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Lateglacial and Holocene vegetation history at Nisi Fen and the Boras mountains, northern Greece

I.T. Lawson,[1]* S. Al-Omari,[2] P.C. Tzedakis,[3] C.L. Bryant[4] and K. Christanis[5]

([1]Department of Geography and the Environment, University of Aberdeen, St Mary's, Elphinstone Road, Aberdeen AB24 3UF, UK; [2]Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK; [3]School of Geography, University of Leeds, Leeds LS2 9JT, UK; [4]NERC Radiocarbon Laboratory, Scottish Enterprise Technology Park, Rankine Avenue, East Kilbride G75 0QF, UK; [5]Department of Geology, University of Patras, GR-26110 Rio-Patras, Greece)

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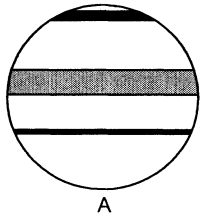

Abstract: New pollen data from three contrasting sites in northern Greece allow an analysis of spatial and temporal patterns of vegetation change during the Holocene and Lateglacial in northern Greece. At the principal site, Nisi Fen, six cores from the thickest surficial peat deposits have yielded a detailed, composite, AMS ^{14}C-dated pollen record covering the period from 20 000 cal. BP almost to the present-day. Cores Kp-4 and Bor-3 were taken from small mires at high elevations in the Boras mountains, a few kilometres to the north of Nisi, in which peat has been accumulating since the mid-Holocene. Our results show that only *Pinus* expanded significantly during the Lateglacial Interstadial, although small thermophilous tree populations were present in the region. The Younger Dryas chronozone is at best marked by subtle vegetational change in favour of steppe taxa. Tree cover increased rapidly at the beginning of the Holocene, with deciduous woodland probably expanding above its present-day altitudinal limits. There is evidence for drier and/or warmer summers, and mild winters, between c. 10 500 and 7500 cal. BP, although the vegetation was not as markedly sclerophyllous as at many sites elsewhere in Greece. The mid-Holocene saw a reorganization of the woodland, with first *Abies* and then *Fagus* becoming important at high altitudes, and an increase in the diversity of deciduous woodland at medium elevations. The suggestion of human impact in the form of a decline in woodland and the appearance of crops in the pollen record can be found at all altitudes in the later Holocene.

Key words: Pollen, Greece, human impact, Lateglacial, Holocene, vegetation history.

Introduction

The Balkan peninsula has some unique characteristics that make it appealing for palaeoenvironmental research: it is known to have been a glacial refugial area for temperate tree taxa (Bennett *et al.*, 1991; Tzedakis, 1993, Tzedakis *et al.*, 2002); it is a biodiversity 'hotspot' (Blondel and Aronson, 1999); and it was probably the first part of mainland Europe to see the adoption of farming technologies (Bailey, 2000; Tringham, 2000). On the whole, however, few parts of the Balkans have been studied in detail in this regard. One exceptional area is central northern Greece (Figure 1), where a relatively dense network of Holocene and Lateglacial pollen sites has been built up since the 1970s (Bottema, 1974, 1982; Gerasimidis and Athanasiadis, 1995; Athanasiadis *et al.*, 2000). Here we have a rare opportunity to study vegetation changes, both in time and space, at many locations within a mountainous region. This paper makes a significant contribution to the body of knowledge in the form of three AMS-dated pollen sequences from contrasting sites, Nisi, Boras, and Kali Pediada, one of which (Nisi) extends through most of the Holocene and Lateglacial. Analysis of the new and existing data permits

*Author for correspondence (e-mail: ian.lawson@abdn.ac.uk) Address from August 2005: School of Geography, University of Leeds, Leeds LS2 9JT, UK.

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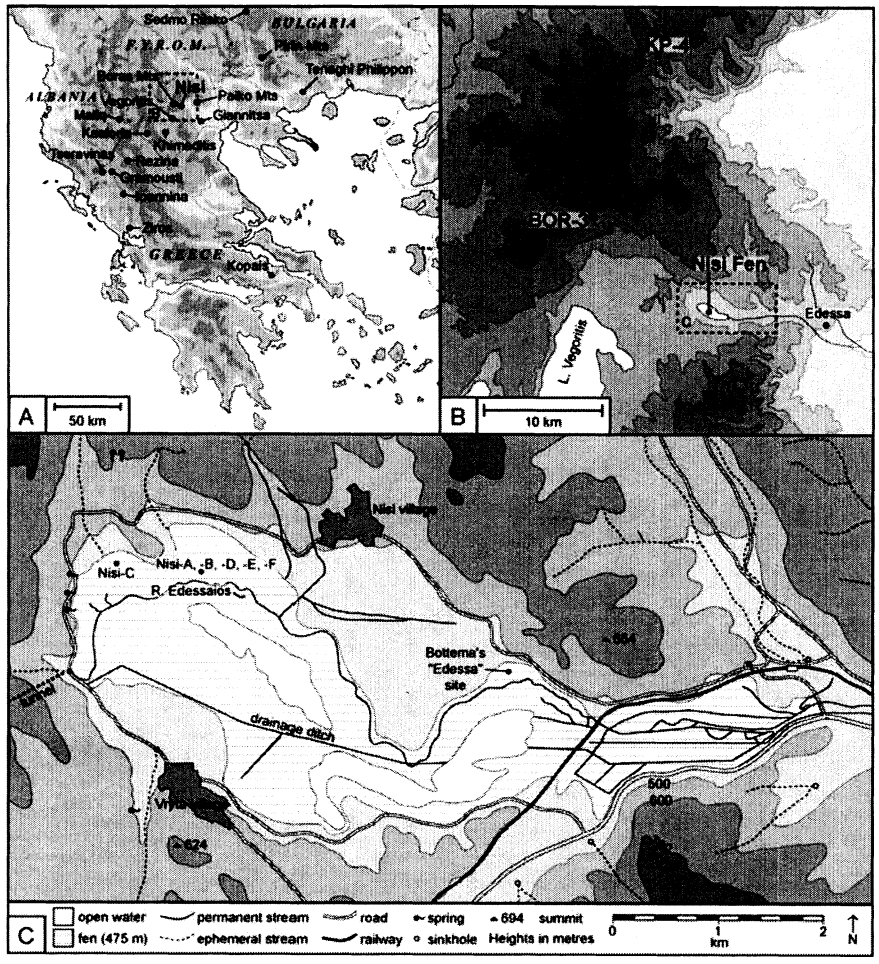

Figure 1 (A) The southern Balkan Peninsula, showing sites mentioned in the text. (B) The topography of the area around Nisi (21°55′E, 40°49′N) and the Boras sites, Kp-4 (41°02′N, 21°53′E) and Bor-3 (40°54′N, 21°47′E). The Boras massif peaks at 2524 m a.s.l.; south of Nisi the Vermion mountains reach 2052 m, while the plain of Pella lies to the northeast. (C) Nisi Fen, showing the relative locations of the different cores reported in this paper. The approximate location of Bottema's 'Edessa' core (Bottema, 1974) is also shown. The artificial tunnel at the western end of the basin, which connects Nisi to Lake Vegoritis, and the numerous drainage ditches, allow control of the hydrology of the basin, which feeds a hydroelectric power station downstream

comparison of the situation in northern Greece with elsewhere in the southern Balkans where suitable data exist.

Study area

Northern Greece experiences a climate that is intermediate between the Mediterranean regime, with high summer temperatures and low summer precipitation, and the continental climate that dominates the interior of the Balkans, with strong seasonal temperature contrasts and a summer precipitation maximum (Furlan, 1977). A precipitation gradient lies across northern Greece, with highest rainfall in the west and lowest in the east. The mountainous nature of the terrain means that climatic conditions also vary with altitude, precipitation increasing and temperatures decreasing upwards. These climatic factors largely determine the regional vegetation, which contains many Mediterranean elements such as *Olea* and *Pistacia* in the lowlands but grades into deciduous woodland at relatively low altitudes compared with other parts of Greece.

