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The Holocene history of highland pine forests in a submediterranean mountain: the case of Gredos mountain range (Iberian Central range, Spain)

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Abstract

The significance of *Pinus sylvestris* and *Pinus nigra* forests in Gredos mountain range in the Iberian botanical literature has been traditionally a matter of controversy. Considered for many botanists to be anthropogenic forests, a high amount of syntaxonomic approaches, cartographies of potential vegetation and dynamic models have been created based on this guesswork.

Nevertheless, this work contributes new data that contradicts this previous hypothesis. For the first time, these data prove the existence of a bioclimatic belt where pine trees dominated during the last 6500 years, clarifying its altitudinal range, surface extension, and its stability. The study is based on the analysis of fossil macrorests and megarests, dated using radiocarbon. The results obtained cohere with the suggestions of other authors that assume the native character of *P. nigra* and *P. sylvestris* in this area, based on data of diverse origin (palynological, historical, toponymical, dendrochronological or geobotanical).

The paper then continues to discuss the geobotanical interpretation of the results and the regional lines of management, as well as the potential causes that could have induced the marked decline of pine forests in the last millennia.

1. Introduction

Pinus sylvestris L and *Pinus nigra* Arn. subsp *salzmannii* (Dunal) Franco are major species in the forest environments of mountainous terrain, both in the Atlantic and the Mediterranean biogeographical regions of the Iberian peninsula.

In the Guadarrama Mountains (Iberian Central range) *P. sylvestris* extends between 1600 and 2100 m, being part of widespread forests that dominate the landscape in the mountainous areas. Further west, another mountain region (Gredos mountain range) presents similar forests with a more important concurrence of *P. nigra* in a smaller area.

Geobotanical interpretations of the significance of *P. sylvestris* and *P. nigra* forests in Gredos mountain range have been object of much controversy. Some authors consider that these forests are products of the recent afforestation programmes and therefore pine groves are not part of the natural vegetation, neither in terminal, nor in serial communities (e.g. Rivas-Martínez, 1987, Rivas-Martínez et al., 1987; Luceño and Vargas, 1991).

Nevertheless, other authors have defended the natural character of *P. nigra* and *P. sylvestris* in this area, on the basis of geobotanical arguments (Laguna, 1879; Willkomm, 1896; Gaussen, 1949; Génova et al., 1988; Gómez Manzaneque, 1988; Regato et al., 1992), historical data (Martínez García and Costa, 2001), toponymic analysis (Mancebo et al., 1993) or palynological works (Franco et al., 1997).

Dendrochronological studies corroborate the last opinion. Richter (1988) studied the forests of Scots pine (*P. sylvestris*) that cover a great part of the territory on the north slope of Gredos and Génova et al. (1993) and García Calvo et al. (2005) studied some relic natural

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populations of both species that still persist on the southern mountainside. The chronological sequences elaborated by these authors date back to the first half of the 17th century (Génova et al., 1993), proving that both species of pine trees were established, at least, before the first important afforestations are documented (Martínez García and Costa, 2001). The palynological studies, numerous at Gredos' northern slopes, reflect a continuous record of *Pinus* pollen between 1400 and 1850 m during the last 6000 years BP. However, there are inaccuracies identifying species within the *Diploxylon* section of Genus *Pinus* with pollen analysis (Moore et al., 1991). Secondly, the microfossil dispersal nature makes it impossible to determine its origin accurately. These facts make it hard to establish precise positional models or to identify the specific dominant taxa.

The conservation of macrofossils (small pieces of wood, pine scales and fruits) and megafossils (trunks, branches and big roots) definitely allows to obtain reliable palaeobotanical proxies to reconstruct past vegetation dynamics, composition and structure with high spatial resolution (e.g.: Ali et al., 2005; Carcaillet and Muller, 2005; Kullman and Kjällgren, 2006).

The finding of numerous trunks (known locally as "*troncas*") in a vast area constitutes an extraordinary fossil record in the Iberian Peninsula. This, combined with other investigations carried out during the last decades, allows the reconstruction of the forest history over the last 6500 years.

2. Study area

2.1. Regional setting

The Iberian Central range divides the Duero and Tajo basins, running from west to east in the Central Iberian Peninsula. The Gredos mountain range is the main mountainous system in the Central System, which is 150 km long and 50 km wide and contains the highest peak in Central Spain (Almanzor, 2592 m) (Fig. 1).

The continental basement is mostly composed of plutonic rocks (granites and gneisses), which were modelled under a horst-graben tectonics.

Climate is montane Mediterranean and it is characterized by a strong summer drought, high seasonal temperature fluctuations and heavy precipitations controlled orographically. Because of the influence of south-western humid winds there is a high asymmetry in the moisture gradient, the mean annual precipitation ranging from 1500–2000 mm in the southern slopes to less than 500 mm in the northern ones.

Below 1100 m evergreen oaks (*Quercus ilex* subsp. *ballota* (Desf.) Samp. and *Quercus suber* L. in the southern slopes) occupy the basal belt, mixed with extensive pinewoods (*Pinus pinea* L.) on sandy or xeric enclaves. Deciduous Pyrenean oak (*Quercus pyrenaica* L.) and Cluster pine forests (*Pinus pinaster* Aiton) extend up to 1400 m. Among these, Holm oaks mixed with *Juniperus oxycedrus* L. grow on shallow lithosols or steep slopes. The tree-line reaches 1800 m with isolated and dispersed stands of *P. nigra* subsp. *Salzmannii* and *P. sylvestris* (Génova et al., 1988; Ruiz de la Torre, 2002). The upper zone is a shrub-dominated community of broom (*Cytisus oromediterraneus* Rivas-Martínez) and prostrate juniper (*Juniperus communis* subsp. *alpina* (Suter) Celak). From 2000 m altitude (depending on the area), open montane grasslands characterized by *Festuca indigesta* Boiss occur.

