

Late Holocene ecological history of *Pinus pinaster* forests in the Sierra de Gredos of central Spain

José Antonio López-Sáez · Lourdes López-Merino ·
Francisca Alba-Sánchez · Sebastián Pérez-Díaz ·
Daniel Abel-Schaad · José S. Carrión

Received: 1 April 2009 / Accepted: 30 June 2009 / Published online: 14 July 2009
© Springer Science+Business Media B.V. 2009

Abstract This article describes the patterns and processes of vegetation change and fire history in the Late Holocene (c. 2400 calendar year BP) palaeoecological sequence of Lanzahíta, Sierra de Gredos in central Spain, and provides the first Iberian pollen sequence undertaken within a monospecific *Pinus pinaster* woodland. These new data reassess not only the autochthonous nature of this pine species in the region and the Iberian Peninsula, but also the naturalness of well-developed cluster pine forests. Conflicts of palaeoecological evidence with phytosociological models of vegetation dynamics in the study region,

and the relationships of *P. pinaster* with fire occurrence in Mediterranean-type ecosystems, are discussed.

Keywords Palaeoecology · Historical biogeography · Vegetation dynamics · *Pinus pinaster* · Holocene · Sierra de Gredos · Spain

Introduction

The cluster or maritime pine (*Pinus pinaster* Aiton) is a western Mediterranean species occurring in Spain, Portugal, continental France and Corsica, Italy (including Pantelleria and Sardinia islands), and the High Atlas and Tunisia in north Africa. In the Iberian Peninsula, *P. pinaster* covers 1.6 million ha, from which 0.6 million are supposedly resulting from direct planting (Gil et al. 1990; Gil 1991; Alía et al. 1995, 1996; DGCN 2002). Its peninsular distribution is patchy and comprises a broad spectrum of substrates (limestone, granite, schist, marly limestone, peridotite), topographies and climates, including from montane sub-humid to Mediterranean semi-arid with summer drought (Nicolás and Gandullo 1967; Alía et al. 1995, 1996, Carrión et al. 2000). Although it is usually forming open forests with dense scrub and mixed forests with oaks and other pine species, *P. pinaster* can occasionally shape monospecific forests (Costa-Tenorio et al. 1990; Blanco et al. 1997).

J. A. López-Sáez (✉) · L. López-Merino · S. Pérez-Díaz
Grupo de Investigación Arqueobiología, CCHS, CSIC,
Albasanz 26-28, 28037 Madrid, Spain
e-mail: joseantonio.lopez@cchs.csic.es

F. Alba-Sánchez
Departamento de Botánica, Facultad de Ciencias, Campus
Universitario de Fuente Nueva, Universidad de Granada,
18071 Granada, Spain

D. Abel-Schaad
Grupo de Investigación Forestal, Departamento de
Ingeniería del Medio Agronómico y Forestal, Escuela de
Ingeniería Forestal, Centro Universitario de Plasencia,
Universidad de Extremadura, Avenida Virgen del Puerto,
06800 Plasencia, Cáceres, Spain

J. S. Carrión
Departamento de Botánica, Facultad de Biología,
Universidad de Murcia, 30100 Murcia, Spain

In this article, we provide palynological data for the c. 2400-year vegetation and fire history of a *P. pinaster*-dominated area of the Sierra de Gredos in central Spain. There are several reasons why this investigation has been considered pertinent. First, because although the available palaeobotanical data are sufficient to assess the natural character of the cluster pine in the Iberian Peninsula (Carrión et al. 2000, and references therein, 2003b; Franco-Múgica et al. 2001, 2005; Carrión 2002; Alcalde et al. 2004; García-Amorena et al. 2007; Rubiales et al. 2009), palaeoenvironmental information associated with monospecific woodlands has so far not been reported.

Second, because it spans the last millennia, for which gaps in the palaeoecological knowledge of the region are particularly significant. For several reasons, including climatic change and human activities, many peat bog basins of the Iberian Peninsula with potential for palaeoecological research are interrupted before that time (Carrión et al. 2009).

Third, the lack of eco-historical information about monospecific stands has given opportunities to unsupported assumptions on cluster pine biogeography; if not about the naturalness of the species (something indisputable), at least definitely over the spatial pattern, magnitude and influence of recent afforestations in current distribution and dynamics. Only seldom, and in particular soil-conditioned situations such as on peridotites, *P. pinaster* communities have been postulated to represent mature forests (Nieto et al. 1989, 1991; Rivas-Martínez et al. 2001, 2002; Valle 2003), being most frequent in the literature the contention that is an invasive species of sclerophyllous scrub or deciduous forest (Izco 1984; Costa 1987; Peinado and Martínez-Parras 1985; Rivas-Martínez, 1987). The situation with *P. pinaster* in the Sierra de Gredos does illustrate this dispute, and while some argue that its local presence results from historical planting (Rivas-Martínez 1963, 1975, 1987; Sánchez-Egea 1975; Rivas-Martínez et al. 1986, 1987; Sánchez-Mata 1989), others stress the lack of evidence for such an activity (Gil 1991; Manuel and Gil 2001). This is not a trivial issue, for many regard that planting cluster pine is inappropriate from a biological perspective and will invariably conduct to failure in forest development (e.g. Rivas-Martínez 1987, 2007; Rivas-Martínez et al. 2002).

Inextricably merged with the former is the assumption that, in absence of human activities,

forests on sufficiently developed soils in the Iberian Peninsula will be dominated by *Quercus* species (Rivas-Martínez 1987). This notion of natural potential vegetation permeates well beyond scholarly articles to deeply penetrate the philosophies that underlie policies on landscape and environmental management. A notorious example is the Habitats Directive and its Natura 2000's interpretation manual of EU habitats (Council of the European Communities 2003). Here lies the fourth reason why this study has been undertaken. Floristically-based, phytosociological models (Rivas-Martínez 1987; Sánchez-Mata 1989), consider that the potential vegetation of the study area, within the mesomediterranean belt, corresponds to an evergreen oak forest (*Pyro bourgaeanae-Quercetum rotundifoliae*), with deciduous oak forest patches (*Luzulo forsteri-Quercetum pyrenicae*) being allegedly pristine in the uppermost, supramediterranean belt between 800 and 1,600 m. The current situation, however, is not of an oak-dominated forest, evergreen or deciduous.

A final implication of this study concerns fire ecology. Charcoal records combined with pollen analysis have been shown to provide contending models of vegetation dynamics in Mediterranean-climate scenarios (e.g. Carcaillet et al. 1997; Turner et al. 2008; Vannièrè et al. 2008; Conedera et al. 2009). This approach may be outstanding for dealing with *P. pinaster*, a species often associated to pyrophilous communities and, indeed, very flammable (Barbero et al. 1998; Calvo et al. 2003, 2008). The palaeo-record presented here provides an opportunity to study these complex interactions in a unique ecosystem, characterised by the prevalence of the cluster pine in the arboreal stratum. Most antecedents relate with regions displaying higher species diversity of forest trees, and therefore it has been difficult to isolate the relationships between fire frequency and *P. pinaster* cover changes (e.g. Carrión and van Geel 1999; Carrión 2002; López-Sáez et al. 2009a).

Methods

Site description

The study area is located in the municipality of Lanzahíta (province of Ávila, Central Spain) on the southern slopes of the eastern massif of the Sierra de

Gredos. A 100-cm sediment core was extracted from a small (150 m²) peat bog (588 m altitude) in the Tiétar Valley (40°13'20"N, 4°56'09"W) (Fig. 1). A granitic bedrock stopped coring at 100 cm depth. The climatic parameters, such as average annual temperatures (15.1°C) and annual rainfall (1,007 mm) were taken from the nearest meteorological station (La Adrada, 1,000 m, 40°18'N and 4°38'W). The soils are from granitic origin and can be classified as humid brown soils (humic cambisols according to the FAO nomenclature) associated with lithosols (Gallardo et al. 1980). The area is situated within the mesomediterranean belt, with a subhumid/humid ombroclimate (Sánchez-Mata 1989).

The vegetation of the peat bog is formed by small oligotrophic bog communities (*Caricetum carpetanae*) dominated by *Carex nigra* (L.) Reichard subsp. *carpetana* (C. Vicioso) Rivas-Martínez, *C. echinata* Murray, *Parnassia palustris* L., *Drosera rotundifolia* L., and towards the drier margins by *Erica tetralix* L. and *Calluna vulgaris* (L.) Hull. Most of the Tiétar Valley is characterised by a dense *P. pinaster* forest with understorey of *Cistus ladanifer* L., *Lavandula stoechas* L., *Rosmarinus officinalis* L., *Thymus*

mastichina (L.) L. and *Cytisus scoparius* (L.) Link. Towards the southern slopes of eastern Sierra de Gredos, maritime pine forests still cover an area of approximately 39,200 ha occupying a wide altitudinal gradient (500 to 1,000 m) (Alfía et al. 1996; Sierra de Grado 1996) (Fig. 1). *Pinus sylvestris* L. and *Pinus nigra* Arnold are more frequent in altitude, shaping the timberline. Riparian forests of black alder (*Alnus glutinosa* (L.) Gaertn.) inhabit the banks of the Eliza river. Today, the valley is cultivated with tobacco, olive trees, watermelon, peppers and asparagus (López-Sáez 2004). The Tiétar Valley is one of the peninsular areas showing a higher incidence of forest fires (Abad et al. 2007), for which exists abundant documentation of the last few decades (Vázquez and Moreno 1998, 2001). Some recent fires have affected areas of above 6,500 ha, including upto 3,500 ha of *P. pinaster* (Pérez et al. 2003).