Nisi Fen occupies a 12 km^2 basin, formed through a combination of tectonic subsidence and karstic erosion (Christanis, 1994), 10 km west of Edessa in northern Greece (Figure 1). The basin contains at least 80 m of mostly limnic sediments, with fen peat capping the deposits in most places. The floor of the basin lies at 475 m a.s.l., with the immediate surrounding hills up to 1000 m a.s.l. on all sides except the east. Further to the south lie the Vermion mountains, peaking at 2052 m a.s.l., while to the north along the frontier with the Former Yugoslavian Republic of Macedonia are the Boras mountains, which reach 2521 m at Kaimaktsalan. The hydrology of the fen is essentially controlled by groundwater, albeit with human interference; the Edessaios river rises from an underground source in the fen and flows to the east through the basin. Although there are some substantial areas of open water, Nisi fen itself is mostly vegetated with a mosaic of *Cladium*, *Phragmites* and *Carex*-dominated communities.

The modern vegetation, especially in the lowlands, shows strong signs of modification by human activity. On the coastal plains and on flat land up to about 500 m a.s.l., agriculture dominates. Cattle graze the fen itself, while steeper slopes are grazed by goats, resulting in a semi-natural scrub-like maquis in which drought-tolerant and grazing-resistant taxa, such as the evergreen *Quercus coccifera*, dominate. Higher up the mountains the vegetation is arranged in altitudinal zones reflecting temperature and moisture gradients. The maquis gives way to mixed deciduous woodland, with *Carpinus orientalis* and *Ostrya carpinifolia* abundant at lower altitudes, and deciduous species of *Quercus* (mainly *Q. pubescens*, *Q. cerris* and *Q. frainetto*), sometimes with abundant *Castanea* and *Tilia tomentosa*, dominating from *c.* 550 to 750–950 m. The next zone, extending to *c.* 1500–1650 m, consists of *Fagus* woodland, sometimes with *Abies* as an important constituent. Above this, *Pinus sylvestris* forms fairly pure but quite open

woodland. Above *c.* 2000 m trees become stunted and scattered, co-occurring with shrubs such as *Juniperus nana*, within a herbaceous matrix. Finally, above *c.* 2300 m, woody species disappear and an alpine tundra ecosystem occurs.

Bottema (1974) published a pollen diagram from a 7.25 m core, which reached bedrock, from the eastern end of the Nisi basin close to the margin of the fen (Figure 1). The base of this sequence, which Bottema named 'Edessa', was dated by ^{14}C to the Holocene/Lateglacial boundary.

The two sites in the Boras mountains presented here were identified and cored as part of a geological survey of montane peatlands (Al-Omari, 1999; Christanis *et al.*, 1999). KP-4 is a core taken from a mire at Kali Pediada (Figure 1) on a plateau at approximately 1725 m a.s.l. Bor-3 is a core from a small mire at 2080 m a.s.l. Both sites are acid mesotrophic mires, their hydrological budget including some groundwater as well as precipitation. Vegetation at both sites is dominated by Cyperaceae, especially *Carex echinata*, *C. pallescens*, and *Eriophorum angustifolium*, with Gramineae and *Sphagnum* co-dominant and small stands of *Pinus sylvestris* close by (Christanis *et al.*, 1999).

Materials and methods

Sampling

Five cores, designated Nisi-A, -B, -D, -E and -F, were taken from Nisi Fen in a location known through a previous study (Christanis, 1994) to hold the thickest sequence of surface peat (Figure 1); a sixth core, Nisi-C, was taken closer to the fen margin. All were taken using a modified Livingstone piston corer except Nisi-D, which was taken using an Edelman peat sampler. The longest sequence, Nisi-E, reached 15.63 m below the surface of the fen. Kp-4 and Bor-3 were taken using a Russian-type corer.

Pollen analysis

Pollen preparation followed standard procedures (Bennett and Willis, 2001): 0.5 cm^3 samples were treated with dilute HCl, dilute NaOH, concentrated HF and acetolysed. An exotic spike was added to each sample in the form of tablets of *Lycopodium* spores (Stockmarr, 1971, 1973). Taxonomic nomenclature follows *Flora Europaea* (Tutin, 1964–80).

The main pollen data set from Nisi presented here (see below) is a composite of analyses undertaken on two cores, Nisi-B and Nisi-E, extracted within a few metres of each other. A minimum of 300 terrestrial grains were counted from each sample, following the recommendations of Maher (1972) and Rull (1987), with the exception of one sample from Nisi-B (5.24 m, 270 grains) and some samples from Bor-3 where pollen concentrations were extremely low.

Sediment description and loss-on-ignition

Sediment description was based on the Troels-Smith system (Troels-Smith, 1955), as adapted by Aaby and Berglund (1986).

Loss-on-ignition was undertaken to provide information on the composition of the sediments and, at Nisi, to permit correlations between sequences. Analysis followed the procedure of Bengtsson and Enell (1986), and included mass readings after heating at 550°C for 6 h, and (Nisi only) at 950°C for 6 h, in order to estimate organic content and carbonate content, respectively.

Radiocarbon dating

Dating was concentrated on the Lateglacial and early Holocene portion of the Nisi record. Five AMS radiocarbon dates from Nisi-B, and one from Nisi-E (Table 1 and Figure 2), were obtained from seeds of *Cladium mariscus*, which were reasonably abundant in some parts of the cores. A second radiocarbon determination was made on macroscopic charcoal fragments from Nisi-E. Each sample was passed through a 250 μm brass sieve using deionized water. Seeds and charcoal were picked by hand under a low-power stereoscopic microscope using metal implements, and were physically cleaned of matrix material as completely as possible. The samples were transferred to glass vials, dried, and their mass was determined before sending to the radiocarbon laboratory for analysis. The samples were further washed using acid–alkali–acid methods before ^{14}C analysis. Consequently they should be free of fulvic and/or humic acid contamination and the terrestrial nature of the samples should mean that they do not suffer from any hard water effect. In addition, two conventional bulk sediment radiocarbon dates from each of Kp-4 and Bor-3 were obtained with analyses performed at the Centre for Isotope Research, Groningen, Netherlands. All dates were calibrated using OxCal (Bronk Ramsey, 1995, 2001) and the INTCAL98 calibration dataset (Stuiver *et al.*, 1998) with 2σ confidence intervals.

Results

Nisi

Sedimentology

Figure 3 shows the sediment composition of Nisi-A, -B, -E and part of Nisi-F. The sediment descriptions for these sequences show broad similarities. Given that these four sequences were all taken from within a few metres of the same spot, the slight differences in their stratigraphies are presumably a reflection of

Table 1 Radiocarbon dates from sequences reported in this paper

Reporting code	Core	Level (m)	Material[a]	Age (^{14}C BP, 1σ)	δ^{13}C (‰)	Calibrated age range (cal. BP, 2σ)
CAMS-59467	Nisi-B	8.10	*Clad.*	6060±40	−27.9	6750–7010
CAMS-59468	Nisi-B	9.20	*Clad.*	4200±40	−26.6	4570–4850
CAMS-59469	Nisi-B	10.50	*Clad.*	9030±40	−27.0	9920–10250
CAMS-59470	Nisi-B	11.10	*Clad.*	5850±40	−27.0	6540–6760
CAMS-59471	Nisi-B	11.70	*Clad.*	9310±50	−26.8	10280–10680
Beta-147751	Nisi-E	10.91	*Clad.*	9560±70	−25.0	10600–11200
Beta-147752	Nisi-E	12.75	Charcoal	11910±70	−23.9	13550–15250
GrN-23594	Bor-3	0.41–0.44	Bulk	420±110	n/a	150–650
GrN-23595	Bor-3	1.04–1.07	Bulk	3770±80	n/a	3920–4410
GrN-23596	Kp-4	0.41–0.46	Bulk	820±120	n/a	550–960
GrN-23597	Kp-4	1.18–1.24	Bulk	5610±160	n/a	5950–6750

[a] *Clad.*, *Cladium mariscus* seeds.