The northern mountainside on the Central part of the Gredos mountain range is almost treeless with the exception of the *P. sylvestris* stands situated on the Iruelas Valley or on the Tormes and Alberche headwaters. Below this altitude, some other isolated stands of *Q. pyrenaica* are located.

The occurrence—in Gredos and in other Iberian mountains—of both species of pines almost in the same altitudinal interval motivated the development of diverse studies with the aim of clarifying the taxa suitability to the ecological parameters. Growth response to climatic oscillation in the Guadarrama range shows that in both taxa growth is limited by summer precipitation,

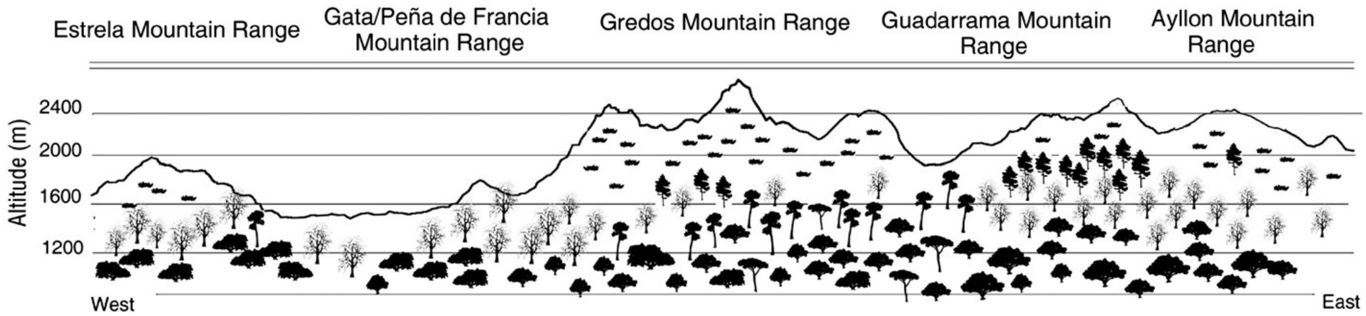

Fig. 1. Schematic representation of the vegetation zonation along the Central Iberian range; view from the South. ▲ Pinewood of Scots pine *P. sylvestris* (including European Black pine *P. nigra*), ✲ Deciduous Pyrenean oak, *Q. pyrenaica*, ♠ Pinewood of *Pinus pinaster*. ⊤ Pinewood of *P. pinea*, ♣ Holm oak (*Q. ilex* subsp *ballota*), ● Cork oak (*Q. suber*), ▬ Shrub dominated community of broom (*C. oromediterraneus, Genista cinerea, Adenocarpus hispanicus*) and prostrate juniper (*J. communis*) and open mountane grasslands. A narrow pine belt at around 1600 m.a.s.l. should be noticed in the Gredos mountain range. From 1600 m altitude, alpine shrub communities and open montane grasslands are represented. Original based on Costa et al. (1997).

resulting in the *P. nigra* having higher climate sensitivity (Génova et al., 1997).

2.2. Site location

Megafossils were located by scrutinizing the mountainous and alpine meadow zones in the study area. The dead pine remnants (stumps and logs) were recovered at the soil's surface or partly buried. Erosive events in peat bogs and streams exposed a high percentage of the said remnants. Other remains were found whilst forest work that involved the opening of trenches (drainage, water captation or forest paths).

The sampled sites are located between 1100 and 1840 m.a.s.l. (location details in Table 1 and Fig. 2). Most of the remains were recovered on the northern slopes of the central part of the Gredos mountain range, between Puerto del Pico and Navalperal de Tormes, in an area that is nowadays treeless. A detailed study of a soil profile was undertaken in the site of Hoyos del Espino-Regajo del Acarreo, a peat bog associated to the stream where a fissure exposed sediments with a high amount of charcoal, strobili, needles and pine scales (Fig. 2).

3. Material and methods

Altogether, 117 megafossil remains (logs, branches and stumps standing upright) from 33 sites were examined (Table 1). The study of macrorests often achieves a higher accuracy with the taxonomic approach than pollen analysis, which usually only gives information on the genus and sometimes does not go farther beyond the family level. For instance, the Iberian species of the genus *Pinus* L. can clearly be differentiated analysing the morphology of their strobili (Mirov, 1967; Farjon, 1984). Moreover, the identification of species based on the xylem is more accurate than the study of pollen morphology (Moore et al., 1991).