Pollen analysis

The core was extracted with a Russian corer and the peat sections placed in PVC tubes and protected in plastic guttering, sealed in polythene tubing, and

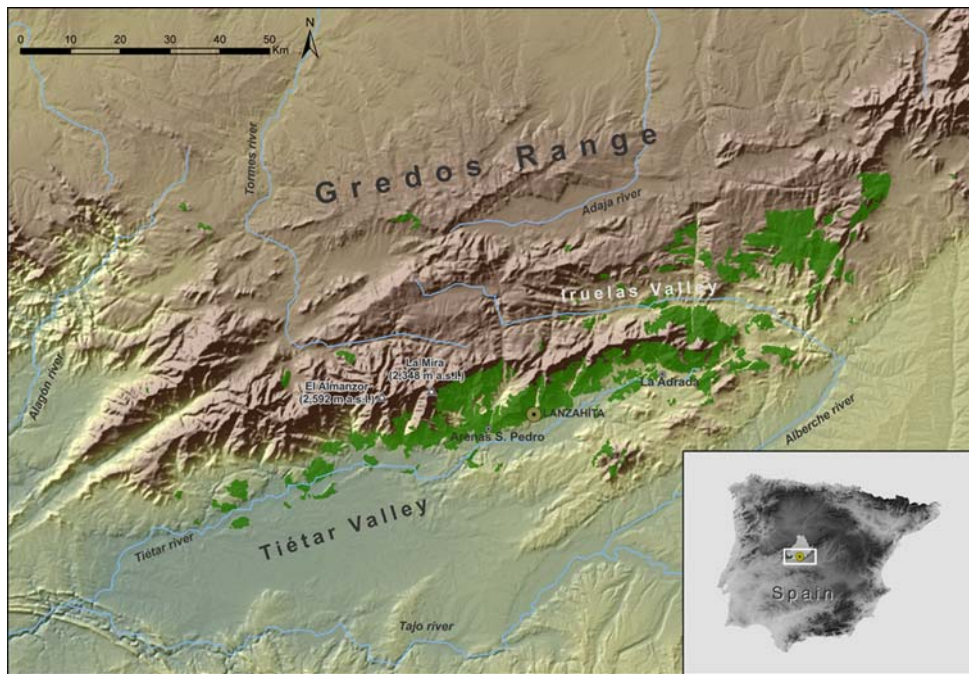


Fig. 1 The study area of southern slopes of Sierra de Gredos (Tiétar Valley, Ávila, Central Spain) and situation of the fossil sequence (Lanzahita peat bog). Light green represents the

modern distribution of the forest formations dominated by *P. pinaster* in the Tiétar Valley

placed in cold storage (4°C) prior to laboratory subsampling at 2 cm intervals. Fifty samples of 1 cm³ were analysed. All samples were treated according to the Faegri and Iversen (1989) method although acetolysis was not carried out to allow the identification of any contamination by modern pollen (Franco-Múgica et al. 1997). One *Lycopodium* tablet per sample was added in order to calculate pollen concentration (grains cm⁻³) (Stockmarr 1971), and these values were divided by deposition time (year cm⁻¹) to calculate pollen accumulation rate (PAR; grains cm⁻² year⁻¹). Small aliquots of the residues were mounted in glycerine, sealed with Histolaque and all recognisable pollen and spores were counted under a light microscope using a 400× magnification, until a pollen amount of at least 500 units was reached. *P. pinaster* was palynologically discriminated from the rest of the pines based on its relatively larger pollen body, short alveoli and thick proximal exine (Carrión et al. 2000). The remaining pine pollen, including doubtful pollen grains, were included in a general *P. sylvestris* type, which, given the flora of this particular region, may also include *P. nigra*. Non-pollen palynomorphs (NPPs) were identified using the nomenclature proposed by van Geel (2001). Palynological identification and counting was aided by the reference collection available at the Laboratory of Archaeobiology at the CSIC, Madrid.

Charcoal analysis

In order to reconstruct local fire history at Lanzahíta, macroscopic charcoal was identified and counted from subsamples of 1 cm³ at every 2 cm depth by sediment sieving. The samples were soaked in a 3% sodium metaphosphate solution (72 h) to deflocculate

any particles, then washed through a 125 µm mesh sieve. Macrocharcoal was identified at a 40× magnification according to Rhodes (1998). Particles >125 µm diameter are not transported far from their source and thus provide information on local fire history (e.g. Whitlock and Larsen 2001). Microscopic charcoal were identified and counted at a magnification of 400× on the same slides used for pollen analysis (Tinner and Hu 2003; Finsinger and Tinner 2005). Charcoal accumulation rates (CHARs) were calculated by sedimentation rate (cm year⁻¹) and are expressed in particles cm⁻² year⁻¹.

Chronology

Seven peat samples were ¹⁴C dated using AMS technique. The dates were calibrated using CALIB 5.0.2 (Stuiver et al. 1998) with the INTCAL04 curve (Reimer et al. 2004) (Table 1). These dates were used to build an age model by linear interpolation (Fig. 2) taking into account the maximum probability intervals at 2 sigma ranges, which is considered to be a robust statistical value (Telford et al. 2004).

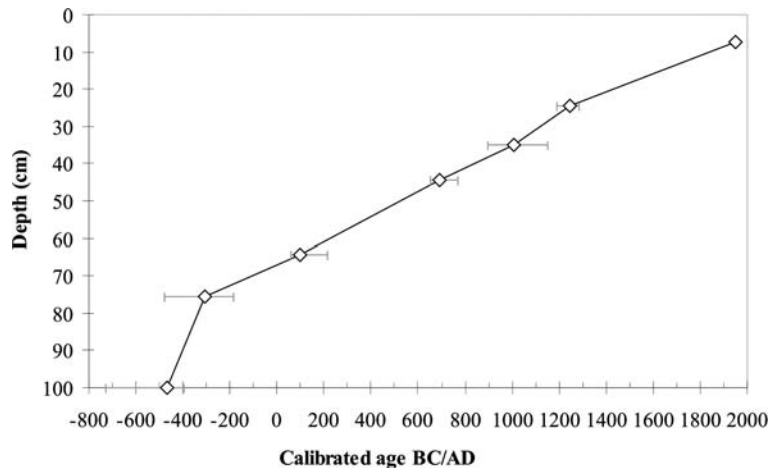
Results and interpretation

The results of identification and counting of pollen grains, spores and NPPs are presented as a percentage diagram (Fig. 3). As it is common with pollen analysis, ferns, aquatics and NPPs were excluded from the total pollen sum in order to avoid biases with local pollen representation. Pollen assemblage zones (PAZ) represent pollen-stratigraphical changes, and were constructed on the basis of agglomerative cluster analysis of incremental sum of squares

Table 1 AMS radiocarbon data from the Lanzahíta peat bog record. Each calibrated radiocarbon date (in parentheses) is presented as a median probability with its 2 sigma interval

Depth (cm)	Radiocarbon date (year BP)	Calibrated age (2σ) (calendar year BP)	Calibrated age (2σ) (calendar year BC/AD)	Laboratory reference
7–8	Modern	–	–	CNA-095
24–25	780 ± 35	667 (706) 762	AD 1188 (1244) 1283	Ua-24879
35	1020 ± 35	799 (940) 1051	AD 899 (1010) 1151	Ua-24878
44–45	1315 ± 29	1179 (1259) 1296	AD 654 (691) 771	CNA-105
64–65	1907 ± 35	1820 (1853) 1928	AD 59 (97) 214	CSIC-1877
75–76	2280 ± 55	2132 (2255) 2430	481 BC (306) 183 BC	Ua-19515
100	2387 ± 32	2342 (2417) 2676	727 BC (468) 393 BC	CSIC-1876

Fig. 2 Age-depth model for Lanzahíta peat bog. Lines connecting each plotted point are linear interpolated sediment-accumulation rates. The horizontal bars show the minimum and maximum ranges at 2σ



(CONISS) with square root transformed percentage data (Grimm 1987). The diagrams were plotted using TILIA and TILIA-GRAPH v. 2.0.b.5 softwares (Grimm 1991). The sequence was divided into five zones (Figs. 3, 4). Figure 4 shows CHARs, PAR, pollen concentration and deposition times related to selected pollen and NPP percentages curves. Sedimentation rates were not constant, but no evidence of an erosive event has been found.

PAZ 1 (100–63 cm): c. 470 BC to AD 140

Pinus pinaster percentages are high (52–62%) indicating a maritime pine forest in the vicinity. Deciduous (4–8%) and evergreen *Quercus* (3–5%) show continuous occurrences, while *Alnus*, *Betula*, *Castanea*, *Fraxinus*, *Juglans*, *Juniperus* and *P. sylvestris* pollen types are low (<3%). The amounts of shrub pollen are between 10 and 19% including *Arbutus unedo*, *C. vulgaris*, *C. ladanifer*, *Erica arborea*, Labiatae undiff., *L. stoechas*, *Phillyrea*, *Pistacia terebinthus* and *Viburnum* types. Herbaceous pollen is between 9 and 21% and PAR very high (42–166, 10^3 grains cm^{-2} year $^{-1}$). Both micro and macrocharcoal particles are present in low concentrations (<70 and <40 particles cm^{-2} year $^{-1}$, respectively).