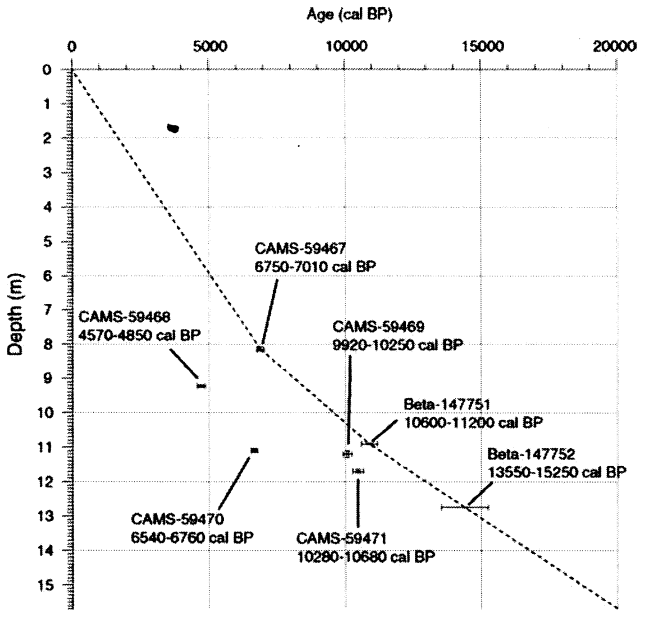

Figure 2 Radiocarbon dates and age model for the composite Nisi-B/E sequence

relatively subtle hydrological or vegetational variations. Below *c.* 12.5 m the sediments are dominated by limnic marls. The upper *c.* 12.5 m of the sediments vary between poorly humified fen peats, fine-grained organic muds, and marls. Mollusc shells (both whole and fragmented), ostracods and fine-grained calcareous material tend to occur together, and are common from *c.* 6 to *c.* 12 m, and again from *c.* 1.5 to *c.* 3.0 m. Lithological boundaries are gradational rather than abrupt throughout.

The loss-on-ignition data for five cores are presented in Figure 4. Nisi-C, which was taken near the edge of the fen, shows quite strong dissimilarity to the other cores, with a generally higher organic content and less carbonate. The data from the other sequences, all taken close to one other, reflect the basic division of organic-rich sediments in the upper ~12.5 m of the sediment sequence, and marls below. The pattern of fluctuations in loss-on-ignition parameters is broadly similar in the various cores, although minor differences occur in the stratigraphic position of fluctuations and the absolute values of the different parameters.

Correlation of the sequences

Synthesis of the pollen data from the five cores analysed from Nisi is based primarily on lithostratigraphic correlation of the sequences (Figure 4). However, because of the possibility of diachroneity in lithological boundaries, the correlation has been tested and adjusted using the pollen data, the regional component of which should be less prone to diachroneity (Lawson, 2001). During this correlation exercise two small blocks of material (9.20–9.30 m and 10.90–11.10 m) were identified from Nisi-B as probably representing contamination, as the sedimentological and palynological data from these blocks did not correspond with equivalent data from the other cores. In the pollen diagrams presented here these suspect data are excluded. The data are plotted on a common 'depth' scale based on these correlations.

Age model

Construction of an age model for Nisi is complicated by two substantially out-of-sequence AMS dates (CAMS-59468 and CAMS-59470). These dates were derived from the two sections of the Nisi-B sequence previously identified by the pollen stratigraphy as representing contamination, confirming the extraneous nature of the material, and were not used in the construction of the age model. The age model shown in Figure 2 is based on linear interpolation between three of the radiocarbon dates. Between 10 and 12 m depth in the combined sequence are three remaining dates that are broadly in agreement, two from Nisi-B and one from Nisi-E. However, given the possibility of contamination of the lower part of Nisi-B, only the date from Nisi-E is used in the interpolation. Biostratigraphic correlation suggests that the age model is in

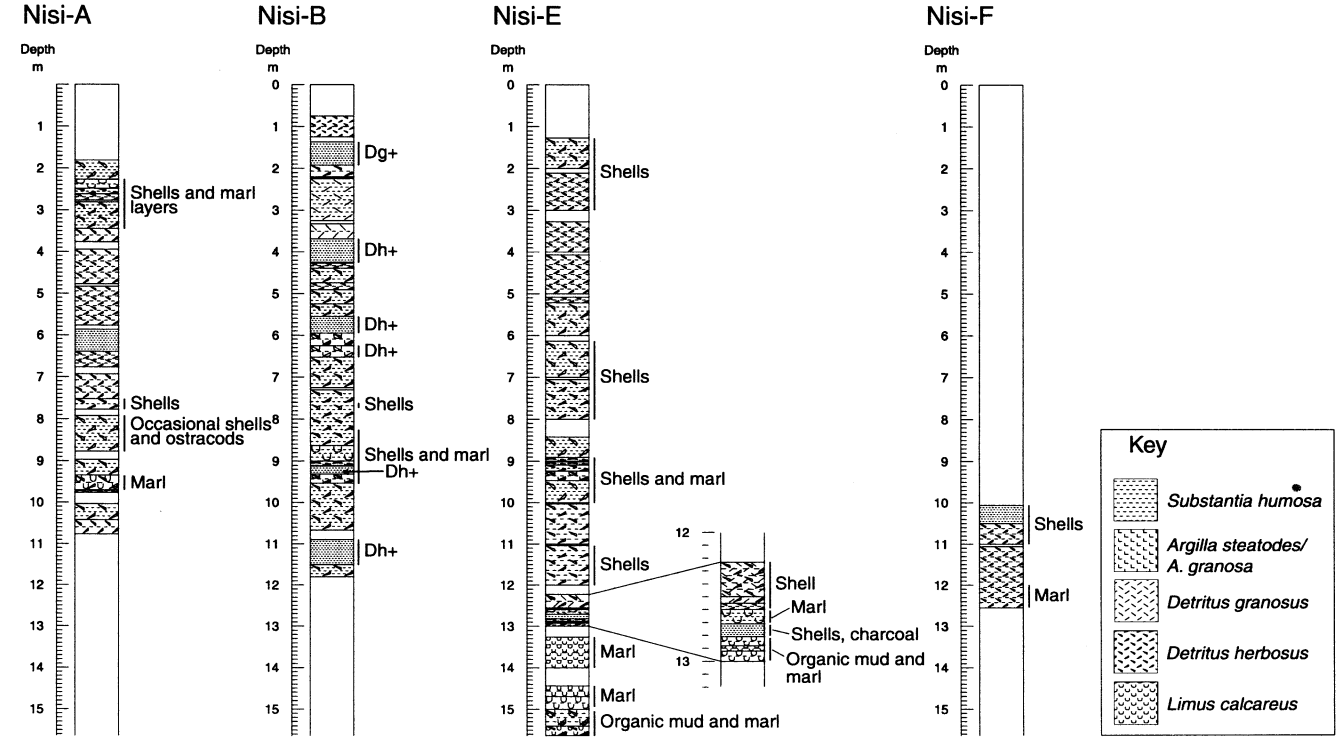

Figure 3 Sediment properties of the Nisi sequences; symbols follow Troels-Smith (1955) and Aaby and Berglund (1986)