A good state of preservation has allowed the analysis of the majority of the wood samples using thin section slides. They were prepared and dyed with safranine red as it is

Table 1
Location and altitude of the studied sites with the radiocarbon ages of the *Pinus sylvestris* samples that were dated

Zonation	Studied sites	UTM coordinates	Age (years BP)	Altitude (masl)
East Zone	San Esteban del Valle (1)	30T 334924 4467023	1815±25	1560
	Serranillos (2)	30T 334942 4463107	2440±60	1580
	Villarejo del Valle (3)	30T 329600 4466500	–	1380
Central Part	Hoyos del Collado (4)	30T 312915 4472776	1670±40	1700
	Hoyos del Espino- La Covacha (5)	30T 316246 4463863	1090±30	1750
	Hoyos del Espino- Pradogrande (6)	30T 314000 4462300	–	1680
	Hoyos del Espino- Regajo del Acarreo (7)	30T 316661 4464047	1300±60	1840
	La Herguijuela- Saucal (8)	30T 308097 4474045	–	1560
	La Herguijuela- Horcajos (9)	30T 310695 4475238		1650
	Navacepeda de Tormes- Cerro Triguero (11)	30T 311600 4462586	2085±25	1560
	Navacepeda de Tormes- Dehesa del Prado de la Casa (10)	30T 312346 4461885	1090±50	1630
	Navalperal de Tormes- Garganta de Gredos (12)	30T 306661 4460653	970±60	1750
	Navalperal de Tormes- Laguna del Cervunal (13)	30T 305800 4463100	4350±60	1790
	Navalperal de Tormes- Roncesvalles (14)	30T 307701 4463855	1560±35	1570
	Navarredonda de Gredos (15)	30T 321105 4472504	–	1560
	San Martín del Pimpollar- Arroyo Arrovalle (16)	30T 326550 4470424	2320±40	1300
	San Martín del Pimpollar- Arroyo de las Hoyuelas (17)	30T 323629 4471534	–	1410
Alto Alberche and Serrota	Cepeda la Mora (18)	30T 327801 4481724	–	1510
	Garganta del Villar (19)	30T 320108 4481597	2430±15	1600
	Hoyocasero (20)	30T 330385 4478293	–	1500
	Navacepedilla de Corneja (21)	30T 315492 4481929	–	1650
	Navadijos (22)	30T 324314 4476124	1750±45	1580
	Navalacruz- Arroyo del Medraero (23)	30T 331425 4482172		1620
	Navalacruz- Arroyo Obreguilla (24)	30T 340500 4478100		1110
	Navalacruz- Astillero (25)	30T 330879 4479167	860±20	1490
	Navalosa (26)	30T 332963 4476959	–	1670
	Navalsauz- La Pobedilla (27)	30T 325880 4476936	–	1440
	Navalsauz- Huertos del Prado de la Casa (28)	30T 326901 4475345		1330
	Navalsauz- La Llanaílla (29)	30T 326064 4475807		1380
	Navaquesera (30)	30T 333879 4476959	5630±70	1620
	San Martín de la Vega del Alberche- Ayo de la Piedad (31)	30T 316431 4478280	–	1500
	San Martín de la Vega del Alberche- Ayo de Pinorredondo (32)	30T 315088 4475772	1170±40	1645
	Villafranca de la Sierra (33)	30T 321032 4483129	2830±60	1800

Table 2
Absolute frequencies of taxa in the sites with megarests in the Gredos mountain range

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Pinus gr sylvestris	2		1	2	1	1	4	2	2	1	2	7	6	1	3	4	1		2	2		1			1	6		1	3	2	2	8	4
Pinus sylvestris	1	1			7	1	1					1						1										1					
Juniperus sp																			1														
Quercus subgen Quercus													3										2					1					
Betula sp												2																					
Salix															1						2						1						
Populus								2																1			2						1
Cytisus scoparius tp					1				1			2																					1
Maloideae																								2									

The names of the sites numbers are listed in Table 1 and the legend of Fig. 2.