PAZ 2 (63–45 cm): c. AD 140–675

Pinus pinaster is at its minimum in this pollen zone, oscillating from 29 to 45%. Other components increase such as *Olea* (4–11%), *Castanea*, *Asphodelus albus* (1–3%), *Aster* (2–6%), Cardueae (1–3%),

Cichorioideae (3–5%) and Poaceae (9–16%). Altogether, these data suggest clearance of the pine woodland, perhaps linked to the local cultivation of olive trees. PAR oscillates between 20 and 80×10^3 grains cm^{-2} year $^{-1}$. This zone is also characterised by rapid accumulation of charcoal, the average influx for macrocharcoal reaching 142 particles cm^{-2} year $^{-1}$, while microcharcoal influx was 713 (<50 μm) and 211 (50–125 μm) particles cm^{-2} year $^{-1}$. This suggests that fire events were of local origin (Whitlock and Larsen 2001). Trends in CHARs correspond with shifts in those pollen assemblages that have higher values of anthropogenic taxa (*Aster*, Cardueae, Cichorioideae, *Rumex acetosella*), *A. albus* and *C. ladanifer*. A large amount of *Pteridium aquilinum* spores occurred in PAZ 2 suggesting fernland spread, which could be related to increased burning (Gliessman 1978; van der Knaap and van Leeuwen 1994). Fungal spores include important counts of the carbonicolous *Chaetomium* (maxima 15%).

PAZ 3 (45–25 cm): c. AD 675–1225

In this zone, *P. pinaster* (53–69%) values are the highest of the sequence and parallel increases in *C. ladanifer*, *Phillyrea* and *P. terebinthus*. Pollen of *Alnus*, *Betula*, *Castanea*, *Fraxinus*, *Juglans*, *Juniperus* and *P. sylvestris* is below 3% and *Olea* disappears. Most of shrubs maintain a continuous and significant presence throughout, reflecting the increased importance of the woodland understorey. Anthropogenic taxa, *A. albus*, Poaceae, *P. aquilinum*

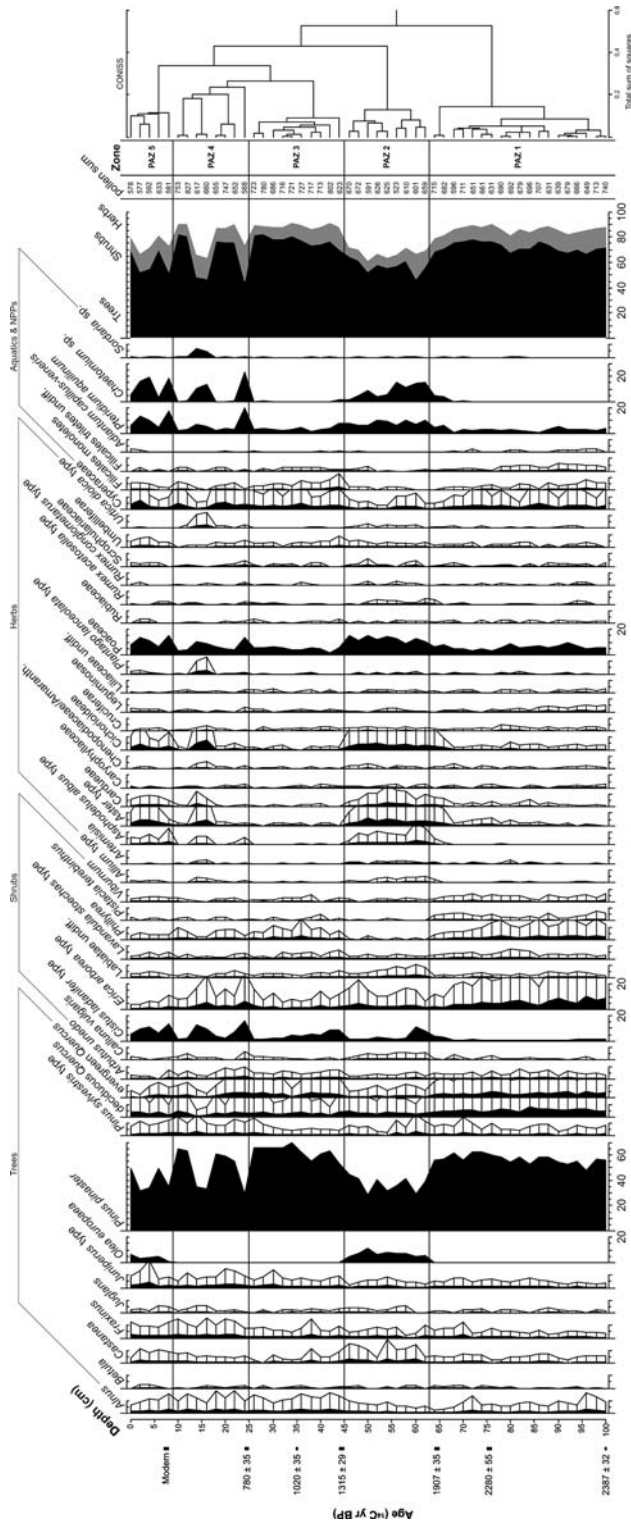


Fig. 3 Pollen and NPP diagram of Lanzahita peat bog. Exaggerated curves show percentage data with 5 × exaggeration

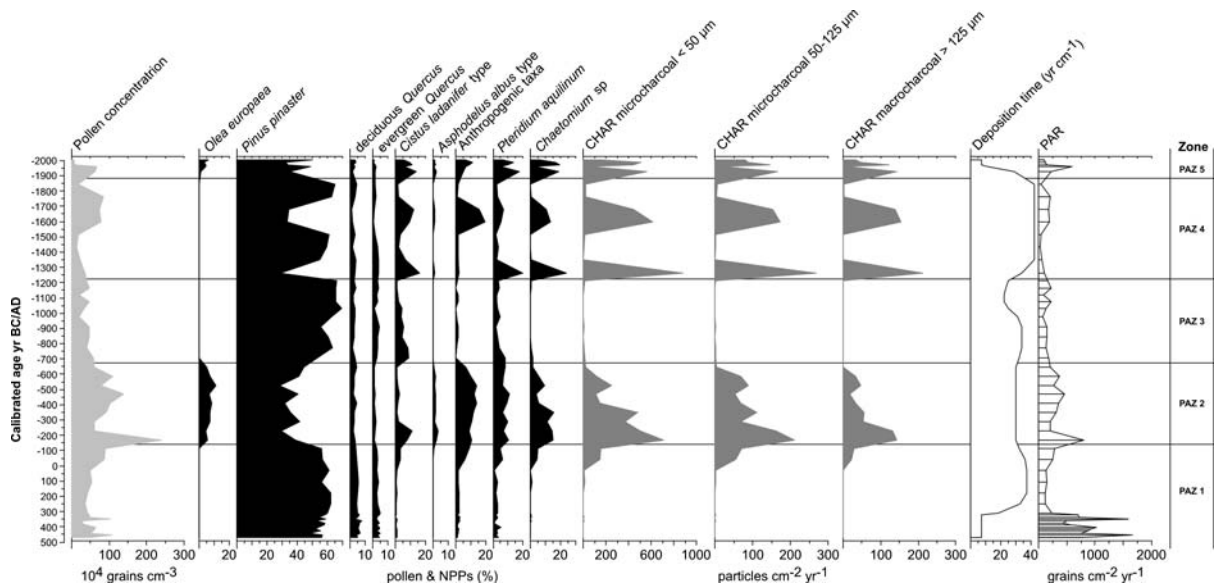


Fig. 4 Charcoal accumulation rates (CHAR), pollen accumulation rate (PAR), deposition time, pollen concentration, and selected pollen and NPP percentage diagram from Lanzahita peat bog

and *Chaetomium* decrease significantly. Charcoal accumulation rates are in their lowest values (<13 particles cm^{-2} year $^{-1}$) while PAR diminishes up to $6\text{--}21 \times 10^3$ grains cm^{-2} year $^{-1}$.

PAZ 4 (25–9 cm): c. AD 1225–1885

In this zone, significant oscillations of *P. pinaster* are noticed (29–65%). *C. ladanifer* (maxima 16%), *E. arborea*, *A. albus*, *Aster*, Cardueae, Cichorioideae (maxima 8%), *Plantago lanceolata*, Poaceae, *Urtica dioica*, *P. aquilinum* (maxima 20%), *Chaetomium* and *Sordaria* show a greater presence in PAZ 4, but *P. pinaster* sharply declines. PAR remains relatively stable ($4\text{--}20 \times 10^3$ grains cm^{-2} year $^{-1}$). The charcoal accumulation rates are higher than those of PAZ 2 zone, suggesting enhanced fire events (c. AD 1265 and c. AD 1600–1680) in relation to the previous fire episode (c. AD 115–170). The strong increase of *Sordaria* (coprophilous fungus, 4–7%) and maxima values of *P. lanceolata* and *U. dioica* indicate woodland clearance and grazing between c. AD 1600–1680.