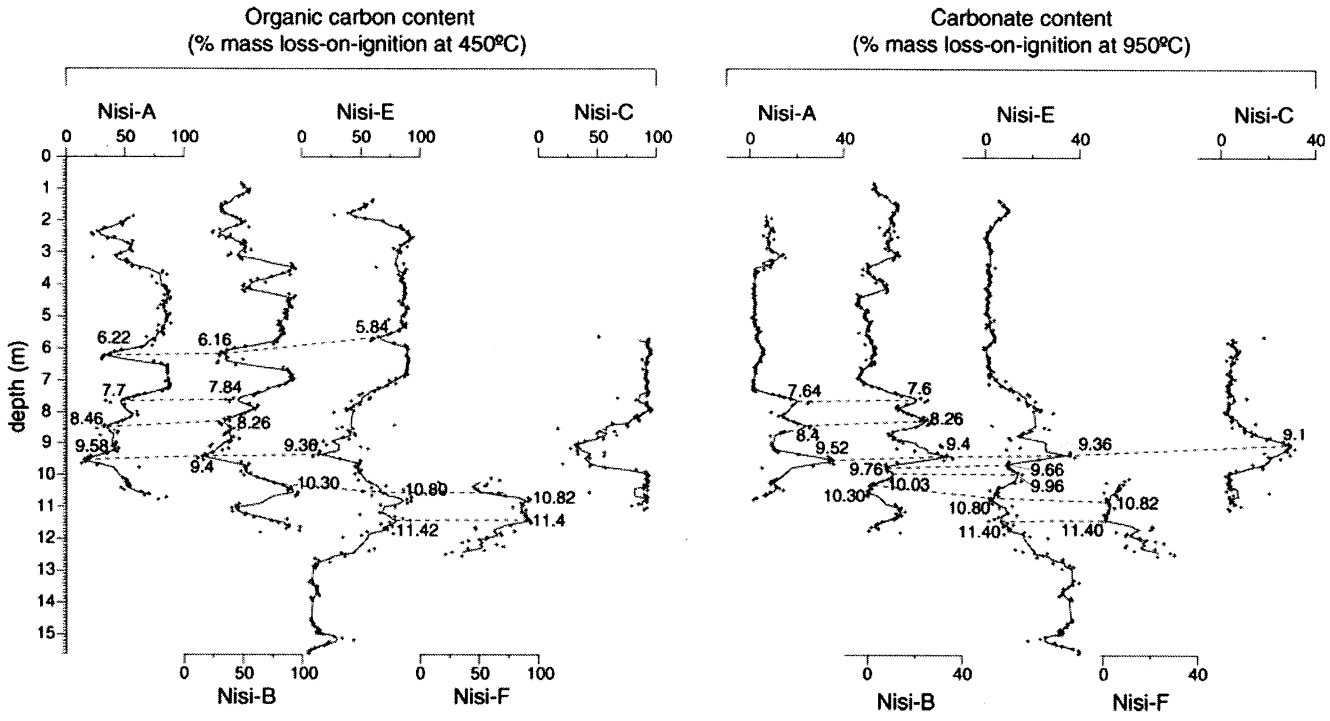

Figure 4 Loss-on-ignition data for Nisi-A, -B, -C, -E and -F, showing tiepoints used to correlate the sequences (including those based on pollen data). Total organic carbon (mass loss between 105°C and 550°C), carbonate (mass loss between 550°C and 950°C) and residue (residue after 950°C, approximately equivalent to the silicate content of the sediment) are presented as % dry weight

broad agreement with that of the Edessa sequence (Bottema, 1974; Lawson, 2001). The age scales shown in the pollen diagrams should be considered approximate, especially where dates are lacking.

The age models for Kp-4 and Bor-3 are based on linear interpolation between the two dates from each sequence, with the top of each sequence defined as 0 cal BP.

Pollen data

Composite pollen diagrams based on data from Nisi-B and -E are presented in Figures 5 and 6. The pollen data were divided into seven zones following a comparison of the results of several different quantitative zonation techniques (Lawson, 2001). *Ostrya*-type includes *Ostrya carpinifolia* and *Carpinus orientalis*.

There is a basic division in the composite data set between relatively low-AP assemblages below *c.* 12 m, and high-AP assemblages above. In the low-AP phase tree pollen oscillates around *c.* 10%, with very high values of *Artemisia*, Chenopodiaceae and Gramineae. The high-AP phase is dominated throughout by deciduous *Quercus* and *Pinus*, with moderate values of *Juniperus*; *Ostrya*-type and *Carpinus betulus* expand at the base of zone N-4, while *Fagus* expands towards the top of zone N-4, and *Platanus* and *Juglans* become important towards the top of the diagram in zones N-6 and N-7. All parts of the sequences exhibit fluctuations in Cyperaceae, monolete spores and aquatic taxa (all of which are outside the pollen sum), and to a lesser extent Gramineae.

Kali Pediada Kp-4

Sedimentology

The stratigraphic, loss-on-ignition and pollen data for Kp-4 are shown in Figure 7 together with the radiocarbon dates. The sediments consist of organic silts and clays below *c.* 0.6 m with well-humified peat, containing both herbaceous and bryophitic material, in the uppermost layers.

Pollen data

Tree taxa dominate the pollen assemblages from Kp-4. In the two lowermost samples, values of *Ostrya*-type, *Corylus*-type and *Betula* are relatively abundant. Above 1.2 m depth the first two of these taxa decline in favour of *Fagus*, *Pinus* and *Abies*. *Betula* values decrease suddenly above 0.6 m, together with a more subtle decline in *Carpinus betulus*, while *Abies* values are low from 0.4 m to the top of the sequence. Gramineae and Cyperaceae dominate the main sum herbs through the whole sequence, although a number of other herbs, notably Compositae, Caryophyllaceae, *Plantago* and Ranunculaceae, are important in the top 0.4 m. Outside the main sum, Pteropsida (fern) spores attain high values in the lowermost samples, declining rapidly as the silicate content of the sediment decreases.

Boras Bor-3

Sedimentology

The data for Bor-3 are shown in Figure 7. The sediments consist of silts and clays with mica flakes below *c.* 0.5 m, with well-humified herbaceous and bryophitic peat above.

Pollen data

AP values in the lowermost five samples from Bor-3 are similar to those from Kp-4, averaging around 50%, with a range of tree taxa including *Pinus*, *Betula*, *Abies*, *Ostrya*-type, and deciduous *Quercus*. However, AP declines to 30–40% above *c.* 0.7 m, with *Betula*, *Abies* and *Ostrya*-type the main taxa to decline. Gramineae and Cyperaceae are the dominant herbs, although Compositae, Caryophyllaceae and *Plantago* are also important, the latter two especially above the decline in AP at *c.* 0.7 m. As at Kp-4, spores are most abundant towards the base of the sequence, although values are generally lower.

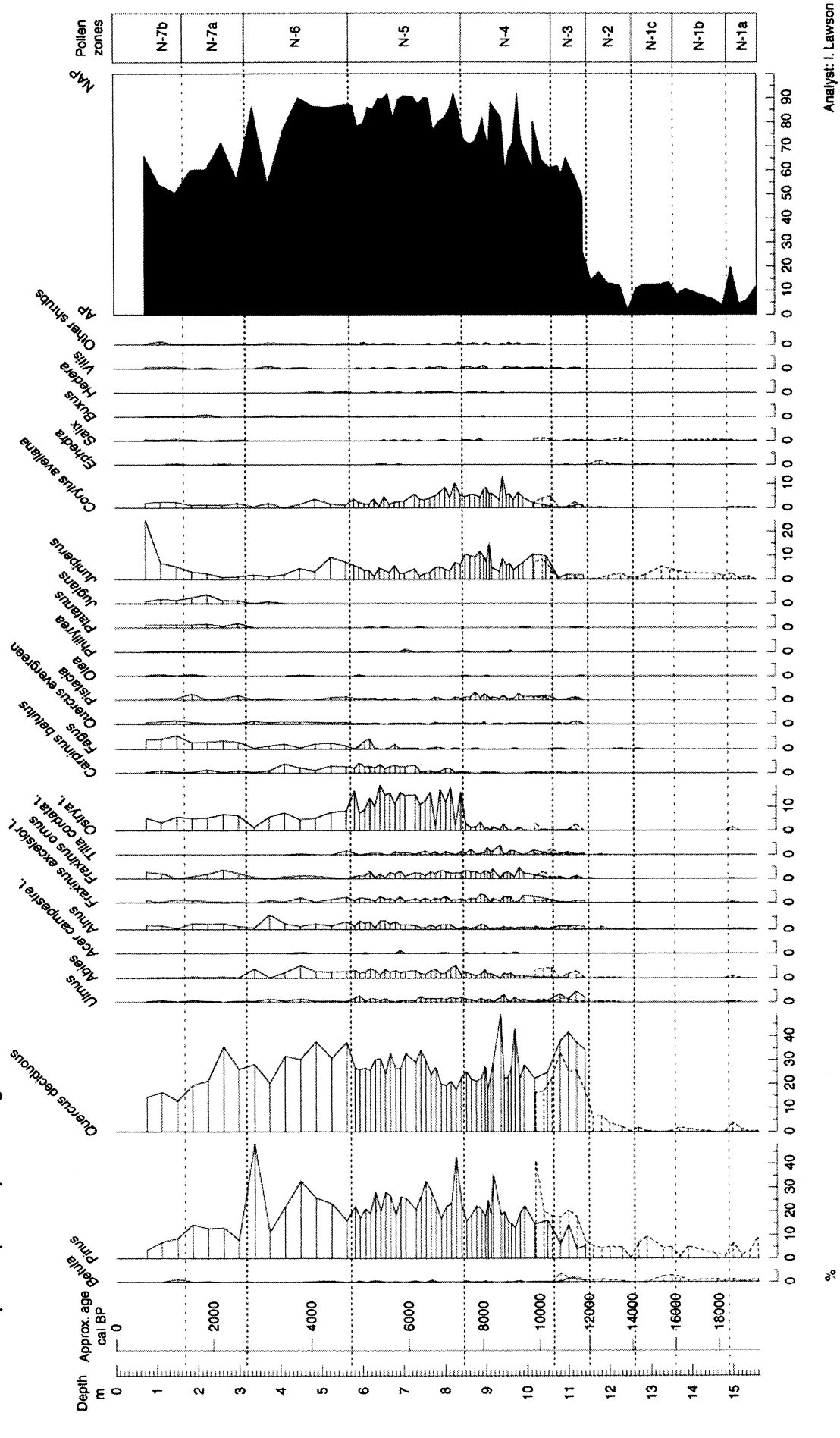

Figure 5 (*Continued*)