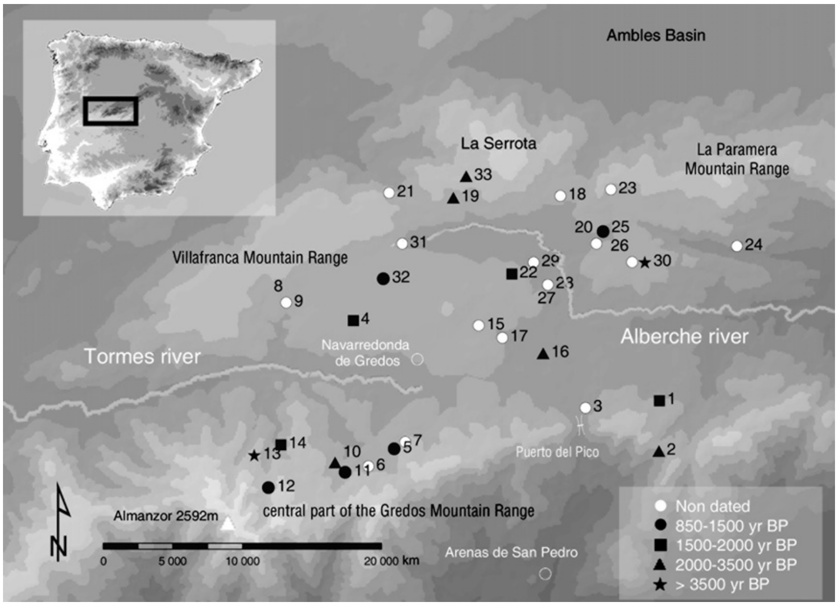

Fig. 2. Location map showing the sampled sites in the Gredos mountain range: San Esteban del Valle (1); Serranillos (2); Villarejo del Valle (3); Hoyos del Collado (4); Hoyos del Espino—La Covacha (5); Hoyos del Espino—Pradogrande (6); Hoyos del Espino—Regajo del Acarreo (7); La Herguijuela—Saucal (8); La Herguijuela—Horcajos (9) Navacepeda de Tormes- Dehesa del Prado de la Casa (10); Navacepeda de Tormes—Cerro Triguero (11); Navalperal de Tormes—Garganta de Gredos (12); Navalperal de Tormes—Laguna del Cervunal (13); Navalperal de Tormes- Roncesvalles (14); Navarredonda de Gredos (15); San Martín del Pimpollar—Arroyo Arrovalle (16); San Martín del Pimpollar—Arroyo de las Hoyuelas (17); Cepeda la Mora (18); Garganta del Villar (19); Hoyocasero (20); Navacepedilla de Corneja (21); Navadijos (22); Navalacruz- Arroyo del Medraero (23); Navalacruz-Arroyo Obreguilla (24); Navalacruz- Astillero (25); Navalosa (26); Navalsauz -La Pobedilla (27); Navalsauz -Huertos del Prado de la Casa (28); Navalsauz -La Llanaílla (29); Navaquesera (30); San Martín de la Vega del Alberche—Arroyo de la Piedad (31); San Martín de la Vega del Alberche—Arroyo de Pinorredondo (32); Villafranca de la Sierra (33).

described in Schweingrüber (1990). The carbonised wood and the easily fractured remains were observed using reflection microscopy.

The identification was made using common keys of wood anatomy identification (Jacquiot, 1955; Greguss, 1955, 1959; Peraza, 1964; García and Guindeo, 1988; de

Palacios, 1997; Schweingrüber, 1990; Schoch et al., 2004) and wherever possible, they were compared with reference collections: U.D. Tecnología de la Madera and U.D. Botánica of the Escuela Técnica Superior de Ingenieros de Montes (U.P.M., Madrid, Spain).

Although considerable research exists on the anatomic discrimination of the European woods, there is a lack of consensus about the identification of the Iberian mountain pines (such as *P. sylvestris*, *P. nigra* and *Pinus uncinata*). Whereas some anatomists propose characters for the taxonomic identification of these species (see Greguss, 1955, 1959; Jacquiot, 1955; García and Guindeo, 1988) other authors believe that our current knowledge does not allow us an unequivocal identification amongst these three species (Schweingrüber, 1990; Carcaillet and Vernet, 2001). The intraspecific variability of the wood anatomy of these species appears to be the cause of this lack of agreement among researchers.

The anatomical features that characterize the wood of the group *P. sylvestris* are (Fig. 3):

(1) Wood without vessels (with tracheids only), that presents resin ducts in early and late-wood (Fig. 3a).
(2) Cross-fields in the radial section with one (rarely two) large fenestriform pinoid pit (Fig. 3b).
(3) Radial tracheids with wall thickenings that appear tooth-like, higher than 5 μm, frequently occupying more than one-half the height of the cell lumen (Fig. 3b).
(4) Uniseriate rays (rarely biseriated) of 3–10 cells height (Fig. 3c), sometimes with resin canals.

The following main features are useful to distinguish *P. sylvestris* from the other Iberian species of the group (*P. uncinata* and *P. nigra*), according to Greguss (1955), Jacquiot (1955), García and Guindeo (1988) and our own observations:

(a) Resin canals with thin-walled epithelial cells.
(b) Transversal ray tracheids with concrescent tooth-shaped walls in early-wood, communicating occasionally as reticulate thickenings.

These features have allowed the identification of species in woods old enough to produce mature wood. Hence, we only selected as identifiable, samples with more than 40 rings, to avoid the higher variability observed in juvenile wood (Sauter et al., 1999; Mutz et al., 2004).

A comparative morphological study was done on fossil strobili, focusing on the diagnostic characters described for the European conifers (Tutin, 1964–1980; Castroviejo et al., 1986–2004). Once the genus and the type were identified, the analysis focused on mountain pines (Galera, 1993; Roig et al., 1997; Alcalde et al., 2001) to obtain the specific range of the remains collected.

Some of the biggest logs were dated with radiocarbon and circular sections were extracted in order to analyse the growth rings. Measurement of the rings in several radial alignments and medium sequences were made. They were adjusted in the time after calibration and depending on the provenance of the dated sample.

Seventeen radiocarbon dates were obtained from samples of wood taken from the outer heartwood rings of the logs. Dates were calibrated using the CALIB 5.0 software (Stuiver and Reimer, 1993, version 5.0) with the IntCal04 dataset (Reimer et al., 2004), and rounded to the nearest 10 years for samples with standard deviations greater than 50

