Journal of Biogeography (J. Biogeogr.) (2007) **34**, 876–899

ORIGINAL ARTICLE

Post-glacial migration of silver fir (*Abies alba* Mill.) in the south-western Alps

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ABSTRACT

Aim Previous studies have failed to reconstruct the regional post-glacial migration pattern of *Abies alba* in southern France. Based on the first exhaustive compilation of palaeoecological data in this region, we present the state-of-the-art and attempt to synthesize the available information concerning glacial refugia and post-glacial migration, and analyse the information with regard to climate and orography.

Location South-western Alps and adjacent areas, southern France.

Methods The work compiles the available palaeoecological data in the south-western Alps (52 sites, 290 radiocarbon dates). The post-glacial migration pattern of *Abies alba* is reconstructed based on 22 selected palynological analyses (11 well-dated reference sites and 11 supplementary ones).

Results The geographical patterns of approaching area limit, immigration and expansion are reconstructed at the scale of the southern French Alps.

Main conclusions Despite previous assertions, the evidence of refugia in southern France is non-existent. The late-glacial records of fir pollen, previously interpreted in French Mediterranean regions and on adjacent foot-hills as possibly reflecting regional refugia, most probably correspond to reworking phenomena or long-distance pollen transport. Fir migration, originating in the Apennine refugia and through the south-western extremity of the Alps, was extremely rapid in the southern French Alps, only spanning a few centuries between 10,100 and 9800 cal. yr BP. The subsequent spread of fir populations was controlled by local parameters, such as the aridity of the inner valleys, which resulted in a delayed expansion in comparison to other regions. *Abies* almost disappeared from the south-western Alps during the Roman era, around 2000 cal. yr BP.

Keywords
***Abies alba*, France, glacial refugia, Holocene, late-glacial, migration, palaeoecology, pollen, topography.**

INTRODUCTION

The continental-scale post-glacial migration patterns of European trees are mainly inferred from pollen, sometimes supported by plant macroremains and genetic data (e.g. Huntley & Birks, 1983; Brewer *et al.*, 2002; Petit *et al.*, 2002; Ravazzi, 2002; Conedera *et al.*, 2004; Giesecke & Bennett, 2004; Terhürne-Berson *et al.*, 2004; van der Knaap *et al.*, 2005). Despite attention being paid to the choice of the palaeodata used, the conclusions may be locally affected by several factors: (1) the irregular geographical and topographic grid, determined by the distribution of lakes and wetlands, (2) the heterogeneous quality of the pollen data, related to sampling methods, pollen sums, determination criteria and taxonomic nomenclature, and (3) the heterogeneous quality of the chronological control. The quality of the chronology mainly

 www.blackwellpublishing.com/jbi
doi:10.1111/j.1365-2699.2006.01665.x

depends on the number of datings and methods used (i.e. radiometric dating of bulk sediment or terrestrial macrofossils, varve counting, or the less suitable regional pollen stratigraphy), and could be affected by the effects of hard water or disturbed sediments. Despite these general limitations, broad-scale reconstructions point to major discrepancies between regions and highlight the south-western Alps as one of the least known regions, where palaeoecological studies still fail to provide a consistent pattern of plant dynamics at the regional scale.

The southern French Alps cover a geographical zone of *c.* 300 by 150 km, and represent the south-western boundary of the Alps. Subjected to contrasting influences of Mediterranean, mountain and continental climates, this region comprises the maximum area of aridity in the whole Alps (Ozenda, 1985). This is reflected by the presence of relict steppe taxa such as *Juniperus thurifera* and *Astragalus alopecurus*. Despite these unfavourable conditions for wetlands, a large number of palaeoecological studies have been carried out over the past half century, since the pioneer work of Becker (1952): notably de Beaulieu (1977), Wegmüller (1977), Coûteaux (1982a), Clerc (1988), David (1993), Fauquette & Talon (1995), Carcaillet (1996), Talon (1997), Nakagawa (1998), Muller *et al.* (2000), Pothin (2000) and Ali (2003). However, the majority of these studies are not computerized in pollen data bases such as the European Pollen Database (EPD), which seriously complicates all attempts to reconstruct vegetation patterns at the regional scale. Furthermore, only a few macrofossil studies have been made in the region, creating a gap in the available data for historical plant biogeography and reconstructions of past vegetation, since macroremains provide useful additional information such as higher taxonomic resolution and smaller spatial scales of origin (Birks & Birks, 2000).

This study is based on the compilation of pollen, macroremains and radiocarbon data currently available from the south-western Alps and adjacent areas, and aims to evaluate the potential of this data set for reconstructing the past dynamics of vegetation at a regional scale. It focuses more specifically on the controversial spatiotemporal pattern of the post-glacial migration of silver fir (*Abies alba*) at the scale of the south-western Alps. The existence of glacial refugia and the migration routes of silver fir in southern France are still not firmly resolved (Nakagawa, 1998; van der Knaap *et al.*, 2005). Despite the inability of palynology to document small stands of trees, particularly in unfavourable climatic contexts (Kullman, 1996, 1998, 2002; Ali *et al.*, 2003, 2005; Brubaker *et al.*, 2005; Tinner & Lotter, 2006), the compiled palaeoecological data could provide evidence for refugial areas in two ways: directly by the comparison between pollen and macrofossil records, and indirectly by the timing of the expansion of fir forests, which should have occurred earlier if it resulted from the spread of local residual populations rather than by immigration from distant areas. The temporal and spatial variability of these processes is discussed in the light of climatic forcing and the orographic context: climatic forcing should result in homogeneous patterns of tree dynamics at a broad scale, whereas physiographical and orographic influences should be more heterogeneous both in time and space. The compiled data set is then used to attempt a preliminary evaluation of the existence of glacial refugia for *Abies* in southern France, and to discuss the migrational response of *Abies* to climate change.

PRESENT AND PAST DISTRIBUTION OF *ABIES* IN EUROPE

Present-day distribution

Abies alba Mill. (= *Abies pectinata* (Lam.) DC) covers the main mountain areas of central and southern Europe (Fig. 1a). This species has populations in Mediterranean climatic zones, in north-eastern Spain (Catalonia), in southern Italy (Calabria) and in southern France (Pre-Alps of Provence, southern Maritime Alps and Pyrenees). In Calabria and in the Pyrenees, *A. alba* populations belong to particular ecotypes, genetically differentiated from other populations (Vicario *et al.*, 1995; Fady *et al.*, 1999), suggesting their ancient separation from the main distribution area. On the other hand, populations in Corsica belong to the Euro-Siberian group (Gamisans, 1999), in agreement with palynological data, which indicate the recent immigration of silver fir to the island (Reille *et al.*, 1999).

Abies alba is generally associated with beech (*Fagus sylvatica*) in lower and middle mountain belts, and with spruce (*Picea abies*) in the upper mountain belt. Moreover, it forms pure forests in the sub-alpine belt in certain zones of the southern Alps, where spruce is absent (Rameau *et al.*, 1989–93). In the southern French Alps and Pre-Alps (alpine foot-hills), *Abies alba* displays a large altitudinal amplitude, ranging from 500 to 2000 m a.s.l. Mediterranean fir forests contain species characteristic of fir–beech forests (including the rare *Androsace chaixii*), generally mixed with *Quercus ilex*, *Quercus pubescens*, *Buxus sempervirens*, *Fagus sylvatica*, *Pinus sylvestris* and some thermophilous species of deciduous oak forests (Tessier du Cros, 1981; Quézel & Médail, 2003). In contrast, the floristic assemblage of the altitudinal fir forests in the Durance Valley is more similar to those from the outer Alps, from which they differ by the occurrence of *Luzula luzulina* and *Listera cordata*. Recent land-use abandonment resulted in abundant regeneration of *Abies alba* within forests of *Pinus sylvestris*, *Pinus uncinata* and *Picea abies*, notably in the southern French and Italian Alps (Motta & Garbarino, 2003; Rameau *et al.*, 1989–93; Quézel & Médail, 2003; Motta & Edouard, 2005).

In Europe, there are four Mediterranean species of *Abies* restricted to small areas (Tutin *et al.*, 1964–80; Quézel & Médail, 2003; Fig. 1a): *Abies pinsapo* Boiss., which could include *Abies marocana* Trabut of Maghreb (Scaltsoyiannes *et al.*, 1999), covers north-facing slopes on limestone mountains in southern Spain; *Abies nebrodensis* (Lojac) Mattei is

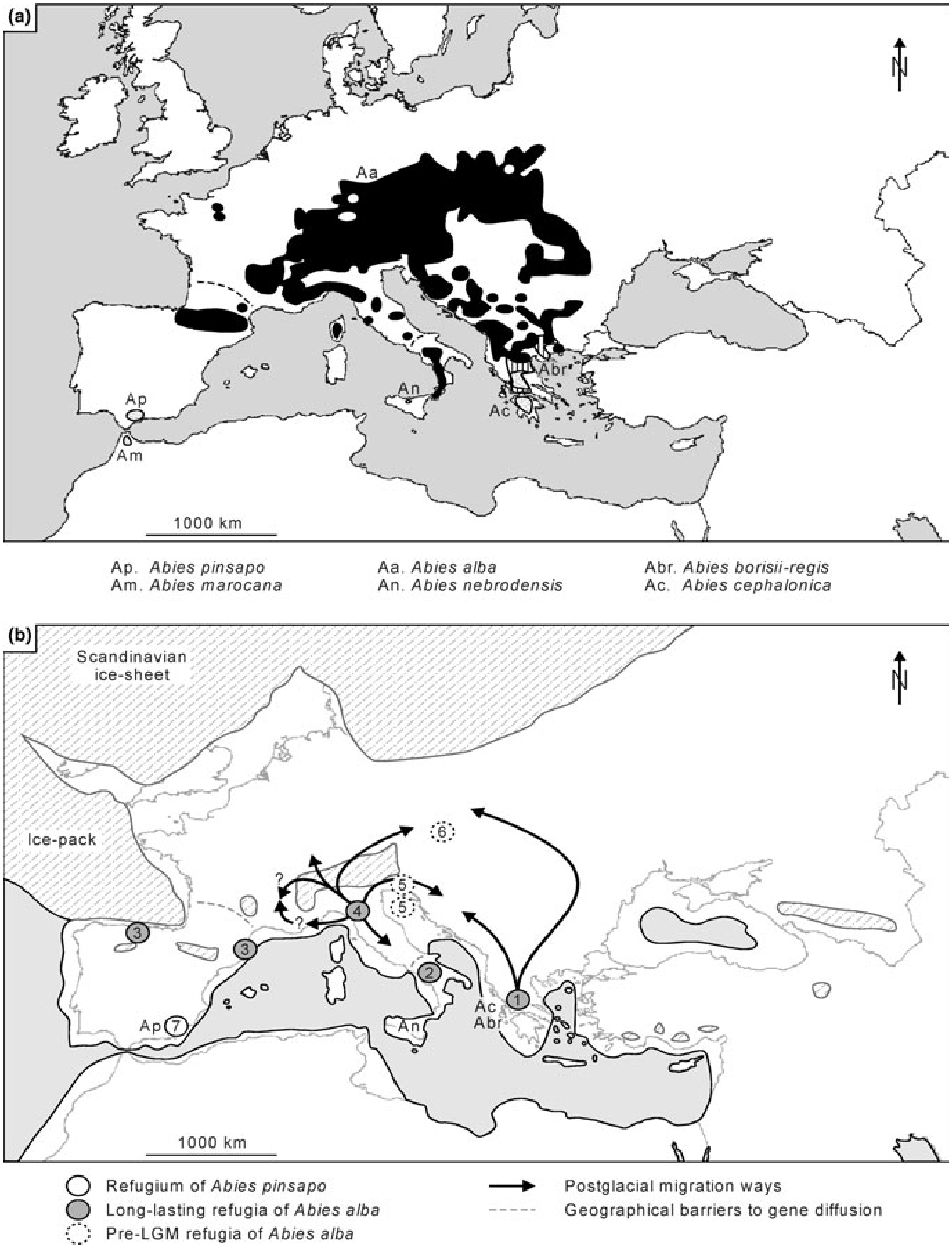

Figure 1 (a) Present range of *Abies* species in Europe (after Tutin *et al.*, 1964–80; Jalas & Suominen, 1973; Quézel & Médail, 2003). (b) Glacial refugia and probable routes of migration of *Abies* species (after Nakagawa, 1998; Terhürne-Berson *et al.*, 2004). Circled numbers refer to refugia locations detailed in the text. LGM is used for Last Glacial Maximum.

