Abrupt vegetation changes in the Segura Mountains of southern Spain throughout the Holocene

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Summary

1 The fossil pollen record of Cañada de la Cruz in the Segura mountains of southern Spain yields insights into high-elevation vegetational dynamics over the last *c*. 8320 years. Phases of xerophytic grassland alternate with high-mountain open pine forests and expansion of deciduous forests and Mediterranean scrub at lower altitudes.

2 Longer-term stable vegetation patterns are interrupted by multidecadal to century-scale shifts at about 7770, 3370, 2630, 1525 and 790 years BP.

3 Some of the vegetation types have no modern analogues and represent high-altitude remnants of widespread last-glacial xerophytic communities. Other species patterns, characteristic of current scrub associations, appeared only within the last 800 years.

4 The sequence fits within the regional context of a generally wet mid-Holocene (*c*. 7700–3300 years BP) characterized by spread of mesophilous vegetation, between drier conditions characterized by greater abundance of xerophytes.

5 The pollen record and current ecological studies on high-elevation vegetation of Mediterranean Spain suggest that control of vegetation is primarily climatic although grazing pressure, which would have pushed vegetation over a threshold for change, cannot be discounted.

Key-words: climate change, historical biogeography, Holocene, palaeoecology, palynology, Spain, vegetation dynamics

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Introduction

Many issues about succession and sensitivity of plant communities cannot be addressed through a biogeographical approach, because our state of knowledge is quite insufficient and every region has its own natural and cultural history (Moore *et al*. 1996). Ecologists are well aware of the importance of the long-term palaeo-perspective and have made efforts to incorporate temporal phenomena into models of vegetation patterns. These studies have largely emphasized disturbance-related, cyclic vegetational dynamics at temporal scales of 10^1–10^2 years (Pickett & White 1985). In contrast, palaeoecological studies may focus on directional changes in environment at temporal scales of 10^2–10^5 years (Bennett 1990).

The Holocene palaeoecological record of Mediterranean Spain remains poorly known. Pollen preserva-

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tion in a number of lowland lake sequences is poor and pollen records from suitable sites tend to be temporally constrained, exacerbating problems of interpretation. A major challenge is to determine the effect of forcing mechanisms of vegetation change, although the influence of millennial-scale climate change and variability is suggested in several sequences (Pons & Reille 1988; Peñalba 1994; Pérez-Obiol & Julià 1994; Burjachs *et al*. 1997; Pantaleón-Cano 1997; Yll *et al*. 1997; Carrión *et al*. 1999). Other pollen records provide evidence for anthropogenic influence from the Neolithic and Bronze Ages onwards (Dupré & Renault-Miskovsky 1990; Stevenson & Harrison 1992; Janssen 1994), and a few for invasion mediated by fire disturbance (Carrión & van Geel 1999). However, the overall Holocene pollen record is puzzling and susceptible to many different interpretations (Carrión *et al*. 2000a).

We have chosen to study the history of high-elevation vegetation in the Segura mountains of southern Spain because its fossil pollen record might yield insights into vegetation dynamics unavailable from the lowland studies. Such vegetation, which has low tree species

diversity, is of limited extent but is clearly defined and presumably has been in existence for at least 10 000 years. In addition, the treeline ecotone is thought to be dynamic and sensitive to climate change because trees are growing near their physiological limits (Peterson 1998). This study has three main goals: (i) to reconstruct the temporal pattern of vegetation change in the Cañada de la Cruz pollen record; (ii) to make inferences about climate and biotic interactions from the palaeoecological record; and (iii) to place this new sequence within the complex picture of regional Holocene vegetation and discuss forcing mechanisms of vegetation change.

Study site

The Cañada de la Cruz (38°04′ N, 2°42′ W, 1595 m a.s.l.) is an intramontane valley lying in the south-central Sierra de Segura within the northern Betic cordillera. The valley is flanked by abrupt mountain relief and a large karstic plateau above 1700 m (Fig. 1), whose bedrock consists of Cretaceous and Jurassic dolomites and limestones. The study site is a temporary shallow lake that extends up to *c.* 0.25 × 2.7 km during high-rainfall years, but normally dries up for 6–8 months per year. The lake has a single outlet stream but has no incoming streams and is fed by direct precipitation and surface runoff from the catchment. The depositional context is a compact bed of brown calcareous clays overlying a small-scale river deposit of calcreted conglomerates. The climate is cold continental Mediterranean. The valley is at the boundary between supra- and oro-Mediterranean vegetation, with inferred mean annual temperatures averaging between 5 °C and 8 °C. Present-day vegetation is characterized by dwarf
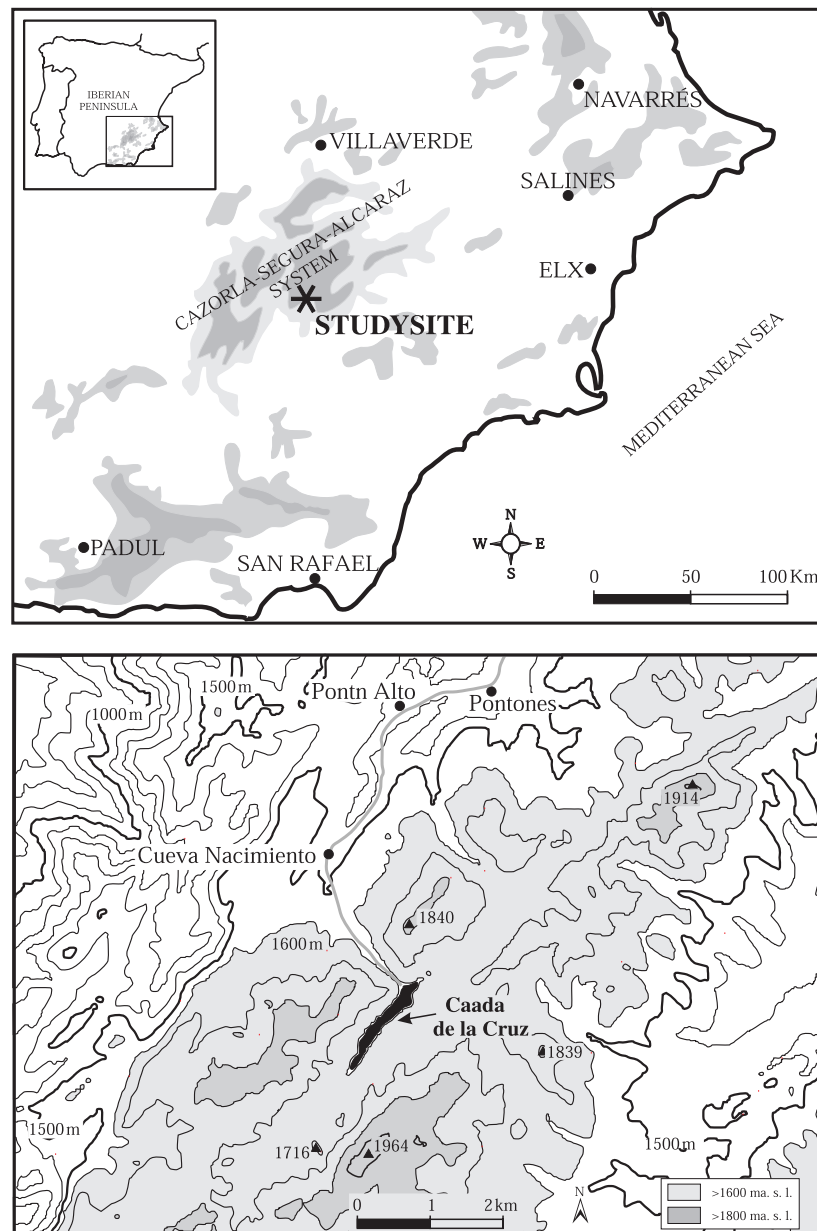

Fig. 1 Location of the study site in the south-central Sierra de Segura (Pontones, Jaén).

junipers (*Juniperus sabina*, *J. communis*), sparse *Pinus nigra* stands, and a thorny prostrate scrub of *Ononis aragonensis*, *Prunus prostrata* and *Rhamnus saxatilis*, with a basal layer of grasses.