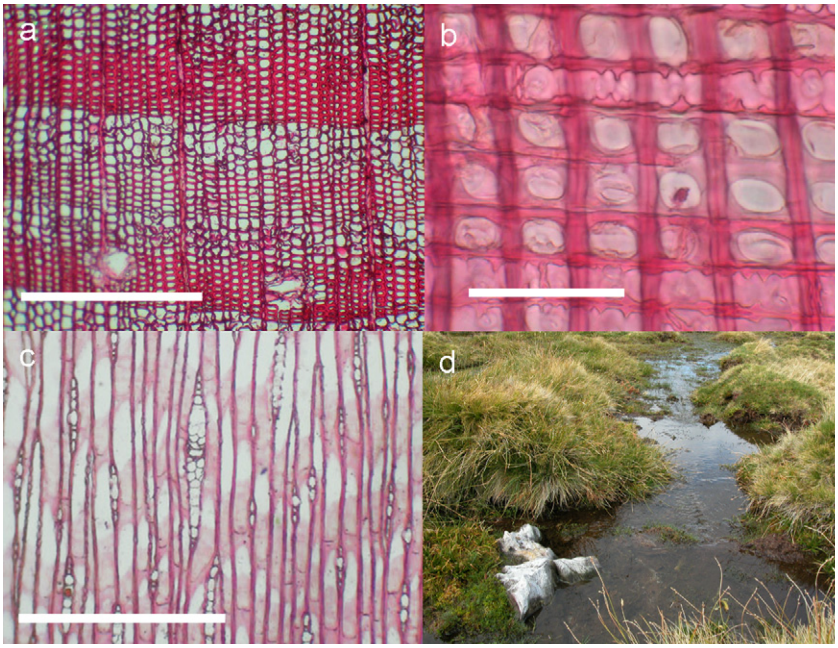

Fig. 3. Wood anatomy of *P. sylvestris*: (a) transversal section, scale bar: 500 μm; (b) radial section, scale bar: 60 μm; (c) tangencial section, scale bar: 400 μm; (d) Upright stump (*in situ*, in its living position) in Paraje de Roncesvalles (Site of Navalperal de Tormes-Roncesvalles).

years. The intercept with 2 sigma and a probability range at $p = 1.0$ and its' means are reported.

New dendrochronological cores of *P. nigra* living trees were extracted in El Arenal County and in the pine forests over the Southern slopes of Puerto del Pico (Cuevas del Valle) (Table 5).

4. Results

The study of the taphonomic processes suffered by megafossils, as well as their abundance and distribution, allows us to suppose that they were not isolated trees in a marginal area different from a forested one. Moreover, in the sites of Pradogrande (Hoyos del Espino) y La Cañada (Navalosa) 27 well-preserved pine cones were recovered, all of them identified as *P. sylvestris* remnants. In the first of the above sites, a detailed study of the charcoal found in the peat-bog was done (Tables 2 and 3).

The totality of the samples was located in a wide altitudinal range. *Pinus* gr. *sylvestris* remains were recovered from 1300 m (Arrovalle, San Martín del Pimpollar, that yield a radiocarbon age of 2320 ± 40 BP) to 1790 m (Laguna del Cervunal, Navalperal de Tormes, dated as 4350 ± 60 BP) (Figs. 4 and 5).

Regarding the identification of the taxa, *Salix* remains correspond with an arboreal species of the genus. Taking into account local ecology it is possible that they might belong to *Salix atrocinerea*. Woods of *Populus* can be assigned either to the boreo-nemoral species *Populus tremula* or the riparian *Populus nigra*. Remains of *Quercus* are of the deciduous type, including marcescents (ring porous, clearly differentiated), with vessels of intermediate size between the evergreen ones (tp *ilex*) and strictly deciduous ones (tp *robur*). Remains of pine cones and charcoal belong mainly to *P. sylvestris*.

Table 3
Absolute frequencies of taxa from charcoal and strobili remains studied in the sites of Pradogrande (Hoyos del Espino) and La Cañada (Navalosa)

Taxa	Sites Pradogrande (Hoyos del Espino)	La Cañada (Navalosa)
Pinus gr sylvestris (charcoal)	36	–
Pinus sylvestris (strobili))	26	1
Cytisus scoparius tp (charcoal)	2	–
Pine cones *(Pinus* sp.*)*	5	–
Non-identifiable charcoal	1	–

A total number of 17 specimens were dated by the conventional radiocarbon dating method, reaching the last 6500 years Cal BP. Most of the dated samples extend over the last 3000 BP years.

Tables 4 and 5 include the results obtained from individual fossil chronologies elaborated from aged specimens of *P. sylvestris* in the same regional range. It is an ensemble of floating chronologies disposed regularly but discontinuously, spanned from 763 BC through 1144 AD. The longest of those ring-width series is close to 200 years, the mean being situated around 100 years. The growth rates of the fossil trees were, in some cases, similar to present-day trees. This was especially true in the bigger logs and in those that were better preserved, as the magnificent trunk located in Puerto de Serranillos.

5. Discussion

5.1. Geobotanical, biogeographical and ecological implications

The taxonomic accuracy resulting from the analysis of the remains supports the hypothesis of the autochthonous character of *P. sylvestris* on these territories. The results are of special significance since these sites constitute the western limit of the species' world range. The 149 fossil remains of *Pinus* that were identified in this study, which span the last 6500 years, are located in a vast area that extends through the Gredos, Serrota, Paramera and Villafranca mountains and the Tormes and Alberche watersheds, exceeding 1000 km^2.