endemic in the north of Sicily and is currently restricted to 50 individuals on the Madonie Range, *Abies cephalonica* Loudon and *Abies borisii-regis* Mattf. both occur in Greece, southwards of the southern limit of silver fir. *Abies borisii-regis* is thought to be a hybrid between *Abies alba* and a Tertiary ancestral fir (Fady *et al.*, 1992; Fady & Conkle, 1993; Fady, 1995).

Finally, *Abies sibirica* forms extensive boreal forests in north-eastern Russia, westwards to *c.* 41° E and southwards to *c.* 55° N (Tutin *et al.*, 1964–80).

Location of glacial refugia

Since fir species cannot be distinguished in palynological analyses, studies related to their glacial refugia generally concern the genus only. Four European regions may be considered as possible glacial refugia for *Abies* (Terhürne-Berson *et al.*, 2004; Fig. 1b):

1. Greece, in the southern Balkans massif (Bottema, 1974; Huntley & Birks, 1983; Lang, 1992; Tzedakis *et al.*, 2002), is the most probable glacial refugial area for the two endemic species *Abies cephalonica* and *Abies borisii-regis*, perhaps in association with *Abies alba*;

2. refugia in southern Italy (Grüger, 1977; Watts, 1985; Bennett *et al.*, 1991; Lang, 1992) are supported by ecophysiological investigations (Larsen, 1986, 1989) and genetic studies (Bergmann *et al.*, 1990; Konnert & Bergmann, 1995; Vicario *et al.*, 1995). These studies suggest moreover that the Calabrian populations of *Abies alba* have remained isolated from those of other European regions since the last glacial maximum (LGM). Southern Italy also comprises the refugial zone of the endemic and currently endangered *Abies nebrodensis*;

3. the Pyrenees and surrounding areas in north-eastern Spain and south-western France (van Campo & Jalut, 1969; Jalut, 1970, 1973a,b; Pons *et al.*, 1974; Uzquiano, 1992; Reille & Lowe, 1993; Pérez-Obiol & Julià, 1994) comprise another important refugial area for *Abies alba*. As for southern Italy, the *Abies* populations of the Pyrenees have been shown to be genetically distinct from those of other European regions (Konnert & Bergmann, 1995; Fady *et al.*, 1999). This suggests that the Pyrenees refugia did not play any role in the northward spread of silver fir during the post-glacial period (Terhürne-Berson *et al.*, 2004);

4. the northern Apennines, in north-western Italy (Bertoldi, 1968, 1980; Bennett *et al.*, 1991; Lowe, 1992; Ponel & Lowe, 1992; Lowe & Watson, 1993; Watson, 1996), the Insubrian southern Alps (Schneider, 1978; Hofstetter *et al.*, 2006) and possibly south-eastern France (de Beaulieu, 1974; Triat-Laval, 1979; Nicol-Pichard, 1987; Nicol-Pichard & Dubar, 1998) would constitute potential refugial areas and the most probable origin for the post-glacial expansion of *Abies alba* throughout northern Europe (de Beaulieu *et al.*, 1984; Clerc, 1988; Brugiapaglia, 1996; Nakagawa, 1998; Terhürne-Berson *et al.*, 2004).

There may have been other glacial refugia of *Abies alba* east of the Alps, but if so they probably disappeared before the LGM, since no palaeobotanical record indicates their survival during the late-glacial (Terhürne-Berson *et al.*, 2004):

5. northern Balkans (Turk *et al.*, 1988–89; Šercelj & Culiberg, 1991; Culiberg & Šercelj, 1995; Gliemeroth, 1995), where *Abies* charcoal is found in Palaeolithic caves, and dated to 38,000 and 20,000 yr BP, respectively;

6. Moravia, in the southern Czech Republic (Willis & van Andel, 2004), where *Abies* charcoal from archaeological layers is preserved below loess deposits and dated between 43,000 and 20,000 yr BP.

Finally, an additional refugial area is suggested, but not for *Abies alba* (Terhürne-Berson *et al.*, 2004):

7. southern Spain (Pons & Reille, 1988) constitutes the most probable refugial area for the endemic *Abies pinsapo*, although no evidence has yet been found.

Late-glacial and post-glacial migration patterns

According to Terhürne-Berson *et al.* (2004) and van der Knaap *et al.* (2005), the most probable routes of migration of *Abies alba* are shown in Fig. 1b. Fir populations in the Pyrenees and Calabria are considered to have been isolated since the last glacial period. Consequently, the most likely origins for the spread of silver fir towards northern Europe are the Balkans Peninsula, the northern Apennines and, maybe, south-eastern France. This related pattern is supported by the work of van der Knaap *et al.* (2005), which, on the basis of pollen-percentage threshold values, showed a northward post-glacial migration route throughout the Alps. Genetic approaches suggest an introgression zone between the eastern and western Mediterranean areas (Konnert & Bergmann, 1995; Liepelt *et al.*, 2002), which could correspond to the contact between the lineages spreading from northern Italy and from Greece, respectively. On the other hand, the post-glacial spread throughout the western Alps was thought to originate from the northern Apennines, the Insubrian southern Alps and possibly south-eastern France (Terhürne-Berson *et al.*, 2004; Hofstetter *et al.*, 2006). Migrating from its northern Italian and Insubrian refugia, silver fir developed in the south-central Alps (Ticino, Switzerland) *c.* 10,000 cal. yr BP, and in the outer Alps (south-eastern Switzerland) around 9000 cal. yr BP (Burga, 1988; Burga & Hussendörfer, 2001). Despite the number of regional syntheses dealing with the post-glacial vegetation history of the southern French Alps (e.g. de Beaulieu, 1977; Clerc, 1988; Nakagawa, 1998), the migration of *Abies alba* is still poorly understood for this area. In particular: (1) the possible existence of glacial refugia in the south-western Alps is not yet elucidated and (2) the direction of the migration routes between the south-western and the north-western Alps remains unknown (Nakagawa, 1998).

MATERIAL AND METHODS

Palaeoecological data

The compiled pollen data set comprises 52 sites, located in the southern French Alps and adjacent hills and mountains, and nine sites in the adjacent plains (Table 1 & Fig. 2). The few computerized data were obtained from the European Pollen Database or directly from the authors. The major part of our data set (*c.* 45 sites) thus consists of published but not computerized data: the *Abies* pollen curves were extracted from published diagrams, and percentages were recalculated when sufficient information was available, with the aim of obtaining a homogeneous and reliable body of data. Pollen percentages are calculated on a pollen sum excluding Pteridophyta spores and local taxa (aquatic plants, Cyperaceae and *Alnus* in sites where its pollen is attributed to a local origin). Macrofossils are used when available to document the local presence of *Abies*.

Table 1 Holocene pollen sequences in the southern French Alps (sites 1–22), adjacent mountainous areas (sites 23–52) and adjacent plains (53–61). Reference sites (**R**, denoted in bold) and supplementary ones (S) are indicated with their respective bioclimatic ranges (Alp, alpine; Sub, subalpine; Mou, mountain) in the column 'Selection'. In the column 'Number of dates', the total number of Holocene radiocarbon dates is indicated, followed by the number of rejected dates (−*x*) and by the number of pre-Holocene ages (+*x*).

	Selection	Site	Nature of site	Longitude	Latitude	Altitude (m)	Geographical zone	Cores	Number of dates	Dating method	Reference
1		Clapeyret	Peatland	07°14′ E	44°09′ N	2260	Mercantour	CL-D38	–	–	de Beaulieu (1977)
								CL-D39	4	Bulk	–
2		Clapouse (la)	Fen	06°47′ E	44°22′ N	2100	Ubaye	CLA	3(−1?)	Bulk	Wegmüller (1977)
3	**R/Mou**	**Corréo**	Marsh	05°59′ E	44°33′ N	1090	Gapençais	**COR**	7(−1)	AMS	Nakagawa (1998)
4	**R/Alp**	**Cristol (lac)**	Lake	06°36′ E	45°00′ N	2248	Briançonnais	CRI-1	2	Bulk	Fauquette & Talon (1995), Fauquette (1995)
								CRI-2	3	AMS	Nakagawa (1998), Nakagawa *et al.* (2000)
								CRI-3	–	–	Fauquette & Talon (1995), Fauquette (1995)
5		Gourre (la)	Marsh	06°11′ E	44°23′ N	992	Gapençais	GOU-1	6(−1)	AMS	S. D. Muller (unpublished data)
6	S/Alp	Lac long inférieur	Lake	07°27′ E	44°03′ N	2093	Mercantour	LLI-1	–	–	de Beaulieu (1974)
								LLI-2	2	Bulk	–
								LLI-D26	6(−2+6)	Bulk	de Beaulieu (1977)
								LLI-D27	–	–	–
								LLI-D28	(+1)	Bulk	–
7	S/Sub	Lauzes (col des)	Lake	06°32′ E	45°46′ N	1784	Briançonnais	CDL-D21	–	–	–
								CDL-D22	4(+6)	Bulk	–
								CDL-D23	–	–	–
8		Lignin	Lake	06°43′ E	44°06′ N	2273	Haut-Verdon	LIG	2(−2)	AMS	Nakagawa (1998)
9		Miroir	Lake	06°48′ E	44°38′ N	2210	Queyras	MIR	1	AMS	–
10	S/Alp	Mouton (lac)	Lake	07°27′ E	44°03′ N	2175	Mercantour	MOU-D29	–	–	de Beaulieu (1977)
								MOU-D30	4	Bulk	–
								MOU-D31	–	–	–
11	S/Mou	Pelléautier	Marsh	06°11′ E	44°31′ N	975	Gapençais	PEL-D1	2	Bulk	de Beaulieu (1977), de Beaulieu & Reille (1983)
								PEL-D2	–	–	–
								PEL-D4	1(−1)	Bulk	–
								PEL-D5	3(+3)	Bulk	–
12		Plaine Alpe	Fen	06°35′ E	44°58′ N	1850	Briançonnais	PA	1	AMS	Muller *et al.* (2000)
13	S/Alp	Plan du Laus	Fen	06°42′ E	44°14′ N	2122	Haut-Verdon	PDL-D16	6	Bulk	de Beaulieu (1977)
14	**R/Sub**	**Pré Rond**	Fen	06°35′ E	44°55′ N	1800	Briançonnais	**PR**	4(−1)	AMS	Muller *et al.* (2000)
15		Raux	Marsh	05°56′ E	44°30′ N	1770	Gapençais	RAU	–	–	Nakagawa (1998)
16		Roche de Rame (la)	Lake	06°35′ E	44°44′ N	950	Embrunnais	RDR-D20	–	–	de Beaulieu (1977)
17		Sabion	Marsh	07°28′ E	44°08′ N	2216	Mercantour	SAB-D33	1	Bulk	–