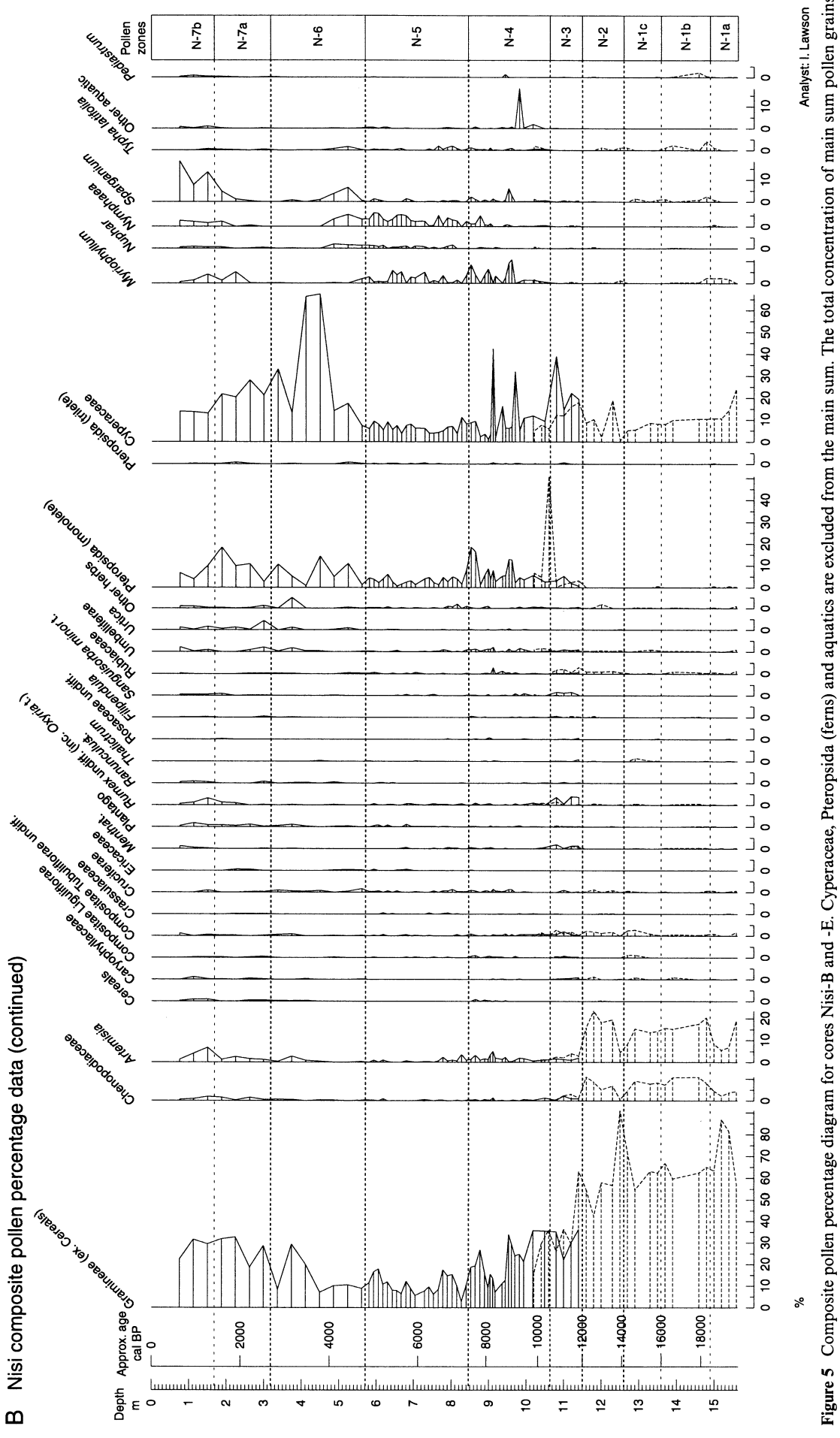

Figure 5 Composite pollen percentage diagram for cores Nisi-B and -E. Cyperaceae, Pteropsida (ferns) and aquatics are excluded from the main sum. The total concentration of main sum pollen grains is also shown. In all diagrams presented in this paper, '*Ostrya*-type' includes pollen of both *Ostrya carpinifolia* and *Carpinus orientalis*

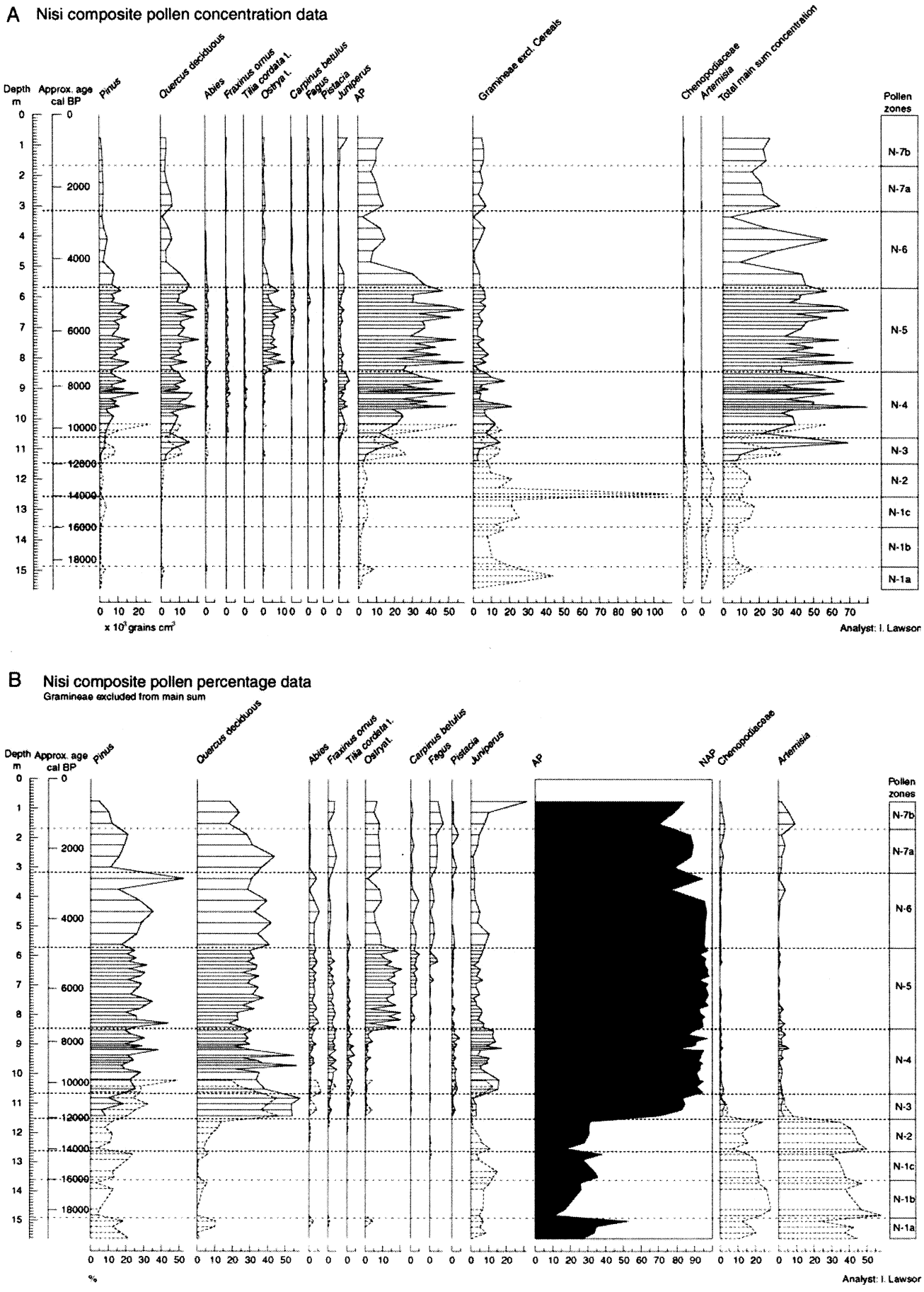

Figure 6 (A) Summary pollen concentration data from Nisi-B and -E. (B) Summary pollen percentage data from Nisi-B and -E, with Gramineae excluded from the sum. The presence of *Phragmites* growing on the fen surface means that the inclusion of Gramineae within the main sum may give a false impression of the importance of this taxon within the regional vegetation (see discussion in the text)