The distribution of the vegetation belts in the Mediterranean region is frequently defined in terms of temperature. They are particularly affected by winter temperatures (e.g. Ozenda, 1975; Quézel and Médail, 2003). The altitudinal extent of the mountain-pine belt in Gredos, obtained from the analysis of macrorests, seems to have been stable during the last 6500 years ranging from 1300 m (the altitudinal lower limit) to around 1850 m (upper limit). This range is lower than the *P. sylvestris* range in Guadarrama, where pine forests are now widely distributed. A significant difference is observed in the lower limit:

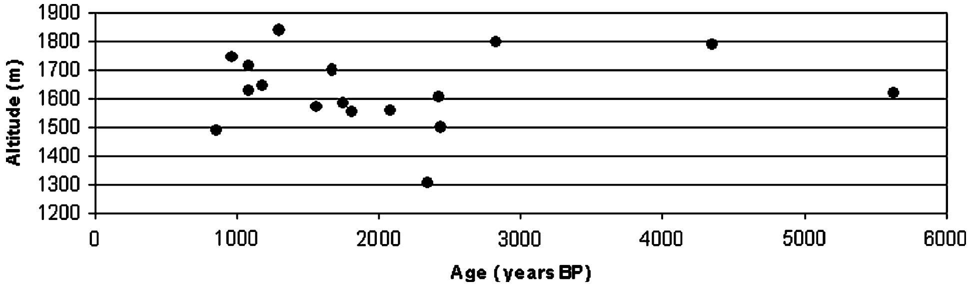

Fig. 4. Radiocarbon age and absolute altitude where the samples were located.

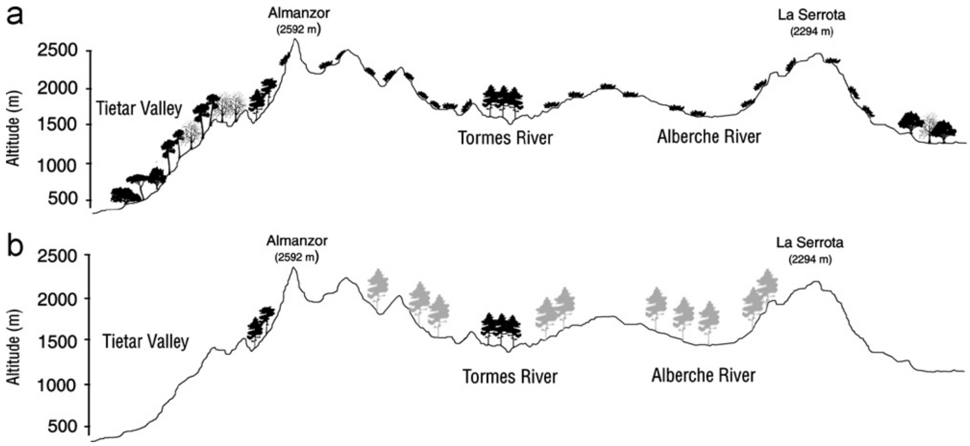

Fig. 5. 🌲: *P. sylvestris*/*P. nigra*. 🌲: *Q. pyrenaica*. ☁, ♠: Sclerophyllous forest with *Q. ilex* subsp ballota and *Q. suber*. 🌲 Pinewoods of *Pinus pinaster*. 🌴: *P. pinea*. ▬: Alpine/subalpine shrub communities (*C. oromediterraneus*, *Genista cinerea*, *Adenocarpus hispanicus*): today representation of the vegetation in a cross section (a). Reconstruction of the pine presence of the *P. sylvestris*/*nigra* group between 3000 and 1000 years BP (b). Trees in black represent sites with nowadays presence of *P. sylvestris*. Trees in grey symbolize the location of sites with remains of the same species.

Table 4
Radiocarbon ages of the studied woods and growth data from the tree ring chronologies

Reference	Id sample	Site	Age 14 Cal yr BP	Years cal BC/AD	Mean	Number of years	Mean width of the tree rings
Pta-9240	NVL006	Navalacruz—Astillero	860 ± 20	1056 AD—1224 AD	1144 AD	57	2.53
Beta-187347	NVT012	Navalperal de Tormes-Pinarejos-Garganta de Gredos	970 ± 60	970 AD—1210 AD	1090 AD	168	0.49
Pta- 9249	HOY009	Hoyos del Espino- Pradogrande	1090 ± 30	893 AD—1013 AD	953 AD	66	1.62
Pta- 9245	SJG010	Navacepeda de Tormes-Cerro Triguero	1090 ± 50	783 AD—1026 AD	904 AD	–	–
Beta-215652	SMV003	San Martín de la Vega del Alberche-Pinorredondo	1170 ± 40	727 AD—975 AD	851 AD	–	–
Pta- 9261	HOY010	Hoyos del Espino-Regajo del Acarreo	1300 ± 60	640 AD—880 AD	760 AD	52	1.78
Pta-9243	NVT013	Navalperal de Tormes-Roncesvalles-Garg. de las Pozas	1560 ± 35	419 AD—574 AD	496 AD	77	3.31
Beta-208810	HOC001	Hoyos del Collado	1670 ± 40	254 AD—530 AD	392 AD	–	–
Pta-9231	NVD001	Navadijos	1750 ± 45	139 AD—398 AD	268 AD	62	1.66
Pta-9235	SEV001	San Esteban del Valle	1815 ± 25	128 AD—312 AD	220 AD	62	1.02
Pta-9247	SJG008	Navacepeda de Tormes- S. Juan de Gredos	2085 ± 25	177 BC—43 BC	110 BC	86	0.74
Beta-215651	SMP005	San Martín del Pimpollar	2350 ± 40	262 BC—727 BC	495 BC		
Pta-9253	GDV002	Garganta del Villar	2430 ± 15	729 BC—409 BC	569 BC	86	3.05
Beta-187348	SER001	Puerto de Serranillos	2440 ± 60	760 BC—400 BC	580 BC	183	1.68
Beta-208822	VLF004	Villafranca de la Sierra-La Serrota	2830 ± 60	1190 BC—840 BC	1015 BC	–	–
Beta-208812	NPT001	Navalperal de Tormes-El Cervunal	4350 ± 60	3330 BC—2870 BC	3100 BC	–	–
Beta-208821	NVQ002	Navaquesera-La Cañada	5630 ± 70	4650 BC—4340 BC	4495 BC	–	–

Calibrated dates were obtained using CALIB 5.0 software (Stuiver and Reimer 1993) version 5.0, with the dataset IntCal04 (Reimer et al., 2004).

