



HAL
open science

**A comparative review of soil charcoal data:
Spatiotemporal patterns of origin and long-term
dynamics of Western European nutrient-poor grasslands**

Vincent Robin, Oliver Nelle, Brigitte Talon, Peter Poschlod, Dominique Schwartz, Marie-Claude Bal, Philippe Allée, Jean-Louis Vernet, Thierry Dutoit

► **To cite this version:**

Vincent Robin, Oliver Nelle, Brigitte Talon, Peter Poschlod, Dominique Schwartz, et al.. A comparative review of soil charcoal data: Spatiotemporal patterns of origin and long-term dynamics of Western European nutrient-poor grasslands. *The Holocene*, 2018, 28 (8), pp.1313-1324. 10.1177/0959683618771496 . hal-01788510

HAL Id: hal-01788510

<https://amu.hal.science/hal-01788510>

Submitted on 9 May 2018

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

A comparative review of soil charcoal data: Spatiotemporal patterns of origin and long-term dynamics of Western European nutrient-poor grasslands

Vincent Robin,¹ Oliver Nelle,² Brigitte Talon,³ Peter Poschlod,⁴ Dominique Schwartz,⁵ Marie-Claude Bal,⁶ Philippe Allée,⁶ Jean-Louis Vernet⁷ and Thierry Dutoit³

Abstract

The nutrient-poor grasslands of Western Europe are of major conservation concern because land use changes threaten their high biodiversity. Studies assessing their characteristics show that their past and on-going dynamics are strongly related to human activities. Yet, the initial development patterns of this specific ecosystem remain unclear. Here, we examine findings from previous paleoecological investigations performed at local level on European grassland areas ranging from several hundred square meters to several square kilometers. Comparing data from these locally relevant studies at a regional scale, we investigate these grasslands' spatiotemporal patterns of origin and long-term dynamics. The study is based on taxonomic identification and radiocarbon AMS dating of charcoal pieces from soil/soil sediment archives of nutrient-poor grasslands in Mediterranean and temperate Western Europe (La Crau plain, Mont Lozère, Grands Causses, Vosges Mountains, Franconian Alb, and Upper-Normandy region). We address the following questions: (1) What are the key determinants of the establishment of these nutrient-poor grasslands? (2) What temporal synchronicities might there be? and (3) What is the spatial scale of these grasslands' past dynamics? The nutrient-poor grasslands in temperate Western Europe are found to result from the first anthropogenic woodland clearings during the late Neolithic, revealed by fire events in mesophilious mature forests. In contrast, the sites with Mediterranean affinities appear to have developed at earlier plant successional stages (pine forest, matorral), established before the first human impacts in the same period. However, no general pattern of establishment and dynamics of the nutrient-poor grasslands could be identified. Local mechanisms appear to be the key determinants of the dynamics of these ecosystems. Nevertheless, this paleoecological synthesis provides insights into past climate or human impacts on present-day vegetation.

Keywords

fire disturbance, grasslands, human clearance, pedoanthracology, radiocarbon AMS dating, taxonomic

identifications Received 14 November 2017; revised manuscript accepted 19 February 2018

Introduction

One of the major lessons from paleoecology is that no fixed reference state or baseline exists, and that vegetation is dynamic in time (Birks et al., 2016). Nevertheless, defining targets for environmental management means identifying trajectories, a key issue for conservation, restoration, or sustainability (Bakker et al., 2000; Egan and Howell, 2001). This involves examining the origins of the ecosystem to determine what its trajectory was before a disturbance shifted the ecosystem onto another trajectory (Balaguer et al., 2014).

Identifying the origin of the ecosystem is particularly important in the case of nutrient-poor grasslands. In Europe, these grasslands, also widely known as semi-natural grasslands, are of major conservation importance, presenting high levels of biodiversity (Poschlod and WallisDeVries, 2002) and being threatened by decreased traditional land use (Kahmen and Poschlod, 2004). Human activities have been identified as the key disturbances triggering the presence of nutrient-poor grasslands for at least several millennia (Goepf, 2007; Poschlod and Baumann, 2010; Poschlod et al., 2009). It is thus assumed that without human deforestation and agro-pastoral activities (Bredenkamp et al., 2002), nutrient-poor grasslands would be restricted to locally

small, extreme habitats like rock outcrops or extremely steep south-facing slopes with edaphic conditions too dry for tree or shrub growth (Ellenberg, 1996).

¹Interdisciplinary Laboratory for Continental Environments, CNRS, University of Lorraine, France

²Baden-Wuerttemberg State Office for Cultural Heritage, Tree-Ring Laboratory, Germany

³Institut Méditerranéen de Biodiversité et d'Ecologie, CNRS, IRD, Aix Marseille Univ, Avignon Univ, France

⁴Institute of Botany, University of Regensburg, Germany

⁵Faculté de géographie et d'aménagement, LIVE, CNRS, Strasbourg University, France

⁶GEOLAB, CNRS, Limoges University, France

⁷Université de Montpellier II, France

Corresponding author:

Vincent Robin, Interdisciplinary Laboratory for Continental Environments, CNRS, University of Lorraine, Campus Bridoux, 8 rue du Général Delestraint, 57070 Metz, France. Email: vincent.robin@univ-lorraine.fr

Over the last decades, the vegetation in most nutrient-poor grasslands (and in other types of grasslands) has been changing due to shrub encroachment. The species typical of the grassland are being excluded, thereby inducing a loss of species richness and diversity (Bonanomi et al., 2013; Habel et al., 2013; Kahmen et al., 2002; Vassilev et al., 2011). Once the human constraint is removed, natural secondary succession takes place (Kahmen and Poschlod, 2004; WallisDeVries et al., 2002). As a consequence of this ongoing habitat change and biodiversity loss, stakeholders have made substantial efforts to conserve and/or restore this type of ecosystem (Dolnik et al., 2009; Schrautzer et al., 2009). Usually, however, not much is known about the primary succession at the spatial scale of present-day grassland distribution, nor about the mechanisms behind the development of such grassland eco-systems. In particular, the respective impacts of recurrent disturbances such as fires, windfalls, and grazing by wild herds remain relatively unexplored (Blakesley and Buckley, 2016; Svenning, 2002; Vera, 1999).

Whether nutrient-poor grasslands are a strictly man-made ecosystem or are of natural origin has been debated for decades (Baumann and Poschlod, 2008; Bush, 1988, 1989, 1993; Thomas, 1989; Wilmans, 1997). This lack of consensus on the origin of nutrient-poor grasslands has so far prevented reference states from being clearly defined (Blakesley and Buckley, 2016). However, recent studies have provided new insights into the local origin and history of various nutrient-poor grasslands in Atlantic, Continental, and Mediterranean Western Europe (Bal et al., 2014; Dutoit et al., 2009; Goepf, 2007; Henry et al., 2010; Poschlod and Baumann, 2010; Schwartz et al., 2005; Vernet, 2006).

Here, we review these studies to investigate whether the origins of the nutrient-poor grasslands show any similarities in chronology and spatial patterns through a large-scale comparison of locally relevant data. Our results are then compared with previous regional pollen data to extend local scale conclusions to the regional scale.

Methods

Studying the long-term history of nutrient-poor grassland communities (e.g. grasslands established on nutrient-poor soils) is challenging because they are generally restricted to specific small areas (e.g. hilltops). Paleo-indicators significant at a relevant spatial scale need to be collected from areas that rarely offer suitable archives recording and preserving the standard paleo-indicators, such as pollen grains. Analysis of charcoal assemblages from soil/sediment has been shown to provide suitable paleo-signals, especially relevant at local scale (Nelle et al., 2013; Thinon, 1978). Therefore, the studies hereunder relied on the analysis of macroscopic charcoal pieces accumulated and preserved locally in the soil/sediment (pedoanthracological approach). The charcoal assemblages are composed of macroscopic pieces of 400 μm or larger, recorded and preserved locally (Dutoit et al., 2009; Talon, 2010; Touflan et al., 2010). Moreover, the macroscopic charcoal assemblages are extracted either from soil horizons formed in-situ, or from soil sediment eroded and deposited in a catchment area. Thus, the spatial relevance of the charcoal data is related to the size of the catchment area (Robin and Nelle, 2014; Robin et al., 2014). Moreover, the presence of fossil assemblages of charcoal is directly related to fire disturbances that could directly explain past changes in communities.

Following Carcaillet and Thinon (1996), a similar protocol was applied to each site, both to sample the macroscopic charcoal assemblages and to analyze them qualitatively and quantitatively. For each study site considered here, the assemblages of macroscopic charcoal pieces were extracted from natural soil or soil sediment archives. Sampling exposures were dug manually to bedrock and are therefore described in terms of soil horizon and/

or levels of soil sediment accumulation (soil stratigraphy; Robin et al., 2014). Between 5 and 10 L of material was sampled for each vertical unit described. These vertical sampling units were defined either according to soil horizon or stratigraphy (Goepf, 2007) or by systematic sampling every 10 cm of depth (Dutoit et al., 2009). The number of exposures per study site varied according to the availability of suitable archive site for sampling and the local sampling strategy to relevantly fit to the surface of the study area (Table 1).

Once sampled, each bag of material was laboratory treated to extract the macroscopic charcoal assemblages. First, the contents of the bag were dried and then weighed. Material larger than 5 mm was excluded by sieving. Next, the dry material was carefully wet-sieved with a deflocculant (Na4P2O7) through a column of sieves of three mesh sizes: 2 mm, 800 μm , and 400 μm . The charcoal pieces were then extracted from mineral and organic sections, for each size class of each sample, by hand-sorting under a binocular microscope.