PAZ 5 (9–0 cm): c. AD 1885–2000

This zone is characterised by oscillations in the *P. pinaster* pollen curve (between 32 and 50%). Also

noteworthy are the continuous presence of *Olea* (1–6%) and the increases of *C. ladanifer*, *A. albus*, *Aster*, Cardueae, Cichorioideae, Poaceae, *P. aquilinum* and *Chaetomium* spores. Increases in micro and macro-charcoal particles suggest local fires at c. AD 1930 and c. AD 1975. A progressive enrichment, between CHARs maxima, in PAR (59×10^3 grains cm^{-2} year $^{-1}$), is observed.

Discussion

Palaeobotanical data demonstrate that the maritime pine is natural of the Iberian Peninsula

Charcoal analysis from several archaeological settlements in Portugal (Figueiral 1995; Figueiral and Terral 2002) demonstrates the presence of *P. pinaster* in coastal and inland areas since c. 33,000 BP and through the Bronze Age (Figueiral and Bettencourt 2004). Recently, 32 stumps were found in situ at Barreiro, at the mouth of the River Tagus, corresponding to stands of *P. pinaster* more than 7,000 years old (García-Amorena et al. 2007). Southwards in western Spain, in the Badajoz province, about 150 km south of the Tiétar Valley, *P. pinaster* charcoal has been found for a c. 2250 calendar year BP, Iron Age settlement in Castillejos II. These

recent findings together with others in northern Iberia (Alcalde et al. 2004; Rubiales et al. 2005, 2007) and the surroundings of the Baetic Cordillera (Rodríguez-Ariza 2000), confirm the natural character of *P. pinaster* in Spain.

Given the difficulties with the palynological identification of *P. pinaster* (Carrión et al. 2000), pollen sequences probably fail to reflect the past cover of this species in the Quaternary forests. In fact, if due regard is made of the current distribution, a good part of the pine pollen in sites like El Carrizal (Franco-Múgica et al. 2005) or Montes Universales (Stevenson 2000) could be from the maritime pine. In any case, there are Pleistocene and Holocene pollen records of *P. pinaster* in almost all the regions of the Iberian Peninsula. Examples include the northern territories (Aira and Saá 1989; Reille 1990, 1991; Ramil 1992; López-Sáez et al. 2009b), Portugal (Mateus 1989; Mateus and Queiroz 1993), the southeastern and eastern regions of Mediterranean-sea influence (Carrión and van Geel 1999; Carrión et al. 2003a, 2003b), the Baetic Cordilleras and adjacent highplains (Carrión 2002; Carrión et al. 2001a, 2001b, 2004, 2007) and Gibraltar (Carrión et al. 2008). The pollen record of the Navarrés peatbog (Valencia, eastern Spain; Carrión and van Geel 1999) shows a synchronous Late Quaternary fluctuation of *P. pinaster*, and *Quercus*-dominated assemblages. It is also noticeable that, during glacial times, *P. pinaster*, although retreated, survived in refugia accompanied by deciduous trees (*Corylus*, *Fraxinus*, *Quercus*) and Mediterranean woody species (*Arbutus*, *E. arborea*, *Olea*, *Phillyrea*, *P. terebinthus*, *Myrtus communis*, *Viburnum tinus*). A similar picture, although more complex in terms of species interactions, is seen in the full-glacial of the Siles lake pollen sequence (Carrión 2002). The pollen record of Lanzahíta described here join to these former findings to warrant not only the autochthonous character of *P. pinaster* in the Iberian Peninsula, but also the naturalness of well-developed cluster pine forests.

The genetic structure of modern populations point to a complex multi-refugia peninsular pattern of *P. pinaster*

Parallel research lines of arguments have led to the hypothesis that the Quaternary climatic changes have

played a major role in the genetic structuring of maritime pine (Baradat and Marpeau 1988; Salvador et al. 2000). It has been hypothesised that the actual distribution of this species is the result of events that occurred during the last glaciation (Baradat and Marpeau 1988; Bahrman et al. 1994). At temperate latitudes, thermophilous species may have consequently been restricted to small southerly ranges with implications for subsequent migration patterns and population genetic structure (McLachlan and Clark 2004). In fact, different maternal lineages in maritime pine may represent different isolated glacial refugia of the species because the existence of a population genetic structure has a main role in adaptation to local environment variation (Petit et al. 1995; Wahid et al. 2004). The typical scattered distribution may have prevented, or limited, gene flow among the different groups of populations, thereby determining genetic drift and high genetic divergence among populations (Vendramin et al. 1998).

Genetic variation patterns across the native range of the species are quite complex (Baradat and Marpeau 1988; Vendramin et al. 1998; Salvador et al. 2000; Burban and Petit 2003) and large genetic differences among populations have been reported at regional and wide-range spatial scales (Salvador et al. 2000; González-Martínez et al. 2001, 2004, 2005). In the Iberian Peninsula, maritime pine populations show high levels of genetic diversity and an important genotype-by-environment interaction that favours the existence of adaptations to local ecological conditions (Alía et al. 1995, 1997; Salvador et al. 2000; Miguel-Pérez et al. 2002). A recent study by Bucci et al. (2007) has identified one “hotspot” of haplotype diversity in central and southeastern Spain and two areas of low haplotypic diversity located in the western peninsula and Morocco. Postglacial developments, starting earlier in the zones of higher diversity, may have contributed to shape the distribution until relatively recently. The picture that emerges from all these genetic studies combined with fossil evidence is that the current-day distribution of maritime pine in the Iberian Peninsula could be explained by the location of glacial refugia, environmental restrictions, Holocene spreads, human impact and fire-mediated replacement dynamics with other Mediterranean conifers (Salvador et al. 2000; Gómez et al. 2005; Gómez and Lunt 2006).

Pinus pinaster forests are natural in southern Sierra de Gredos

The Lanzahíta pollen diagram covers a c. 2700-year record of vegetation history from the southern slopes of Sierra de Gredos (Tiétar Valley). The landscape of the study area from c. 470 BC to AD 140 (PAZ 1) and c. AD 675–1225 (PAZ 3) is dominated by a dense pinewood of *P. pinaster* with patches of evergreen and deciduous *Quercus*. Plausibly, this represents not only some local patchiness but a regional signal of the mountain vegetation belts (*P. sylvestris* and/or *P. nigra* at highest altitudes), as seen in the modern landscape (Sánchez-Mata 1989). Studies of pollen rain support this view (Andrade et al. 1994). Qualitatively, the PAZ 1 and PAZ 3 pollen assemblages match well with the composition and structure of modern communities (Barkman 1990) such as the *Pinus-Phillyrea* woodland type characterised by *P. pinaster*, *A. unedo* L., *C. ladanifer*, *E. arborea* L., *V. tinus* L., *Pistacia* sp. and *Phillyrea* sp.

The continuous dominance of maritime pine throughout the Late Holocene support the contention that the *P. pinaster* belt in the Tiétar Valley is of natural origin. Taking into account the detailed Spanish *P. pinaster* chorology given by Alía et al. (1996, 1997), Lanzahíta site is located in a recognised natural stand for this taxon (Sierra de Gredos). Our results reveal the natural presence of maritime pine in the study area before the Roman occupation of the southern slopes of Sierra de Gredos.

Mediaeval documentary records make reference the Lanzahíta pine forests. The *Consignación de Rentas* sent by Cardinal Gil Torres to the Bishop of Ávila in 1250, listed, under the heading of ‘pines’, the forests of many localities in southern Gredos such as Arenas de San Pedro, La Parra, Lançaita (Lanzahíta) or La Adrada (González 1974). The *Libro de la Montería de Alfonso XI* (1350) also refers the presence of maritime pine forests in the Tiétar Valley, some of which are reflected in current toponyms, demonstrating unequivocally their existence during the Late Middle Ages in the study area (Martínez-Ruiz 1998; Chavarría 1999). Thus, the recovery in the percentages of *P. pinaster* in the first half of PAZ 4 (c. AD 1265–1515) could be related with mediaeval regulations for the prevention of forest fires in the Sierra de Gredos such as *Fuero del Barco de Ávila* (1211), the ordinances of Rincón (1472) and La Adrada (1502) (Martínez-Ruiz 1998). In

fact, it is at a later date to such regulations where maritime pine pollen percentages decreased again coinciding with a new charcoal accumulation rate maximum.

Afforestations with maritime pine were unimportant in the Iberian Peninsula before 1887 (Gil 1991). The oldest management project of the forests in the Sierra de Gredos dates from 1885 (Iruelas Valley) and the second was written in 1918 for the pine forest of Santa Cruz del Valle. The remaining forests of the valley were not managed until the last half of the 20th century (Sierra de Grado 1996). Therefore, no historical document reflects afforestation of the study area with maritime pine before the dates discussed above. Rather, toponymic information indicates the common occurrence of *P. pinaster* woodlands throughout the Sierra de Gredos (Gil 1991; Chavarría 1999). The large-scale coniferous reafforestation in the Sierra de Gredos is reflected in the pollen diagram (PAZ 5) after c. AD 1960.

