dev 6 L. II and Dev 5B L. IV) indicate plant formations where this taxon was dominant, with rare *Pinus cembra* individuals.

Discussion

The plant assemblage identified during phase 1 is composed of pioneer species (*Pinus uncinata*, *Betula* cf. *pubescens*, and *Populus tremula*) colonizing the poor rocky soils of the valley after deglaciation. This result supports previous pollen analysis interpretations. In fact, pollen analyses for this period report an increase of *Pinus* type *sylvestris* (de Beaulieu, 1977; Nakagawa et al., 2000); however, a specific identification could not be achieved. These authors assume that they were dealing with *Pinus uncinata* above 1600 m a.s.l., based only on comparison with modern ecological analogs. This pine formation was probably well established, and few environmental perturbations occurred, favoring the deposit of homogenous travertine facies observed in the Tioures 1 formation.

During phase 2, the development of *Pinus cembra* in the valley appears to have induced a gradual regression of the previous pioneer vegetation dominated by *Pinus uncinata*. In fact, this last species does not support the presence of more competitive taxa (Rameau et al., 1993). The climatic warming, characterizing the early Holocene period, triggered a pedogenesis process (Ballandras, 1997; Descroix and Gautier, 2002) favoring the development of *Pinus cembra*, which requires deep soils. This vegetation dynamics could be explained as a competition between *Pinus uncinata* and *Pinus cembra* reinforced by the climatic warming. The profile Dev 3 is mainly composed of travertine facies (Fig. 2) and also testifies to homeostatic conditions (few environmental perturbations) around the site, despite fire events responsible for the deposit of altered travertine levels of the sequence (levels II and IV). The development of *Pinus cembra* (ca. 7600 B.P.) shown by the charcoal record is surprising. In fact, according to regional pollen analyses, this period is characterized mainly by the development of *Betula*. The establishment of conifer species such as *Pinus cembra* occurred later (de Beaulieu, 1977; Wegmüller, 1977; Tessier et al., 1993; Fauquette and Talon, 1995; Nakagawa et al., 2000). Our results show that *Pinus cembra* was established in the Aigue Agnelle Valley at least 2000 yr before its first sustained pollen record (5700 B.P., according to Nakagawa et al., 2000). This discrepancy shows that local vegetation dynamics could be different from the regional model provided by pollen analyses. This micro-regional specificity may be explained by the incidence of local parameters such as exposure, topography, and soil features. Present-day field observations show, for example, that *Pinus cembra* develops better on schist than on limestone substratum (Contini and Lavarello, 1982; Petitcolas et al., 1997).

The development of *Larix/Picea* is generally interpreted as a consequence of woodland clearance in relation to human activities involving the use of fire (Talon, 1997; Carcaillet, 1996, 1998). During phase 3, we noted the development of *Larix/Picea*. According to archaeological data from this area, human settlement is recorded only from the Bronze Age (Ancel, 1997; Barge et al., 1998; Leveau and Martinez, 2002). Pollen analyses also indicate the development of *Larix decidua* during this period before significant anthropogenic perturbations (de Beaulieu, 1977; Nakagawa et al., 2000). But is this development a consequence of sporadic human presence in the valley or a result of climatic variations and wild-fire events? Present-day observations of subalpine vegetation dynamics show that the development of woody vegetations dominated by *Larix decidua* requires sustained perturbations in space and time. Consequently, we assume that sporadic human-induced disturbances cannot be responsible for the *Larix/Picea* development identified in our study.

However, it is currently believed that the Holocene is characterized by significant climatic variations with the alternation of amelioration phases (high temperatures and/or lower rainfall) and deterioration phases (decrease in temperatures and/or higher rainfall) (Burga and Perret, 1997; Magny, 1993, 2002). During amelioration

TABLE 2

Frequencies of taxa based on analysis of charcoal fragments from Deveze formations

	Profile 3 Level II %	Profile 5A Level III %	Profile 6 Level II %	Profile 5B Level IV %
<i>Larix/Picea</i>	5	71.9	76	94.8
<i>Pinus cembra</i>	24.5	4.3	4.9	1.6
<i>Pinus</i> sp.	47	18.6	10.6	2.4
<i>Betula</i> sp.	12.5	—	2	—
<i>Ericaceae</i> (<i>Vaccinium</i> type)	4.5	—	—	—
<i>Salix</i> sp.	—	—	1.4	—
Gymnosperms	6.5	5.2	5.1	1.2
Total fragments studied	200	210	350	250

phases, conditions were optimal for the occurrence of wild fires. In fact, litter was probably dry, creating an important fire hazard and thus triggering fire episodes (Trabaud, 1989; Carcaillet and Richard, 2000). It is possible that the development of *Larix/Picea* in the Aigue Agnelle Valley, during this period was a consequence of natural fire perturbations. However, we do not eliminate the possibility of human causation. Furthermore, this development corresponds to the deposition of strong detrital facies in travertine sequences and landslide events as a result of important perturbations around the site.

Phase 4 is also characterized by the dominance of *Larix/Picea*. At this stage, this development appears to be a direct consequence of human activities such as pastoral practices related to the settlement of semipermanent habitation beginning ca. 4000 B.P. (Courtois, 1961; Ancel, 1997; Barge et al., 1995, 1998). During this period, a mosaic plant formation might have been established, e.g., with woodlands at the margins of pasture patches.

After at least ca. 1700 B.P., the intensification of human activities in the valley was probably responsible for the total regression of woody vegetation on the southern slope. At the present day, the Aigue Agnelle Valley contains large pasture areas with intensive pastoral activities.

Conclusion

In the Aigue Agnelle Valley, four phases in the vegetation dynamics have been recognized. During the early Holocene (9800 B.P.), *Pinus uncinata* colonized the area, along with *Betula* cf. *pubescens* and *Populus tremula*. This pioneer vegetation seems to have been replaced by another, dominated by *Pinus cembra*, due to climatic warming (ca. 7600 B.P.). The mid-Holocene (ca. 5600 B.P.) was characterized by the regression of *Pinus cembra* correlated with *Larix/Picea* development (probably *Larix decidua*). This vegetation dynamic could be a consequence of natural fire perturbations, but we do not reject the possibility of anthropogenic origin. *Larix/Picea* dominated at ca. 2900 B.P. and 1700 B.P., while *Pinus cembra* was rare. This vegetation dynamic is correlated with the development of semi-permanent human settlements in the Massif beginning in the Bronze Age, inducing an intensive exploitation of woodland and then favoring the spread of *Larix/Picea*.

This interdisciplinary paleoenvironmental approach based on the analysis of time-stratified plant remains (imprints and charcoal fragments) and morphosedimentary facies from the Aigue Agnelle travertine sequences shows that these deposits provide reliable data to characterize spatiotemporal organization of subalpine vegetation. In comparison to pollen analysis that generally reveals the global trend of vegetation dynamics (regional scale), plant remains enclosed in travertine sequences allow us to characterize the microdynamics (local scale) that occurred within these global changes of the vegetation.

Consequently, the analysis of pollen and plant remains from travertine sequences, particularly in the subalpine areas, constitute complementary paleobotanical approaches.

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