Methods

A sediment core (total depth 274 cm) that reached bedrock was raised from a central point in the dry lake during late summer using a 6-cm piston sampler. The core was extruded in the field, wrapped in cling film and placed in labelled sections of PVC guttering cut lengthways. Upon return to the laboratory the core was wrapped in heavy-duty plastic sheet and placed in a dark cold-store at 4 °C to prevent desiccation and reduce microbial activity. Subsamples of sediment for pollen analysis were taken at 2–4 cm intervals throughout the core. Pollen was only found in the uppermost 128 cm of the sediment core, corresponding to a uniform clayey bed *c*. 1.5 m depth, without signs of erosive contacts or internal changes in colour, texture and structure. During the intervals of substantial change in the pollen spectra, samples were counted every 1 cm. No macrofossil or charcoal remains were found throughout the sediment core. Extraction of pollen follows the standard procedure described in Moore *et al*. (1991). Mineral separation with zinc chloride density 2.0 was used for all the samples. Exotic *Lycopodium* tablets of a known concentration were added to calculate pollen concentrations.

After chemical and physical treatment, at least 400 pollen grains were identified under a light microscope using the reference collection of the Laboratory of Palynology at the University of Murcia and criteria detailed in previous papers (e.g. Carrión & van Geel 1999). *Pinus pinaster* was palynologically separated from the most abundant *P. nigra* type by its larger pollen body, shorter alveoli and thicker proximal exine (see Carrión *et al.* 2000b for further details). Identification of non-pollen microfossils was aided by the

Table 1 Radiocarbon age determinations on bulk sediment from the Cañada de la Cruz sequence. Ages are given in uncalibrated years BP

Laboratory code	Depth (cm)	^{14}C years BP	Analysis
Pta-8009	0–2	1955/1956 AD	Standard
Pta-7999	3–4	750 ± 90	Standard
Pta-7883	8–10	790 ± 70	Standard
GrA-13531	20–21	1500 ± 50	AMS
GrA-14159	22–23	1550 ± 40	AMS
GrA-14161	27–28	2130 ± 40	AMS
Beta-141044	37–38	2630 ± 140	Standard
Pta-8342	43–45	2740 ± 50	Standard
GrA-14160	83–84	3350 ± 40	AMS
Pta-8339	84–86	3370 ± 20	Standard
Pta-8340	86–88	3385 ± 30	Standard
Beta-141046	106–108	5820 ± 40	AMS
Beta-141047	115–117	7770 ± 40	AMS
Beta-13532	126–128	8320 ± 50	AMS

descriptions and microphotographs of Van Geel *et al.* (1989) and Carrión & van Geel (1999). Pollen percentage and pollen concentration diagrams were constructed using Tilia 1.12 and TiliaGraph 1.18 programs (Grimm 1992). Hygrophyte pollen (*Polygonum*, Cyperaceae, *Typha*), algal and fungal spores and other non-pollen palynomorphs (largely Type 128) were excluded from pollen sum. The delimitation of percentage pollen zone boundaries was aided by stratigraphically constrained incremental sum-of-squares analysis (CONISS analysis, Grimm 1992) using a square-root transformation and chord-distance dissimilarity measure for all pollen taxa. Nomenclature for plant vascular species follows Valle *et al.* (1989) and Mota *et al.* (1993).

A chronology was established on the basis of 14 radiocarbon dates (Table 1). Samples consisted of bulk organic sediment, dated by the AMS method where necessary because of low carbon content in the organic extracts. The dates may be affected by a hard-water error, although internal consistency suggests that this is unlikely and an age-depth model based on interpolated ages between adjacent pairs of dates was therefore constructed (Fig. 2).
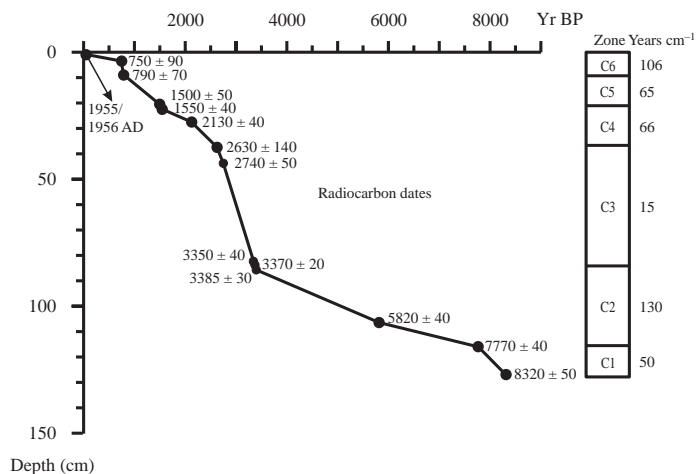
Fig. 2 Sediment depth and pollen stratigraphy to radiocarbon age relationships from the Cañada de la Cruz section. Lines connecting each plotted point are interpolated sediment accumulation rates.

Table 2 Taxonomic and ecological definition of selected pollen types of Figure 3

Pollen type	Suggested taxon/taxa	Indication of present-day ecology
Poaceae	*Helictotrichon filifolium* Henrard, *Festuca hystrix* Boiss., *Poa ligulata* Boiss., *Koeleria vallesiana* Gaudin, etc.	Xerophytic grassland-scrub above treeline, rocky substrates and basal layer of high-altitude pine forests
Juniperus	*Juniperus sabina* L., *J.communis*, *J. thurifera* L., *J. phoenicea* L.	Xerophytic grassland-scrub. Continental situations
Asteraceae	*Jurinea humilis* DC., *Scorzonera albicans* Cosson, etc.	Rocky substrates in xerophytic grassland-scrub
Lamiaceae	*Thymus serpylloides* Bory, *Teucrium polium* L., etc.	Xerophytic scrub
Caryophyllaceae	*Dianthus subacaulis* Vill., *Arenaria tetraquetra* L.	Xerophytic grassland-scrub
Brassicaceae	*Vella spinosa Boiss.*	Xerophytic scrub
Helianthemum	*Helianthemum croceum* Desf.	Xerophytic grassland-scrub
Genisteae	*Echinospartium boissieri* Rothm., *Genista longipes* Pau, *Erinacea anthyllis* Link	Xerophytic scrub. Degradation stages of pine and oak forests?
Helleborus	*Helleborus foetidus* L.	Degradation stages of forests?
Berberis	*Berberis hispanica* Boiss.	Degradation stages of forests?
Ephedra nebrodensis	*Ephedra nebrodensis (rare)*	Cold continental situations and stressful soils below 1600 m
Chenopodiaceae	Several species	Xerophilous in lowlands
Artemisia	*Artemisia campestris* L., *Artemisia herba-alba* Asso	Xerophilous in lowlands
Juglans	*Juglans regia* L.	Arboriculture in mesic areas
Olea	*Olea europaea* L. var. *sylvestris*, *Olea europaea* L. var. *europaea*	Xerothermophilous scrub. Arboriculture in lowlands
Vitis	*Vitis vinifera* L.	Cultivated
Pteridium aquilinum	*Pteridium aquilinum* (L.) Khuhn	Clearance of deciduous forests
Plantago lanceolata	*Plantago lanceolata* L., *P. sempervirens* Crantz	Agro-pastoral activities
Cerealia	*Triticum*, *Hordeum*, *Oryza*	Crop cultivation
Centaurea aspera	*Centaurea* sev. sp.	Weeds
Papaver	*Papaver*, *Roemeria*	Weeds (crop cultivation)

Results

SOURCE AREA

High-elevation vegetation of the Betic mountain system is limited in extent and, because of its topographic situation, the study site is well-placed to record shifts in the treeline occurring from about 1600 m upwards (Fig. 1). Although there are no pollen rain records for the area, pollen catchments for similar mountain top sites of the Spanish Central System included a low-altitude signal caused by ascending air flows along slopes (Vázquez & Peinado 1993; Andrade *et al*. 1994). The pollen sequence of Cañada de la Cruz can thus allow insights into the vegetation history throughout the Segura mountains since *c*. 8320 years BP.