Charcoal pieces were then randomly selected from the extracted charcoal assemblages for taxonomic identification, in balanced proportions from the three size classes of each sample. The charcoal pieces were identified according to wood anatomy criteria, since carbonization of wood fixes the wood anatomy so that it remains visible with only minor deformation and shrinking (Braadbaart and Poole, 2008; Théry-Parisot, 2001). The charcoal pieces were identified under an incident light microscope, mainly at magnifications of $\times 200$ and $\times 500$, and compared with charred wood reference collections and wood anatomy atlases (Jacquiot, 1955; Jacquiot et al., 1973; Schweingruber, 1990).

The macroscopic charcoal signals were actually further quantified per identified taxa, and/or in total amount per vertical unit of sampling, and/or in total amount per profile of sampling, and/or in charcoal concentration per kilo of sampled material smaller than 5 mm. However, the present comparative study only considered the taxonomically identified charcoal pieces that were directly dated. For each study area, chronological information was gathered from the radiocarbon dating of various quantities of single charcoal pieces, after their formal taxonomic identification. Only these latter data provide insights without reference to the complex and unclear taphonomic processes. These taphonomic processes may significantly influence the recording and preservation of soil charcoal assemblages. In particular, bioturbation causes mixing of assemblages, and fragmentation of the charcoal pieces causes quantitative bias in records (Carcaillet, 2001a, 2001b; Robin et al., 2012). Poorly documented such processes mean that extensive extrapolation is required for taxonomic and chronological interpretation of any unidentified or undated pieces in charcoal assemblages, often with questionable results (Carcaillet and Vernet, 2001; Giesecke, 2016; Robin et al., 2016; Willis et al., 2001).

Since the data on radiocarbon ages and the corresponding taxa identification for single charcoal pieces are less likely to involve extrapolation, the database for this comparative approach uses the C14 measurements of each study site and the corresponding identified taxa. Our database moreover eliminates potential comparative biases due to site-specific variations in sampling strategy at local scale. Nevertheless, of the large quantity of charcoal pieces extracted overall from the different study sites, only a small proportion were identified and dated. Thus, the level of representativeness of the identified and dated taxa at the scale of each investigated site was also taken into account (Table 2).

Study sites

We considered six Western European nutrient-poor grasslands, ranging widely from nutrient-poor Mediterranean grasslands to nutrient-poor subalpine grasslands in very wet areas, where soil charcoal data were available (Figure 1 and Supplementary material, available online):

Table 1. General biotic and abiotic characteristics of the various nutrient-poor grasslands compared here.

Site	Crau	Causses	Mont Lozère	Vosges	Franconian Alb	Upper-Normandy
Key reference	Henry et al. (2010)	Vernet (2006)	Bal et al. (2014)	Schwartz et al. (2005); Goepf (2007)	Poschold and Baumann (2010)	Dutoit et al. (2009)
'GPS43°N344°E5						
Surface	55,000 ha	34,000 ha	700 ha	3500 ha	70 ha	32 ha
Altitude (m a.s.l.)	5–55		1450–1670	1000–1350	340–440	50–110
Topographie	Flat	700–1000m Flat with small depression	Medium slopes	Medium slopes	Steep slopes	Steep slopes
Vegetation physiognomy	Semi-arid steppe	Pre-steppic (herbaceous systems with shrubby vegetation and some trees)	Pre-steppic (herbaceous systems with shrubby vegetation and some trees)	High and dense herbaceous system (chaumes) and forests	Limestone grasslands, shrubs, and forests	Chalk grasslands, shrubs, and forests
Type of soil	Truncated Leptic Cambisol	Dolomitic Cambisol	Hyperdystric Cambisol	Hyperdystric Cambisol and Umbric Leptosol	Rendzic Leptosol	Rendzic Leptosol
Type of archive	Soil	Soil	Soil	Soil	Soil	Soil
Number of profile of sampling	14	85 _a	4	13	17	5
Total number of identified	11 taxa	25	6	17 _b	7	21
Total number of identified	597 pieces	3142	1541	>some hundredc	1052	68

includes single subsurface sampling (Vernet, 2006) only (Friedericaa, in respect to compilation by Goepf, 2007).



Figure 1. Map showing location of the six compared nutrient-poor grasslands in Western Europe (map under GNU-free documentation license).

1. La Crau (Henry et al., 2010): This plain area is situated in South-Eastern France, ca. 50 km north-west of Marseille. The plain is a fossilized river bed formed by Durance river deposits between 2,000,000 and 70,000 years ago (Molliex et al., 2013). In this flat topography, stone cover amounts to ca. 50%, and average soil depth is 40 cm, covering a 1–5 m thick layer of impermeable conglomerate. Soils of the study area (Crau de Miramas) are Truncated Leptic Cambisol originating from the dissolution and removal of carbonates after soil deposition by the Durance river between 70,000 and 125,000 years ago (Riss-Würm inter-glacial period). It should also be noted that soil abrasion by eolian deflation occurred in this area between 10,000 and 75,000 years ago, resulting in the erosion of the upper silty layer (Molliex et al., 2013). Thus, the alluvial water table is inaccessible to plant roots. Moreover, dryness is also induced by the Mediterranean climate, with a mean temperature of 14.5°C and a yearly precipitation of 500–600 mm (Buisson and Dutoit, 2006). Previous palynological studies realized at the regional scale (Triat-Laval, 1982) showed that during the late Neolithic and Bronze Age, the landscape was already covered by matorral vegetation and *Pinus pinea/halepensis* forests but not by forest dominated by the late successional species *Quercus ilex*. Today, the Mediterranean nutrient-poor grassland plant community, also called ‘steppe of La Crau’ or ‘Coussoul’, is characterized by the dominance of a perennial Poaceae tussock species, *Brachypodium retusum*, while in the western part *Thymus vulgaris* is the dominant plant species. Since antiquity, from 100 BC to fourth/fifth century AD in this area, the plain has chiefly been used for sheep grazing (Badan et al., 1995). No traces of shrub encroachment have therefore been observed in its central part since the 19th century (Buisson and Dutoit, 2006). A total of 14 soil profiles were sampled at different locations in the remaining area of the plain of La Crau, from which 23 single charcoal pieces were dated.
2. Mont Lozère (Bal et al., 2014): This study site is situated in South-Central France, in the southern part of the mountainous area of the Massif Central. Mont Lozère is a 30-km-long mountain range, oriented northwest–southeast, ranging from 900 to 1700 m a.s.l. It is a granitic area, with marked relief. De Beaulieu and Gilot (1972) put forward the hypothesis of a human origin for the grassland, consistent with pollen data showing the opening of the beech-forest landscape by agro-pastoral activities during the same period as in the Causses, in the middle Neolithic–Chalcolithic.

Table 2. Radiocarbon ages of the charcoal pieces from the various nutrient-poor grasslands compared here, with information about charcoal assemblages.