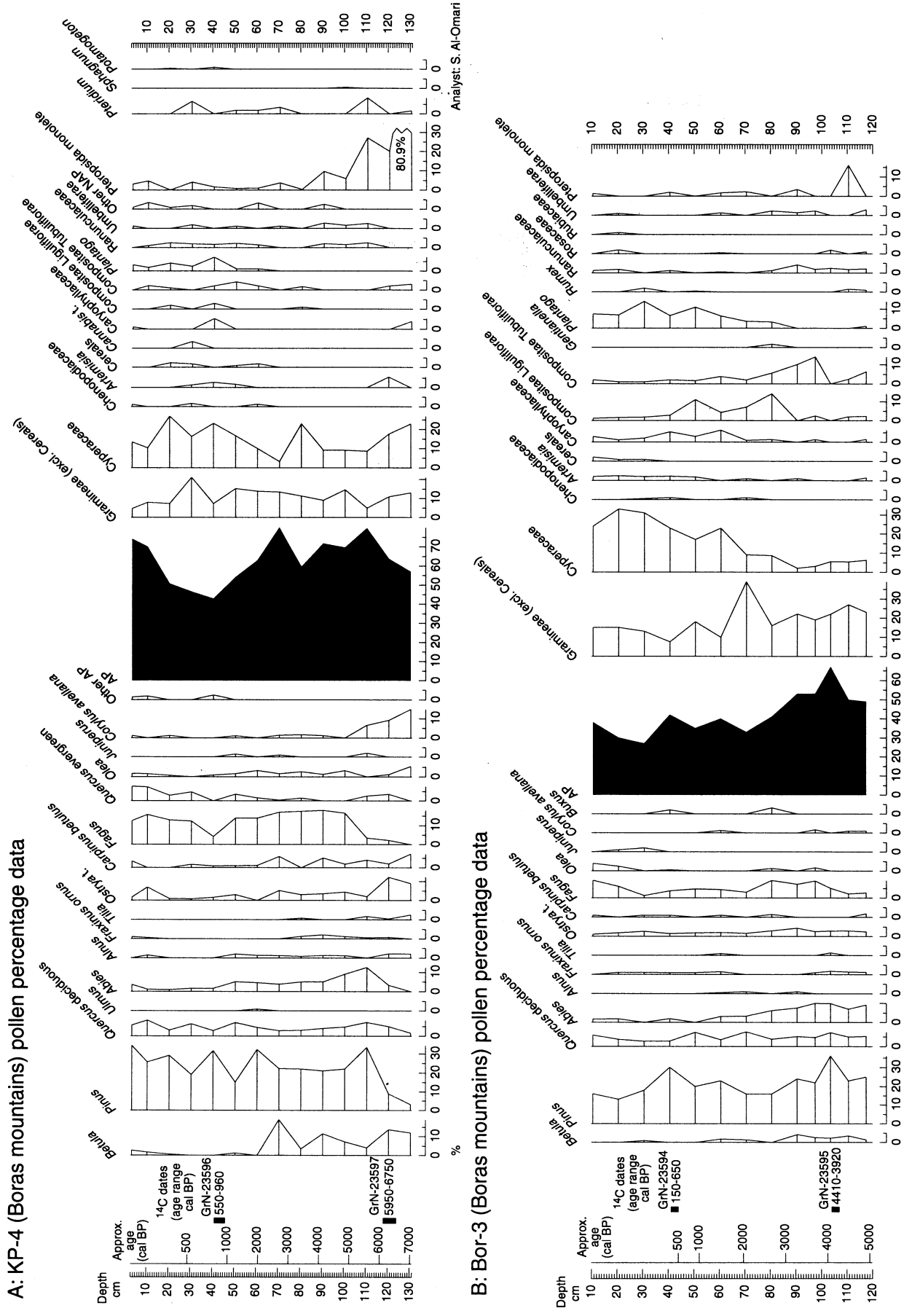

Figure 7 Palynological data from (A) Kp-4 and (B) Bor-3. Pollen data are shown as percentages with Gramineae and Cyperaceae included in the main sum.

Discussion

The following discussion focuses mainly on the data from Nisi, taking into account the results from Kp-4 and Bor-3, as well as other sites in the region, as appropriate.

Palynological variations between cores

One of the most notable features of the composite pollen percentage diagram from Nisi-B and -E (Figure 5) is that, although the patterns of the taxa in the two cores are very similar in the area of overlap, the absolute values of some taxa differ consistently. Variations in the percentage abundance of pollen types such as Cyperaceae, Pteropsida and Gramineae (the latter probably largely constituting *Phragmites*) are presumably a reflection of the dynamic metre-scale vegetation mosaic that exists on the fen surface today and that can reasonably be assumed to have occurred in the past. Of the upland taxa – those absent from the fen itself – *Pinus* and deciduous *Quercus* show the greatest absolute differences. In order to assess the between-core variation in the pollen data, limited counts were made of a number of samples from cores Nisi-A, -C and -D. Figure 8 shows that there is a high degree of correspondence between the stratigraphic patterns from one core to the next, although absolute values differ; for example, *Pinus* values are generally higher in Nisi-E than in the other cores over the overlapping section.

Sedimentological work at Nisi, and observations of the patterns of change of aquatic and fen taxa in the pollen records, strongly suggest that the shallow water environments of the Nisi basin were not stable over time or space; small changes in groundwater level, the processes of infilling and terrestrialization, and/or varying subsidence rate in different parts of the basin are probably responsible for the observed facies changes. This shifting patchwork of sedimentary facies might account for the observed differences in the pollen record of upland taxa if the taphonomy of this pollen differs between facies. The pollen rain from the uplands is expected to be well mixed during atmospheric or fluvial transport to the fen (Tauber, 1965; Davis, 2000). Processes that might differentially filter the upland pollen rain as the pollen becomes incorporated in the sediment include the winnowing of buoyant *Pinus* pollen by wind and wave action on patches of open water (Davis *et al.*, 1971; Davis and Brubaker, 1973); differential subaquatic resuspension of different pollen taxa (Davis, 1968); and differential preservation under variably anoxic conditions (cf. Cushing, 1967).