Floristic-phytosociological models conflict with palaeoecological data about the “natural” potential vegetation

The data provided by the Lanzahíta pollen record (Figs. 3, 4) appear not to fit into the floristically-based phytosociological model of vegetation change for the study area, which, as mentioned earlier, postulates that an oak forest is the “climax” vegetation of the Tiétar Valley (Rivas-Martínez 1963, 1975; Sánchez-Mata 1989). This is to say that the forest patches of *P. pinaster* are incidental and mainly derived from afforestations. The vegetation history at Lanzahíta spans a relatively recent period, which was not free of human impact, probably in the form of prehistoric pastoralism and historical agriculture, as in other regions of the Iberian Peninsula (e.g. van der Brink and Janssen 1985; van der Knaap and van Leeuwen 1995; Carrión et al. 2003a). On the other hand, it is difficult to isolate natural from man-made events since they often overlap in historical records and have similar effects on the present-day landscape. In any case, if contextualised in the Holocene pollen succession of the central mountain systems of Iberia (Ruiz-Zapata et al. 1996; Franco-Múgica et al. 1997, 2001; van der Knaap and van Leeuwen 1997), it seems that Lanzahíta is just another record reflecting the multi-millennial resilience of Holocene pinelands.

In sum, this might be another case of “failure” in the dynamic model by phytosociologists. Many allegedly pristine oak woodlands of the Iberian Peninsula and Balearic Islands are indeed pine and pine-oak mixed forests, as seen in pollen records of the pre-anthropogenic phases of the Holocene (e.g. Peñalba 1994; Franco-Múgica et al. 2001, 2005; Ruiz-Zapata et al. 2002; Carrión and Díez 2004). The potentiality of *Quercus ilex* forests under dry and sub-humid ombroclimates was early discussed by Reille and Pons (1992), and similar disagreements are found year by year in other regions such as recently in Slovenia (Andric and Willis 2003). The conflict between palynology and phytosociology has extended to the Canary Islands, where pre-anthropogenic forests have been shown to be dominated by *Quercus-Carpinus* forests (de Nascimento et al. 2009), thus contradicting the conventional “wisdom” about laurel forests (Rivas-Martínez et al. 1993).

Maritime pine forests linked to fire occurrence

Overall, the Lanzahíta palaeoecological sequence reflects the association of *P. pinaster* with fire occurrence. From the charcoal evidence, it even appears that the vegetation changes recorded in PAZ 2 (c. AD 140–675), PAZ 4 (c. AD 1225–1885) and PAZ 5 (c. AD 1885–2000) may have been a consequence of intensifying fire regimes and olive tree cultivation. The fires could have been anthropogenically induced, since the first important charcoal peak (c. AD 115–170) coincides with the first Roman rural settlements in the area (Martino 2004), the second (c. AD 1265) with the Christian repopulation of the Tiétar Valley (Mariné 1995), the third (c. AD 1600–1680) with the height of the “Concejo de La Mesta” transhumance system (Troitiño 1987) and high values for anthropozoogenous taxa (*P. lanceolata*, *U. dioica*) and coprophilous fungi (*Sordaria* sp.) (López-Sáez and López-Merino 2007), and the last two-ones (c. AD 1930 and c. AD 1975) with intensive fire forests reported in the vicinity of Lanzahíta peat bog (Vázquez and Moreno 2001). Hypothetically, burning by local communities may have provoked woodland clearance, permitting the expansion of heliophytic and pyrophytic communities such as those dominated by *C. ladanifer* or *A. albus* (Franco-Múgica et al. 2005). The abundance of anthropogenic taxa and carbonicolous ascospores in

these zones supports this hypothesis (López-Sáez et al. 1998).

Other Holocene pollen records have linked the presence and/or expansions of *P. pinaster* with fire events, continued fire occurrence or intensification of burning. The Navarrés pollen record shows that, around 6000 BP, maritime pine was involved in a post-fire replacement of *Pinus* forests towards oak-dominated vegetation (Carrión and van Geel 1999). *P. pinaster* exhibited here an ecological behaviour closer to evergreen oaks than *P. nigra*, and became favoured by anthropogenic disturbance. A partial, competitively-mediated replacement of *P. nigra* by *P. pinaster* in absence of human activities has been reported in the early Holocene of the Segura Mountains in southern Spain (Carrión 2002). In a pedoanthracological study undertaken in Corsica, Carcaillet et al. (1997) showed a late Holocene expansion of *Quercus ilex*, *P. pinaster* and *E. arborea* after burning of a *P. nigra* forest.

Fire is a natural factor of many Mediterranean landscapes and has an important influence on the biological productivity and composition of several ecosystems (Calvo et al. 2008). The role of fire as a disturbance that generally favours the *Pinus* genus is well recognised, fire being a major factor in the dynamics of Mediterranean pine forests (Barbero et al. 1998). In Spain, the maritime pine is one of the conifer forest types most frequently subject to fire, which affects 33% of all such forests (Pérez and Moreno 1998). Seed production and the life-history strategy of maritime pine are related to forest fire regimes and their communities of natural origin occur in lightning-prone mountains (González-Martínez et al. 2002; Fernandes and Rigolot 2007) such as the Sierra de Gredos (Vázquez and Moreno 2001). Among the *P. pinaster* populations across Spain, those located on the southern slopes of Sierra de Gredos are particularly subject to frequent arsons (Vázquez and Moreno 1998, 2001; Abad et al. 2007). The study area is very sensitive to the risk of forest fires due to the sharp orography, abundant storms and pronounced summer deficit, as well as high temperatures in the inner valley. Owing to this high frequency, the maritime pine forests in this area have acquired a series of adaptative characteristics that help their perpetuation in fire-prone Gredos environments such as early flowering, presence of serotinous cones, an important canopy seed bank and a thick bark (Gil et al.

1990; Tapias et al. 2001, 2004; Fernandes and Rigolot 2007; Calvo et al. 2008). However, regardless of the high seed germination capacity of *P. pinaster* after a fire (Torres et al. 2006), its forest regeneration is dependent on post-fire environmental conditions which affect seed germination and seedling establishment (Rodrigo et al. 2004; Calvo et al. 2008).

Competitive effects on the establishment of *P. pinaster* seedlings can also be expected in forests where the dominant understorey species consist mostly of woody (such as *Quercus pyrenaica* or *C. ladanifer*) and herbaceous resprouters (Calvo et al. 2003), but understorey vegetation appears to have a positive influence on the height of maritime pine seedlings (Calvo et al. 2008). In fact, in the studied area *C. ladanifer* plays an important role in the pattern of recolonization of *P. pinaster* stands after wildfire (e.g. PAZ3). This shrub species is a pioneer after a fire, for it germinate rapidly from a persistent soil seed bank which is stimulated by a thermal increase (Calvo et al. 2003). Vázquez and Moreno (2001) have confirmed the tendency for fires to be highly aggregated in space in the southern slopes of Sierra de Gredos and furthermore it was also evidenced that reburning tended to occur preferentially in certain areas such as Lanzahíta. The result of these tendencies is a concentration of the likely impacts of fires in the study area with low elevations, lower slopes and deeper soils. Under such an accelerated fire cycle, maritime pine forest would not regenerate naturally without management, which would lead to lasting vegetation change (Pérez and Moreno 1998).

Acknowledgements This study was funded by the projects HAR2008-06477-C03-03/HIST, CGL-2006-2956-BOS (Plan Nacional I + D + i, Ministry of Education and Science, Spain), CSD2007-00058 (Consolider Program, Consejo Superior de Investigaciones Científicas, Spain) and Paleodiversitas Network (Fundación Séneca, Murcia). Milagros Tapia Ariza, Paco Peón, Mariano Martín and Daniel Sánchez-Mata provided guidance and advice throughout the study. We thank the personnel of Ayuntamiento de Lanzahíta for logistical support. G. Reher corrected the final English version of the manuscript.