Area	Laboratory reference	Identified taxa	Depth layer (min–max)	¹⁴ C age yr BP	Calibrated age yr BP	Representativeness of the taxa
Crau	Poz20310	<i>Sclerophyllous Quercus</i>	10–20	105 ± 35	149–11	+++
	Poz22605	<i>Sclerophyllous Quercus</i>	10–20	340 ± 30	481–311	+++
	Poz22609	<i>Thymus</i> sp.	15–25	350 ± 30	492–315	++
	Poz20306	<i>Sclerophyllous Quercus</i>	0–10	420 ± 30	524–435	+++
	Poz22599	<i>Rosaceae</i>	0–10	600 ± 30	654–541	+++
	Poz22602	Monocotyledon	10–20	875 ± 30	833–726	+++
	Poz22598	<i>Pinus halepensis/pinea</i>	10–20	1785 ± 30	1816–1686	+++
	Poz20299	<i>Pinus halepensis/pinea</i>	20–30	1790 ± 30	1817–1687	+++
	Poz20300	<i>Cupressus</i> spp.	20–30	1820 ± 30	1827–1693	++
	Poz20309	<i>Pinus halepensis/pinea</i>	35–45	2025 ± 30	2061–1895	+++
	Poz22611	<i>Pinus halepensis/pinea</i>	35–45	2045 ± 30	2114–1926	+++
	Poz20298	<i>Quercus</i> sp.	5–15	2115 ± 30	2154–1998	+
	Poz22594	<i>Pinus halepensis/pinea</i>	0–5	2120 ± 30	2155–1999	+++
	Poz20307	<i>Prunus</i> spp.	10–20	3305 ± 35	3614–3451	+++
	Poz22603	<i>Prunus</i> spp.	10–20	3335 ± 35	3643–3475	+++
	Poz22600	<i>Lavandula</i> sp.	10–20	3355 ± 35	3648–3547	+
	Poz22607	<i>Prunus</i> spp.	20–30	3400 ± 40	3730–3560	+++
	Poz22612	<i>Phillyrea</i> spp.	10–20	3430 ± 30	3731–3592	++
	Poz22601	<i>Prunus</i> spp.	10–20	3430 ± 30	3731–3592	+++
	Poz22610	<i>Prunus</i> spp.	0–10	3435 ± 35	3779–3606	+++
	Poz20301	<i>Prunus</i> spp.	5–15	3560 ± 35	3932–3814	+++
	Poz22608	<i>Taxus baccata</i>	10–20	3745 ± 35	4163–3984	+
	Poz22597	<i>Pinus halepensis/pinea</i>	5–15	3995 ± 35	4535–4408	+++
Mont Lozère	UGAMS11151	<i>Fagus sylvatica</i>	20–30	900 ± 25	911–741	+++
	UGAMS11753	<i>Fagus sylvatica</i>	10–20	1140 ± 25	1146–971	+++
	UGAMS11354	<i>Fagus sylvatica</i>	30–40	1670 ± 25	1620–1528	+++
	UGAMS9237	<i>Prunus</i> spp.	20–30	2180 ± 25	2308–2121	+++
	UGAMS11152	<i>Fagus sylvatica</i>	30–40	2170 ± 25	2308–2112	+++
	UGAMS14226	<i>Betula</i> spp.	50–60	2490 ± 25	2723–2485	+
	UGAMS14228	<i>Fagus sylvatica</i>	50–60	2730 ± 25	2870–2768	+++
	UGAMS9239	<i>Prunus</i> spp.	70–80	3790 ± 30	4257–4084	+++
	UGAMS9240	<i>Prunus</i> spp.	70–80	3820 ± 30	4354–4093	+++
	UGAMS11353	<i>Fagus sylvatica</i>	50–70	4010 ± 25	4525–4422	+++
	UGAMS11755	<i>Fagus sylvatica</i>	50–70	4030 ± 25	4569–4424	+++
	UGAMS11754	<i>Fagus sylvatica</i>	40–50	4850 ± 25	5645–5487	+++
	UGAMS9238	<i>Prunus</i> spp.	50–60	4870 ± 30	5655–5583	+++
UGAMS14227	<i>Prunus</i> spp.	50–60	5320 ± 25	6185–6001	+++	
Grands Causses	GifA99508	<i>Fagus sylvatica</i>	0–20	10 ± 60	269–0	+
	GifA9950	<i>Fagus sylvatica</i>	0–20	30 ± 50	268–0	+
	Lyon1693	<i>Fagus sylvatica</i>	10–20	95 ± 45	272–11	+
	Erl5597	<i>Fagus sylvatica</i>	15–20	102 ± 47	273–10	+
	Lyon1696	<i>Pomoideae</i>	15–20	115 ± 40	273–10	++
	Lyon1425	<i>Pinus type sylvestris</i>	20–25	150 ± 30	284–60	+++
	AA49141	<i>Pomoideae</i>	30–45	158 ± 32	285–0	++
	Lyon1423	<i>Fagus sylvatica</i>	10–20	170 ± 45	297–59	+
	GifA99506	<i>Fagus sylvatica</i>	0–15	170 ± 60	302–56	+
	Lyon1691	<i>Fagus sylvatica</i>	10–20	180 ± 35	301–71	+
	AA49134	<i>Buxus</i> sp.	0–20	201 ± 33	305–0	++
	Lyon1692	<i>Fagus sylvatica</i>	15–20	215 ± 40	423–82	+
	Erl5599	<i>Fagus sylvatica</i>	0–20	224 ± 48	430–73	+
	Lyon1424	<i>Buxus</i> sp.	15–20	260 ± 45	464–146	++
	Lyon 1419	<i>Fagus sylvatica</i>	10–20	265 ± 45	468–148	+
	Lyon1420	<i>Fagus sylvatica</i>	15–25	280 ± 45	480–151	+
	Lyon1697	Deciduous <i>Quercus</i>	15–20	1045 ± 40	1059–910	+
	Lyon1421	<i>Pinus type sylvestris</i>	20–30	2570 ± 50	2776–2489	+++
	GifA99501	<i>Pinus type sylvestris</i>	0–15	2990 ± 60	3351–2996	+++
	GifA99503	<i>Pinus type sylvestris</i>	15–30	3020 ± 60	3369–3031	+++
	GifA99504	<i>Pinus type sylvestris</i>	15–30	3040 ± 60	3380–3068	+++
	GifA99502	<i>Pinus type sylvestris</i>	15–30	3100 ± 60	3448–3166	+++
	Lyon1422	<i>Fagus sylvatica</i>	15–30	3200 ± 50	3561–3342	+
GifA99500	<i>Pinus type sylvestris</i>	0–15	4180 ± 60	4849–4566	+++	
GifA99505	<i>Pinus type sylvestris</i>	0–50	4805 ± 50	5644–5331	+++	
Lyon1694	<i>Pinus type sylvestris</i>	0–10	5180 ± 50	6061–5753	+++	
Lyon1695	<i>Pinus type sylvestris</i>	0–15	5320 ± 100	6295–5912	+++	
	GifA99689	<i>Pinus type sylvestris</i>	0–15	5620 ± 70	6565–6285	+++

Table 2. (Continued)

Area	Laboratory reference	Identified taxa	Depth layer (min–max)	¹⁴ C age yr BP	Calibrated age yr BP	Representativeness of the taxa
Vosges	Poz12463	<i>Abies</i> spp.	0–5	190 ± 30	302–32	+++
	Poz12467	<i>Fagus sylvatica</i>	20–30	250 ± 30	325–150	+++
	Poz6154	<i>Acer</i> spp.	20–25	570 ± 30	646–528	+++
	Poz12449	<i>Fagus sylvatica</i>	16–21	750 ± 30	728–664	+++
	Poz12464	<i>Acer</i> spp.	20–30	765 ± 30	732–668	+++
	Poz12450	<i>Ericaceae</i>	16–21	915 ± 30	920–762	++
	Poz12447	<i>Abies</i> spp.	16–21	935 ± 25	920–793	+++
	Poz12453	<i>Genista</i> spp.	56–61	1000 ± 30	967–822	+
	Poz6147	<i>Acer</i> spp.	70–75	1280 ± 30	1288–1176	+++
	UtC11538	<i>Fagus sylvatica</i>	100–120	1301 ± 45	1304–1172	+++
	UtC11527	<i>Abies</i> spp.	20–25	1494 ± 30	1416–1309	+++
	UtC11531	<i>Abies</i> spp.	100–120	1930 ± 60	2000–1717	+++
	UtC11529	<i>Populus</i> spp.	70–75	1968 ± 32	1993–1865	+
	UtC11539	<i>Juniperus</i> spp.	20–25	2113 ± 35	2155–1994	++
	Poz6150	<i>Fraxinus</i> spp.	50–55	2125 ± 35	2297–2001	++
	Poz6145	<i>Juniperus</i> spp.	50–55	2135 ± 30	2300–2004	++
	Poz6144	<i>Juniperus</i> spp.	70–75	2210 ± 30	2320–2148	++
	UtC10893	<i>Acer</i> spp.	30–40	2339 ± 37	2488–2307	+++
	Poz12451	<i>Vaccinium</i> sp.	36–41	2445 ± 35	2704–2358	++
	UtC10895	<i>Fagus sylvatica</i>	25–35	2456 ± 47	2711–2361	+++
	UtC10894	<i>Fagus sylvatica</i>	50–60	2510 ± 90	2754–2357	+++
	Poz12455	<i>Calluna</i> sp.	56–61	2725 ± 30	2873–2761	++
	Poz6149	<i>Fagus sylvatica</i>	70–75	2930 ± 35	3175–2963	+++
	UtC11528	<i>Acer</i> spp.	50–55	3030 ± 60	3379–3060	+++
	Poz12459	<i>Abies</i> spp.	30–35	3060 ± 35	3361–3177	+++
	Poz12465	<i>Fraxinus</i> spp.	20–30	3260 ± 35	3570–3399	++
	Poz12469	<i>Fraxinus</i> spp.	70–80	3300 ± 35	3611–3450	++
	Poz12454	<i>Fagus sylvatica</i>	56–61	3330 ± 35	3641–3466	+++
	Poz12458	<i>Acer</i> spp.	30–35	3400 ± 35	3723–3565	+++
	Poz12457	<i>Fagus sylvatica</i>	30–35	3460 ± 30	3830–3641	+++
	Poz6151	<i>Corylus</i> sp.	20–25	3850 ± 35	4408–4155	+
	Poz12452	<i>Sorbus</i> sp.	36–41	3885 ± 35	4420–4230	+
	Poz12468	<i>Abies</i> spp.	70–80	4370 ± 35	5039–4855	+++
Poz6143	<i>Fagus sylvatica</i>	100–120	5580 ± 40	6437–6296	+++	
UtC11530	<i>Tilia</i> spp.	70–75	6970 ± 60	7932–7685	+	
Poz12460	<i>Salix</i> spp.	40–45	9260 ± 60	10,580–10,256	+	
Poz12461	<i>Fabaceae</i>	40–45	9520 ± 50	11,089–10,660	+++	
Poz6208	<i>Pinus type sylvestris</i>	50–55	9570 ± 50	11,125–10,724	+++	
Poz6153	<i>Pinus type sylvestris</i>	20–25	10,170 ± 170	12,410–11,260	+++	
Poz6146	<i>Abies</i> spp.	90–100	18,200 ± 100	22,348–21,810	+++	
Franconian Alb	Erl6167	<i>Pinus type sylvestris</i>	0–9	302 ± 48	487–285	+++
	Erl6168	<i>Pinus type sylvestris</i>	9–16	399 ± 122	654–267	+++
	Erl6170	<i>Pinus type sylvestris</i>	16–26	425 ± 49	538–425	+++
	Erl6169	<i>Pinus type sylvestris</i>	5–16	510 ± 54	570–479	+++
	Erl6165	<i>Pinus type sylvestris</i>	0–9	573 ± 49	655–520	+++
	Erl6166	<i>Pinus type sylvestris</i>	9–20	581 ± 49	656–525	+++
	Erl6163	<i>Pinus type sylvestris</i>	12–20	1565 ± 50	1555–1352	+++
	Erl6164	<i>Pinus type sylvestris</i>	11–18	1674 ± 52	1710–1514	+++
Upper-Normandy	AA59139	<i>Taxus baccata</i>	20–40	105 ± 35	149–11	++
	AA59138	<i>Fagus sylvatica</i>	20–40	210 ± 35	223–138	++
	Poz6334	<i>Fagus sylvatica</i>	20–40	300 ± 30	461–347	++
	AA59134	Deciduous <i>Quercus</i>	15–35	365 ± 35	503–315	+++
	AA59142	Deciduous <i>Quercus</i>	55–80	460 ± 60	560–425	+++
	AA59143	Deciduous <i>Quercus</i>	55–80	795 ± 40	784–671	+++
	AA59135	Deciduous <i>Quercus</i>	35–55	1190 ± 35	1185–1048	+++
	AA59136	<i>Fagus sylvatica</i>	35–55	1990 ± 40	2043–1864	++
	AA59140	<i>Taxus baccata</i>	55–80	3260 ± 40	3573–3394	++
	AA59141	Deciduous <i>Quercus</i>	55–80	3680 ± 45	4102–3892	+++
	AA59137	<i>Taxus baccata</i>	35–55	3905 ± 40	4437–4230	++
	AA59133	<i>Taxus baccata</i>	15–35	3975 ± 60	4585–4239	++
	AA59144	<i>Fagus sylvatica</i>	0–15	5435 ± 40	6305–6181	++
	AA59145	Deciduous <i>Quercus</i>	35–55	5840 ± 40	6747–6533	+++