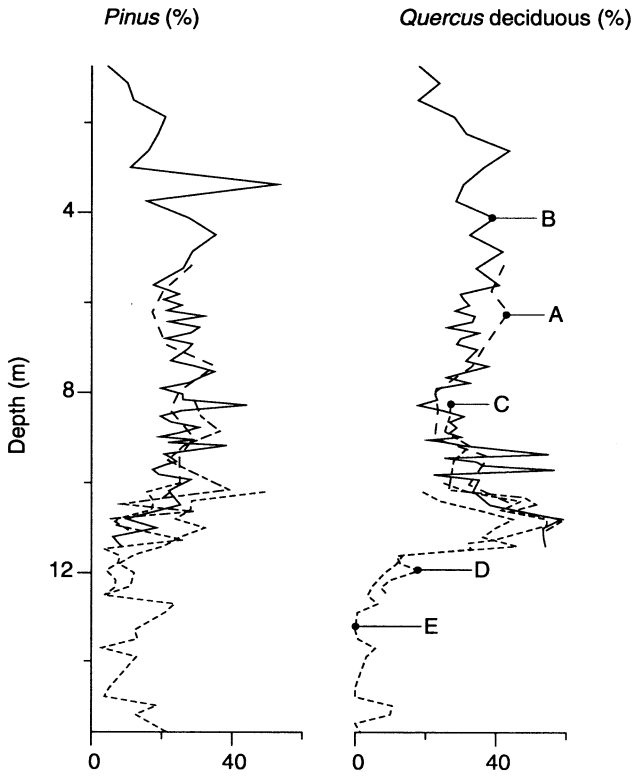

Figure 8 Comparison of *Pinus* and deciduous *Quercus* pollen percentages from five Nisi cores. In this diagram Gramineae are excluded from the pollen sum. Counts from Nisi-A, -C and -D are to *c.* 100 terrestrial grains per sample

These observations raise the possibility that variation in sediment facies at a single core site over time might cause variation in upland pollen taphonomy, leading to stratigraphic changes in the pollen record that reflect local, hydrological change, rather than change in the regional vegetation. This is an issue that potentially affects almost every pollen record, not just Nisi. However, in this case, comparison of the composite pollen diagram (Figure 5) with the lithological columns for Nisi-B and -E (Figure 3) shows that major changes in non-local, non-aquatic taxa do not, as a rule, occur in concert with major lithological changes (e.g., from peats to marls). This suggests that stratigraphic changes in the upland taxa in the pollen data from Nisi do primarily reflect real vegetation changes, not facies changes.

The further significance of this is that sequences from shallow lake environments, particularly in Greece where hydrological budgets are usually finely balanced and lake levels can vary significantly from season to season and from year to year, so causing rapid facies shifts, are likely to be 'noisy' compared with pollen sequences from deeper, larger, more sedimentologically stable lakes. This is especially true for taxa such as Gramineae and Cyperaceae, which are often included in the pollen sum, despite the fact that both families include semi-aquatic species. (Figure 6B shows the effect of excluding Gramineae from the pollen sum at Nisi; the result is substantially smoother curves for upland taxa, which are likely to be more representative of the pattern of regional vegetation change.)

The multicore work at Nisi therefore suggests that the substantial variations in pollen data, especially where influenced by the local presence of *Phragmites*, from other sites in northern Greece such as Khimaditis, Giannitsa and Edessa (Figure 1; Bottema, 1974) are likely to be taphonomic artefacts of the depositional setting. This conclusion may also apply to the upland mire sites (cf. Bunting, 2003). At Kastoria and, especially, Vegoritis (Figure 1; Bottema, 1974, 1982), both of which are somewhat deeper lakes, the problem should be less acute, and indeed the pollen data from these sites plot to give much smoother curves.

Lateglacial (zones N-1 and N-2; *c.* 20 000–12 000 cal. BP)

During the part of the last glacial represented in the Nisi sequence the pollen data suggest an open, lightly wooded landscape. AP percentages are low at around 5–15%. Tree populations were dominated by *Betula*, *Pinus* and *Juniperus* with varying amounts of deciduous *Quercus* during the period recorded by zone N-1 leading to a more sustained expansion during N-2. Fluctuations in the abundance of tree pollen in the sequence are possibly due to rapid changes in climatic conditions; similar patterns are seen at the nearby site of Khimaditis (Bottema, 1974). Single-sample increases in the pollen percentages of some other temperate trees, particularly *Ostrya*-type and *Fraxinus ornus*, suggest that these trees may

have been present in the region in sufficient abundance to appear in the pollen record during particularly favourable periods; again, similar features appear in the Khimaditis data.

Most of the main-sum NAP consists of *Artemisia* and Chenopodiaceae, indicating a steppic environment in which Gramineae were almost certainly also important. However, much of the fluctuation in Gramineae abundance is likely to be attributable to *Phragmites* populations growing on the fen. The basin seems to have undergone substantial hydrological changes. Sediments vary from marls to organic muds; changes in the sedimentary environment are to some extent reflected in changes in aquatic taxa such as *Nymphaea* and *Myriophyllum*. Although in some cases (e.g., subzone N-1a) it appears that AP broadly follows changes in the organic content of the sediment, comparison of the loss-on-ignition data from the various Nisi cores shows that sedimentological conditions were rarely uniform across the sites, suggesting that climatically forced hydrological changes may not be expressed straightforwardly in any single core.

In short, the data from Nisi, like Bottema's work from Khimaditis, indicate the presence of fluctuating populations of *Quercus*, *Pinus*, *Juniperus* and *Betula* during the last part of the glacial, with woodland always subordinate to open, steppe communities. Sporadic presence suggests that temperate trees (*Ostrya carpinifolia/Carpinus orientalis* and *Fraxinus ornus*) were present at times during or possibly throughout the interval. Pollen diversity (Odgaard, 1999) was low compared with the Holocene, or even in comparison with Lateglacial western Greece (Lawson, 2001; Lawson *et al.*, 2004), suggesting a relatively uniform vegetation.

In most pollen diagrams from Europe we see an expansion of temperate taxa during the Lateglacial Interstadial (Bølling/Allerød chronozone; Mangerud *et al.*, 1974), followed by a contraction of these taxa during the Lateglacial Stadial (Younger Dryas chronozone). Such a pattern is clearly visible in many pollen diagrams from Iberia (e.g., Peñalba *et al.*, 1997), southern France (e.g., Reille and Lowe, 1993) and Italy (e.g., Allen *et al.*, 2000), where it is usually expressed as an expansion and contraction of deciduous *Quercus* and/or *Pinus*. This basic pattern is also seen very clearly in three separate diagrams from the Kopais basin of south-central Greece (Allen, 1990; Tzedakis, 1999; Okuda *et al.*, 1999), at sites in the mountains of southwest Bulgaria, where *Pinus* and *Betula* are more important than deciduous *Quercus* (e.g., Bozilova and Tonkov, 2000; Tonkov, 2001; Tonkov *et al.*, 2002; Stefanova and Ammann, 2003) and in Romania (Björkman *et al.*, 2002, 2003). This pattern is thought to be a reflection of climatic change, from cold and/or dry conditions in the full glacial, to warm and/or wet conditions during the Lateglacial Interstadial, back to cold/dry conditions during the Lateglacial Stadial, and finally to warm/wet interglacial conditions at the beginning of the Holocene.

However, this pattern of vegetational change is not so clear in the pollen record from Nisi, where deciduous *Quercus* shows no expansion during the Lateglacial (zone N-1c) and *Pinus* expands only slightly, then contracts in zone N-2, when *Artemisia* and Chenopodiaceae expand. Data from the nearby site of Khimaditis (Bottema 1974), albeit at low resolution, show a similar response; Tenaghi Philippon in northeast Greece (Wjimstra, 1969; Rossignol-Strick, 1995) and Maliq in Albania (Denèfle *et al.*, 2000) are also similar. (Sites in western Greece are considerably different from this, and from each other; Lawson *et al.*, 2004).

The likely explanation for the observed patterns of Lateglacial vegetation change is that the variations between sites are not due to differences in the trajectory or magnitude of climatic change at each site, but to spatial and altitudinal variation in climatic factors at any given time in the past. Present-day climatic trends are towards lower average temperatures in the north than in the south, and for temperatures to decrease with increasing altitude, while precipitation is markedly higher in western Greece than in the east, and tends to increase with altitude. It seems likely that broadly similar geographical and altitudinal patterns would have occurred during the Lateglacial. Lateglacial vegetation communities therefore would be more likely to be dominated by *Quercus* in the south and/or at low altitudes (e.g., Kopais and Tseravinas), and by *Pinus* in the north and/or at higher altitudes (e.g., Nisi, Khimaditis and Tenaghi Philippon). In general, the pollen data from Lateglacial sites across the southern Balkans reflect this pattern, supporting this explanation, although there are some exceptions – in particular, sites in Epirus, where orographic precipitation may account for high deciduous *Quercus* values throughout the Lateglacial (Lawson *et al.*, 2004).