POLLEN STRATIGRAPHY

The pollen stratigraphy is shown in Figs 3–7. *Pinus nigra* type and Poaceae dominate the pollen record and show abrupt shifts in abundance at about 8320, 7770, 3370, 2630, 1525 and 790 years BP. Zones C1, C3 and C5 are dominated by Poaceae. Zones C2, C4 and C6 are dominated by *Pinus*. Poaceae-dominated zones are also characterized by *Juniperus*, *Artemisia*, *Ephedra nebrodensis*, Chenopodiaceae, Asteraceae and, partially, Lamiaceae and *Helianthemum* (Fig. 3). However, the *Artemisia* and *Ephedra nebrodensis* curves are different in zones C2 and C5, Lamiaceae shows a

particular maximum in C6, and *Juniperus* and Poaceae show lags in maxima for zones C2 and C3. Table 2 indicates the present-day habitat indications of these species. *Pinus*-dominated zones show relatively high values of deciduous *Quercus*, *Fraxinus*, *Acer*, *Pinus pinaster*, evergreen *Quercus*, and *Erica arborea* (Fig. 4, Table 3), although there are observable lags in appearance, disappearance and in the timing of particular peaks, especially of *Pinus nigra* type in relation to *Quercus* types, *P. pinaster* and *Erica arborea* types. From zone C4 upwards, there is also concordance between *Pinus nigra* type and meso-thermophilous taxa such as *Alnus*, *Betula*, *Ononis*, *Prunus*, *Rhamnus*, *Ephedra fragilis* and *Pistacia* (Fig. 4). Patterns of hygrophyte pollen, spores and non-pollen palynomorphs generally correlate with pollen curves (Fig. 5, Table 4). The pollen concentration curves for selected taxa (Fig. 6) show similar trends to the percentage curves and support their palaeoecological reliability. Pollen stratigraphy and vegetational developments are summarized in Fig. 7 and Tables 5 and 6.