+: taxa with low frequency; ++: taxa with medium frequency; +++: taxa with high frequency.

- Soils are influenced by the leucogranite substratum (silicate rock) and belong to Hyperdystric Cambisol. Mean annual temperature is 6.5°C and yearly precipitation is 1500 mm. Old and traditional agricultural systems, where nutrients were translocated through sheep grazing to arable fields, led to this nutrient-poor vegetation (Bal et al., 2014). Vegetation distribution along the slopes of Mont Lozère can be divided as follows: from 400 to 900 m a.s.l. forests are dominated by *Quercus pubescens* and *Quercus petraea*; from 900 to about 1400 m a.s.l. forests are dominated by *Fagus sylvatica*, with a few *Abies alba*; and above 1400 m a.s.l. lie *Nardus stricta* grasslands with *Vaccinium myrtillus*, *Calluna vulgaris*, *Cytisus oro-mediterraneus*, and *Genista purgans*. Sporadically, early successional species such as *Pinus sylvestris*, *Betula pen-dula*, and *Juniperus nana* are encountered. Four soil profiles were sampled in the *Nardus stricta* grasslands, along an altitudinal transect from 1450 m to 1670 m a.s.l. A total of 14 single charcoal pieces was selected and dated.
3. Grands Causses (Causse Méjean & Causse Larzac; Vernet, 2006): The site of Grands Causses is situated in the same region as Mont Lozère and includes two areas, Causse Méjean and Causse Larzac. Both are located on a Jurassic calcareous-dolomitic plateau from 700 to 1000 m a.s.l., with an active Karstic system (Corbel, 1954). Soils belonging to Dolomitic Cambisol occurred on Jurassic calcareo-dolomitic substrate. Mean annual temperature is 8–9°C and yearly precipitation 1000–1200 mm (Météo France online data). Supramediterranean forest species grow in close proximity to oromediterranean and mediterraneo-montane species (Lecompte and Cohen, 1985). Both areas have distinct zones of forest, dominated by *Pinus sylvestris*, and grassland traditionally grazed by sheep. Because of the lack of wetlands and peat bogs on the calcareous-dolomitic plateau of the Causses, only one reference was found concerning previous palynological investigations (Van Campo and Aymonin, 1962), simply suggesting the existence of a forest of *Pinus sylvestris* in the Mesolithic. Moreover, prehistoric traces have already shown that the spread of human settlement in the Causse Méjean began during the Neolithic period, with a peak during the late Neolithic–Chalcolithic. This assumption is based on data from the distribution of archeological remains and is confirmed by the results of Vernet (2006), which support the existence of several phases of fire affecting pine forests in the northern areas of the Causse during the period 4800–3000 BP cal. yr. Soil and sediment samples in the Grands Causses were taken from natural small topographical depressions, such as dolines, at various locations on the plateau. To ensure the comparability of the data on grass-land history, only samples from open areas were taken into consideration here. A total of 216 samples were collected from 85 subsurface locations and yielded a total of 28 dates (26 from Causse Méjean and 2 from Causse Larzac).
 4. Vosges Mountains (Rossberg and Hohneck; Goepf, 2007; Schwartz et al., 2005): The Vosges are a range of low mountains in North-Eastern France, ca. 120 km long, oriented north–south and formed of sandstone and crystalline stones. Their altitude ranges from ca. 300–1424 m a.s.l. Average annual temperature is 8°C (Gerardmer station, Météo France), and yearly precipitation is from 1800 to 2000 mm (Météo France on-line data). Janssen and Janssen-Kettlitz (1972) showed a slight increase of pollen from non-forested herbaceous species in the Bronze Age around 2500 yr BP, but no signs of the existence of former open areas have been detected. Soils from the Vosges sites belong to Hyperdystric Cambisol and Umbric Leptosol originating from the degradation of biotite porphyroid granites under mountainous climate conditions. The grasslands are mainly in the southern half of the massif, where the elevation of the relief leads to what are known as ‘chaumes’, above ca. 1000 m a.s.l. The vegetation communities of these grasslands include mainly *Nardus stricta*, *Festuca ovina*, and *Festuca rubra*. They have been grazed by cattle for centuries. Some dwarf shrubs also occur, such as *Vaccinium myrtillus* and *Calluna vulgaris*. Sites were investigated on two chaumes: the Rossberg site, with two soil profiles providing 18 radiocarbon dates, and the Hohneck site, with 11 soil profiles providing 22 radio-carbon dates (Schwartz et al., 2014).
 5. Franconian Alb (Baumann, 2006; Poschlod and Baumann, 2010): This study site includes several sampling areas in the central and southern Franconian Alb (or Franconian Jura), in South-Eastern Germany. It is a relatively low mountain range, part of the Jura, reaching ca. 600 m a.s.l. and mainly composed of limestone from the Jurassic period. Poschlod and Baumann (2010) in the same survey compared two different methodological approaches (soil charcoal and pollen analyses) on these sites. Their results show that the peaks of *Pinus* pollen fully correspond to the periods to which the charcoal found in the calcareous grasslands were dated. Soils of the Rendzic Leptosol type occurred on Jurassic Malm. Mean annual temperature is around 7–8°C, and yearly precipitation is 600–700 mm (Baumann, 2006). The main phytosociological association is *Gentiano-Koelerietum*. A total of 17 profiles from four different sampling areas in formerly grazed grasslands were investigated, and eight radiocarbon dates were obtained.
 6. Upper-Normandy (France; Dutoit et al., 2009): The study site is the chalk hillsides of Saint-Adrien situated ca. 100 km north-west of Paris, in the Lower Seine Valley of Upper-Normandy. The Seine River and its tributaries, such as the Bequet River, shaped the geomorphology of cliffs and rocky outcrops on chalk from the Cretaceous period, with hills ranging from 50 to 110 m a.s.l. Pre-vious palynological studies in the Seine valley showed that forest openings began to occur in the Pre-Boreal Period but that this extensively forested landscape dominated by *Fagus sylvatica* was probably not conducive to large areas of chalk grassland until the late Neolithic (Huault, 1986). The soils of the studied site are Rendzic Leptosol originating from the degradation of the chalk outcrop since the beginning of the post-Glacial period 9,000 years ago. The local topography of steep slopes induces shallow soil, with low water-availability for vegetation. Thus, vegetation is nutrient-poor dry grassland dominated by *Sesleria albicans* and *Bromus erectus*, grazed by sheep, goats, and cattle for centuries (Dutoit et al., 2003). Mean annual temperature is around 10°C, and yearly precipitation is 800 mm. Five profiles were sampled, one at the base of the hillside and four at the top. The latter four profiles are in an area comparable to the minimum sampling area required to provide a good representation of the floristic composition, richness, and diversity of chalk grassland communities (around 500 m²; Dutoit et al., 2003). In total, 14 single charcoal pieces were dated.