Table 1 continued

	Selection	Site	Nature of site	Longitude	Latitude	Altitude (m)	Geographical zone	Cores	Number of dates	Dating method	Reference
18		Siguret	Lake	06°33′ E	44°47′ N	1066	Embrunnais	SIG-D17	–	–	–
								SIG-D18	1(+1)	Bulk	de Beaulieu (1977), de Beaulieu & Reille (1983)
								SIG-D19	2	Bulk	–
								SIG-1980	1(+6)	Bulk	de Beaulieu & Reille (1983)
19	**R/Mou**	**St-Léger**	Lake	06°20′ E	44°25′ N	1308	Gapençais	SL-D9	3	Bulk	de Beaulieu (1977)
								SL-D10	5	Bulk	–
								SL-D11	1	Bulk	–
								SL-B135m	12(−1)	AMS	Digerfeldt *et al.* (1997)
20		Vallon du Loup	Fen	06°24′ E	44°24′ N	2010	Ubaye	VDL-D15	–	–	de Beaulieu (1977)
21	S/Alp	Vallon de Provence	Fen	06°24′ E	44°23′ N	2075	Ubaye	VDP-D12	1(+1)	Bulk	–
								VDP-D13	6	Bulk	–
22		Vars (col de)	Lake	06°43′ E	44°33′ N	2070	Embrunnais	VAR-D25	2	Bulk	de Beaulieu (1977)
23		Alpe de Vénosc	Fen	06°09′ E	44°58′ N	1644	Oisans	ADV	–	–	Coûteaux (1962)
24		Besset (le)	Fen	06°28′ E	45°11′ N	1834	Maurienne	BES	3(−1)	Bulk	Wegmüller (1977)
25		Boites	Lake	05°53′ E	45°03′ N	1560	Taillefer	BOI	–	–	Nakagawa (1998)
26		Brande	Peatland	06°08′ E	45°05′ N	1820	Oisans	BRA	–	–	Coûteaux (1982a, 1984
27		Canard (lac)	Peatland	05°57′ E	45°04′ N	2055	Taillefer	CAN-1A	5(−2?)	Bulk	Ponel *et al.* (1992)
28		Chirens	Bog	05°34′ E	45°25′ N	460	Chartreuse	CHI-2a	1	Bulk	Wegmüller (1977)
								CHI-2b	3	Bulk	–
29		Deux-Alpes	Peat	06°09′ E	45°05′ N	1650	Romanche	DA	–	–	Coûteaux (1983a)
30		Faudon (lac de)	Lake	06°13′ E	44°36′ N	1577	Champsaur	FAU	9	AMS	M. Court-Picon (unpublished data)
31	S/Mou	Forest en Dévoluy	Fen	05°54′ E	44°45′ N	1460	Dévoluy	FED-D8	5(+1)	Bulk	de Beaulieu (1977)
								FED	3(+1)	Bulk	Wegmüller (1977)
32		Fourchu (lac)	Peatland	05°56′ E	45°03′ N	1070	Taillefer	FOU	3	Bulk	Ponel *et al.* (1992)
33	**R/Sub**	**Gouille (la)**	Peatland	06°12′ E	45°26′ N	1800	Belledonne	**GO-1**	3	AMS	David (2001)
								GO-2	6	AMS	–
34		Grand Lemps	Pond	05°25′ E	45°28′ N	500	Terres-Froides	GL-1	–	Bulk	Clerc (1988)
								GL-2	6	Bulk	–
								GL-3	5(−1)	Bulk	–
								GL-4	1(−1)	Bulk	–
35		Grand Ratz	Marsh	05°36′ E	45°20′ N	650	Chartreuse	GR	5(−1)	Bulk	–
36		Gypsières (les)	Fen	06°24′ E	45°04′ N	2500	Maurienne	GYP	–	–	Wegmüller (1977)
37		Laux du Villardon (le)	Pond	06°03′ E	44°44′ N	1090	Champsaur	LDV	7(−2)	AMS	Pothin (2000)
38		Lauza (le)	Fen	06°13′ E	44°39′ N	1140	Champsaur	LAU-1	3	Bulk	Wegmüller (1977)
								LAU-2	8(−1)	AMS	M. Court-Picon (unpublished data)
39	**R/Alp**	**Lauzons (lac des)**	Fen	06°17′ E	44°47′ N	2180	Champsaur	**LDL**	11(−1)	AMS	–
40		Libouse	Meadow	06°13′ E	44°38′ N	1455	Champsaur	LIB	9	AMS	–

Table 1 continued

	Selection	Site	Nature of site	Longitude	Latitude	Altitude (m)	Geographical zone	Cores	Number of dates	Dating method	Reference
41	S/Mou	Luitel (col)	Bog	05°60′ E	45°05′ N	1250	Taillefer	LUI	3	Bulk	Wegmüller (1977)
42	**R/Mou**	**Montsec**	Marsh	05°48′ E	45°14′ N	1130	Taillefer	MON-1	–	–	Nakagawa (1998)
								MON-2	5	AMS	–
43		Muzelle (la)	Peatland	06°06′ E	44°57′ N	2140	Oisans	MUZ	–	–	Coûteaux (1982b, 1983b
44	**R/Mou**	**Peuil**	Bog	05°39′ E	45°07′ N	970	Vercors	**PEU**	3(+1)	AMS	Nakagawa (1998)
45	**R/Alp**	**Plan des Mains**	Marsh	06°35′ E	45°21′ N	2080	Maurienne	**PDM**	5(−1)	Bulk	David (1995b, 1997)
									8	AMS	David (1997)
46	**R/Mou**	**Praver**	Lake	05°51′ E	45°04′ N	1170	Taillefer	**PRA**	7	AMS	Nakagawa (1998)
47	**R/Alp**	**Pré Bérard**	Fen	06°30′ E	45°14′ N	2020	Maurienne	**PB**	3	AMS	David & Barbero (2001)
48	S/Mou	Sagne de Canne	Fen	06°06′ E	44°37′ N	1270	Champsaur	SDC	7	AMS	M. Court-Picon (unpublished data)
49	S/Alp	Soie (la)	Peatland	06°27′ E	45°09′ N	2110	Maurienne	SOI	5(−1)	Bulk	Wegmüller (1977)
50		St-Hilaire-du-Rosier	Marsh	05°19′ E	45°08′ N	190	Vercors	SHR	(+2)	Bulk	Clerc (1985, 1988)
51		St-Julien-de-Ratz	Lake	05°37′ E	45°21′ N	650	Chartreuse	SJR-1	2(+2)	Bulk	–
								SJR-2	5(−3)	Bulk	Clerc (1988)
52	S/Mou	St-Sixte	Pond	05°37′ E	45°27′ N	650	Chartreuse	SSI-1	3	Bulk	Clerc (1985, 1988)
								SSI-2	4(−1)	Bulk	Clerc (1988)
53		Baux de Provence	Marsh	04°48′ E	43°41′ N	2	Rhone valley	D9	–	–	Triat-Laval (1979)
								D10	6(−1)	Bulk	–
54		Beauchamp-Panières	Marsh	04°53′ E	43°32′ N	45	Rhone valley	D5	–	–	–
								D6	(+1)	Bulk	–
								D7	4(−1+4)	Bulk	–
55		Berre (Pointe de)	Lagoon	05°09′ E	43°27′ N	1.5	Rhone valley	D26	5(−4?)	Bulk	–
								D27	–	–	–
56		Biot	Estuary	07°07′ E	43°38′ N	?	Côte d'Azur	Biot-D1	6(−1?)	Bulk	Nicol-Pichard & Dubar (1998)
57		Courthezon	Marsh	04°52′ E	44°05′ N	32	Rhone valley	D1	–	–	Triat-Laval (1979)
								D2	5(+2)	Bulk	–
58		Frignants	Lagoon	04°29′ E	43°31′ N	0.7	Rhone delta	D23	4(+2)	Bulk	–
59		Meyranne	Marsh	04°43′ E	43°37′ N	2	Rhone valley	D15	–	–	–
								D16	3	Bulk	–
60		Molleges	Marsh	04°56′ E	43°37′ N	50	Rhone valley	D8	1(+1)	Bulk	–
61		Tourves	Marsh	05°56′ E	43°25′ N	298	Provence	Tourves	5(−1+3)	Bulk	Nicol-Pichard (1987)