References

- Abad J, García F, Cepeda C (2007) La situación de los incendios en el Valle del Tiétar. *Observat Medioamb* 10:123–143
- Aira MJ, Saá MP (1989) Contribución al conocimiento de la vegetación holocena (3000–2210 B.P.) de la provincia de Pontevedra a través del análisis polínico. *Anales J Bot Madrid* 45:461–474
- Alcalde C, García-Amorena I, Gómez-Manzanaque F, Maldonado J, Morla C, Postigo JM, Rubiales JM, Sánchez L (2004) Nuevos datos de carbones y maderas fósiles de *Pinus pinaster* Aiton en el Holoceno de la Península Ibérica. *Invest Agr: Sist Recur For fuera de serie* 15:2–163
- Alía R, Gil L, Pardos JA (1995) Performance of 43 *Pinus pinaster* provenances of 5 locations in Central Spain. *Silvae Genet* 44:75–81
- Alía R, Martín S, De Miguel J, Galera R, Agúndez D, Gordo J, Catalán G, Gil L (1996) Las regiones de procedencia de *Pinus pinaster* Aiton. DGCONA, Madrid
- Alía R, Moro J, Denis JB (1997) Performance of *Pinus pinaster* Ait. provenances in Spain: interpretation of the genotype-environment interaction. *Can J For Res* 27:1548–1559
- Andrade A, Valdeolmillos A, Ruiz-Zapata B (1994) Modern pollen spectra and contemporary vegetation in the Paramera Mountain range (Ávila, Spain). *Rev Palaeobot Palynol* 82:127–139
- Andric M, Willis KJ (2003) The phytogeographical regions of Slovenia: a consequence of natural environmental variation or prehistoric human activity? *J Ecol* 91:807–821
- Bahrman N, Zivy M, Damerval C, Baradat P (1994) Organization of the variability of abundant proteins in seven geographical origins of maritime pine (*Pinus pinaster* Ait.). *Theor Appl Genet* 88:407–411
- Baradat P, Marpeau A (1988) Le pin maritime (*Pinus pinaster* Ait.). Biologie et génétique des terpènes pour la connaissance et l'amélioration de l'espèce. Université Bordeaux I, Bordeaux
- Barbero M, Loisel R, Quézel P, Richardson DM, Romane F (1998) Pines of the Mediterranean Basin. In: Richardson DM (ed) *Ecology and biogeography of Pinus*. Cambridge University Press, Cambridge, pp 153–170
- Barkman JJ (1990) A tentative typology of European scrub and forest communities based on vegetation texture and structure. *Vegetatio* 86:131–141
- Blanco E, Casado M, Costa M, Escribano R, García-Antón M, Génova M, Gómez-Manzanaque G, Gómez-Manzanaque F, Moreno J, Morla C, Regato P, Sainz-Ollero H (1997) Los bosques ibéricos. Una interpretación geobotánica. Editorial Planeta, Barcelona
- Bucci G, González-Martínez SC, Le Provost G, Plomion C, Ribeiro MM, Sebastiani F, Alía R, Vendramin GG (2007) Range-wide phylogeography and gene zones in *Pinus pinaster* Ait. revealed by chloroplast microsatellite markers. *Mol Ecol* 16:2137–2153
- Burban C, Petit RJ (2003) Phylogeography of maritime pine inferred with organelle markers having contrasted inheritance. *Mol Ecol* 12:1487–1495
- Calvo L, Santalla S, Marcos E, Valbuena L, Tárrega R, Luis-Calabuig E (2003) Regeneration after wildfire in communities dominated by *Pinus pinaster*, an obligate seeder, and others dominated by *Quercus pyrenaica*, a typical resprouter. *For Ecol Manag* 184:209–223
- Calvo L, Santalla S, Valbuena L, Marcos E, Tárrega R, Luis-Calabuig E (2008) Post-fire natural regeneration of a *Pinus pinaster* forest in NW Spain. *Plant Ecol* 197:81–90

- Carcaillet C, Barakat HN, Panaiotis C, Loisel R (1997) Fire and late-Holocene expansion of *Quercus ilex* and *Pinus pinaster* on Corsica. *J Veg Sci* 8:85–94
- Carrión JS (2002) Patterns and processes of late quaternary environmental change in a montane region of southwestern Europe. *Quat Sci Rev* 21:2047–2066
- Carrión JS, Díez MJ (2004) Evolución de la vegetación mediterránea en Andalucía a través del registro fósil. In: Herrera C (ed) *El monte mediterráneo en Andalucía*. CSIC, Estación Biológica de Doñana, Madrid pp 21–28
- Carrión JS, van Geel B (1999) Fine-resolution upper Weichselian and Holocene palynological record from Navarrés (Valencia, Spain) and a discussion about factors of Mediterranean forest succession. *Rev Palaeobot Palynol* 106:209–236
- Carrión JS, Navarro C, Navarro J, Munuera M (2000) The distribution of cluster pine (*Pinus pinaster*) in Spain as derived from palaeoecological data: relationships with phytosociological classification. *The Holocene* 10:243–252
- Carrión JS, Andrade A, Bennet KD, Navarro C, Munuera M (2001a) Crossing forest thresholds: inertia and collapse in a Holocene sequence from south-central Spain. *The Holocene* 11(6):635–653
- Carrión JS, Munuera M, Dupré M, Andrade A (2001b) Abrupt vegetation changes in the Segura Mountains of southern Spain throughout the Holocene. *J Ecol* 89:783–797
- Carrión JS, Sánchez-Gómez P, Mota JF, Yll EI, Chaín C (2003a) Fire and grazing are contingent on the Holocene vegetation dynamics of Sierra de Gádor, southern Spain. *The Holocene* 13:839–849
- Carrión JS, Yll EI, Walker M, Legaz A, Chaíns C, López A (2003b) Glacial refugia of temperate, Mediterranean and Ibero-North African flora in south-eastern Spain: new evidence from cave pollen at two Neandertal man sites. *Global Ecol Biogeogr* 12:119–129
- Carrión JS, Willis KJ, Sánchez Gómez P (2004) Holocene forest history of the eastern plateaux in the Segura Mountains (Murcia, southeastern Spain). *Rev Palaeobot Palynol* 132:219–236
- Carrión JS, Fuentes N, González-Sampérez P, Quirante LS, Finlayson JC, Fernández S, Andrade A (2007) Holocene environmental change in a montane region of southern Europe with a long history of human settlement. *Quat Sci Rev* 26:1455–1475
- Carrión JS, Finlayson C, Fernández S, Finlayson G, Allué E, López-Sáez JA, López-García P, Gil-Romera G, Bailey G, González-Sampérez P (2008) A coastal reservoir of biodiversity for upper pleistocene human populations: palaeoecological investigations in Gorham's Cave (Gibraltar) in the context of the Iberian Peninsula. *Quat Sci Rev* 27:2118–2135
- Carrión JS, Fernández S, González-Sampérez P, Leroy SAG, Bailey GN, López-Sáez JA, Burjachs F, Gil-Romera G, García-Antón M, Gil-García MJ, Parra I, Santos L, López-García P, Yll EI, Dupré M (2009) Quaternary pollen analysis in the Iberian Peninsula: the value of negative results. *Internet Archaeol* 25: 1–53 (http://intarch.ac.uk/journal/issue25/carrion_toc.html)
- Chavarría JA (1999) Toponimia del Alto Tiétar (Ávila/Toledo) en el Libro de la Montería de Alfonso XI. SEVAT, Madrid
- CN DG (2002) Plan Forestal Español. Ministerio de Medio Ambiente, Madrid
- Conedera M, Tinner W, Neff C, Meurer M, Dickens AF, Krebs P (2009) Reconstructing past fire regimes: methods, applications, and relevance to fire management and conservation. *Quat Sci Rev* 28:555–576
- Costa M (1987) El País Valenciano. In: Peinado M, Rivas-Martínez S (eds) *La vegetación de España*. Universidad de Alcalá de Henares, Alcalá de Henares, pp 281–308
- Costa-Tenorio M, García-Antón M, Morla-Juaristi C, Sainz-Ollero H (1990) La evolución de los bosques de la Península Ibérica: una interpretación basada en datos paleobiogeográficos. *Ecología fuera de serie* 1:31–58
- Council of the European Communities (2003) Regulation (EC) No 1/2003 of 16 December 2002 on the implementation of the rules on competition laid down in Articles 81 and 82 of the Treaty', OJ L 1, 04.01.2003, pp 1–25
- de Nascimento L, Willis KJ, Fernández-Palacios JM, Criado C, Whittaker RJ (2009) The long-term ecology of the lost forests of La Laguna, Tenerife (Canary Islands). *J Biogeogr* 36:499–514
- Faegri K, Iversen J (1989) Textbook of pollen analysis. John Wiley, Chichester
- Fernandes PM, Rigolot E (2007) The fire ecology and management of maritime pine (*Pinus pinaster* Ait.). *For Ecol Manage* 241:1–13
- Figueiral I (1995) Charcoal analysis and the history of *Pinus pinaster* (cluster pine) in Portugal. *Rev Palaeobot Palynol* 89:441–454
- Figueiral I, Bettencourt AMS (2004) Middle/Late bronze age plant communities and their exploitation in the Cávado Basin (NW Portugal) as shown by charcoal analysis: the significance and co-occurrence of *Quercus* (deciduous)–*Fabaceae*. *Veg Hist Archaeobot* 13:219–232
- Figueiral I, Terral JF (2002) Late Quaternary refugia of Mediterranean taxa in the Portuguese Estremadura: charcoal based palaeovegetation and climatic reconstruction. *Quat Sci Rev* 21:549–558
- Finsinger W, Tinner W (2005) Minimum count sums for charcoal-concentration estimates in pollen slides: accuracy and potential errors. *The Holocene* 15:293–297
- Franco-Múgica F, García-Antón M, Sainz-Ollero H (1997) Impacto antrópico y dinámica de la vegetación durante los últimos 2000 años BP en la vertiente septentrional de la Sierra de Gredos: Navarredonda (Ávila, España). *Rev Paléobiol* 16:29–45
- Franco-Múgica F, García-Antón M, Maldonado-Ruiz J, Morla-Juaristi C, Sainz-Ollero H (2001) The Holocene history of *Pinus* forests in the Spanish Northern Meseta. *The Holocene* 11:343–358
- Franco-Múgica F, García-Antón M, Maldonado-Ruiz J, Morla-Juaristi C, Sainz-Ollero H (2005) Ancient pine forest on inland dunes in the Spanish northern meseta. *Quat Res* 63:1–14
- Gallardo JF, Cuadrado S, González-Hernández MI (1980) Suelos forestales de la vertiente sur de la Sierra de Gredos. In: IOATO (ed) *Anuario del Centro de Edafología y Biología Aplicada de Salamanca*, vol 8. CSIC, Salamanca, pp 155–188
- García-Amorena I, Gómez-Manzaneque F, Rubiales JM, Granja HM, Soares G, Morla C (2007) The late quaternary coastal