Results

Soil charcoal synthesis

A total of 127 single charcoal pieces from the six study sites were radiocarbon dated (Bal et al., 2014; Dutoit et al., 2009; Goepf, 2007; Henry et al., 2010; Poschlod and Baumann, 2010;

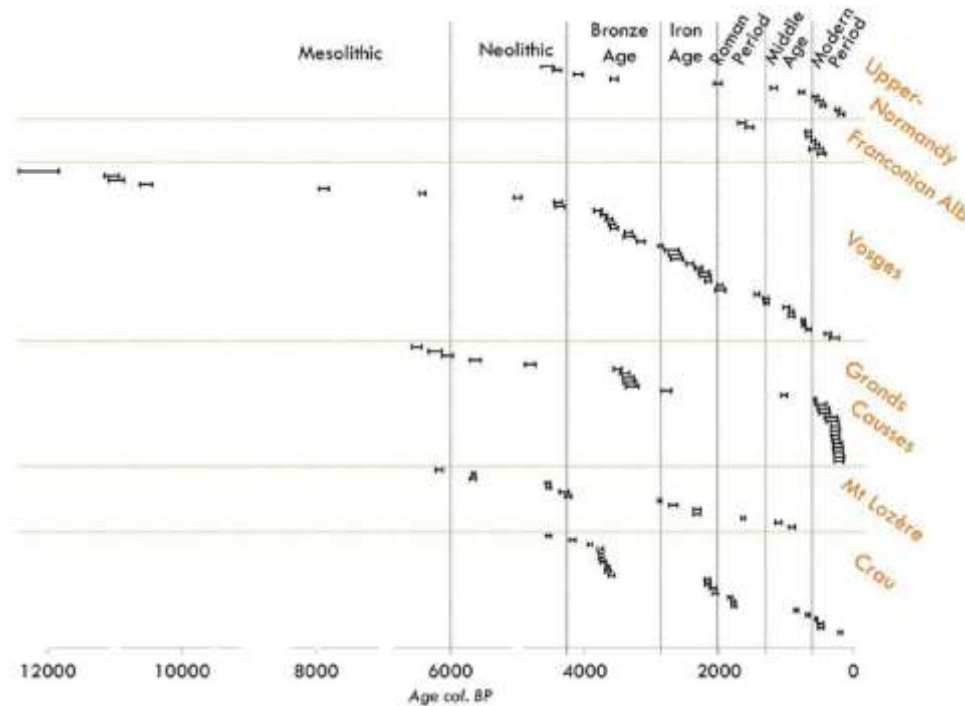


Figure 2. Age distribution of the dated charcoal pieces from the six compared nutrient-poor grasslands in Western Europe, related to the chrono-cultural phases with which the dated charcoal pieces are contemporaneous.

Schwartz et al., 2005; Vernet, 2006; Table 2). When considered together, the ^{14}C -AMS data compiled show an uneven distribution, both within and between study areas (Figure 2). Obviously, it can be postulated that some soil charcoal pieces could have been lost through charcoal fragmentation and/or soil erosion (Robin and Nelle, 2014). However, the absence of charcoal dates for some periods, for instance, from La Crau area before 5000 cal. BP, or before 2000 cal. BP in the Franconian Alb, cannot be attributed to the absence of soils, as they were forming or already developed during the early Holocene. While it is true that the soil of La Crau area has been truncated (Molliex et al., 2013), that occurred between 10,000 to 70,000 years ago and not during the period for which dates are lacking. To avoid any over-interpretation, the chronological data are not extrapolated here to the total quantities of charcoal per soil layer; we interpret the chronological data exclusively with reference to the single charcoal pieces dated from each study site.

A clear clustering of dates is only observed during three periods at La Crau: the end of the Neolithic/Bronze Age, the Roman period, and the Medieval period/early Modern period. In Mont Lozère, clustering is less marked: some dates are found loosely grouped in the early Neolithic, others in the late Neolithic, then in the Iron Age, with a few isolated dates during the Roman and Medieval periods. The radiocarbon dataset for Grands Causses shows more dates during the Neolithic, the Bronze Age, and the Modern period, with only a few dates during the Medieval period. The two Vosges areas show differences in the temporal distribution of dates: Hohneck has a few dates occurring together during the early Iron Age, with others during the Medieval period and the Bronze Age, while the Rossberg dates are more concentrated in the Iron Age and the Roman period, with fewer Medieval period dates. Only the Franconian Alb has no dates older than Roman times. Seven dates relate either to the Roman period or to the late Medieval period/early Modern period. The Upper-Normandy dates are more or less grouped in the late Neolithic/Bronze Age and Medieval period/early Modern period. The taxonomic spectrum of the dated charcoal pieces from the various study sites show 30 different taxa in total. The large number of taxa revealed by charcoal analysis in these study areas, compared with single-site or regional studies (e.g. Robin et al., 2013, 2014), is due to their very diverse biogeographic contexts.

Therefore, to ensure comparability between study areas, the dated taxa are grouped here by functional type, according to their life-history traits with respect to plant community succession as described in the specialist literature (Denslow, 1980; Rameau et al., 1999, 2005, 2008). Some are early successional taxa, which could indicate a possibly short-lived expansion of shrubs and trees: sclerophyllous *Quercus* spp., *Pinus pinea/halepensis* and *Pinus* type *sylvestris* (including *Pinus nigra*, *Pinus sylvestris* and *Pinus uncinata*), *Cupressus* spp., *Prunus* spp., *Phillyrea* spp., *Acer* spp., *Genista* spp., *Populus* spp., *Juniperus* spp., *Fraxinus* spp., *Vaccinium* spp., *Calluna* sp., *Corylus* sp., *Buxus* sp., *Betula* spp., *Salix* spp., while some characterize strictly open habitats (*Lavandula* sp., *Thymus* sp.). A second group consists of taxa tolerant to competition, with *Taxus* spp., *Sorbus* spp., and *Tilia* spp. The last group consists of late successional taxa, with *Fagus* sp., deciduous *Quercus* and *Abies* sp., which are trees that could close the canopy and restrict plants of open vegetation.

The greater number of taxa in the early successional group can be explained by the selection process. Charcoal pieces were usually selected, so as to provide dating as accurate as possible with respect to the fire event. Thus, short-lived species were chosen, and these species are often early successional. Therefore, the dating of the successional groups is not interpreted quantitatively (i.e. by frequency of taxa occurrence) but only qualitatively (i.e. by site-to-site comparison of the chronological occurrence of successional groups). The taxonomic results interpreted according to chronological data are shown in Figure 3.

The plain of La Crau mainly contained early successional species like *Pinus pinea/halepensis*, *Phillyrea* sp. (cf. *angustifolia*), and *Prunus* sp. at the end of the Neolithic or during the Bronze Age. For these periods, there is no evidence of late successional species. The only dated late successional taxon is from the Roman period. Mont Lozère had early successional taxa before La Crau, notably *Prunus* sp., as well as late successional taxa such as *Fagus sylvatica*. Both were already present during the early Neolithic. Then, both groups are dated at various periods during the middle and late Holocene.

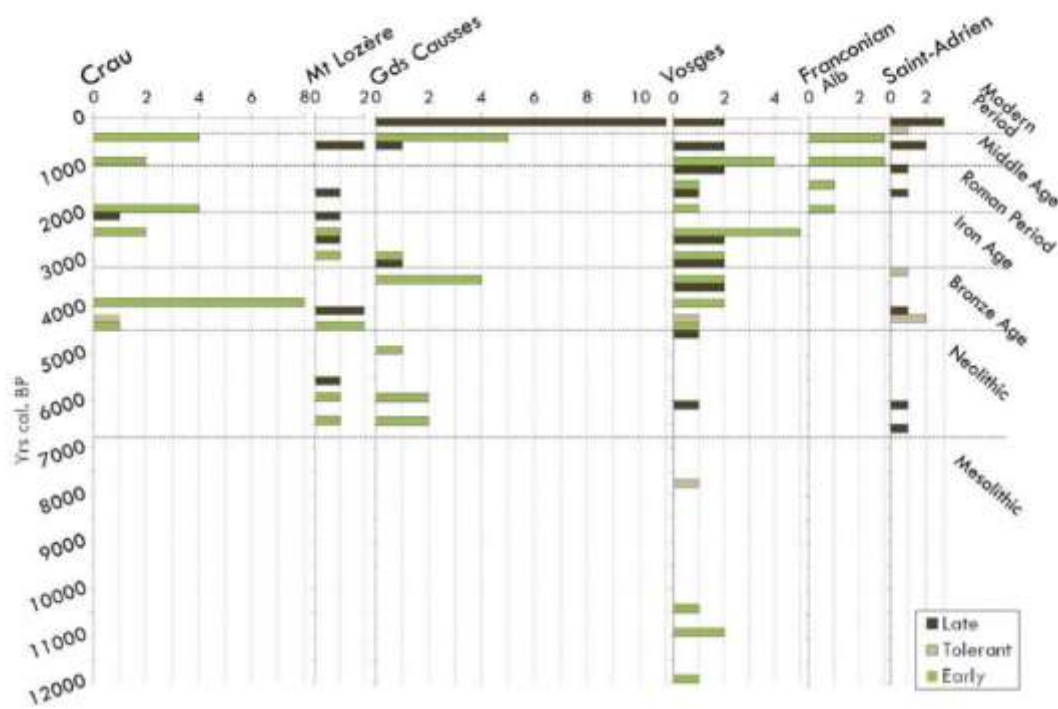


Figure 3. Number of dated charcoal pieces on a time axis per investigated grassland in Western Europe, and per successional group of the identified taxon, related to the chrono-cultural phases with which the dated charcoal pieces are contemporaneous.

On the Grands Causses, several dates for the early successional taxon *Pinus* type *sylvestris* are from the late Mesolithic/early Neolithic (as early as the dates for the early successional taxa on Mont Lozère). The dates for late successional taxa are much later, starting with *Fagus sylvatica* in the late Bronze Age. The subsequent late successional taxa all date from the Modern period. Early successional taxa also show several dates from the Modern period; however, there are more prior occurrences, during the Bronze and Iron Ages. The Vosges contains the oldest dated taxa of the entire dataset, with early successional taxa such as *Pinus* type *sylvestris*, and *Salix* spp. from the Mesolithic. It also contains both a tolerant taxon (*Tilia* spp.) and a late successional taxon (*Fagus sylvatica*) dated to the late Mesolithic. Then, from the late Neolithic onward, various taxa from both late and early successional groups occur regularly, up to the Modern period. In the Franconian Alb, the only taxon from the early successional group dated was *Pinus* type *sylvestris*, from the Roman period to the Medieval period and the Modern period. However, observations of the charcoal assemblages reveal late successional taxa such as *Fagus sylvatica*, *Abies* sp., and deciduous *Quercus*, along with early successional taxa such as *Juniperus* and *Ligustrum*. In Upper-Normandy, no early successional taxa are dated. Thus, although they were most likely present locally at some stages of the forest dynamic, the absence of dating and their weak occurrence within the local soil charcoal assemblages suggest that this vegetation stage did not burn locally. The oldest dating is for late successional taxa from the late Mesolithic; they subsequently occur sporadically in more recent periods, along with tolerant taxa such as *Taxus baccata*.