SUDDENNESS OF THE POLLEN-STRATIGRAPHICAL CHANGES

Each 1 cm of sediment-accumulation represents, on average, 50 years in zone C1, 130 years in zone C2, 15 years in zone C3, 66 years in zone C4, 65 years in zone C5 and 106 years in zone C6 (Fig. 2). As the sharpest changes in the pollen record generally occur within 1–2 cm, we estimate that vegetational transitions
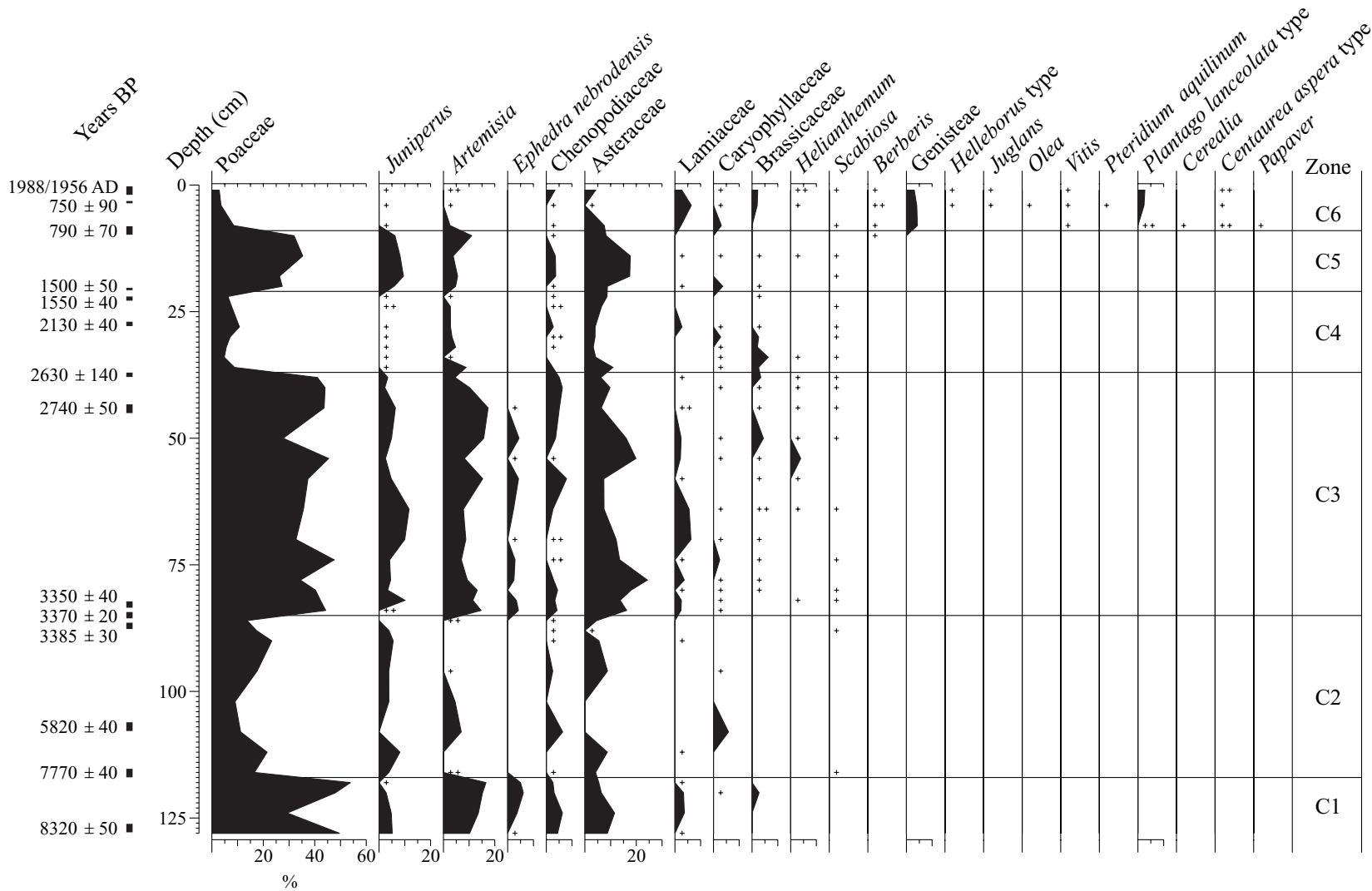
Fig. 3 Pollen diagram for shrubs and herbs, and anthropogenic indicators. Points indicate pollen frequencies below 2%. Ages are given in uncalibrated years BP.
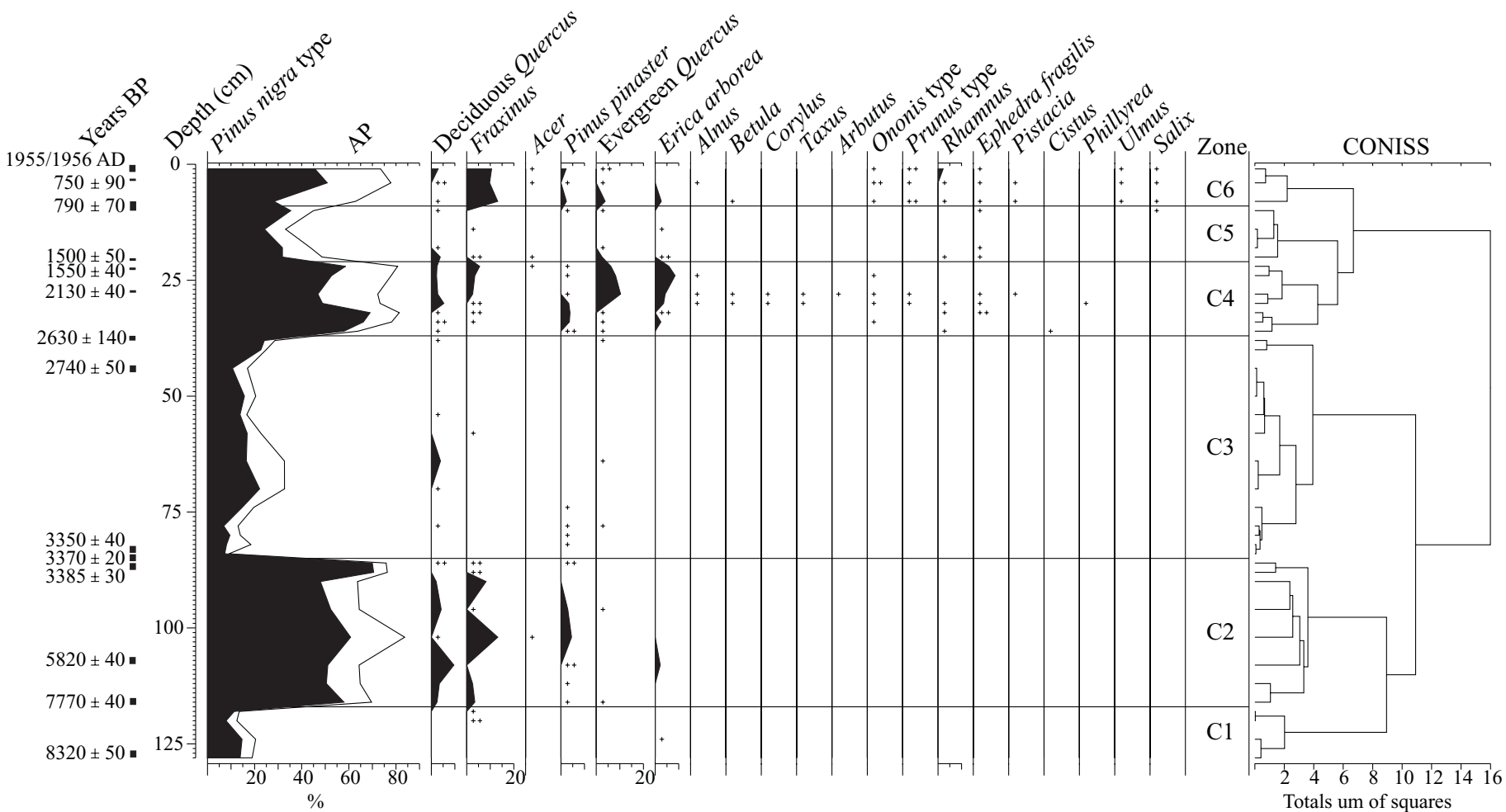
Fig. 4 Pollen diagram of Cañada de la Cruz for trees and shrubs, and sum of arboreal pollen, AP. Delimitation of percentage pollen zone boundaries was aided by stratigraphically constrained incremental sum-of-squares (CONISS) analysis (Grimm 1992) using a square-root transformation and chord-distance dissimilarity measure for all pollen taxa. Points indicate pollen frequencies below 2%. Ages are given in uncalibrated years BP.
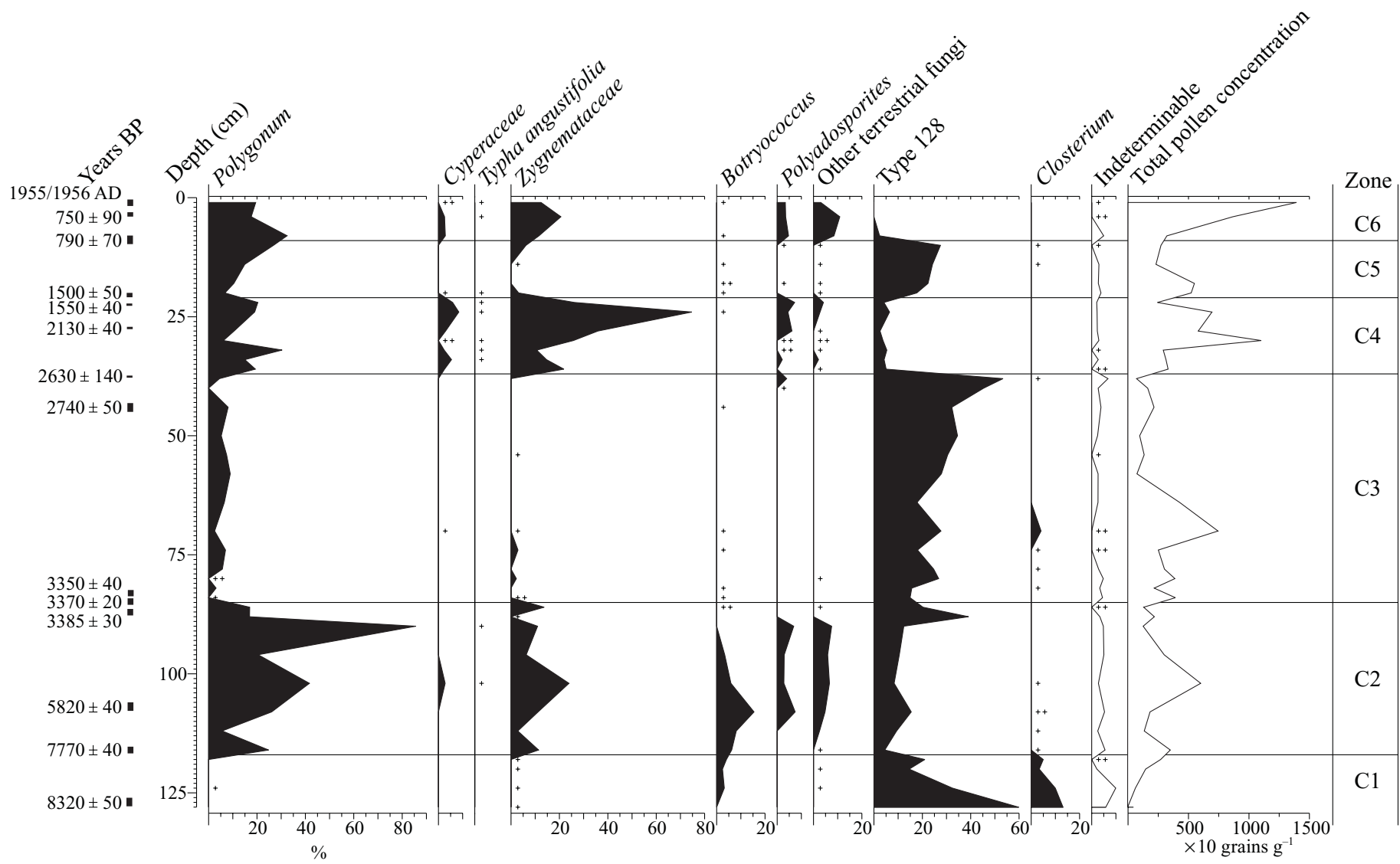
Fig. 5 Pollen diagram for hygrophyte pollen, spores and non-pollen palynomorphs, and total pollen concentration. All types excluded from pollen sum. Points indicate pollen frequencies below 2%. Ages are given in uncalibrated years BP. See Table 4 for taxonomic adherence of spore types.
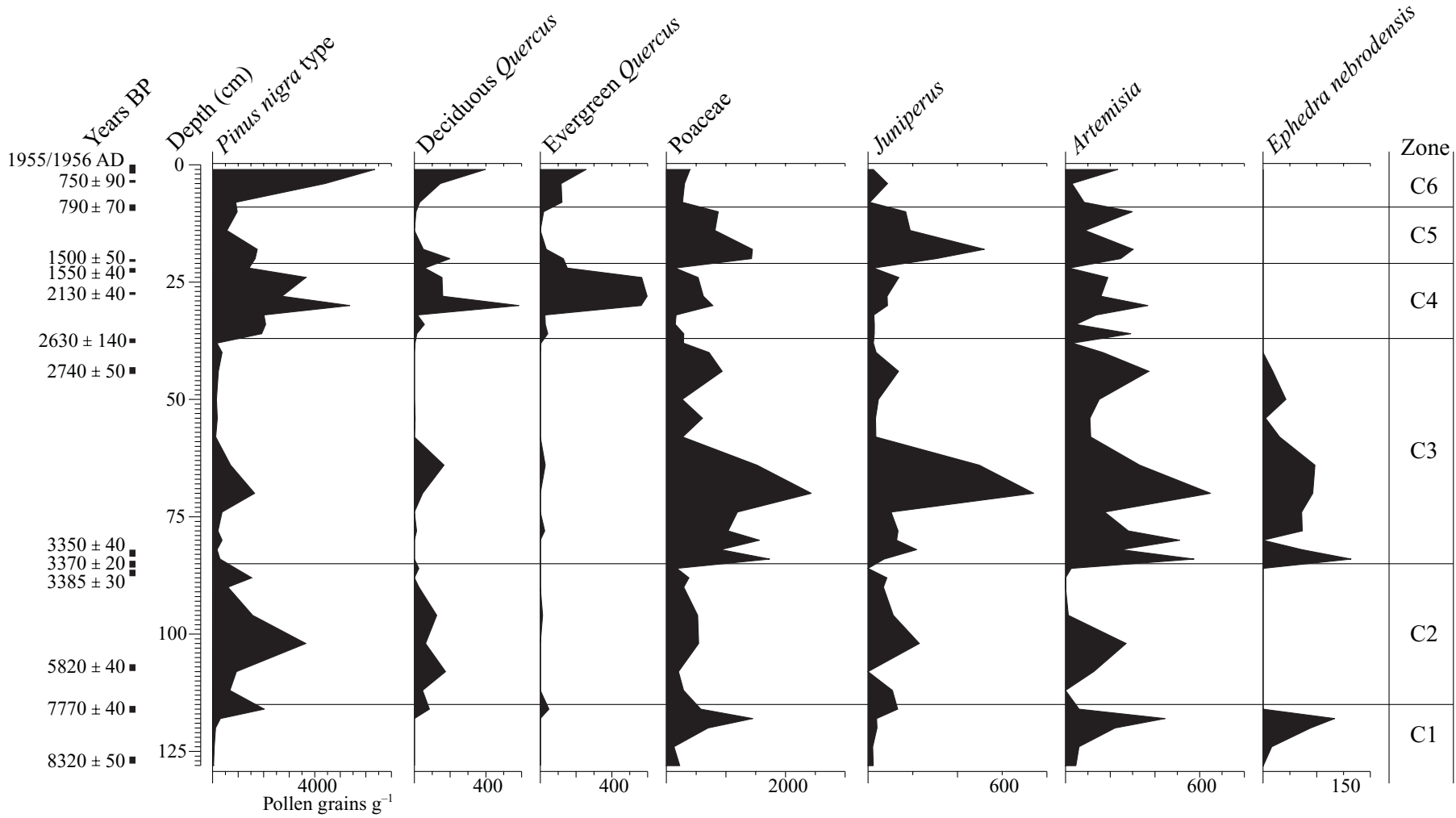
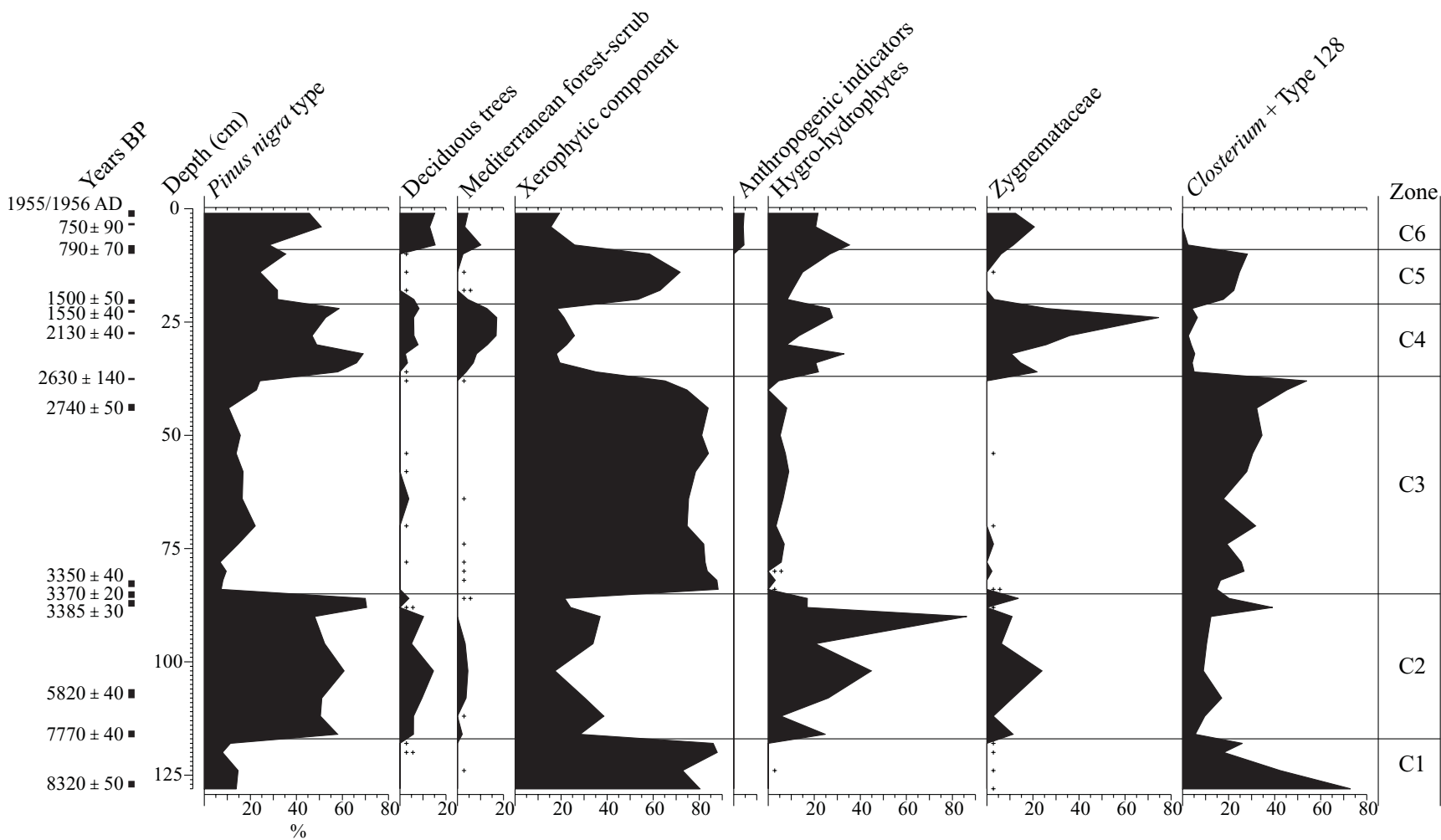**Fig. 6** Concentration diagram for selected types.