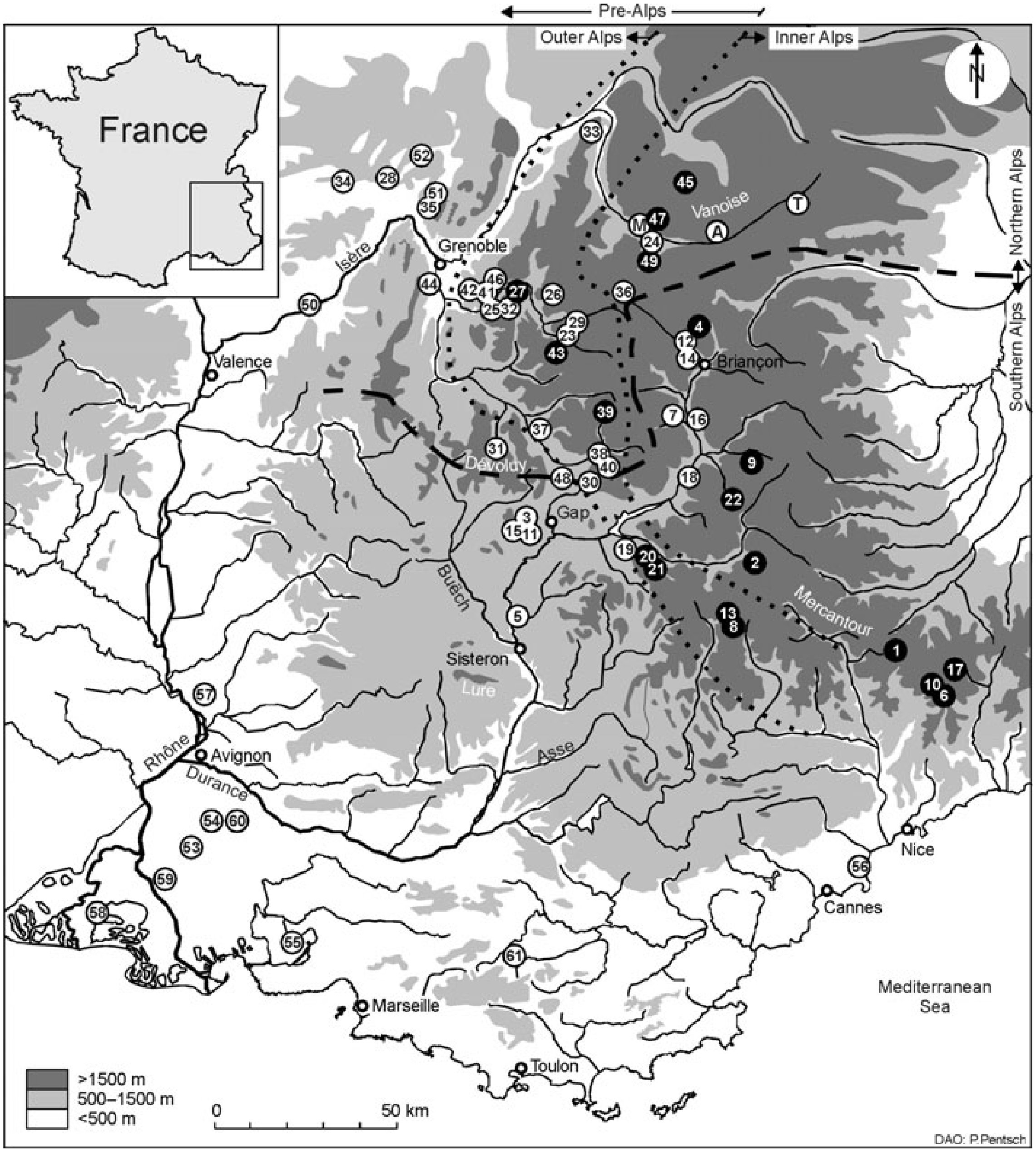

Figure 2 Location of sites in the south-western Alps and adjacent areas. Site numbers refer to Table 1, except the sites denoted A (Aussois), M (St-Michel-de-Maurienne) and T (travertine sequences of St-Génix and Termignon). Sites located above 2000 m a.s.l., i.e. above the present-day tree line, are noted in white on black.

Chronological control

The chronological setting of the study is provided by 290 ^{14}C dates performed on sedimentary sequences (see Appendix S1 in Supplementary Material), four U/Th dates and 14 ^{14}C dates performed on travertine deposits and on charcoal from soils, respectively (Table 2). As for pollen data, radiocarbon dates were obtained partly from the authors directly and partly from previously published papers, which did not always give all the relevant information. Among the 52 pollen sequences available in the study area, only 44 have at least one radiocarbon date, often of variable quality. Consequently, we first selected a reference body of high-quality sequences, by excluding: (1) sequences dated on bulk sediments, because the use of uncontrolled dated material may result in dating errors caused by hard-water effects, and (2) those with fewer than three radiocarbon dates or an incomplete Holocene record. The so-defined reference body contains 11 pollen sequences, characterized by a consistent accelerator mass spectrometry (AMS) radiocarbon dating carried out on terrestrial plant macrofossils. Second, this reference body is compared with 11 supplementary sites, well dated on bulk sediments, in order to

Table 2 U/Th ages of travertine sequences containing *Abies* remains (St-Génix, Termignon) and ^{14}C ages of *Abies* charcoals from soils in Savoie, northern French Alps (St-Michel-de-Maurienne, Aussois; from Carcaillet, 1996; Carcaillet & Muller, 2005).

Site	Longitude	Latitude	Altitude (m)	Laboratory code	Level/depth	Measured age (yr BP)	Calendar age (cal. yr BP)
Aussois 1	45°15′ N	06°45′ E	1750	Lyon-870(OxA)	15–30 cm	3675 ± 55	3842–4149
				AA-20464	15–30 cm	1025 ± 100	733–1170
Aussois 4	45°15′ N	06°45′ E	1900	Lyon-871(OxA)	30–50 cm	4730 ± 45	5324–5586
				Lyon-872(OxA)	30–50 cm	3990 ± 40	4301–4568
				Lyon-873(OxA)	30–50 cm	3745 ± 45	3932–4238
Maur 6	45°15′ N	06°30′ E	1770	Lyon-865(OxA)	20–40 cm	4040 ± 55	4407–4811
				Lyon-866(OxA)	40–60 cm	4605 ± 45	5052–5467
				Lyon-867(OxA)	60–85 cm	6070 ± 50	6753–7155
				Lyon-868(OxA)	60–85 cm	5550 ± 55	6204–6445
				AA-14776	90–120 cm	5590 ± 65	6209–6500
Maur 13	45°15′ N	06°30′ E	1770	Lyon-1078(OxA)	35–40 cm	4100 ± 50	4444–4821
				Lyon-302(OxA)	45–60 cm	3580 ± 65	3692–4083
				Lyon-869(OxA)	65–80 cm	4455 ± 55	4873–5292
				AA-20476	110–130 cm	3800 ± 65	3988–4407
St-Génix	45°17′ N	06°55′ E	1695	Ifm-Geomar, Kiel	A-3	7908 ± 195	7713–8103
				Ifm-Geomar, Kiel	A-9	5300 ± 133	5167–5433
				Ifm-Geomar, Kiel	B-4	3025 ± 149	2876–3174
Termignon	45°18′ N	06°49′ E	1537	Ifm-Geomar, Kiel	3–2	6010 ± 350	5660–6360

refine the geographical coverage. The remaining poorly dated sites are used to verify the consistency of the regional vegetation dynamics.

Because the varying duration of the ^{14}C year is likely to bias the interpolation of conventional radiocarbon ages, the chronology used is only based on calibrated radiocarbon dates. Despite the above-mentioned problems, conventional ages (uncalibrated ^{14}C years) are still commonly used, even in broad-scale syntheses based on between-site correlations (e.g. Terhürne-Berson *et al.*, 2004). Calibrated ages (cal. yr BP) are computed with the CALIB 5.0 program (Stuiver & Reimer, 1993), using the calibration data set INTCAL04.14C (Reimer *et al.*, 2004) (Table 3). Age-depth models (Fig. 3) were constructed by interpolating the simplest curve connecting calibrated dates within the 2-sigma confidence intervals (smooth spline interpolation; Guiot & Goeury, 1996). They integrate stratigraphic changes, which may result in abrupt variations in sedimentation rate. Confidence intervals, taking into account the thickness of dated levels, are interpolated to all samples of each pollen sequence, in order to evaluate the influence of radiocarbon age uncertainties on the precision of the reconstruction (Davis *et al.*, 1986).

Phases of *Abies* migration from pollen data

Watts (1973), Birks (1986), Lang (1992) and van der Knaap *et al.* (2005) discuss the interpretation of the different phases of tree migration from pollen-stratigraphic patterns. According to these authors, we can pinpoint the three following phases in *Abies* pollen curves: (1) approaching area limit, corresponding to the first scattered occurrences (less than 1%), (2) immigration (i.e. first arrival) and establishment of fir populations, corresponding to the beginning of the continuous curve, often combining around 1% occurrences, and (3) expansion of fir populations, corresponding to the beginning of the strong increase in pollen percentages.

Low percentages may cause problems in interpretation, notably due to their high sensitivity to the size of the pollen sum, counting errors, long-distance transport and possible contamination (van der Knaap *et al.*, 2005). Furthermore, rare or scattered trees, whose local past presence is evidenced by dated macroremains, can escape detection by pollen (Kullman, 1996, 1998, 2002; Ali *et al.*, 2003, 2005; Brubaker *et al.*, 2005; Tinner & Lotter, 2006). The ages interpolated for the approaching area limit are thus more questionable than the ones proposed for the subsequent phases. Moreover, local- and stand-scale parameters, e.g. altitude, size of the lake or peat basin, and local vegetation structure, may create variance between pollen records. Indeed, large basins and sites located above the tree line record much better the regional vegetation than small basins and sites at lower altitudes, which essentially trap a more local pollen rain (Jacobson & Bradshaw, 1981; Muller *et al.*, 2006). To sum up, the interpretation is adapted to each diagram and problematic ages are excluded.

RESULTS

Approaching area limit

The first scattered pollen occurrences may be interpreted as the approaching area limit of silver fir (Figs 4 & 5). The earliest are recorded around 11,000 cal. yr BP in southern Mercantour and Grenoble Pre-Alps, i.e. at both extremities of the southern French Alps (Fig. 6). The important uncertainties of the related radiocarbon ages, ranging from ±280 to ±680 years,

Table 3 Calibrated radiocarbon dates for selected sites: reference ones (bold print) and supplementary ones (normal print).

	Site	Core	Depth (cm)	Sample code	^{14}C age (yr BP)	Calibrated interval 2σ	Used age (cal. yr BP)
3	**Corréo**	**COR**	177.5	GrA-6601	2580 ± 80	2370–2850	2850
			301–302.5	GrA-7789	5450 ± 80	6000–6400	6400
			390	GrA-6612	5810 ± 80	6410–6790	6790
			530.5–534.5	GrA-6602	7110 ± 80	7750–8150	8150
			579–582	GrA-6595	7550 ± 80	8180–8520	8520
			649–652	GrA-6607	9670 ± 90	10750–11230	11230
			713.5–720.5	GrA-6597	9220 ± 480	9150–11970	Reject
4	**Cristol (lac)**	CRI-1	40–50	Ly-6109	1970 ± 65	1740–2110	2110
			60–70	Ly-6110	2500 ± 80	2360–2740	2740
		CRI-2	67.5–70	GrA-6611	5040 ± 80	5610–5920	5610
			102.5–105	GrA-6613	6380 ± 90	7030–7470	7470
			117.5–120	GrA-6609	7910 ± 80	8560–9000	8780
31	Forest en Dévoluy	FED-D8	60–65	Ly-1144	5100 ± 150	5580–6270	5925
			120–125	Ly-1143	7570 ± 190	7980–8970	8600
			125–135	Ly-782	8310 ± 180	8720–9630	9000
			138–143	Ly-1142	8440 ± 320	8610–10210	9600
			145–155	Ly-781	9220 ± 220	9770–11100	10435
			170–175	Ly-780	10850 ± 300	11830–13360	12595
33	**Gouille (la)**	**GO-1**	102	AA-20086	2490 ± 120	2310–2840	2575
			180	AA-20085	3950 ± 60	4160–4570	4365
			220	AA-20084	4715 ± 70	5320–5590	5455
		GO-2	170	AA-20083	6200 ± 70	6910–7270	7090
			200	AA-20082	8105 ± 75	8730–9280	8730
			240	AA-20080	8190 ± 85	9000-9430	9215
			256	AA-20081	8325 ± 80	9090–9490	9400
			290	AA-20079	8715 ± 75	9530–10120	9825
			388	AA-20078	9640 ± 170	10440–11600	11020
6	Lac long inférieur	LLI-D26	40–45	Ly-1244	2660 ± 190	2330–3320	2825
			60–65	Ly-1243	3740 ± 160	3640–4530	4085
			80–85	Ly-1242	4770 ± 300	4650–6200	5425
			100–105	Ly-1241	5670 ± 170	6020–6890	6890
			130–135	Ly-1240	8730 ± 220	9270–10370	9270
			140–145	Ly-1239	9330 ± 220	9930–11210	9930
			212–217	Ly-1208	11270 ± 230	12830–13610	Reject
			217–225	Ly-1207	10430 ± 210	11410–12840	12840
			225–235	Ly-1206	10970 ± 370	11820–13660	13300
			235–245	Ly-1205	12040 ± 370	13220–15070	13700
			245–255	Ly-1237	12170 ± 280	13460–15010	14200
			255–265	Ly-1236	12510 ± 370	13670–15700	15000
			266–278	Ly-1235	13460 ± 410	14790–17210	16000
7	Lauzes (col des)	CDL-D22	45–50	Ly-1234	2980 ± 130	2810–3450	2810
			190–195	Ly-1279	5680 ± 170	6020–6890	6455
			280–285	Ly-1280	7510 ± 150	8010–8590	8590
			373–378	Ly-1281	9860 ± 200	10710–12040	11375
39	**Lauzons (lac des)**	**LDL**	18–19	AA-46928	729 ± 50	560–720	640
			22–23	AA-46929	929 ± 31	740–930	835
			29–30	AA-46930	1249 ± 32	1070–1270	1170
			34–35	AA-46931	1947 ± 46	1800–1980	1890
			44–45	AA-46933	2949 ± 53	2940–3260	3100
			60–61	AA-46934	4136 ± 52	4450–4830	4640
			77–78	AA-46935	5547 ± 65	6200–6330	6460
			96–97	AA-46937	5242 ± 55	5910–6180	Reject
			117–118	AA-46938	7679 ± 58	8340–8550	8445
			124–125	AA-46939	8007 ± 46	8610–8990	8800
			142–144	AA-46940	9701 ± 71	10490–11000	10745