Discussion

The presence of macroscopic charcoal pieces in natural soils indicates the importance of fire as a disturbance in the opening of the ecosystem, as pointed out by the local scale investigations at each site (Bal et al., 2014; Dutoit et al., 2009; Goepp, 2007; Henry et al., 2010; Poschlo and Baumann, 2010; Schwartz et al., 2005; Vernet, 2006). From Prehistoric times until the beginning of the Modern

period, our synthesis on soil charcoal data shows that nutrient-poor grasslands existed throughout the study region.

However, caution should be used in interpreting these data, since the charcoal proxy here comes from soil/soil sediment archives. While it was possible to identify the geographical origin of the charcoal signal here by the catchment area of each sampling, taphonomical processes make recording and preservation of such charcoal assemblages inadequate for reliable interpretation. This is an issue particularly regarding transfer of the results to a larger geographical range, such as the regional scale. For instance, there is no relation between the depth of sampling and the measured radiocarbon ages (Carcaillet, 2001a, 2001b). This is why our study sites simply represent a few areas in different landscapes from Northern to Southwestern Europe. Moreover, the spatial distribution of this soil charcoal sampling was designed to capture reliable local information: taxonomic identifications and radio-carbon dating, independently of the archive, to permit their comparison at regional scale. Actually, taxonomic identification and radiocarbon dating yield only partial information, since we have no guarantee that we dated the oldest charcoal pieces of a specific taxa or that we identified all the taxa historically present in the study areas (probably overlooking taxa that did not burn locally for certain chronological periods). Nevertheless, they provide some evidence of the local presence of formally identified taxa for a dated period on the site sampled.

The ^{14}C age distribution points to fire activity occurring locally during the Mesolithic, and from the Neolithic at various sites, but still sporadically. This shows the early role of fire in the dynamics of nutrient-poor grasslands. From the late Neolithic to the Bronze Age, fire activity progressively spread throughout the study sites, consistent with fire history patterns at continental scale in Europe (Carcaillet et al., 2002; Power et al., 2008) and in the Mediterranean (Vannière et al., 2008). However, we were unable to identify clear synchronicities between fires events dated at local scale in different regions. Thus, the fire events in nutrient-poor grasslands at local scale are highly heterogeneous, probably due to the existence of local semi-open mosaics of fuel and to specific local scale fire regime drivers, like local vegetation dynamics, human activities,

and potential effects from recurrent grazing by wild herds in the Mesolithic (Robin et al., 2012). However, during this period, the impacts of wild herds on the degree of vegetation opening (in space and time) could not be reliably assessed from natural bone archaeological traces (Svenning, 2002). Thus, the key impact of wild herds on vegetation openness and maintenance of nutrient-poor grasslands during the Mesolithic periods in Europe is still purely a hypothesis (Vera, 1999), as the precise dynamics of wild herds have not yet been determined.

However, identifying the ignition sources of the dated char-coal is challenging. The soil charcoal database does not enable us to assess directly whether fire activity is related to human activities or to climate forcing, since the fire responsible for the presence of charcoal assemblages can be either natural or human-made. In addition, the charcoal recorded might result from the domestic use of wood for cooking, even out of archaeological archives or be related to clearly identified human occupation sites such as La Crau plain (Henry et al., 2010). However, the taxonomic identification and radiocarbon dating of these charcoal pieces possibly from 'hearths' still provide direct evidence of the local presence of some taxa for some periods. From the local charcoal assemblages, therefore, two groups of sites can be distinguished: one at northernmost latitudes (i.e. Upper-Normandy, Vosges, Franconian Alb), and one with Mediterranean affinities (i.e. Grands Causses, Mont Lozère, La Crau).

For the first group, the impact of man-made fire is plausible considering that the burnt vegetation is identified as originating from low flammable forest systems since at least the Neolithic for the Vosges and Normandy sites (i.e. presence of *Fagus sylvatica*, *Abies* sp., and/or deciduous *Quercus*; Dutoit et al., 2009; Goepf, 2007; Poschlod and Baumann, 2010; Schwartz et al., 2005; Figure 3). The role played by human disturbance in the emergence of grassland ecosystems has already been pointed out by paleo-investigations of other European grassland sites (e.g. Bush, 1988, 1989). These studies feed into the debate on whether human disturbance should be seen as causing the development of grassland or as maintaining existing grassland inherited from cold periods (Bush, 1993; Thomas, 1989). The soil charcoal dataset for the sites considered here supports the hypothesis that nutrient-poor grasslands in Western Europe are the result of woodland opening since the Neolithic, which became even more marked during the Bronze Age, Roman Empire, and Medieval Age. This is consistent with the Holocene vegetation history of Western Europe: reestablishment of closed canopy forest during the early/middle Holocene (ca. 8–4 ka yr BP), followed by progressive afforestation related to human activities and use of natural resources (e.g. Berglund et al., 1996; Kalis et al., 2003; Robin et al., 2014). This is especially marked for the late Holocene (ca. the last 4 ka yr BP), which saw the onset of human use of fire as a tool to open wooded areas (Marlon et al., 2008), related to the development of cultural landscapes (Gaillard et al., 2007).

For the second group (Grands Causses, La Crau), with the sites at lower latitudes, fires may have occurred naturally due to the presence of highly flammable vegetation (e.g. pine woodland; Bal et al., 2014; Henry et al., 2010; Vernet, 2006; Figure 3). The importance of wildfire related to summer drought as a key disturbance during the Holocene in the Mediterranean region has already been shown (Vannière et al., 2011), supporting climate determinism (Combourieu-Nebout et al., 2013; Jalut et al., 2009; Pons and Quezel, 1998; Thiebault, 1997). In La Crau, the charcoal assemblages show a degradation of pre-existing matorral vegetation and pine forests by fire and grazing during the Neolithic, before any advanced forest succession established locally (Bazile-Robert, 1987; Henry et al., 2010). In the Grands Causses sites, the same pattern emerges even earlier, with fire occurrences in pioneer forests from

the beginning of the Mesolithic and the Neolithic (Bal et al., 2014; Vernet, 2006). This early successional vegetation type remained dominant during the Neolithic, probably because the Mediterranean climate and soil erosion slowed primary plant successions (Carrion et al., 2003; Grove and Rackham, 2003). Human activities intensified the effect of climate constraint, keeping open ecosystems dominated by herbaceous plant communities, notably through grazing (Henry et al., 2010; Vernet, 2006).

A relatively similar phenomenon has been observed in Central Europe, where natural grasslands occurred even before the start of agricultural activities in the early Neolithic (5500 BC). However, their area was estimated to be relatively small and grassland patches were probably rather fragmented in a dominantly forested landscape matrix. Thus, large-scale enlargement of grasslands is not expected to have occurred before the Iron Age (Hájková et al., 2011; Hejzman et al., 2012; Kuneš et al., 2015; Pokorný et al., 2015).

Finally, on Mont Lozère, the finding of some *Fagus sylvatica* dates from the Neolithic points to the presence of mature stands before the establishment of grassland. However, for the same period and from the same charcoal assemblages, pioneer forest vegetation was also found (i.e. *Betula* spp., *Salix* spp., *Corylus avellana*; Bal et al., 2014). Thus, it can be postulated that the *Fagus* dates do not result from dense closed forests. The high altitude of the Mont Lozère grasslands sampled, with their wet mountain climate, explain the differences from La Crau and even from Grands Causses, where climate conditions are much drier. However, for those three study sites with Mediterranean affinities, it is clearly shown that the first fire events occurred in non-mature forest stages, as revealed by charcoal assemblages. This is an important distinction, marking them out at large scale from the study sites at northernmost latitudes, where the first fire occurrences were in late successional forest stages.

Concerning the last few hundred years, the absence of charcoal from this period in La Crau, Mont Lozère, and the Franconian Alb may indicate a continuous openness of these grasslands. This may have led to higher floristic diversity for sites not plowed during the Modern period (Dutoit et al., 2003; Forey and Dutoit, 2012; Gibson and Brown, 1992; Karlík and Poschlod, 2009; Römermann et al., 2005). Grassland diversity has already been linked to late Iron Age human population density (Pärtel et al., 2007). Conversely, the abundance of young charcoal from *Fagus* should indicate that the other grasslands are younger and would quickly disappear if human land use stopped. These grasslands would certainly differ floristically. However, since our sites are situated in different biogeographic areas, testing this hypothesis would require discriminating climatic factors from those linked to history and landscape organization at the regional and local scale across Europe (Cousins and Eriksson, 2002).