Fig. 7 Synthetic pollen diagram of Cañada de la Cruz. See Tables 2–4 for definition of ecological groups. 'Deciduous trees': deciduous *Quercus*, *Fraxinus angustifolia*, *Acer*, *Alnus*, *Betula*, *Corylus*, *Ulmus*, *Salix*. 'Mediterranean forest-scrub': *Pinus pinaster*, evergreen *Quercus*, *Erica arborea*, *Arbutus*, *Ephedra fragilis*, *Pistacia*, *Cistus*, *Phillyrea*. 'Xerophytic component': Poaceae, *Juniperus*, *Artemisia*, *Ephedra nebrodensis*, Chenopodiaceae, Asteraceae, Lamiaceae, Caryophyllaceae. 'Anthropogenic indicators': *Juglans regia*, *Olea*, *Vitis*, *Pteridium aquilinum*, *Plantago lanceolata*, Cerealia, *Centaurea aspera*, *Papaver*. 'Hygro-hydrophytes': *Polygonum*, Cyperaceae, *Typha angustifolia*. Points indicate pollen frequencies below 2%. Ages are given in uncalibrated years BP.

Table 3 Taxonomic and ecological definition of selected pollen types of Figure 4. P = mean annual precipitation (mm). T = mean annual temperature (°C)

Pollen type	Suggested taxon/taxa	Indication of present-day ecology
Pinus nigra	*Pinus nigra* Arnold, *Pinus sylvestris* L.? (not present in the region)	High-altitude (1600–2100 m) pine forests and mixed pine-oak forests at mid altitudes
Ononis	*Ononis aragonensis* Asso	High-altitude open pine forests
Prunus	*Prunus prostrata* Labill.	High-altitude open pine forests
Rhamnus	*Rhamnus saxatilis* Jacq.	High-altitude open pine forests
Deciduous *Quercus*	*Quercus faginea* Lam., *Quercus pyrenaica* Willd? (rare)	Deciduous oak forests, *c.* 1200–1600 m, P > 600, T > 8
Taxus	*Taxus baccata* L.	Deciduous forests, steep gullies
Acer	*Acer granatense* Boiss. *A. monspessulanum* L.	Deciduous oak forests, mid-altitude pine forests
Betula	*Betula pendula* Roth.	
Corylus	*Corylus avellana* L.	Deciduous forests, P > 1000
Ulmus	*Ulmus minor* Miller	Riparian forests
	Ulmus glabra Hudson	Deciduous forests
Salix	Several species	Riparian forests
Fraxinus	*Fraxinus angustifolia* Vahl	Mainly riparian forests
Evergreen *Quercus*	*Quercus rotundifolia* Lam.	Evergreen oak and mixed pine-oak forests below 1500 m, P 350–600
Pinus pinaster	*Pinus pinaster* Aiton	Pine and mixed forests below 1500 m
Erica arborea	*Erica arborea* L.	Evergreen oak forests
Arbutus	*Arbutus unedo* L.	Oak forests below 1500 m
Pistacia	*Pistacia lentiscus* L.	Thermophilous, Mediterranean oak forest-scrub below 900 m
	P. terebinthus L.	Mesothermophilous, oak forests
Phillyrea	*Phillyrea angustifolia* L.	Thermophilous, Mediterranean oak forest-scrub below 1100 m
Ephedra fragilis	*Ephedra fragilis* Desf.	Xerothermic scrub in lowlands

Table 4 Taxonomic definition and ecological indication of selected pollen types of Figure 5. Indication refers to present-day ecology (pollen) and palaeoecological data (non-pollen palynomorphs)

Pollen Type	Suggested taxon/taxa	Indication
Polygonum	*Polygonum salicifolium* agg. Brouss.	Hygrophilous, temporary stagnant soils
Cyperaceae	*Carex, Cyperus, Scirpus, Schoenus*	Hygrophilous, stagnant soils, lake and pool margins
Typha	Typha angustifolia *L.*	Hydrophilous, lake margins
Zygnemataceae	Sum of *Zygnema, Mougeotia,* and *Spirogyra* zygospores and aplanospores	Meso- to eutrophic stagnant shallow water
Polyadosporites	*Polyadosporites* (Jarzen & Elsik 1986)	Organic matter decomposition (fungal activity)
Other terrestrial fungi	Sum of Types 1, 8B and 55 (Van Geel *et al.* 1983, 1986, 1989)	Organic matter decomposition
Type 128	Types 128A and 128B (Van Geel *et al.* 1989)	Assemblage characteristic of mesotrophic oxygen-rich fresh water during dry, cold stages in
Closterium	Closterium idiosporum-type zygospores (Van Geel *et al.* 1989)	Mediterranean Spain (Carrión & van Geel 1999)

must have occurred at the multidecadal to century scale. Determining transition times more accurately is not possible given the multidecadal error of radiocarbon dating and the inconstancy of sediment accumulation rates (Fig. 2). Transition times estimated in Table 6 should therefore be taken as only approximate. However, changes at the century scale are clear during the transitions from C2–C3 upwards.