- forests of western Iberia: a study of their macroremains. *Palaeogeogr Palaeoclimatol Palaeoecol* 254:448–461
- Gil L (1991) Consideraciones históricas sobre *Pinus pinaster* Aiton en el paisaje vegetal de la Península Ibérica. *Est Geogr* 202:5–27
- Gil L, Gordo J, Alía R, Catalán G, Pardos JA (1990) *Pinus pinaster* Aiton en el paisaje vegetal de la Península Ibérica. *Ecología fuera de serie* 1:469–495
- Gliessman SR (1978) The establishment of bracken following fire in tropical habitats. *Am Fern J* 68:41–44
- Gómez A, Lunt DH (2006) Refugia within refugia: patterns of phylogeographic concordance in the Iberian Peninsula. In: Weiss S, Ferrand N (eds) *Phylogeography in Southern European Refugia: evolutionary perspectives on the origins and conservation of European biodiversity*. Springer, Dordrecht, pp 1–42
- Gómez MA, Vendramin GG, González-Martínez SC, Alía R (2005) Genetic diversity and differentiation of two Mediterranean pines (*P. halepensis* Mill. & *P. pinaster* Ait.) along a latitudinal cline using cpSSR markers. *Divers Distrib* 11:257–263
- González J (1974) La Extremadura castellana al mediar el siglo XIII. *Hispania* 127:265–424
- González-Martínez SC, Salvador L, Agúndez D, Alía R, Gil L (2001) Geographical variation of gene diversity of *Pinus pinaster* Ait. in the Iberian Peninsula. In: Müller-Starck G, Schubert R (eds) *Genetic response of forest systems to changing environmental conditions*. Kluwer, Dordrecht, pp 161–171
- González-Martínez SC, Gerber S, Cervera MT, Martínez-Zapater JM, Gil L, Alía R (2002) Seed gene flow and fine-scale structure in a Mediterranean pine (*Pinus pinaster* Ait.) using nuclear microsatellite markers. *Theor Appl Genet* 104:1290–1297
- González-Martínez SC, Mariette S, Ribeiro MM, Burban C, Raffin A, Chambel MR, Ribeiro CAM, Aguiar A, Plomion C, Alía R, Gil L, Vendramin GG, Kremer A (2004) Genetic resources in maritime pine (*Pinus pinaster* Ait.): molecular and quantitative measures of genetic variation and differentiation among maternal lineages. *For Ecol Manage* 197:103–115
- González-Martínez SC, Gil L, Alía R (2005) Genetic diversity estimates of *Pinus pinaster* in the Iberian Peninsula: a comparison of allozymes and quantitative traits. *Invest Agr: Sist Recur For* 14:3–12
- Grimm EC (1987) A Fortran 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Comp Geosci* 13:13–35
- Grimm EC (1991) *Tilia* and *Tilia*. Graph, version 2.0 and TG View version 1.6.2. Illinois State Museum, Springfield
- Izco J (1984) Madrid Verde. MAPA–CAM, Madrid
- López-Sáez JA (2004) Vegetación y evolución del paisaje de Lanzahíta. In: González JM, Chavarría JA, López-Sáez JA (eds) *Lanzahíta (Ávila). Historia, naturaleza, tradiciones*. SEVAT, Madrid, pp 27–38
- López-Sáez JA, López-Merino L (2007) Coprophilous fungi as a source of information of anthropic activities during the prehistory in the Amblés Valley (Ávila, Spain): the archaeopalynological record. *Rev Esp Micropal* 39:103–116
- López-Sáez JA, van Geel B, Farbos-Texier S, Diot MF (1998) Remarques paléocologiques à propos de quelques palynomorphes non-polliniques provenant de sédiments quaternaires en France. *Rev Paléobiol* 17:445–459
- López-Sáez JA, López-Merino L, Alba-Sánchez F, Pérez-Díaz S (2009a) Contribución paleoambiental al estudio de la trashumancia en el sector abulense de la Sierra de Gredos. *Hispania* 231:9–38
- López-Sáez JA, López-Merino L, Mateo MA, Serrano O, Pérez-Díaz S, Serrano L (2009b) Palaeoecological potential of the marine organic deposits of *Posidonia oceanica*: a case study in the NE Iberian Peninsula. *Palaeogeogr Palaeoclimatol Palaeoecol* 271:215–224
- Manuel C, Gil L (2001) De quelques mythes répandus sur les forêts espagnoles. *Sud-Ouest Européen* 11:83–90
- Mariné M (1995) El patrimonio arqueológico de la Sierra de Gredos. In: Troitiño MA (ed) *Gredos: territorio, sociedad y cultura*. Diputación Provincial de Ávila, Ávila, pp 19–48
- Martínez-Ruiz E (1998) El bosque del Valle del Tiétar en la Historia. Un bosque emblemático bajomedieval. *Trasierra* 3:9–30
- Martino D (2004) Tierras con historia: Lanzahíta. In: González JM, Chavarría JA, López-Sáez JA (eds) *Lanzahíta (Ávila). Historia, naturaleza, tradiciones*. SEVAT, Madrid, pp 41–74
- Mateus JE (1989) Lagoa Travessa: a Holocene pollen diagram from the South-West coast of Portugal. *Revista de Biología* 14:17–94
- Mateus JE, Queiroz PF (1993) Os estudos de vegetação quaternária em Portugal; contextos, balanço de resultados, perspectivas. In: Carvalho GS, Ferreira AB, Senna-Martínez JC (eds) *O Quaternário em Portugal. Balanço e perspectivas*. Edições Colibri, Lisboa, pp 105–131
- McLachlan JS, Clark JS (2004) Reconstructing historical ranges with fossil data at continental scales. *For Ecol Manage* 197:139–147
- Miguel-Pérez I, González-Martínez SC, Alía R, Gil L (2002) Growth phenology and mating system of maritime pine (*Pinus pinaster* Aiton) in central Spain. *Invest Agr: Sist Recur For* 11:193–204
- Nicolás A, Gandullo JM (1967) *Ecología de los pinares españoles. I. Pinus pinaster* Ait. I.F.I.E., Madrid
- Nieto JM, Cabezudo B, Trigo MM (1989) Series de vegetación edafófilas de las Sierras Tejeda y Almijara (Málaga-Granada; España). *Acta Bot Malacit* 14:161–170
- Nieto JM, Pérez A, Cabezudo B (1991) Biogeografía y series de vegetación de la provincia de Málaga (España). *Acta Bot Malacit* 16:417–436
- Peinado M, Martínez-Parras JM (1985) *El paisaje vegetal de Castilla-La Mancha*. Junta de Comunidades de Castilla-La Mancha, Toledo
- Peñalba C (1994) The history of the Holocene vegetation in northern Spain from pollen analysis. *J Ecol* 82:815–832
- Pérez B, Moreno JM (1998) Fire-type and forestry management effects on the early postfire vegetation dynamics of a *Pinus pinaster* woodland. *Plant Ecol* 134:27–41
- Pérez B, Cruz A, Fernández F, Moreno JM (2003) Effects of the recent land-use history on the postfire vegetation of uplands in Central Spain. *For Ecol Manage* 182:273–283
- Petit RJ, Barhman N, Baradat PH (1995) Comparison of genetic differentiation in maritime pine (*Pinus pinaster* Ait.) estimated using isozyme, total protein and terpenic loci. *Heredity* 75:382–389