Table 3 continued

	Site	Core	Depth (cm)	Sample code	^{14}C age (yr BP)	Calibrated interval 2σ	Used age (cal. yr BP)
42	**Montsec**	**MON-2**	45.5–49.5	GrA-7790	450 ± 50	320–620	620
			90.5–92.5	GrA-7791	1850 ± 60	1620–1920	1920
			145.5–149.5	GrA-6599	7560 ± 90	8190–8540	8190
			246–249	GrA-7792	8830 ± 100	9560–10190	10190
			310	GrA-6600	9940 ± 140	11100–12000	11550
10	Mouton (lac)	MOU-D30	55–60	Ly-247	3000 ± 190	2750–3610	3180
			115–120	Ly-1249	8220 ± 200	8610–9540	8610
			125–130	Ly-1248	7930 ± 170	8410–9250	9250
			200–205	Ly-1246	9340 ± 240	9920–11230	10570
44	**Peuil**	**PEU**	50.5–54.5	GrA-6585	6810 ± 80	7510–7830	7670
			75.5–79.5	GrA-6590	8120 ± 90	8720–9400	9400
			105.5–109.5	GrA-6610	9670 ± 90	10750–11230	10750
			224	GrA-6584	11230 ± 90	12940–13270	13105
13	Plan du Laus	PDL-D16	240–250	Ly-995	5820 ± 150	6300–6980	6300
			305–325	Ly-960	7310 ± 140	7860–8390	8000
			450–455	Ly-996	8630 ± 200	9140–10220	9200
			460–465	Ly-997	8320 ± 180	8730–9660	9400
			510–520	Ly-998	8970 ± 210	9540–10570	10055
			570–590	Ly-961	8820 ± 370	9000–11070	10800
45	**Plan des Mains**	**PDM**	70	AA-15114	2455 ± 60	2360–2710	2535
			78–80	AA-15115	2740 ± 60	2750–2960	2855
			96	AA-15116	3330 ± 60	3410–3700	3700
			107–108	AA-15117	4025 ± 65	4300–4810	4300
			123	A-7942	4345 ± 260	4240–5590	Not used
			152	AA15118	5502 ± 95	6010–6490	6200
			170	A-7943	6765 ± 230	7170–8040	Not used
			196	A-7944	8450 ± 290	8650–10190	Not used
			210	A-7945	9900 ± 420	10290–12690	Reject
			220	AA-15119	8515 ± 90	9300–9690	9300
			239	AA-15120	8870 ± 100	9630–10220	9800
			244	A-7941	8825 ± 650	8350–11810	Not used
			259	AA-15121	9100 ± 100	9920–10550	10550
46	**Praver**	**PRA**	197.5	GrA-6580	810 ± 80	570–920	920
			231–234	NUTA-	1520 ± 120	1180–1700	1180
			327	GrA-6582	2060 ± 80	1830–2300	2065
			603	GrA-6586	4540 ± 80	4890–5460	5175
			795	GrA-6608	7830 ± 320	8040–9440	8740
			815.5–819.5	GrA-6588	8520 ± 90	9300–9700	9300
			893–897	GrA-6587	9460 ± 90	10440–11100	10770
47	**Pré Bérard**	**PB**	255	Ly-404	5850 ± 55	6500–6780	6500
			440	Ly-405	7490 ± 60	8190–8400	8400
			525	Ly-406	8660 ± 65	9530–9890	9710
14	**Pré Rond**	**PR**	92	Lyon-648	3965 ± 50	4250–4570	4500
			115	Poz-10818	4660 ± 40	5310–5570	5500
			136–140	Poz-10819	7900 ± 50	8590–8980	Reject
			160	Lyon-649	7660 ± 65	8360–8590	8475
48	Sagne de Canne	SDC	26–27	AA 50236	1083 ± 32	930–1060	1060
			34–35	AA 50235	1888 ± 35	1720–1920	1720
			46–47	AA 50234	2179 ± 35	2070–2320	2320
			59–60	AA 50233	3378 ± 37	3480–3700	3480
			79–80	AA 50232	3996 ± 38	4320–4770	4770
			94–95	AA 50231	6736 ± 45	7510–7670	7510
			119–120	AA 50230	7858 ± 58	8520–8980	8750
49	Soie (la)	SOI	70	B-2462	3050 ± 100	2960–3450	3205
			120	B-2461	3290 ± 120	3260–3830	Reject
			170	B-2460	6790 ± 110	7440–7910	7600

Table 3 continued

	Site	Core	Depth (cm)	Sample code	^{14}C age (yr BP)	Calibrated interval 2σ	Used age (cal. yr BP)
			220	B-2459	7670 ± 110	8200–8720	8600
			290	B-2458	8950 ± 130	9610–10380	9995
19	**St-Léger**	**SL-B135m**	260.0	Ua-4127	970 ± 65	730–1050	890
			342.5	Ua-4126	1195 ± 70	970–1270	1270
			402.5	Ua-4125	1665 ± 60	1410–1700	1700
			462.5	Ua-4124	2490 ± 65	2360–2730	2360
			612.5	Ua-4123	3405 ± 65	3480–3830	3830
			625.0	Ua-4140	3650 ± 80	3720–4230	3975
			652.5	Ua-4139	4860 ± 85	5330–5860	Reject
			715.0	Ua-4138	4580 ± 80	4970–5580	5400
			745.0	Ua-4137	5220 ± 105	5740–6270	6270
			767.5	Ua-4122	6920 ± 65	7620–7930	7620
			777.5	Ua-4136	7255 ± 90	7880–8310	8310
			800.0	Ua-4135	8975 ± 105	9700–10370	10035
21	Vallon de Provence	VDP-D13	140–150	Lv-840	3840 ± 70	4000–4420	4210
			235–245	Lv-841	5680 ± 70	6320–6630	6320
			280–290	Lv-842	6010 ± 110	6570–7170	6900
			360–370	Lv-843	7080 ± 75	7730–8020	8020
			385–390	Lv-844	7880 ± 120	8430–9010	8600
			453–458	Ly-1284	9750 ± 200	10560–11950	11255

prevent us from detecting an obvious geographical pattern for this phase.

Immigration phase

The immigration of silver fir is first recorded immediately prior to 10,000 cal. yr BP, both in southern Mercantour and in the Grenoble Pre-Alps (Figs 5 & 6). Macroremains indicate the local presence of *Abies* since 9300 cal. yr BP near Grenoble, 8700 cal. yr BP on the Belledone Massif, 8500 cal. yr BP in the Middle Durance Valley and 7900 cal. yr BP in the Maurienne Valley (Tables 3 & 4). The immigration phase spans *c.* 1000 years, not only within the whole study area but also within small regions such as the Middle Durance, the Grenoble Pre-Alps and the Maurienne Valley. The approximate synchronicity of records both in the north and the south of the western Alps does not provide evidence for obvious migration routes (Fig. 7).

Expansion phase

The first development of dense fir forests, recorded in the different zones of the outer French Alps between 9600 and 9000 cal. yr BP, appears to have been relatively synchronous based on the reliability and precision of the chronologies (Fig. 6). Here, the lack of a clear geographical pattern is likely to result from the expansion of already present populations established during the *immigration phase.* The build-up of the fir population is thus mainly controlled by local ecological conditions. However, two sequences located in the high Durance Valley (Col des Lauzes, Pré Rond; numbers 7 and 14, Fig. 2) suggest a later expansion of fir populations beginning around 6600–6500 cal. yr BP. This is supported by the late ages obtained on *Abies* macroremains in the Guisane Valley (5500 and 4700 cal. yr BP; Table 4). This indicates a delay of several millennia in the spread of fir forests in the central part of the dry continental western Alps.

DISCUSSION

Testing the hypothesis of glacial refugia of fir in the south-western Alps and adjacent areas

Several glacial refugia of *Abies* have been postulated in south-eastern France based on pollen occurrences: (1) in the Maritime Alps (de Beaulieu, 1974; Nicol-Pichard & Dubar, 1998; Terhürne-Berson *et al.*, 2004), (2) on coastal palaeoval-leys close to the Rhone Delta (Triat-Laval, 1979, 1982), (3) in eastern Provence (Nicol-Pichard, 1987), and (4) in the Grenoble Pre-Alps (Clerc, 1988).