Discussion

HOLOCENE PINE FORESTS

Pinus nigra is the most likely pine-pollen producing species in Cañada de la Cruz, as it currently dominates

high-altitude karstic reliefs on limestones, although in relatively sparse stands (Mota *et al.* 1993), and historical documents describe its prominence since the 15th century AD (Sánchez-Gómez *et al.* 1995). The main alternative, *P. sylvestris*, prefers siliceous substrates, and even if the species coexist, *P. nigra* is more tolerant of the aridity that characterizes the northern Betics (Sánchez-Gómez *et al.* 1995). The remaining Iberian species (*P. pinea, P. halepensis*) are not well-adapted to high-mountain climates (Barbero *et al.* 1990). Regional charcoal-analytical data come from coastal and lowland settlements (Rodríguez 1992) and, hence, cannot clarify this problem.

Pollen of *Pinus pinaster* increases during the *P. nigra* and *Quercus*-dominated periods (Fig. 4). These findings

Table 5 Pollen-stratigraphical changes in the Cañada de la Cruz sequence (Figs 3–7). Numbers in brackets refer to relative pollen percentages

Zone Pollen characteristics	Aquatic types and non-pollen microfossils
C6 **Pinus nigra** (45–51) Ev. *Quercus* (1–3) *P. pinaster* (2) Dec. *Quercus* (2) *Fraxinus* (9–12) *Berberis* (2) Genisteae (4–5) *Plantago* (2) Ocurrence of *Acer, Alnus, Salix, Ulmus, Betula, Pistacia, Ephedra fragilis, Ononis, Prunus, Rhamnus, Olea, Juglans, Vitis, Centaurea, Papaver*	*Polygonum* **Zygnemataceae** *Polyadosporites* *Cyperaceae* Typha
C5 **Poaceae** (28–39) *Juniperus* (6–9) *Artemisia* (4–10) Asteraceae (8–15)	**Type 128** *Closterium*
C4 **Pinus nigra** (52–70) Ev. *Quercus* (1–10) *Erica arborea* (3–10) *Pinus pinaster* (1–4) *Ephedra* fragilis (1–2) Dec. *Quercus* (1–4) *Fraxinus* (2–4) Occurrence of *Corylus, Alnus, Betula, Acer, Taxus, Arbutus, Pistacia, Phillyrea, Cistus, Ononis, Prunus, Rhamnus*	**Zynemataceae** *Polygonum* Cyperaceae *Typha* *Polyadosporites*
C3 **Poaceae** (31–46) *Artemisia* (10–18) *Juniperus* (3–11) *Ephedra nebrodensis* (1–5) Chenopodiaceae (2–8) Asteraceae (9–24) Lamiaceae (1–4) *Helianthemum* (1–2) Brassicaceae (1–4)	**Type 128** *Closterium*
C2 **Pinus nigra** (51–72) Dec. *Quercus* (3–9) *P. pinaster* (1–4) *Fraxinus* (2–12) Occurrence of *Acer* and *Erica arborea*	*Polygonum* **Zygnemataceae** *Botryococcus* *Polyadosporites*
C1 **Poaceae** (35–55) *Artemisia* (10–17) *Juniperus* (1–6) *Ephedra nebrodensis* (2–6) Lamiaceae (1–3)	**Type 128** *Closterium*

Table 6 The Cañada de la Cruz vegetation history and estimated duration of stages and transitions

Aprox. age (years BP)	Stage/transition	Aprox. duration (years)	Local vegetation	Mid- and low-altitude developments
790–1955 AD	C6	745	Open pine forest	Expansion of cluster pine, deciduous and evergreen oak forests, and Mediterranean scrub. Agriculture, increased grazing pressure
790 ± 70	C5–C6	65–212	Forest expansion	
1525–790	C5	735	Grassland with juniper scrub and pines	Expansion of xerophytes
1500 ± 50 1550 ± 40	C4–C5	66–130	Forest regression	
2630–1525	C4	1105	Open pine forest	Expansion of cluster pine, deciduous and evergreen oak forests, and Mediterranean scrub
2630 ± 140	C3–C4	30–130	Forest expansion	
3370–2630	C3	740	Grassland with juniper scrub	Expansion of xerophytes
3370±20	C2–C3	35–70	Forest regression	
7770–3370	C2	4400	Pine forest with juniper	Expansion of cluster pine and deciduous oak forests
7770 ± 40	C1–C2	50–130	Forest expansion	
8320–7770	C1	550	Grassland with juniper scrub	Expansion of xerophytes

agree with previous palaeoanthracological and palynological data in support of the natural character of *P. pinaster* communities in mid-altitude montane regions of the Iberian Peninsula, at least since the Upper Pleistocene (Figueiral 1995; Carrión *et al.* 2000). A recent study of the genetic variability and migration pathways of *Pinus pinaster* suggests that southern Iberia was a dispersal centre for the species after the last glaciation (Salvador *et al.* 2000).

VEGETATION TYPES LACKING MODERN ANALOGUES

Present-day vegetation at this altitude could not produce the high pollen frequencies observed for *Artemisia*,

Ephedra nebrodensis and Chenopodiaceae in Cañada de la Cruz, even if the possibility of long-distance transport is considered (Andrade *et al.* 1994). Such pollen assemblages are a common feature of Pleistocene cold stages, often in the context of thermoclastic scree and periglacial lithology (Dupré 1988), and may be regarded as a remnant of glacial vegetation at this site. This vegetation, being adapted to full-glacial climatically stressful environments, progressively reduced its range and became extinct throughout the Holocene with *Artemisia, Ephedra* and Chenopodiaceae showing species-specific rates of change (Fig. 3). Thus, *Ephedra nebrodensis* retreated at *c.* 2740 years BP, and has become rare in the region, whereas *Artemisia* only reduced in high-altitude abundance during the last

millennium and Chenopodiaceae was still increasing as recently as *c.* 750 years BP.

Several assemblages of pollen types that match the present-day composition of high-altitude communities have appeared relatively recently. *Prunus-Ononis-Rhamnus* understorey dates from *c.* 2500 years BP (Fig. 4). *Helleborus foetidus* and thorny species such as *Berberis hispanica*, *Erinacea anthyllis*, *Genista longipes* and *Echinospartium boissieri*, assembled only during the last 800 years (Fig. 3).

FORCING MECHANISMS OF VEGETATION CHANGE

Several lines of reasoning support the view that climate change has influenced vegetational developments at Cañada de la Cruz, although response times cannot be measured, and it remains open to debate whether climate alone or in combination with other factors (e.g. human disturbance) is ultimately responsible for the observed rapid shifts in vegetation.

Current ecological studies

The picture emerging from the Cañada de la Cruz sequence is of *Pinus*-Poaceae dynamics in agreement with phytosociological models for the oro-Mediterranean belt. The ecotone between pine forest and xerophytic grassland-scrub, which would have changed altitudinal position at least five times over the last 8320 years, is known to be sensitive to thermal lapse rate, wind intensity, summer length and rainfall distribution (Valle *et al.* 1989). The upper altitudinal limit of angiosperm forests in the region is also strongly influenced by mean annual temperatures (Rivas-Martínez 1990). Overall, therefore, the high-elevation boundary conditions at Cañada de la Cruz mean that rapid vegetation changes do not necessarily require pronounced shifts in climate.