Conclusion

Comparing the locally relevant chronological and taxonomic data for the six study areas revealed no clear pattern of nutrient-poor grassland development and dynamics between areas in contrasting parts of Europe. Local-scale mechanisms appear to be the dominant drivers of these ecosystems. It can be concluded that the origin and history of European nutrient-poor grasslands are related to a combination of climatic constraint and/or human influence impacting vegetation dynamics at local or at least 'infra-regional' scale. Nevertheless, we observed a clear distinction between the sites under Mediterranean influence (i.e. Grands Causses, Mont Lozère, and La Crau), where matorral and pioneer forest stages were already established when the first human impacts occurred during the Neolithic, and the sites at central Europe latitudes (i.e. Upper-Normandy, Vosges, and Franconian Alb), where the grassland appears to result more from anthropogenic woodland clearing from the Neolithic onwards. Moreover, comparisons between local

pedoanthracological data and previous regional pollen data clearly show how the results can be additional for a better understanding of the spatial areas really affected by vegetation changes. Here, charcoal-based data suggest a Prehistoric origin for nutrient-poor grasslands (from the Neolithic to the Bronze age) but their extension in space appears to have occurred no earlier than the Middle-Ages according to most of the regional pollen analyses previously realized in our study regions.

Acknowledgements

We thank Marjorie Sweetko for English language revision.

Funding

This publication was made possible by the financial support for a research stay to Oliver Nelle and Vincent Robin provided by the University of Avignon.

ORCID iD

Peter Poschlod <https://orcid.org/0000-0003-4473-7656>

References

- Badan O, Brun J-P and Congès G (1995) Les bergeries romaines de la crau d'Arles. Les origines de la transhumance en Provence. *Gallia* 52: 263–310.
- Bakker JP, Grootjans AP, Hermy M et al. (2000) How to define targets for ecological restoration? Introduction. *Applied Vegetation Science* 3: 1–72.
- Bal MC, Allée P and Liard M (2014) Charcoal from soil: The origin of *Nardus stricta* grassland and the history of a mountain cultural landscape (Mont Lozère, France) since the Neolithic period. *Quaternary International* 366: 3–14.
- Balaguer L, Escudero A, Martín-Duque JF et al. (2014) The historical reference in restoration ecology: Redefining a cornerstone concept. *Biological Conservation* 176: 12–20.
- Baumann A (2006) *On the vegetation history of calcareous grasslands in the Franconian Jura (Germany) since the Bronze age*. PhD Thesis, University of Regensburg.
- Baumann A and Poschlod P (2008) Did calcareous grasslands exist in prehistoric times? An archaeobotanical research on the surroundings of the prehistoric settlement above Kall-münz (Bavaria, Germany). *British Archaeological Reports International Series* 1807: 25–37.
- Bazile-Robert E (1987) Végétations pré-néolithiques d'après l'anthracanalyse de sites préhistoriques du sud de la France. In: Guilaine J, Courtin J, Roudil JL et al. (eds) *Premières communautés paysannes en Méditerranée occidentale*. Paris: CNRS Edition, pp. 81–85.
- Berglund BE, Birks HJB, Ralska-Jasiewiczowa M et al. (1996) *Palaeoecological Events during the Last 15,000 Years: Regional Synthesis of Palaeoecological Studies of Lakes and Mires in Europe*. Hoboken, NJ: John Wiley and Sons.
- Birks HJB, Felde VA, Bjune AE et al. (2016) Does pollen-assembly richness reflect floristic richness? A review of recent developments and future challenges. *Review of Palaeobotany and Palynology* 228: 1–25.
- Blakesley D and Buckley P (2016) *Grassland Restoration and Management*. Exeter: Pelagic Publishing.
- Bonanomi G, Incerti G and Allegrezza M (2013) Assessing the impact of land abandonment, nitrogen enrichment and fairy-ring fungi on plant diversity of Mediterranean grasslands. *Biodiversity and Conservation* 22: 2285–2304.
- Braadbaart F and Poole I (2008) Morphological, chemical and physical changes during charcoalification of wood and its relevance to archaeological contexts. *Journal of Archaeological Science* 35: 2434–2445.
- Bredenkamp GJ, Spada F and Kazmierczak E (2002) On the origin of northern and southern hemisphere grasslands. *Plant Ecology* 163: 209–229.
- Buisson E and Dutoit T (2006) Creation of the natural reserve of La Crau: Implications for the creation and management of protected areas. *Journal of Environmental Management* 80: 318–326.
- Bush MB (1988) Early Mesolithic disturbance: A force on the landscape. *Journal of Archaeological Science* 15: 459–462.
- Bush MB (1989) On the antiquity of British chalk grasslands: A response to Thomas. *Journal of Archaeological Science* 16: 555–560.
- Bush MB (1993) An 11400 years paleoecological history of a British chalk grassland. *Journal of Vegetation Science* 4: 47–66.
- Carcaillet C (2001a) Are Holocene wood-charcoal fragments stratified in alpine and subalpine soils? Evidence from the Alps based on AMS 14C dates. *The Holocene* 11: 231–242.
- Carcaillet C (2001b) Soil particles reworking evidences by AMS 14C dating of charcoal. *Comptes Rendus de l'Académie des Sciences – Series IIA – Earth and Planetary Science* 332: 21–28.
- Carcaillet C and Thion M (1996) Pedoanthracological contribution to the study of the evolution of the upper treeline in the Maurienne Valley (North French Alps): Methodology and preliminary data. *Review of Palaeobotany and Palynology* 91: 399–416.
- Carcaillet C and Vernet J-L (2001) Comments on 'The Full-Glacial Forests of Central and Southeastern Europe' by Willis et al. *Quaternary Research* 55: 385–387.
- Carcaillet C, Almquist H, Asnong H et al. (2002) Holocene bio-mass burning and global dynamics of the carbon cycle. *Chemosphere* 49: 845–863.
- Carrión JS, Sánchez-Gómez P, Mota JF et al. (2003) Holocene vegetation dynamics, fire and grazing in the Sierra de Gádor, southern Spain. *The Holocene* 13: 839–849.
- Combourieu-Nebout N, Peyron O, Bout-Roumazeilles V et al. (2013) Holocene vegetation and climate changes in the central Mediterranean inferred from a high-resolution marine pollen record (Adriatic Sea). *Climate of the Past* 9: 2023–2042.
- Corbel J (1954) Les phénomènes karstiques dans les Grands Causses. *Revue de Géographie De Lyon* 29: 287–315.
- Cousins SAO and Eriksson O (2002) The influence of management history and habitat on plant species richness in a rural hemiboreal landscape, Sweden. *Landscape Ecology* 17: 517–529.
- De Beaulieu J-L and Gilot E (1972) Végétations holocènes du mont Lozère: Analyses polliniques et datages. *Comptes Rendues Académie des Sciences* 274: 1641–1644.
- Denslow JS (1980) Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* 46: 18–21.
- Dolnik C, Dengler J, Jandt U et al. (2009) Dry grasslands in a changing environment – Special feature with contributions from the 5th dry grassland meeting 2008 in Kiel. *Tuexenia* 29: 331–337.
- Dutoit T, Buisson E, Roche P et al. (2003) Land use history and botanical changes in the calcareous hillsides of Upper-Normandy (North-Western France): New implications for their conservation management. *Biological Conservation* 115: 1–19.
- Dutoit T, Thion M, Talon B et al. (2009) Sampling soil wood charcoals at a high spatial resolution: A new methodology to investigate the origin of grassland plant communities. *Journal of Vegetation Science* 20: 349–358.
- Egan D and Howell EA (2001) *The Historical Ecology Hand-book: A Restorationist's Guide to Reference Ecosystems*. Washington, DC: Island Press.