As noted by Nakagawa (1998), the lack of synchronicity in the spread of fir between the French Alps and the Massif Central, where it developed after 7000 cal. yr BP (de Beaulieu *et al.*, 1984), implies that the Rhone Valley constituted a geographical barrier to its progression and suggests it is highly improbable that refugia persisted at low altitudes, within its alluvial basin and in the adjacent plains of Provence (Fig. 2). The discontinuous occurrences of *Abies* pollen (Table 4) recorded in the low Rhone Valley (Triat-Laval, 1979) and in Provence (Nicol-Pichard, 1987) during the late-glacial period consequently do not provide evidence for regional refugia. The record at Biot (number 56, Fig. 2) could indicate the persistence of fir in lower valleys of the Mediterranean coastal rivers (Nicol-Pichard & Dubar, 1998). However, its expansion is dated there around 9500–9030 cal. yr BP, which would imply

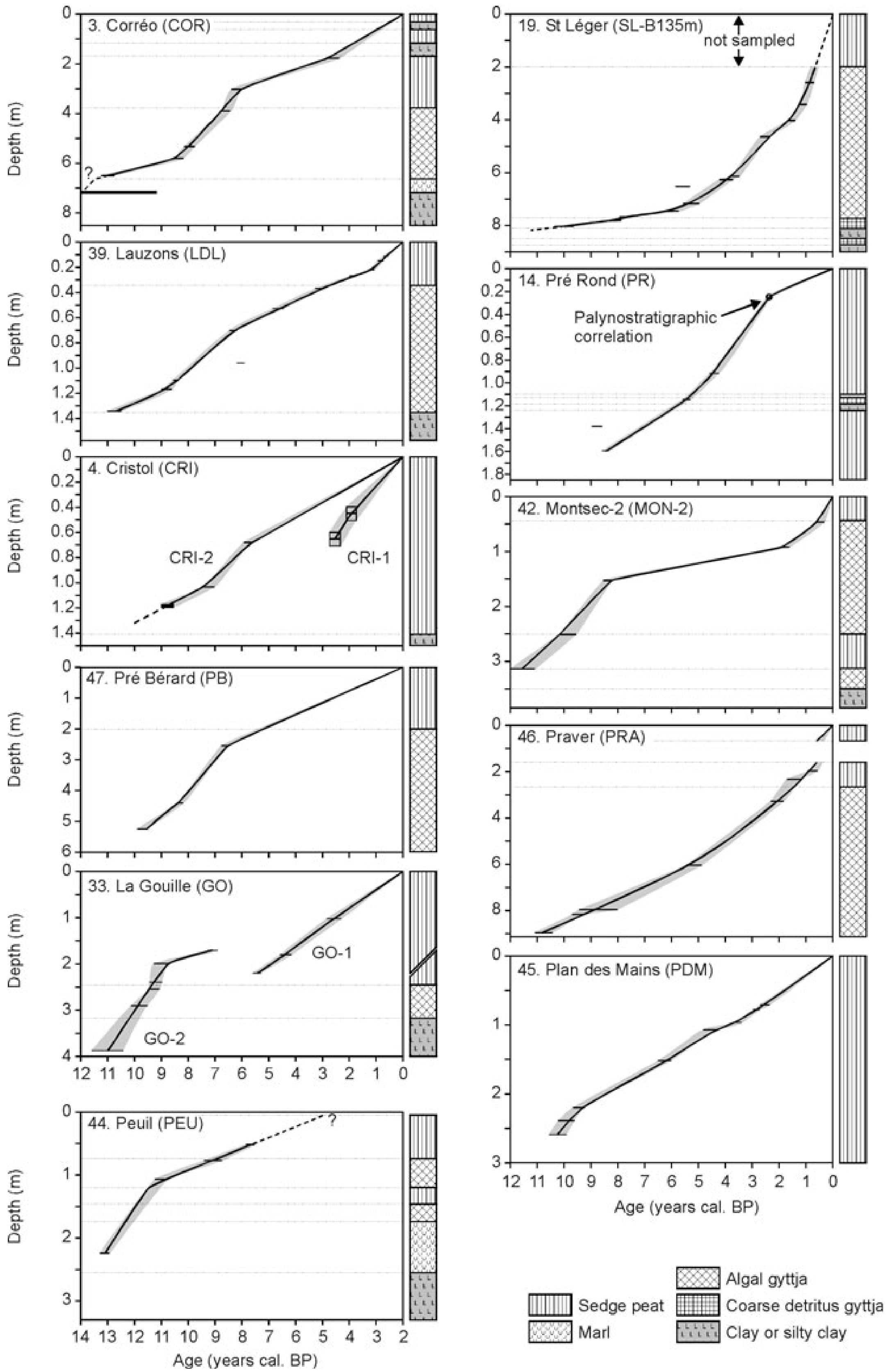

Figure 3 Age-depth models for selected well-dated sites in the south-western Alps and adjacent areas. Error bars correspond to the 2-sigma confidence intervals (95.4%). All time scales span from 12 to 0 cal. ka BP, except for the Peuil site.

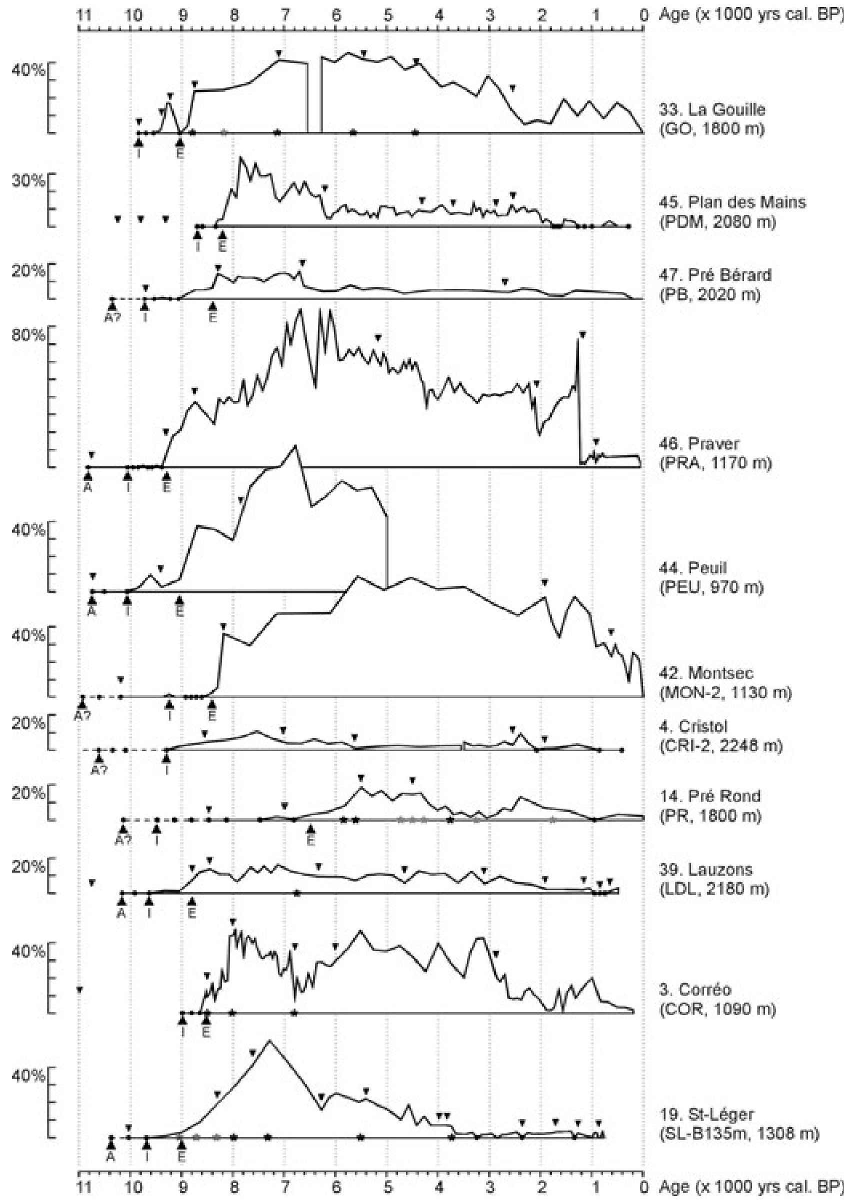

Figure 4 Pollen and macrofossil records of *Abies* in selected sites in the south-western Alps and adjacent areas, dated by AMS of terrestrial plant macroremains. Triangles indicate radiocarbon dates. Macroremains are indicated by asterisks. Arrows and letters noted below the curves indicate the main steps of *Abies* migration: A, approaching area limit; I, migration (= first arrival); E, expansion (= population built up). Pollen percentages are based on a 100% sum excluding fern spores, Cyperaceae and aquatic taxa, and *Alnus* for COR and MON-2.

a non-equilibrium response to climate change, since the temperature increase was shown to occur 1 millennium before (Digerfeldt *et al.*, 1997; Davis *et al.*, 2003). With regard to the absence of a late-glacial diffusion of *Abies* in the French Mediterranean regions, its late expansion at Biot suggests arrival from Italy.

In the southern French Alps, the late-glacial sequences show sporadic and irregular occurrences of *Abies* pollen (Table 4). Recently, Terhürne-Berson *et al.* (2004) consider that the pollen of *Abies* found at the base of the first, poorly dated pollen sequences from Lac Long Inférieur (LLI-1 and LLI-2; de Beaulieu, 1974; Table 4) indicates a glacial refugium in southern Mercantour. This reinterpretation surprisingly does not take into account the later work of de Beaulieu (1977), which clearly shows, on the basis of supplementary pollen analyses (LLI-D26 to LLI-D28; Table 4), that the previous late-glacial pollen records resulted from contamination and that *Abies* did not persist during the LGM in altitudinal zones of the French Maritime Alps. The most continuous late-glacial records of *Abies* pollen in the southern French Alps are those of Pelléautier and la Roche de Rame, located in the middle Durance Valley (central part of the western Alps). However, in the first site, only one core among five shows any pre-Holocene pollen occurrences of *Abies*, and both sites are surrounded by others with no or only discontinuous late-glacial pollen records of fir (Table 4), which also eliminates the middle Durance as a potential refugial area.

Finally, in the northern French Alps, the results obtained by Nakagawa (1998) show similar, irregular late-glacial records of *Abies* pollen and do not justify the regional fir refugia postulated in the Grenoble Pre-Alps by Clerc (1988) and de Beaulieu *et al.* (1992). No macroremains from peat or lake sediments, plant imprints from travertine or charcoal from soil support the existence of *Abies* refugia in the western Alps and

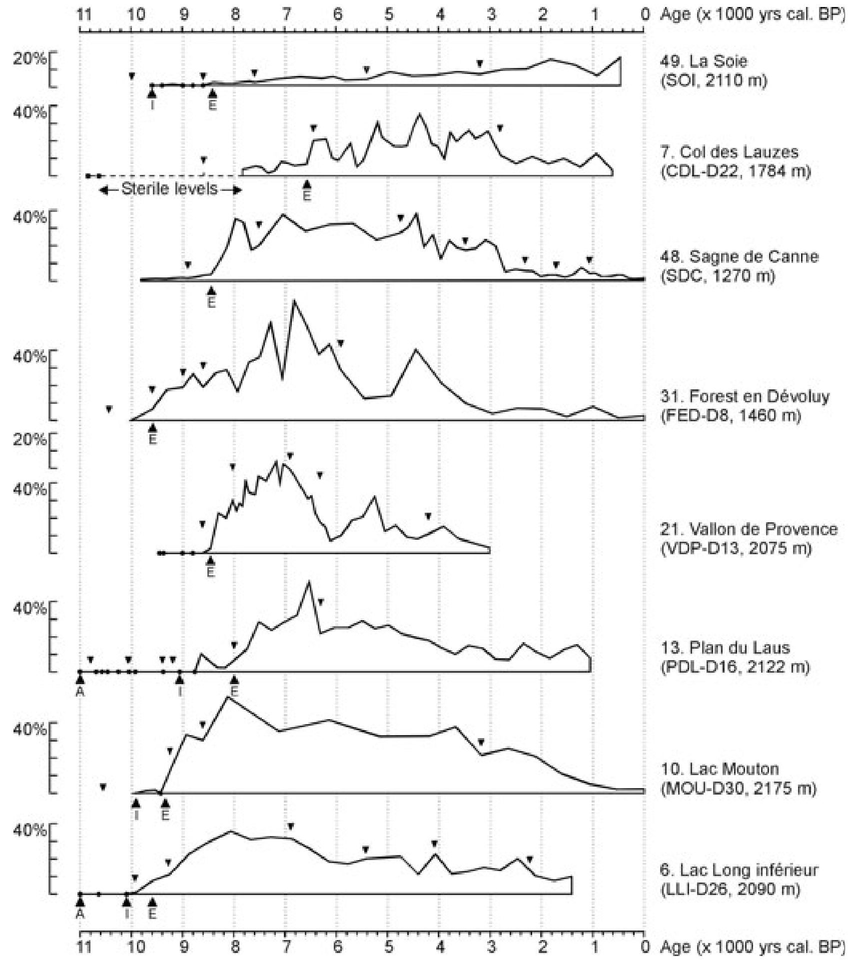

Figure 5 Pollen records of *Abies* in selected bulk-dated sites of the southern French Alps and adjacent areas. Symbols as in Fig. 4.