Table 5
Tree ring chronologies obtained in the Gredos mountain range

Location	Author(s)	Species	Geographic location	Altitude (m)	*N*	Chronology length
Navarredonda	K. Richter	*P. sylvestris*	40°20′–5°08′	1500	24	1769-1985 (217 years)
Hoyos del Espino	K. Richter	*P. sylvestris*	40°20′–5°10′	1500	21	1813-1985 (173 years)
Cuevas del Valle (*)	D. García & M. Génova	*P. sylvestris*	40°19′–5°01′	1500/1700	28	1740-2003 (264 years)
Piedralaves/Casavieja (*)	M. Génova	*P. nigra*	40°21′–4°40′	1300/1500	31	1667-1991 (325 years)
El Arenal (*)	M. Génova & D. García	*P. nigra*	40°17′–5°07′	1300/1600	51	1686-2002 (317 years)

The sites marked with (*) correspond with studies that have been recently enlarged or are today unpublished. *N*: number of sequences.

the fossil record suggests that the lower limit is around 1300 m, 400 m lower than many botanists consider natural for pine trees in eastern parts of the Iberian Central range, such as Guadarrama where this limit is defined around 1600–1800 (e.g. Rivas Martínez, 1982; Izco, 1984; Rivas Martínez et al., 1987; Martín et al., 1998). The lower limit for the altitude range of the fossil record is also lower than the upper limit of the range for the potential vegetation series of *Q. pyrenaica* in the Iberian Central range, which is defined around 1800 m (Sánchez Mata, 1989).

Although there is not enough data to present detailed climate inferences, the observations cohere with the global climate reconstructions that suggest a relative stability since 7000 Cal BP (e.g. COHMAP-Members, 1988; Davis et al., 2003; Andersen et al., 2004; Heiri et al., 2004). The data provided by the nearest meteorological stations is also coherent with the climatic parameters that characterize today *P. sylvestris* and *P. nigra* mountain forests (Gandullo and Sánchez Palomares, 1994).

The highlands and the northern slopes (Alto Alberche, Alto Tormes and Serrota mountains) situated in the rain shadow of winter winds, today have a climate with larger seasonal temperature variances and marked summer droughts than southern slopes. These conditions allow mountain pines to continue their dominance preventing *Q. pyrenaica* colonization. Nevertheless, the southern slopes, under the influence of a more temperate and humid climate, unfavourable to pines, could provide the conditions for the establishment of broadleaved communities, such as *Q. pyrenaica*.

Acknowledgement of the existence of a mountain pine forest belt through the last six millennia in Gredos shows that palaeophytogeographical work contradicts current assumptions about the occurrence of pine species in the Mediterranean ambit (Carrión et al., 2000). The results suggest that the vegetal succession models created from syntaxonomical studies that ignore the natural pine communities in these western mountains should be revised.

5.2. *Causes of the pine decline*

Concerning the whole Iberian Central range, different authors suggest that there is a relationship between the deforestations of the last millennia, linked with climatic changes, and the anthropogenic disturbances that occurred during the Lateglacial and Holocene (Mancebo et al., 1993; Van der Knaap and Van Leeuwen, 1995; Franco et al., 1997; Martínez García and Costa, 2001).

Firstly, it is important to note that the relative magnitude of the climatic change through the end of the Quaternary and its significance for vegetation dynamics, differ highly depending on the location of the mountain within the whole range. In the westernmost portion of the Iberian Central range, wetter climatic conditions and temperate temperatures occurred around 9000 BP, resulting in an accelerated autogenic vegetational succession. The outcome of competition in those environments is the expansion of *Quercus*, while *Pinus* concentrations decline early, stopping them from being dominant as a forestry unit since the onset of the Holocene. The regional pollen diagrams of the Portuguese Estrela mountain range (van den Brink and Janssen, 1985), especially those from Lagoa Comprida and Charco da Candieira (Janssen and Woldringh, 1981; Van der Knaap and Van Leeuwen, 1994, 1995) show this pattern of early vegetal succession.

The Sierra de Guadarrama (east from Gredos) is characterized by sharp temperature contrasts that result in a more continental climate. Hence, pine forests here were the most extensive vegetation type during the whole Holocene. During the last millennium they went through a regression that did not result in the increase of dominance of other tree taxa such as *Quercus* (Franco et al., 1998). This temporal decline of the Guadarrama pinewoods is interpreted here just as the result of anthropogenic disturbance (Martínez García and Costa, 2001).

The Gredos mountain range, located between the two preceding mountains, reflects the gradient oceanicity/continentality that has been previously described from west to east. Here, pine forests maintained their hegemony during the Holocene, but experienced a progressive decline as times went by. Increases of *Quercus* (Franco et al., 1997) or of *Quercus* and *Betula* synchronically in western Gredos (Atienza, 1993; Franco, 1995) are recorded. Pine forests from the southern slopes of Gredos, directly exposed to the western oceanic influences, were the most affected by this process.