Palynological evidence in support of climatic control

The correlation between Poaceae, *Artemisia*, Chenopodiaceae, *Juniperus* and *Ephedra nebrodensis* suggests cold arid conditions for the stages in which pollen of these taxa increase in value, namely at *c.* 8320–7770 years BP, 3370–2630 years BP, and to a lesser extent, 1525–790 years BP. Declines of these herbaceous assemblages correspond with increases in value of pollen of mesophilous (*Quercus*, *Pinus pinaster*, *Fraxinus*, *Acer*, *Erica arborea*, *Alnus*, *Betula*, *Corylus*, *Arbutus*, *Ulmus*) and thermophilous (*Pistacia*, *Cistus*, *Phillyrea*, *Ephedra fragilis*, *Olea*) taxa. Thus, the montane climate must have been relatively warmer and wetter during *c.* 7770–3370, 2630–1525 and 790 years BP to the present. During these stages, invasion of high-elevation grassland-scrub by pines is consistent with upward displacement of deciduous forests and expansion of evergreen forest and scrub.

Anthropogenic pollen indicators and human influence

From *c.* 790 years BP there is palynological evidence of arable agriculture and pastoralism (Fig. 3). Anthropogenic indicators include *Plantago lanceolata* type, Cerealia, *Vitis*, *Centaurea aspera* type and *Papaver*. The presence of *Olea*, *Juglans*, *Pteridium aquilinum*, *Helleborus*, *Berberis* and Genisteae, and partially the high pollen records of *Fraxinus* during zone C6, may also be related to human activity (Table 2). The association of Genisteae and *Berberis* with anthropogenic indicators suggests that they may be related to the expansion of thorny scrub following historical overgrazing of high-altitude grassland.

The intensity and timing of human impact on vegetation varied from one part of south-eastern Spain to another. Thus, while peripheral and lowland sites such as Navarrés, Elx and Salines (Fig. 1) show anthropogenic pollen indicators since Chalcolithic and Neolithic times (Burjachs *et al.* 1997; Carrión & van Geel 1999), there is no firm palynological evidence of human disturbance in Villaverde until *c.* 2000 years BP (Carrión *et al.* in press), and in Cañada de la Cruz prior to *c.* 790 years BP (Fig. 3). However, as in other mountain ranges of the peninsula (Janssen 1994), grazing by flock animals may have occurred many thousands of years before the last millenium but left no traces in the landscape. The area is indeed a suitable place for grazing and human habitation in the summer, and it is therefore conceivable that high-elevation vegetation was pushed over a threshold by locally increased grazing pressure. *Artemisia* and Chenopodiaceae could be then viewed as anthropozoochores and Asteraceae, Lamiaceae, Caryophyllaceae, Brassicaceae, *Helianthemum* and *Scabiosa* as indicative of grazing-induced spiny scrub currently defined by *Jurinea humilis*, *Cirsium gregarium*, *Carduncellus araneosus*, *Thymus serpylloides*, *Teucrium polium*, *Arenaria tetraquetra*, *Dianthus subacaulis*, *Ptilotrichum spinosum*, *Vella spinosa*, *Helianthemum croceum* and *Scabiosa andryaefolia* (Table 2).

Documentary evidence is scarce, but it is clear that agricultural practices existed in these mountains from Roman times, and that important urban expansion had already taken place during Islamic times, when the flanks of the Segura mountains were dotted with a string of villages practising irrigation, separated by large areas of pasture (De la Cruz 1980).

Palaeolimnological changes

The stratigraphy of palaeolimnological indicators in Cañada de la Cruz is compatible with climatic control of vegetation stages. Zones C1, C3 and, to a lesser extent, C5, characterized by *Closterium* and Type 128 (Tables 4 and 5, Fig. 5) and increased minerogenic influx (Fig. 2), may represent stages with comparatively poor-nutrient water in the context of low temperatures and short summers leading to treeless catchment

vegetation. Zones C2, C4 and C6, with characteristic Zygnemataceae-dominated assemblages, decomposing fungi and hygrophyte pollen, would represent moderate eutrophication and temporary colonization of the lake by marginal vegetation within a more forested landscape and milder climate. *Polygonum* may also indicate shifts to longer snow-free periods and mesic summer conditions. The absence of peaty layers and preserved macroremains suggests, however, that prolonged dessication of the basin, organic matter decomposition and mineralization occurred throughout the sequence.

Palaeoecological correlation

Pollen records of the Iberian Peninsula exhibit asynchronies with vegetation change during the Holocene (Carrión *et al.* 2000a). Several of these may reflect insufficient or imprecise chronological control, but others clearly need explanation in terms of ecological and historical factors (Bennett & Willis 1995).

The lowland pollen record from nearby Villaverde (Carrión *et al.* 2001) joins Cañada de la Cruz and other pollen sequences from the semiarid Almería littoral (Pantaleón-Cano 1997) and southern Iberian mountain valleys (Carrión & van Geel 1999) in suggesting a generally wet mid-Holocene stage characterized by spread of mesophilous vegetation, preceded and followed by drier conditions that are inferred from a higher abundance of xerophytes. However, there are centurial- to millennial-scale lags in vegetational developments and, for instance, the onset of humid conditions occurs perceptibly earlier in Cañada de la Cruz (*c.* 7700 years BP) and the aridification trend starts earlier in Almería (*c.* 5000 years BP) and Villaverde (*c.* 4500 years BP). It is therefore possible that a long-term influence of climate change at the regional level induced a xerophytization trend from lowland to high-elevation sites, and brought about the spread of deciduous trees and Mediterranean vegetation from mountain to littoral areas.

It is not possible to fit the Cañada de la Cruz and Villaverde sequences into an overall picture of Holocene climate variation based on biological and geological proxies obtained from regional archives, as palaeoecological correlation is limited by insufficient evidence.

CONCLUDING REMARKS

Most pollen records from the Iberian Peninsula reveal gradual shifts in vegetation or relatively stable vegetation patterns throughout the Holocene (Dupré 1988; Peñalba 1994; Franco *et al.* 1998; Sánchez-Goñi & Hannon 1999), although sudden changes have occasionally been reported (Carrión & van Geel 1999). Two major transitions in the pollen record at Villaverde occurred over decades and involved changes in the dominant trees in the forest, whereas others were smooth and may be due to natural competition (Car-

rión *et al.* 2001). The sequence of Cañada de la Cruz also suggests that pollen may be a successful indicator of rapid shifts in Mediterranean vegetation but establishing the mechanism responsible is more difficult. The climate hypothesis provides an adequate explanation at Cañada de la Cruz, but not at Villaverde, where other ecological factors produced important lags in vegetational developments (Carrión *et al.* 2001).

Webb (1986) predicted that when several species, each with different ecological relationships to climate, are present in the vegetation, then most climatic changes will tend to elicit an immediate (i.e. 50–80-year) response in the vegetation by altering the competitive balance. The availability of large openings, such as those found today in the oro-Mediterranean vegetation belt, may have been an important determinant of the high rates of tree expansion after *c.* 7770, 2630 and 790 years BP. Subsequent regressions (after *c.* 3370 and 1500 years BP) may have been due to increased disturbance linked to climatic changes. Increases in wind intensity would have damaged trees in the winter by desiccation and reduced productivity by lowering the ambient temperature during the shorter summer months, although it is unlikely that timberline communities experienced fire or other types of disturbance that create openings in less stressful environments (Richardson & Rundel 1998). Although we cannot test the hypothesis that pastoral activities provoked forest depletion, it is difficult to conceive that any Holocene vegetation remained outside the influence of human activity, at least after neolithization at *c.* 5500 years BP (Carrión & Dupré 1997).

The abrupt changes in the pollen record at Cañada de la Cruz at *c.* 7700–7800 and 3300–3400 years BP are synchronous with periods of abrupt oscillations and rapid transitions in the climates of north Africa and the Sahel (Gasse 2000) and the North Atlantic region (Lauritzen 1996). However, the relationships between the Holocene pollen record and abrupt climatic oscillations inferred from other proxies are far from clear. Hypothetically, high-frequency forcings may have been dampened by the inertia of the vegetation system, and sustained forcings might tend to have more significant impact on vegetation. Better understanding of these forcings in addition to new high-resolution palaeoecological records will significantly improve our ability to explain current distributional patterns and vulnerability of Mediterranean vegetation.

References

Andrade, A., Valdeolmillos, A. & Ruiz-Zapata, B. (1994) Modern pollen spectra and contemporary vegetation in the Paramera Mountain range (Ávila, Spain). *Review of Palaeobotany and Palynology*, **82**, 127–139.