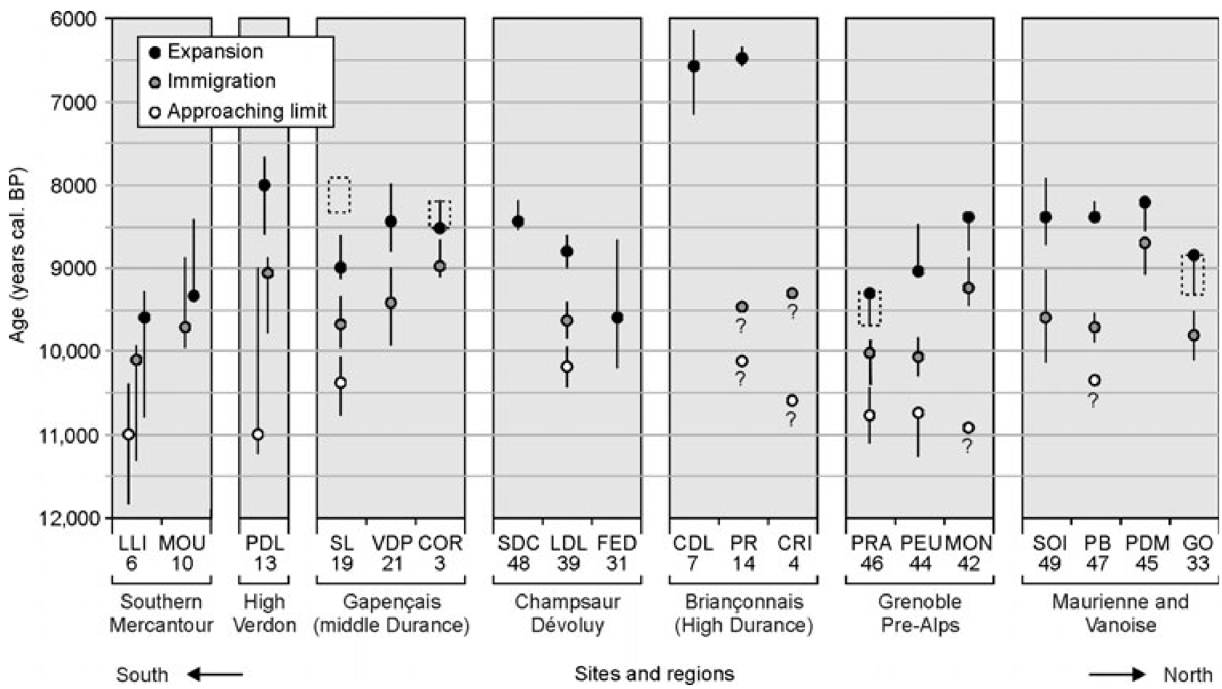

Figure 6 Pattern of *Abies* migration in the southern French Alps. Radiocarbon dates performed on *Abies* macroremains are circled by a dashed line. The code and the reference number of the sites are noted below the diagrams. The interrogation points (?) indicate the ages obtained by extrapolation, with the aim of distinguishing these from those obtained by interpolation.

Table 4. Pollen occurrences of *Abies* in late-glacial sequences of south-western Alps and adjacent Mediterranean regions. The number of open dots corresponds to the number of pollen occurrences, three dots meaning three and more than three occurrences. Grey shading indicates periods for which evidence was recorded.

	Sites	Old Dryas	Bölling	Alleröd	Younger Dryas	Pre-boreal
South-western Alps						
7	CDL-D21	○				
	CDL-D22					
	CDL-D23					
3	COR		○○			
4	CRI-1				○	
	CRI-2					○
5	GOU-1		○○			
6	LLI-D26					○
	LLI-D27			○		
	LLI-D28					○
10	MOU-D29					○○○
13	PDL-D16					
11	PEL-D2					○○○
	PEL-D3	○○	○	○		○
	PEL-D5					
	PEL-D6					
	PEL-D7					
16	RDR-D20	○○	○○○	○		○○○
18	SIG-D17		○○○			
	SIG-D19					○
19	SL-D9	○			○	○○
	SL-D11			○○	○	
20	VDL-D15					
21	VDP-D12					
	VDP-D13					
Mediterranean region						
53	Baux					○
54	Beauchamp			○		
55	Berre					○
56	Biot			○	○○○	○○○
57	Courthezon					
58	Frignants					○○
59	Meyranne					○○○
60	Molleges					○
61	Tourves			○○○	○○○	○○○

adjacent regions east of the Rhone Valley. Late-glacial pollen occurrences of *Abies* in the southern French Alps should therefore be considered as resulting from long-distance transport from the northern Apennines refugia (central Italy) or reworking from older sediments. Consequently, the regular pollen record of *Abies*, from 10,000 years ago in the western Alps (David, 1995a,b; Digerfeldt *et al.*, 1997; Nakagawa, 1998), would reflect its spread from Italian refugia. The consistent patterns of approaching area limit and immigration (Fig. 6), which show the earliest records in both the northern and southern extremities of the western Alps, suggest its arrival from distant regions.

The pattern and dynamics of fir migration in the south-western Alps

As mentioned above, the important uncertainties concerning the oldest radiocarbon dates and the rarity of well-dated sites present serious difficulties in reconstructing the geographical pattern of *Abies* migration at the regional scale. However, the data presented allow us to establish some general features and to propose some hypotheses.

The oldest pollen records of *approaching area limit* and *immigration* of *Abies* are located both at the southern extremity of the Alps and in the western foot-hills close to Grenoble (Fig. 7), which could suggest simultaneous migration routes from the north and the south. The speed of the colonization by fir within the western Alps appears extremely rapid, at the scale of the time intervals observed within small regions and, for the most part, within the radiocarbon age errors (Fig. 6). On the one hand the rapidity of this process prevents the clear separation of actual dynamics from dating errors, but on the other hand it could be considered as supporting the idea of a multiorigin migration. However, the later ages of establishment of *Abies* in the north-western Alps (de Beaulieu *et al.*, 1992; David, 1995a,b; David *et al.*, 2001) and adjacent Jura (Richard, 1983; Reille, 1989) contradict the hypothesis of a migration route from the north and would rather support the idea of a northward spread throughout the south-western Alps, i.e. the French or Italian Alps. According to this second hypothesis, the rate of *Abies* range extension through the south-western Alps may be inferred from the dates of its establishment in southern Mercantour and in Grenoble Pre-Alps (Fig. 6): it appears to be up to 0.12 km year^{-1}, and close to 2.3 km year^{-1} if the estimated ages are correct, which is consistent with the apparent maximum range extension rate reported at a European scale by Davis (1981) and Huntley & Birks (1983). It must be noted that this roughly estimated rate also depends on the time interval between samples, and could be improved by increasing the temporal resolution of the palynological sequences used.

The slight delay of fir migration between the outer and the inner Alps (Fig. 7) and the location of the oldest *Abies* records within the wetter regions (Fig. 8) suggest a first wave of immigration restricted to the Pre-Alps as early as 10,100 cal. yr BP, before the colonization of the inner altitudinal zones between 9700 and 9000 cal. yr BP. Associated with the rapidity of the fir expansion over the entire French Alps, this diachronism could indicate that its migration was not only related to climate change but also controlled by dispersion processes, physiography and orographically induced precipitation patterns (Fig. 8). The quantitative pollen-based climate reconstructions for the south-western Alps (Digerfeldt *et al.*, 1997; Davis *et al.*, 2003), in agreement with independent European studies (e.g. von Grafenstein *et al.*, 1998, 1999; Magny *et al.*, 2001, 2003; Heiri *et al.*, 2003, 2004), date the abrupt increase in temperature and precipitation of the beginning of the Holocene at *c.* 10,500 cal. yr BP, i.e. several centuries before the first pollen evidence for *Abies* immigration

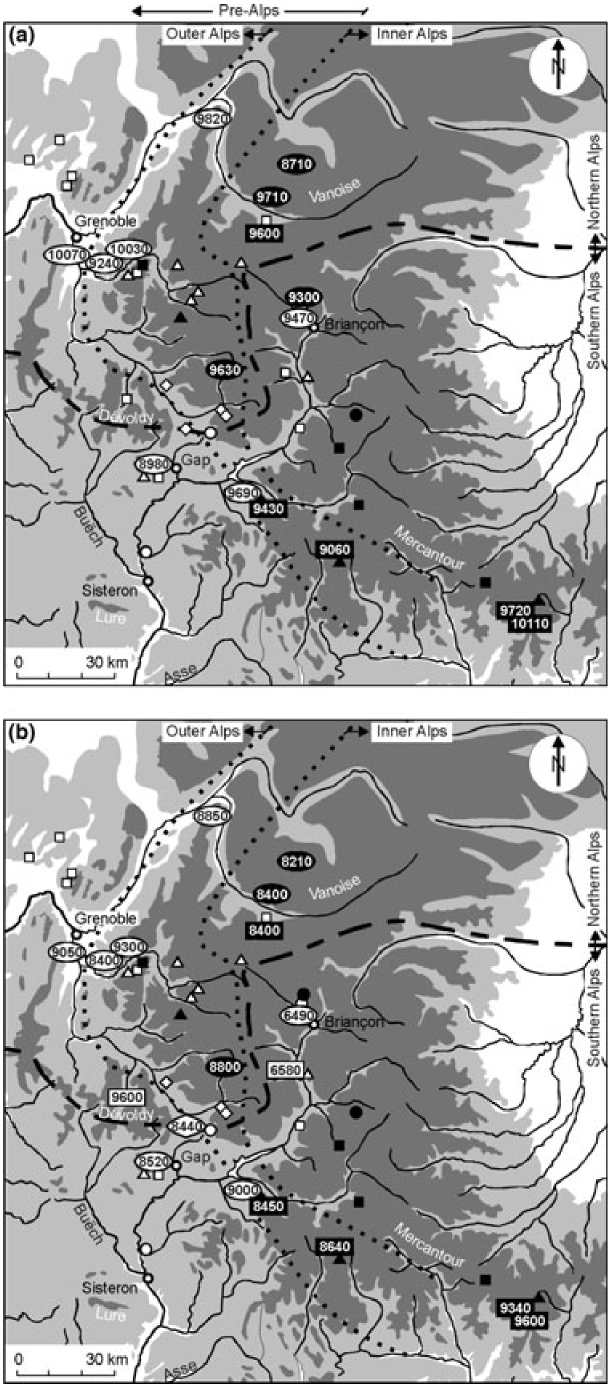

Figure 7 Pattern of migration (a) and expansion (b) of *Abies* in the south-western Alps and adjacent areas. The shape of sites indicates the type of dating: undated sequences (△), dating by AMS of terrestrial macroremains (○), by AMS of bulk sediments (◇) or by the conventional method using bulk sediments (□). For comments and legends, refer to Fig. 2.