However, climate is not the only controlling factor in the general retraction of the pinewoods of Gredos during the Holocene, especially when we consider its northern slopes and highlands. Autoecological studies that have been carried out for *P. sylvestris* and *P. nigra* in the Iberian Peninsula (Gandullo and Sánchez-Palomares, 1994) compared with the climatic, physiographic and soil parameters of Gredos, locate these mountains into the optimum for both species. Moreover, the modelling frameworks applied under the Breiman's random forest and neural networks algorithms present an extended potential area in the Central System mountain range (Benito et al., 2006). Consequently, abiotic parameters are not the only factors that control vegetal distribution, but there are other restrictions that should be considered as an essential part of the present day landscape interpretation. Human activity, accelerating the deforestation and erosion processes, seems to be the main factor determining the forest dynamics during historic times. The disappearance of almost all the pinewood in the Tormes and Alberche watersheds can be associated with anthropogenic activities during the Late Holocene.

5.3. Relationships between anthropogenic influence and ecological processes

Among the previously exposed factors, fire concurrence, either of anthropogenic or climatic origin, constitutes the trigger process that probably destabilized the dominance of established tree populations. This was exacerbated by the occurrence of exclusively anthropogenic activities such as tree cuttings, pasture and agriculture. Even considering regional variations, the regression of the mountain forests due to those causes is a generalized phenomenon in the whole Iberian Peninsula. In the mountains of Central Iberia, the correspondence between historic data seems to be connected with the descent of the arboreal covering. In Charco da Candieira (Portugal) any climatic signal in the pollen trends appears to be obscured by the anthropogenic signal from around 5500 BP (Van der Knaap and Van Leeuwen, 1995) although it was not until ca 2000 BP when most of the pollen diagrams have identified the anthropogenic signal as large-scale deforestation. In the Bejar mountain range, Atienza et al. (1990, 1991) detect that human impacts intensified at around 4000 BP. The mountains of Guadarrama and the nearby Ayllón mountain range suffered the same deforestation trends (Gil García, 1992; Vázquez and Ruiz-Zapata, 1992; Franco et al., 1997).

In Gredos, signs of human disturbance can be detected on the pollen records from around 2000 BP onwards, intensifying over the last 1000 years (Andrade et al., 1990, Dorado, 1993; Andrade et al., 1996; Franco et al., 1997). On one hand, the Roman occupation began in the first century B.C. (approx. 2000 BP); on the other hand the establishment of the "*Honrado Concejo de la Mesta*" transhumance system in the thirteenth century (ca 700 BP) seems to match with the historic turning points that are pointed out by the palaecological reconstructions.

The use of fire as a tool to clear vast forest terrains with different purposes (defence, agriculture or grazing) could be the crucial factor in the general decline of mountain pinewood in Gredos. The findings of charcoal samples in Hoyos del Espino-Pradogrande confirm the hypothesis of fire occurrence in mountain areas, at least during the last two millennia. Some studies of post-fire vegetation dynamics in Mediterranean areas reveal that, following large fires, *P. nigra* and *P. sylvestris* forests had high probability of evolving toward other successional stages dominated by other tree species or grasslands (Retana et al., 2002; Rodrigo et al., 2004). Resprouters, such as *Q. pyrenaica*, are favoured because of their ability to persist *in situ* through disturbance events such as fire, and they are also decisively involved in the succession patterns of the dominant species (Gracia et al., 2002). Other shrub communities of these Mediterranean mountains, dominated by species of Leguminosae (gen. *Adenocarpus*, *Cytisus*, *Genista*), also have higher resilience to fire than mountain pines (Fernández-Santos and Gómez-Gutiérrez, 1994; Fernández-Santos et al., 2004). Fire damage on ectomycorrhizal fungi of mountain pines should be also considered, since they can critically affect the persistence and stability of forests (Harvey et al., 1980; Dahlberg, 2002). The importance of those fungi in the survival rate of seedlings has been proven in pine stands (Honrubia et al., 1996; Amaranthus et al., 2004).

The expansion of extensive grazing systems could have had a growing importance towards the end of the Holocene. Seed and seedling predation and the barrier created by the herbaceous layer are today the mechanisms blocking the encroachment of *P. sylvestris* onto Mediterranean mountain environments, limiting regeneration and potential expansion of the forest (Castro et al., 2002). These statements agree with the hypothesis argued by other researchers for *P. nigra* in the Central Iberian range (Génova et al., 1988). Hence, fires, forest cuttings and the simultaneous increase of grazing could probably be the critical factors controlling the recolonization ability of the surviving trees.

Therefore, regarding forest management, *Pinus* stands differentiation into potential, permanent or anthropogenic forests becomes problematic. Under the context of current concern about biodiversity loss and the 'best practice' management policies of natural resources, it is essential to develop the research of today's relict pine stands. Dendrochronological studies appear to be an excellent tool to achieve these aims (Génova et al., 1993).

The processes limiting regeneration of some of the stands that persist today (e.g. Hoyocasero, southern slopes of the central part of the Gredos mountain range), must be studied in detail in order to propose the measures that guarantee their conservation, following the results of studies carried out in other marginal distribution areas.

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