- Ramil P (1992) La vegetación cuaternaria de las sierras septentrionales de Lugo a través del análisis polínico. Ph.D. thesis, Universidad de Santiago de Compostela, Santiago
- Reille M (1990) Recherches pollenanalytiques dans l'extrémité orientale des Pyrénées: données nouvelles de la fin du glaciaire à l'actuel. *Ecol Medit* 16:317–357
- Reille M (1991) Quelques exemples de séquences polliniques polluées par la matière organique intruse: conséquence pour l'histoire de la végétation des Pyrénées (France). *Palynosciences* 1:143–144
- Reille M, Pons A (1992) The ecological significance of sclerophyllous oak forests in the western part of the Mediterranean basin: a note on pollen analytical data. *Vegetatio* 99–100:13–17
- Reimer PJ, Baillie MGL, Bard E, Bayliss A, Beck JW, Bertrand CJH, Blackwell PG, Buck CE, Burr GS, Cutler KB, Damon PE, Edwards RL, Fairbanks RG, Friedrich M, Guilderson TP, Hogg AG, Hughen KA, Kromer B, McCormac G, Manning S, Ramsey CB, Reimer RW, Remmele S, Southon JR, Stuiver M, Talamo S, Taylor FW, van der Plicht J, Weyhenmeyer CE (2004) IntCal04 terrestrial radiocarbon age calibration, 26–0 ka BP. *Radiocarbon* 46:1029–1058
- Rhodes AN (1998) A method for the preparation and quantification of microscopic charcoal from terrestrial and lacustrine sediment cores. *The Holocene* 8:113–117
- Rivas-Martínez S (1963) Estudio de la vegetación y flora de las Sierras de Guadarrama y Gredos. *Anal Inst Bot Cavanilles* 21:5–330
- Rivas-Martínez S (1975) Mapa de vegetación de la provincia de Ávila. *Anal Inst Bot Cavanilles* 32:1493–1556
- Rivas-Martínez S (1987) Memoria del mapa de series de vegetación de España, 1: 400.000. M.A.P.A.-I.C.O.N.A., Madrid
- Rivas-Martínez S (2007) Mapa de series, geoserias y geopermaseries de vegetación de España. Memoria del mapa de la vegetación potencial de España, parte 1. *Itin Geobot* 17:1–436
- Rivas-Martínez S, Fernández-González F, Sánchez-Mata D (1986) Datos sobre la vegetación del Sistema Central y Sierra Nevada. *Opusc Bot Pharm Complut* 2:3–136
- Rivas-Martínez S, Belmonte D, Cantó P, Fernández-González F, Fuente V, Moreno JM, Sánchez-Mata D, Sancho LG (1987) Piornales, enebrales y pinares oromediterráneos (*Pino-Cytisium oromediterranei*) en el Sistema Central. *Lazaroa* 7:93–124
- Rivas-Martínez S, Wildpret W, Díaz TE, Pérez de Paz PL, del Arco M, Rodríguez O (1993) Excursión guide. Outline vegetation of Tenerife Island (Canary Islands). *Itin Geobot* 7:5–169
- Rivas-Martínez S, Fernández-González F, Loidi J, Lousã M, Penas A (2001) Syntaxonomical checklist of vascular plant communities of Spain and Portugal to association level. *Itin Geobot* 14:5–341
- Rivas-Martínez S, Díaz TE, Fernández-González F, Izco J, Loidi J, Lousã M, Penas A (2002) Vascular plant communities of Spain and Portugal. Addenda to the Syntaxonomical checklist of 2001. *Itin Geobot* 15:5–922
- Rodrigo A, Retana J, Pico FX (2004) Direct regeneration is not the only response of mediterranean forest to large fires. *Ecology* 85:716–729
- Rodríguez-Ariza MO (2000) El paisaje vegetal en la Depresión de Vera durante la Prehistoria Reciente. Una aproximación desde la Antracología. *Trab Prehist* 57:145–156
- Rubiales JM, Hernández L, Morla C, García-Amorena I, Sanz C, Alfaro E (2005) Nuevas aportaciones al conocimiento de los paisajes vegetales en el Holoceno de la cuenca del Duero. In: *Actas IV Congreso Forestal Español*. S.E.C.F., Zaragoza, CD-Rom
- Rubiales JM, García-Amorena I, Génova M, Gómez Manzanque F, Morla C (2007) The Holocene history of highland pine forests in a submediterranean mountain: the case of Gredos mountain range (Iberian Central range, Spain). *Quat Sci Rev* 26:1759–1770
- Rubiales JM, García-Amorena I, García-Álvarez S, Morla C (2009) Anthracological evidence suggests naturalness of *Pinus pinaster* in inland southwestern Iberia. *Plant Ecol* 200:155–160
- Ruiz-Zapata MB, Gil MJ, Dorado M (1996) Climatic changes in the Spanish Central zone during the last 3000 BP based on pollinic analysis. In: *Diachronic climatic impacts on water resources with emphasis on Mediterranean region*. NATO ASI Series, vol 36. Springer, Berlin, pp 9–23
- Ruiz-Zapata MB, Gil MJ, Dorado M, Valdeolmillos A, Vegas J, Pérez-González A (2002) Clima y vegetación durante el Tardiglacial y el Holoceno en la Sierra de Neila (Sistema Ibérico Noroccidental). *Cuat Geomorf* 16:9–20
- Salvador L, Alía R, Agúndez D, Gil L (2000) Genetic variation and migration pathways of maritime pine (*Pinus pinaster* Ait.) in the Iberian Peninsula. *Theor Appl Genet* 100:89–95
- Sánchez-Egea J (1975) El clima. Los dominios climáticos y los pisos de vegetación de las provincias de Madrid, Ávila y Segovia: ensayo de un modelo fitoclimático. *Anal Inst Bot Cavanilles* 32:1039–1078
- Sánchez-Mata D (1989) Flora y vegetación del Macizo Oriental de la Sierra de Gredos (Ávila). *Institución Gran Duque de Alba, Ávila*
- Sierra de Grado R (1996) ¿Es el *Pinus pinaster* espontáneo en la Sierra de Gredos? *Montes* 43:5–8
- Stevenson AC (2000) The Holocene forest history of the Montes Universales, Teruel, Spain. *The Holocene* 10:603–610
- Stockmarr J (1971) Tablets with spores used in absolute pollen analysis. *Pollen Spores* 13:615–621
- Stuiver M, Reimer PJ, Bard E, Beck JW, Burr GS, Hughen KA, Kromer B, McCormac G, van der Plicht J, Spurk M (1998) INTCAL98 Radiocarbon age calibration, 24000–0 cal BP. *Radiocarbon* 40:1041–1083
- Tapias R, Gil L, Fuentes-Utrilla P, Pardos JA (2001) Canopy seed banks in Mediterranean pines of southeastern Spain: a comparison between *Pinus halepensis* Mill., *P. pinaster* Ait., *P. nigra* Arn. and *P. pinea* L. *J Ecol* 89:629–638
- Tapias R, Climent J, Pardos JA, Gil L (2004) Life histories of Mediterranean pines. *Plant Ecol* 171:53–68
- Telford RJ, Heegaard E, Birks HJB (2004) The intercept is a poor estimate of a calibrated radiocarbon age. *The Holocene* 14:296–298
- Tinner W, Hu FS (2003) Size parameters, size-class distribution and area-number relationship of microscopic charcoal: relevance for fire reconstruction. *The Holocene* 13:499–505

- Torres O, Calvo L, Valbuena L (2006) Influence of high temperatures on seed germination of a special *Pinus pinaster* stand adapted to frequent fires. *Plant Ecol* 186:129–136
- Troitiño MA (1987) Dinámica espacial y lógica de ordenación en un espacio de compleja organización humana: el área de Gredos. *An Geogr Univ Complut* 7:365–376
- Turner R, Roberts N, Jones MD (2008) Climatic pacing of Mediterranean fire histories from lake sedimentary microcharcoal. *Global Planet Change* 63:317–324
- Valle F (ed) (2003) Mapa de Series de Vegetación de Andalucía. Ed. Rueda, Madrid
- van der Brink LM, Janssen CR (1985) The effect of human activities during cultural phases on the development of montane vegetation in the Serra da Estrela, Portugal. *Rev Palaeobot Palynol* 44:193–215
- van der Knaap WO, van Leeuwen JFN (1994) Holocene vegetation, human impact, and climatic change in Serra da Estrela, Portugal. *Dissert Bot* 234:497–535
- van der Knaap WO, van Leeuwen JFN (1995) Holocene vegetation and degradation as responses to climatic change and human activity in the Serra da Estrela, Portugal. *Rev Palaeobot Palynol* 89:153–211
- van der Knaap WO, van Leeuwen JFN (1997) Late glacial and early Holocene vegetation succession, altitudinal vegetation zonation, and climatic change in the Serra da Estrela, Portugal. *Rev Palaeobot Palynol* 97:239–285
- van Geel B (2001) Non-pollen palynomorphs. In: Smol JP, Birks HJB, Last WM (eds) Tracking environmental change using lake sediments, vol 3: Terrestrial, algal and siliceous indicators. Kluwer, Dordrecht, pp 99–119
- Vannièr B, Colombaroli D, Chapron E, Leroux A, Tinner W, Magny M (2008) Climate versus human-driven fire regimes in Mediterranean landscapes: the Holocene record of Lago dell'Accesa (Tuscany, Italy). *Quat Sci Rev* 27:1181–1196
- Vázquez A, Moreno JM (1998) Fire frequency and fire rotation period in areas with different potential vegetation types in peninsular Spain. In: Trabaud L (ed) Fire management and landscape ecology. International Association of Wildland Fire, Washington, pp 305–314
- Vázquez A, Moreno JM (2001) Spatial distribution of forest fires in Sierra de Gredos (Central Spain). *For Ecol Manag* 147:55–65
- Vendramin GG, Anzidei M, Madaghiele A, Bucci G (1998) Distribution of genetic diversity in *Pinus pinaster* Ait. as revealed by chloroplast microsatellites. *Theor Appl Genet* 97:456–463
- Wahid N, González-Martínez SC, El-Hadrami I, Boulli A (2004) Genetic structure and variability of natural populations of Maritime pine (*Pinus pinaster* Aiton) in Morocco. *Silvae Genet* 53:93–99
- Whitlock C, Larsen CPS (2001) Charcoal as a fire proxy. In: Smol JP, Birks HJB, Last WM (eds) Tracking environmental change using lake sediments, vol 3: Terrestrial, algal and siliceous indicators. Kluwer, Dordrecht, pp 75–97