in the French Alps. Since this date, the climatic conditions of the south-western Alps would have been as favourable to *Abies* development as today's. In this context, the successive 8.2 ka-type cooling events would have favoured its rapid expansion, as proposed for Central Europe by Tinner & Lotter (2006). This implies a complex response of the *Abies* range extension to early Holocene climate change: the 8.2 ka-type events would have controlled the timing of its spread while orographic parameters would have determined its spatial pattern. Finally, the rapidity of the early Holocene expansion of fir through the south-western Pre-Alps could be partly induced by the enhancement of its capacities of dispersion and colonization by the absence of competitors, such as spruce (*Picea abies*) and beech (*Fagus sylvatica*).

The expansion and the dominance of fir forests in the south-western Alps

The formation of dense forests dominated by *Abies alba* began as early as 9600 cal. yr BP in southern Mercantour and maybe in Dévoluy, a northern and wet-oceanic massif located north of the city of Gap (Fig. 7). However, most populations of *Abies* expanded between 9000 and 8500 cal. yr BP, both in the southern (de Beaulieu, 1977; de Beaulieu & Reille, 1983; Digerfeldt *et al.*, 1997; Nakagawa, 1998) and in the northern outer French Alps (Nakagawa, 1998; David *et al.*, 2001; David, 2001). Fir forests were particularly well developed between 1000 and 1500 m a.s.l., although they reached and even exceeded 2000 m in numerous regions (e.g. Wegmüller, 1975; de Beaulieu, 1977; Tessier *et al.*, 1993; David, 1995b, 2001; David & Barbero, 2001; Carcaillet & Muller, 2005; Muller *et al.*, 2006). This extension is supported by the altitudinal location of present-day relict fir stands in the high Durance Valley. Macroremains found in peatlands, lake sediments, soils and travertine sequences document the local development of *Abies* in the French Alps from 1090 to 1900 m, between 9700–9300 and 1170–733 cal. yr BP (Tables 3 & 4).

As for the migration phase (Fig. 8), the expansion of *Abies* was delayed in the inner Alps. It occurred later, between 8400 and 8200 cal. yr BP in the Vanoise Massif and the Maurienne Valley (David, 1995a,b; David & Barbero, 2001), and around 6500 cal. yr BP in the high Durance valley (de Beaulieu, 1977; Muller *et al.*, 2000). Because the Briançon region is the most arid zone in the whole Alps (Ozenda, 1985), the present-day rarity of *Abies* in this zone was ascribed for a long time to the climatic conditions there being unfavourable to its growth. Indeed, many experimental and dendrochronological studies report the elevated susceptibility of *Abies alba* to drought (e.g. Aussenac, 1980; Lévy & Becker, 1987; Becker, 1989; Tan & Bruckert, 1992; Guicherd, 1994; Desplanque *et al.*, 1998a,b). However, its expansion occurred during an arid period of the Holocene, with major lake-level lowering (Digerfeldt *et al.*, 1997), and resulted in the formation of extended subalpine forests, which developed on both sides of the valleys (Muller *et al.*, 2000; Carcaillet & Muller, 2005). Despite the apparent lack of a relation between the general climate dynamics and the spread of fir forests, their very late expansion in the high Durance Valley (Fig. 6) could have resulted from harsh climatic conditions within the region. Besides, even if *Abies* constituted real forests up to the high inner valleys, the fir forests appear never to have attained an

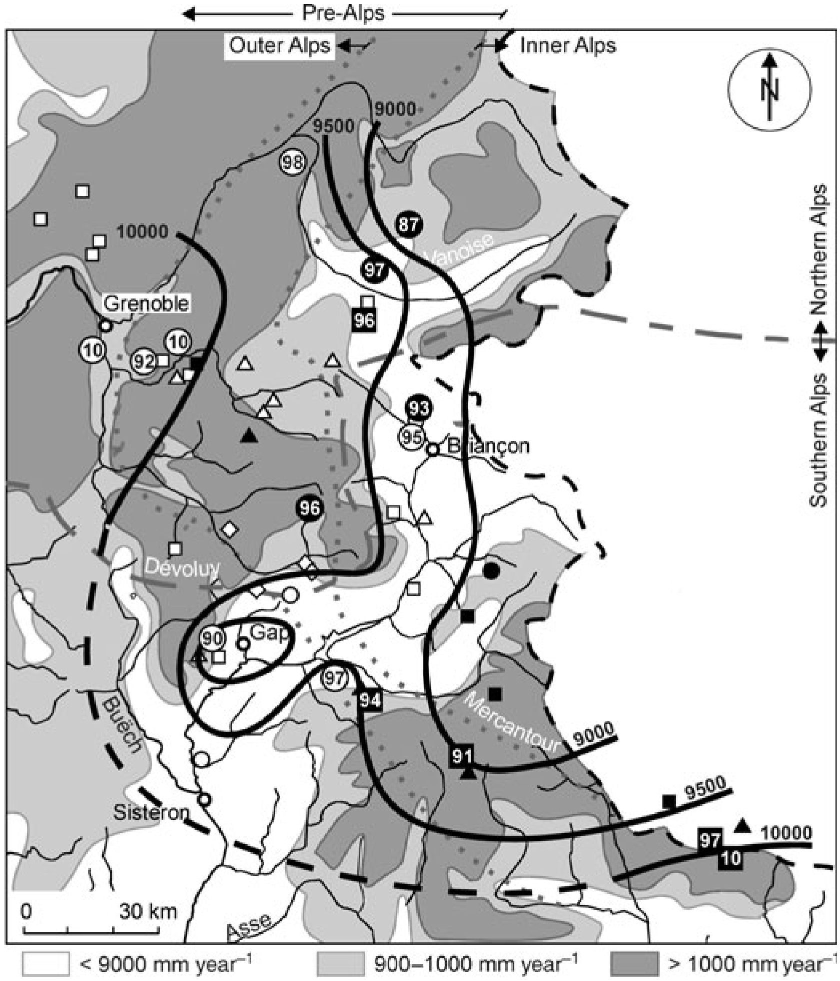

Figure 8 Possible isochrones of *Abies* migration (black lines) and present-day isohyets, linking points with identical annual precipitation (grey lines, delimiting greyed zones) in the southern French Alps (from Office National de la Météorologie, 1946). For comments and legends, refer to Fig. 2.

abundance there similar to the wet-oceanic foot-hills and Pre-Alps.

CONCLUSIONS

The compiled palaeoecological data set allows the detection of some regional features concerning the post-glacial history of *Abies alba* in the south-western Alps. First, the late-glacial pollen sequences currently available from the French Alps and adjacent areas do not provide proof for the presence of glacial refugia for fir. The irregular late-glacial pollen records from south-eastern France may have resulted from sediment reworking or long-distance pollen transport from the Apennine and Insubrian refugia, which we regard as the only certain origins for the fir populations in west-central Europe. Second, whereas the data are still insufficient for a precise reconstruction of the migration patterns, they provide evidence for the rapid spread of *Abies* throughout the south-western Alps, which only occurred over a few centuries, at a rate estimated, in a first approximation, to be around 2.3 km year^{-1}. This feature, implying a non-limiting climate (i.e. a non-equilibrium state), supports the idea of an immigration from distant refugia, later than the climate improvement at the late-glacial–Holocene transition. Third, we demonstrate a delayed expansion of *Abies* in the inner valleys compared with external foot-hills, which may be attributed to their well-known aridity. Climatic conditions consequently appear to have influenced the post-glacial history of *Abies* in the south-western Alps more through their spatial heterogeneity than through their temporal changes.

These results clearly point to the need for such regional syntheses, allowing reliable data to be distinguished from biased data within the whole available data set, and consequently provide valuable past regional biogeographical patterns. Such work should ideally be realized before broad-scale reconstructions, in an attempt to avoid the propagation of erroneous local reconstructions, often related to a selection of unreliable data. Moreover, our study points to the lack of high-resolution, well-dated pollen and macrofossil sequences in the south-western Alps (Fig. 8). An intensive research effort on selected sites could allow more precise reconstructions of the patterns of post-glacial migration of trees, and the determination of the respective influences of external factors (climate, physiography, disturbances) and internal ones (succession, competition, etc.).

Finally, the compiled data set allows us to evaluate the status of the present-day forests of *Pinus*, *Larix* and *Fagus* in the south-western Alps, as well as the biogeographical significance of the relict fir populations in the Durance Valley. The first ones clearly benefited from the decline of *Abies*, dated between 5500 and 3500 cal. yr BP (de Beaulieu & Goeury, 2004), and they may therefore be considered as secondary forests. *Abies* almost completely disappeared from most of the south-western Alps during the Roman era, around 2000 cal. yr BP. Only some limited fir stands persisted until today in remote areas. A map, dated to AD 1770 (Cassini, 1779–82), shows the existence of the present-day *Bois de la Sapée*, on the north-face of the Lure Massif (Provence, France), whose name is based on the French name for fir (*sapin*). This archive attests to the survival of fir stands in the southern massifs during a period of severe forest exploitation for domestic use and industries (Barruol *et al.*, 2004). The relict fir forests of the high Durance Valley probably owed their survival to their location at high elevations, around 2000 m a.s.l., and on steep slopes. A particular case is the Boscodon fir forest, in the Durance Valley, at the boundary between the Pre-Alps and the inner Alps: during the Middle Ages, this forest benefited from protection by the monks of the Boscodon Abbaye.

ACKNOWLEDGEMENTS

We thank H. J. B. Birks, J. N. Haas, W. O. van der Knaap, R. J. Whittaker and an anonymous referee for their constructive suggestions which helped to improve the manuscript. The research has been partly supported by the Eclipse-CNRS programme and by the French national ECCO programme (INSU). This publication is contribution 2006-064 of the Institut des Sciences de l'Evolution de Montpellier. The compiled pollen data set is available as supplementary material online (Supplementary Appendix S2).

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1. Conventional and AMS radiocarbon dates in the southern French Alps and adjacent areas.

Appendix S2. French Alps pollen data base.

This material is available as part of the online article from: http://www.blackwell-synergy.com/http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2006.01665.x (This link will take you to the article abstract).

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Editor: John Birks