- Ellenberg H (1996) *Vegetation Mitteleuropas Mit Den Alpen*. 5th Edition. Stuttgart: Eugen Ulmer.
- Forey E and Dutoit T (2012) Vegetation, soils and seed banks of limestone grasslands are still impacted by former cultivation one century after abandonment. *Community Ecology* 13: 194–202.
- Gaillard MJ, Dutoit T, Hjelle K et al. (2007) European cultural landscape – Insights into origins and development. In: Krzywinski K, O’Connell M and Küster H (eds) *Cultural Landscapes in Europe*. Delmenhorst: Aschenbeck and Holstein Publishers, pp. 35–44.
- Gibson CWD and Brown VK (1992) Grazing and vegetation change: Deflected or modified succession? *Journal of Applied Ecology* 29: 120–131.
- Giesecke T (2016) Did thermophilous trees spread into central Europe during the Late Glacial? *New Phytologist* 212: 15–18.
- Goepf S (2007) *Origine, histoire et dynamique des Hautes-Chaumes du massif vosgien – Déterminismes environnementaux et actions de l’Homme*. PhD Thesis, University of Strasbourg.
- Grove AT and Rackham O (2003) *The Nature of Mediterranean Europe: An Ecological History*. New Haven, CT: Yale University Press.
- Habel JC, Dengler J, Janišová M et al. (2013) European grassland ecosystems: Threatened hotspots of biodiversity. *Biodiversity and Conservation* 22: 2131–2138.
- Hájková P, Roleček J, Hájek M et al. (2011) Prehistoric origin of the extremely species-rich semi-dry grasslands in the Bílé Karpaty Mts (Czech Republic and Slovakia). *Preslia* 83: 185–204.
- Hejman M, Hejmanová P, Pavlů V et al. (2012) Origin, history, management and plant species composition of grasslands in Central Europe – A review. *Grassland Science in Europe* 17: 554–567.
- Henry F, Talon B and Dutoit T (2010) The age and history of the French Mediterranean steppe revisited by soil wood charcoal analysis. *The Holocene* 20: 25–34.
- Huault MF (1986) Etude palynologique d’un sondage dans le marais de La Harelle, Heurteville (Seine-Maritime). *Revue Archéologique de L’ouest* 1: 23–27.
- Jacquot C (1955) *Atlas d’anatomie des bois et des conifères*. Paris: Centre Technique du Bois et Fonds Forestier National.
- Jacquot C, Trenard Y and Dirol D (1973) *Atlas d’anatomie des bois d’Angiospermes*. Paris: Centre Technique du Bois et Fonds Forestier National.
- Jalut G, Dedoubat JJ, Fontugne M et al. (2009) Holocene circum-Mediterranean vegetation changes: Climate forcing and human impact. *Quaternary International* 200: 4–18.
- Janssen CR and Janssen-Kettilitz EL (1972) A post-Atlantic pollen sequence from the tourbière du Tanet (Vosges, France). *Pollen et Spores* 14: 67–77.
- Kahmen S and Poschold P (2004) Plant functional trait responses to grassland succession over 25 years. *Journal of Vegetation Science* 15: 21–32.
- Kahmen S, Poschold P and Schreiber K-F (2002) Conservation management of calcareous grasslands: Changes in plant species composition and response of functional traits during 25 years. *Biological Conservation* 104: 319–328.
- Kalis AJ, Merkt J and Wunderlich J (2003) Environmental changes during the Holocene climatic optimum in central Europe – Human impact and natural causes. *Quaternary Science Reviews* 22: 33–79.
- Karlík P and Poschold P (2009) History or abiotic filter: Which is more important in determining the species composition of calcareous grasslands? *Preslia* 81: 321–340.
- Kuneš P, Svobodová-Svitask H, Kolar J et al. (2015) The origin of grasslands in the temperate forest zone of east-central Europe: Long-term legacy of climate and human impact. *Quaternary Science Reviews* 116: 15–27.
- Lecompte M and Cohen M (1985) Le climat du Causse Méjan (830–1247m): montagnard et méditerranéen ? *Méditerranée* 56: 31–35.
- Marlon JR, Bartlein PJ, Carcaillet C et al. (2008) Climate and human influences on global biomass burning over the past two millennia. *Nature Geoscience* 1: 697–702.
- Molliex S, Siame LL, Bourlès DL et al. (2013) Quaternary evolution of a large alluvial fan in a periglacial setting (Crau Plain, SE France) constrained by terrestrial cosmogenic nuclide (Be-10). *Geomorphology* 195: 45–52.
- Nelle O, Robin V and Talon B (2013) Pedoanthracology: Analysing soil charcoal to study Holocene palaeoenvironments. *Quaternary International* 289: 1–4.
- Pärtel M, Helm A, Reitalu T et al. (2007) Grassland diversity related to the Late Iron Age human population density. *Journal of Ecology* 95: 574–582.
- Pokorny P, Chytrý M, Juricková L et al. (2015) Mid-Holocene bottleneck for central European dry grasslands: Did steppe survive the forest optimum in northern Bohemia, Czech Republic? *The Holocene* 25: 716–726.
- Pons A and Quezel P (1998) A propos de la mise en place du climat méditerranéen. *Comptes Rendus de L’académie des Sciences* 327: 755–760.
- Poschold P and Baumann A (2010) The historical dynamics of calcareous grasslands in the central and southern Franconian Jurassic mountains: A comparative pedoanthracological and pollen analytical study. *The Holocene* 20: 13–23.
- Poschold P and WallisDeVries MF (2002) The historical and socioeconomic perspective of calcareous grasslands: Lessons from the distant and recent past. *Biological Conservation* 104: 361–376.
- Poschold P, Baumann A and Karlík P (2009) Origin and development of grasslands in central Europe. In: Veen P, Jefferson R, de Smidt J et al. (eds) *Grasslands in Europe of High Nature Value*. Uitgeverij: KNNV Publishing, pp. 15–25.
- Power MJ, Marlon J, Ortiz N et al. (2008) Changes in fire regimes since the Last Glacial Maximum: An assessment based on a global synthesis and analysis of charcoal data. *Climate Dynamics* 30: 887–907.
- Rameau JC, Mansion D and Dumé G (1999) *Flore forestière française tome 2: Montagnes*. Paris: IDF.
- Rameau JC, Mansion D and Dumé G (2005) *Flore forestière française tome 1: Plaines et collines*. Paris: IDF.
- Rameau JC, Mansion D, Dumé G et al. (2008) *Flore forestière française tome 3: Montagnes*. Paris: CNPPF – IDF.
- Robin V and Nelle O (2014) Contribution to the reconstruction of central European fire history, based on the soil charcoal analysis of study sites in northern and central Germany. *Vegetation History and Archaeobotany* 23: 51–65.
- Robin V, Bork H-R, Nadeau M-J et al. (2014) Fire and forest history of central European low mountain forest sites based on soil charcoal analysis: The case of the eastern Harz. *The Holocene* 24: 35–47.
- Robin V, Nadeau M-J, Grootes PM et al. (2016) Palaeobotanical and climate data support the plausibility of temperate trees spread into central Europe during the Late Glacial. *New Phytologist* 212: 19–21.
- Robin V, Rickert B-H, Nadeau M-J et al. (2012) Assessing Holocene vegetation and fire history by a multiproxy approach: The case of Stodthagen Forest (Northern Germany). *The Holocene* 22: 337–346.
- Robin V, Talon B and Nelle O (2013) Pedoanthracological contribution to forest naturalness assessment. *Quaternary International* 289: 5–15.
- Römermann C, Dutoit T, Poschold P et al. (2005) Influence of former cultivation on the unique Mediterranean steppe of France and consequences for conservation management. *Biological Conservation* 121: 21–33.
- Schrautzer J, Jansen D, Breuer M et al. (2009) Succession and management of calcareous dry grasslands in the Northern Franconian Jura, Germany. *Tuexenia* 29: 339–351.

- Schwartz D, Goepp S, Ertlen D et al. (2014) Les défrichements anciens dans les massifs du Hohneck et du Rossberg. Une histoire revisitée des Hautes-Chaumes vosgiennes. In: Rothiot J-P and Husson J-P (eds) *La Bresse et ses vallées*. Epinal: Editions de la Fédération des Sociétés Savantes des Vosges, Racines Bressanes, Maison des Loisirs et de la Culture, pp. 61–76.
- Schwartz D, Thion M, Goepp S et al. (2005) Premières datations directes de défrichements protohistoriques sur les chaumes secondaires des Vosges (Rossberg, Haut-Rhin). Approche pédoanthracologique. *Comptes Rendus de Geoscience* 337: 1250–1256.
- Schweingruber FH (1990) *Anatomy of European Woods*. Bern; Stuttgart: Verlag Paul Haupt.
- Svenning JC (2002) A review of natural vegetation openness in north-western Europe. *Biological Conservation* 104: 133–148.
- Talon B (2010) Reconstruction of Holocene high-altitude vegetation cover in the French Southern Alps: Evidence from soil charcoal. *The Holocene* 20: 34–44.
- Théry-Parisot I (2001) *Economie des combustibles au Paléolithique*. Paris: CNRS.
- Thiebault S (1997) Early-Holocene vegetation and the human impact in central Provence (Var, France): Charcoal analysis of the Baume de Fontbrégoua. *The Holocene* 7: 343–349.
- Thion M (1978) La pédoanthracologie: une nouvelle méthode d'analyse phytochronologique depuis le Néolithique. *Comptes Rendus de L'académie des Sciences* 287: 1203–1206.
- Thomas KD (1989) Vegetation of the British chalklands in the Flandrian period: A response to Bush. *Journal of Archaeological Science* 16: 549–553.
- Touflan P, Talon B and Walsh K (2010) Soil charcoal analysis: A reliable tool for spatially precise studies of past forest dynamics: A case study in the French Southern Alps. *The Holocene* 20: 45–52.
- Triat-Laval H (1982) Pollen analyse de sédiments quaternaires récents du pourtour de l'Étang de Berre. *Ecologia Mediterranea* 8: 97–115.
- Van Campo M and Aymonin G (1962) Le problème de l'histoire de la flore et de la végétation dans les Cévennes méridionales, vu sous l'angle de l'analyse pollinique. *Flora* 152: 679–688.
- Vannièr B, Colombaroli D, Chapron E et al. (2008) Climate versus human-driven fire regimes in Mediterranean landscapes: The Holocene record of Lago dell'Accesa (Tuscany, Italy). *Quaternary Science Reviews* 27: 1181–1196.
- Vannièr B, Power MJ, Roberts N et al. (2011) Circum-Mediterranean fire activity and climate changes during the mid-Holocene environmental transition (8500–2500 cal. BP). *The Holocene* 21: 53–73.
- Vassilev K, Pedashenko H, Nikolov SC et al. (2011) Effect of land abandonment on the vegetation of upland semi-natural grasslands in the Western Balkan Mts., Bulgaria. *Plant Biosystems* 145: 654–665.
- Vera FWM (1999) *Grazing Ecology and Forest History*. Oxford: CABI Publishing.
- Vernet J-L (2006) History of the *Pinus sylvestris* and *Pinus nigra* ssp. *salzmanni* forest in the Sub-Mediterranean mountains (Grands Causses, Saint-Guilhem-le-Désert, southern Massif Central, France) based on charcoal from limestone and dolomitic deposits. *Vegetation History and Archaeobotany* 16: 23–42.
- WallisDeVries MF, Poschlod P and Willems JH (2002) Challenges for the conservation of calcareous grasslands in north-western Europe: Integrating the requirements of flora and fauna. *Biological Conservation* 104: 265–273.
- Willis KJ, Rudner E and Sümegi P (2001) Reply to Carcaillet and Vernet. *Quaternary Research* 55: 388–389.
- Wilmans O (1997) On the history of Central European dry grassland communities since the Late-Glacial: Methods, facts, hypotheses. *Phytocoenologia* 27: 213–233.