Barbero, M., Bonin, G., Loisel, R. & Quèzel, P. (1990) Changes and disturbances of forest ecosystems caused by human activities in the western part of the mediterranean basin. *Vegetatio*, **87**, 151–173.

Bennett, K.D. (1990) Milankovitch cycles and their effects on species in ecological and evolutionary time. *Paleobiology*, **16**, 11–21.

Bennett, K.D. & Willis, K.J. (1995) The role of ecological factors in controlling vegetation dynamics on long temporal scales. *Giornale Botanico Italiano*, **129**, 243–254.

Burjachs, F., Giralt, S., Roca, J.R., Seret, G. & Julià, R. (1997) Palinología holocénica y desertización en el Mediterráneo occidental. *El Paisaje Mediterráneo a Través del Espacio y del Tiempo. Implicaciones en la Desertificación* (eds J.J. Ibáñez, B.L. Valero & C. Machado), pp. 379–394. Geoforma Editores, Logroño, Spain.

Carrión, J.S., Andrade, A., Bennett, K.D., Munuera, M. & Navarro, C. (2001) Crossing forest thresholds. Inertia and collapse in a Holocene sequence from south-central Spain. *The Holocene*, **11**, 635–653.

Carrión, J.S. & Dupré, M. (1997) Late quaternary vegetational history at Navarrés, eastern Spain. A two-core approach. *New Phytologist*, **134**, 177–191.

Carrión, J.S., Munuera, M., Navarro, C., Burjachs, F., Dupré, M. & Walker, M.J. (1999) The palaeoecological potential of pollen records in caves: the case of Mediterranean Spain. *Quaternary Science Reviews*, **18**, 1061–1073.

Carrión, J.S., Munuera, M., Navarro, C. & Sáez, F. (2000a) Paleoclimas e historia de la vegetación cuaternaria en España a través del análisis polínico. Viejas falacias y nuevos paradigmas. *Complutum*, **11**, 1–27.

Carrión, J.S., Navarro, C., Navarro, J. & Munuera, M. (2000b) The distribution of cluster pine (*Pinus pinaster*) in Spain as derived from palaeoecological data: relationships with phytosociological classification. *The Holocene*, **10**, 243–252.

Carrión, J.S. & 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. *Review of Palaeobotany and Palynology*, **106**, 209–236.

De la Cruz, E. (1980) *Ordenanzas Del Común de la Villa de Segura y su Tierra de 1580*. Instituto de Estudios Gienenses, Jaén, Spain.

Dupré, M. (1988) *Palinología y Paleoambiente. Nuevos Datos Españoles. Referencias*. Serie de Trabajos Varios, no. 84. Servicio de Investigación Prehistórica, Valencia, Spain.

Dupré, M. & Renault-Miskovsky, J. (1990) El hombre y su impacto en las zonas bajas mediterráneas. Datos palinológicos de sedimentos arqueológicos holocenos. *Archivo de Prehistoria Levantina*, **20**, 133–141.

Figueiral, I. (1995) Charcoal analysis and the history of *Pinus pinaster* (cluster pine) in Portugal. *Review of Palaeobotany and Palynology*, **89**, 441–454.

Franco, F., García-Antón, M. & Sainz-Ollero, H. (1998) Vegetation dynamics and human impact in the Sierra de Guadarrama, Central System, Spain. *Holocene*, **8**, 69–82.

Gasse, F. (2000) Hydrological changes in the African tropics since the Last Glacial Maximum. *Quaternary Science Reviews*, **19**, 189–211.

Grimm, E. (1992) *Tilia*, Version 1.12. Illinois State Museum, Research and Collection Center, Springfield, USA.

Janssen, C.R. (1994) Palynological indicators for the extent of the impact of man during Roman times in the western part of the Iberian Peninsula. *Evaluation of Land Surfaces Cleared from Forests in the Mediterranean Region During the Time of the Roman Empire* (ed. B. Frenzel), pp. 15–22. Gustav Fischer, Stuttgart, Germany.

Lauritzen, S.E. (1996) Calibration of speleothem stable isotope against historical records: a Holocene temperature curve for north Norway? *Climatic Change: the Karst Record* (ed. S.E. Lauritzen), pp. 78–80. Special Publication no. 2. Karst Waters Institute, Charles Town, West Virginia.

Moore, P.D., Chaloner, B. & Stott, P. (1996) *Global Environmental Change*. Blackwell Science, Oxford, UK.

Moore, P.D., Webb, J.A. & Collinson, M.E. (1991) *Pollen Analysis*, 2nd edn. Blackwell Science, Oxford, UK.

Mota, J., Valle, F. & Cabello, J. (1993) Dolomitic vegetation of South Spain. *Vegetatio*, **109**, 29–45.

Pantaleón-Cano, J. (1997) Estudi palinològic de sediments litorals de la província d'Almería. Transformacions del paisatge vegetal dins un territori semiàrid. PhD thesis, Universidad Autónoma de Barcelona, Barcelona, Spain.

Peñalba, M.C. (1994) The history of the Holocene vegetation in northern Spain from pollen analysis. *Journal of Ecology*, **82**, 815–832.

Pérez-Obiol, R. & Julià, R. (1994) Climatic change on the Iberian Peninsula recorded in a 30 000-yr pollen record from lake Banyoles. *Quaternary Research*, **41**, 91–98.

Peterson, K.L. (1998) Climate, limiting factors and environmental change in high-altitude forests of western North America. *Climatic Variability and Extremes: the Impacts on Forests* (eds M. Beniston & J.L. Innes), pp. 191–208. Springer-Verlag, Heidelberg, Germany.

Pickett, S.T.A. & White, P.S. (1985) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York, USA.

Pons, A. & Reille, M. (1988) The Holocene and upper Pleistocene pollen record from Padul (Granada, Spain). A new study. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **35**, 145–214.

Richardson, D.M. & Rundel, P.W. (1998) Ecology and biogeography of *Pinus*: an introduction. *Ecology and Biogeography of Pinus* (ed. D.M. Richardson), pp. 3–46. Cambridge University Press, Cambridge, UK.

Rivas-Martínez, S. (1990) Bioclimatic belts of west Europe (relations between bioclimate and plant ecosystems). *Folia Botanica Matritensis*, **7**, 1–22.

Rodríguez, O. (1992) Human–plant relationships during the Copper and Bronze Ages in the Baza and Guadix Basins. *Les Charbons de Bois, les Anciens Écosystemes et le Rôle de L'homme* (ed. J.L. Vernet), pp. 451–464. Bulletin de la Société botanique de France, Paris, France.

Salvador, L., Alía, R., Agúndez, D. & Gil, L. (2000) Genetic variation and migration pathways of maritime pine (*Pinus pinaster* Ait) in the Iberian Peninsula. *Theoretical and Applied Genetics*, **100**, 89–95.

Sánchez-Gómez, P., Carrión, J.S., Jordán, J. & Munuera, M. (1995) Aproximación a la historia reciente de la flora y vegetación en las Sierras de Segura Orientales. *Albasit*, **21**, 87–111.

Sánchez-Goñi, M.F. & Hannon, G.E. (1999) High-altitude vegetational pattern on the Iberian Mountain Chain (north-central Spain) during the Holocene. *Holocene*, **9**, 39–57.

Stevenson, A.C. & Harrison, R.J. (1992) Ancient forests in Spain: a model for land-use and dry forest management in south-west Spain from 4000 BC to 1900 AD. *Proceedings of the Prehistoric Society*, **58**, 227–247.

Valle, F., Gómez-Mercado, F., Mota, J.F. & Díaz de la Guardia, C. (1989) *Parque Natural de Cazorla, Segura Y Las Villas. Guía Botánico-Ecológica*. Rueda, Madrid, Spain.

Van Geel, B., Coope, G.R. & Van der Hammen, T. (1989) Palaeoecology and stratigraphy of the lateglacial type section at Usselo (The Netherlands). *Review of Palaeobotany and Palynology*, **60**, 25–129.

Vázquez, R. & Peinado, M. (1993) Relations between modern pollen rain and vegetation in the Sierra de Guadarrama (Madrid, Spain). *Ecologia Mediterranea*, **19**, 59–76.

Webb, T. III (1986) Is vegetation in equilibrium with climate? How to interpret late-Quaternary pollen data. *Vegetatio*, **67**, 75–91.

Yll, E.I., Pérez-Obiol, R., Pantaleón-Cano, J. & Roure, J.M. (1997) Palynological evidence for climatic change and human activity during the Holocene on Minorca (Balearic Islands). *Quaternary Research*, **48**, 339–347.