Early Holocene (zones N-3 to N-5; *c.* 12 000–5000 cal BP)

A substantial increase in the extent of forest cover can be inferred from the data at the beginning of zone N-3 (*c.* 12 000 cal. BP). AP increases sharply, from 13% to 65%, and pollen concentrations show a similar increase, making it clear that this represents a significant increase in the abundance of trees in the landscape. The bulk of the expansion is seen in deciduous *Quercus* and *Pinus*, and these taxa probably dominated the woodland with relatively small numbers of other taxa. Given its low pollen productivity, the moderate increase in *Abies* may represent a considerable increase in the extent of *Abies* woodland, probably in the uplands. Abundant *Rumex* and *Sanguisorba minor*-type pollen suggests that unshaded, treeless patches were abundant in the landscape. The records for this period from the nearby sites of Edessa and Khimaditis-I (zones X1 and X2 in both cases; Bottema, 1974) are extremely similar.

At about 10 500 cal. BP those thermophilous tree taxa that became continuously present in N-3, notably *Ostrya*-type, *Tilia cordata*-type, *Carpinus betulus*, *Fraxinus ornus* and *Pistacia* (but not *Fagus*), become more abundant, marking an increase in woodland diversity.

Pistacia peaks during zone N-4 (approximately 10 500–7500 cal BP), along with increases in *Juniperus*, *Vitis* and other maquis taxa such as evergreen *Quercus* and *Phillyrea*. This suggests an expansion of sclerophyllous lowland vegetation, possibly in response to climatic change as the change approximately coincides with the period of peak Holocene summer insolation. A similar early Holocene '*Pistacia* event' is seen throughout the eastern Mediterranean (Rossignol-Strick, 1995). The Nisi data suggest that the warm, dry summers and mild winters extended into the presently sub-Mediterranean climatic zone of northern Greece. However, taxa such as *Olea* and *Phillyrea*, which are important constituents of the early Holocene vegetation in many other Mediterranean sites, are present only at very low values at Nisi, suggesting that such a northern site did not experience great extremes of summer drought and/or winter warmth.

Zone N-5, beginning *c.* 7500 cal. BP, is characterized by an early increase and sustained abundance of *Ostrya*-type pollen. Other changes include a decline in *Pistacia* and increases in *Abies* and, later, *Fagus*. These features signal a reorganization of woodland, with increased diversity. A similar pattern of change is clearly visible in diagrams from nearby sites (Edessa, Khimaditis-I: Y1/Y2 zone boundary; Kastoria: zone Z1; Giannitsa: above 6.5 m; Bottema, 1974) and has been attributed to factors including competitive, autogenic interac-

tions among trees, soil development and a change in climate towards cooler, wetter conditions (e.g., Willis, 1994).

The sediments throughout zones N-3 to N-5 are variously organic muds, peats and marls. Together with rapid fluctuations in the abundance of fen vegetation, especially Gramineae (probably largely *Phragmites*) and Cyperaceae, this suggests that local changes in the depositional environment at the core sites occurred throughout the Holocene. Possible mechanisms for such stratigraphic variability include rapid changes in the regional hydrological budget, and episodic tectonic subsidence.

Late Holocene (zones N-6 and N-7; *c.* 5000–500 cal. BP)

The upper two zones of the Nisi record chart the decline of woodland in the region. At the base of zone N-6 the composition of the AP changes: *Ostrya*-type declines markedly, with smaller decreases in *Ulmus*, *Fraxinus ornus* and *Tilia*. These decreases are balanced by increases in deciduous and evergreen *Quercus*. At the top of N-6 *Juglans* makes its first appearance; *Juglans* is a tree crop, possibly introduced (Bottema, 1980). The change in woodland composition could well be attributable, at least in part, to an increase in grazing, favouring the less edible evergreen *Quercus* and *Juniperus*; the present open maquis vegetation of lowland Greece is considered to be largely a product of heavy grazing (Rackham and Moody, 1996; Grove and Rackham, 2001). Other maquis taxa, including *Pistacia* and, to a lesser extent, *Olea* and *Phillyrea*, all expand during N-7.

In the middle of N-6, a rapid decline in AP is recorded, with a number of herb taxa contributing to the event including *Artemisia*, *Cannabis* type, Cereals, *Plantago*, Umbelliferae and *Urtica*; Gramineae also expand. Thereafter AP slowly declines to the top of the sequence. Although climatic causes cannot be ruled out, the most likely explanation is human agency. The herb taxa responsible for the decrease in AP, both within N-6 and throughout N-7, are all typical indicators of agricultural activity (Behre, 1981; Bottema, 1982).

These vegetational changes – a decrease in woodland diversity, the expansion of maquis taxa, an overall decline in AP, and the spread of ruderal herbs and crops – are clearly visible in diagrams from other low- to mid-altitude sites in the vicinity. The records from Khimaditis-I (Bottema, 1974), Giannitsa (Bottema, 1974) and Vegoritis (core 8; Bottema, 1982) show almost identical changes to those at Nisi. In the Edessa sequence *Castanea* is sporadically present during the late Holocene; its absence from Nisi suggests that it had a patchy distribution. At Kastoria (Bottema, 1974), the rise in *Juglans* and *Platanus* occurs above a date of 1095 ± 60 ^{14}C BP (920–1180 cal. BP), although this date may well be inaccurate (Bottema, 1980). Values of *Fagus* and *Pinus* are somewhat higher at Kastoria than at Nisi, probably a reflection of Kastoria's higher elevation (650 m a.s.l.). Here the extent of the decline in AP and rise in NAP is even more marked than at Nisi, perhaps because the lake at Kastoria is surrounded by a wide belt of flat land suitable for farming, unlike Nisi where the area of cultivable land was very small before artificial drainage began in the 1950s (Christanis, 1994).

While strong similarities exist between the data from Nisi and other low- to mid-altitude sites, the upland sites show differences that probably reflect the character of upland vegetation. Both Kp-4 and Bor-3 were taken from relatively small mires (Kp-4, 1.2 km^2; Bor-3, 0.01 km^2) and as such are likely to have relatively small pollen catchments (Jacobson and Bradshaw, 1981), reflecting mainly local vegetation, although moderate values of certain taxa restricted to low elevations, such as *Olea*, are presumably attributable to transport from the foothills. Willis (1992) found a similar situation with regard to upward dispersal of pollen in northwest Greece. The high values of Pteropsida (fern) spores at the base of both diagrams, coinciding with low loss-on-ignition values, probably reflect poor pollen preservation favouring the robust Pteropsida spores in the mineral deposits underlying the true peat.

In general, the pollen records from the two sites are quite similar. Perhaps the most striking difference between them is that AP is generally much higher at Kp-4. Most of the difference is attributable to *Pinus* and *Fagus*, suggesting that over the period covered by Kp-4 the site, the lower of the two at 1725 m a.s.l., was situated close to the junction between the *Fagus*/*Abies* and *Pinus* altitudinal vegetation belts. Tonkov (2001, 2003) and Stefanova and Ammann (2003) have argued that higher summer insolation during the early Holocene may have been responsible for the expansion of mixed deciduous woodland in southwest Bulgaria to much higher altitudes than are achieved today; the data from Kp-4 suggest that a similar situation pertained in northern Greece, as *Fagus* today generally occurs at slightly lower altitudes. Large amounts of *Betula* pollen may also relate to trees growing within *Fagus* or mixed deciduous woodland; *Betula* is not common at the tree-line in northern Greece today (Strid and Tan, 1997).

Kp-4 and Bor-3, like other montane sites in the Boras and Paiko ranges (Gerasimidis and Athanasiadis, 1995), show a decline in AP in the later part of the Holocene (somewhat smaller and less rapid than that recorded at Nisi), and an expansion of herbs including Compositae, *Plantago*, and *Urtica*. Climate change is a possible cause. A decrease in temperature would most likely lead to a depression of the altitudinal belts of vegetation, and hence a reduction in *Fagus* and *Abies* in favour of *Pinus* at Kp-4. This is, indeed, the pattern seen at Kp-4, although it is very subdued. However, a similar pattern could result from increased anthropogenic disturbance. The sharp decline in *Betula*, which would otherwise be expected to increase in response to disturbance, is consistent with increased grazing – as are the increases in *Plantago* in Kp-4 and in *Plantago* and Compositae in Bor-3, as these taxa include many species favoured by grazing. It is also notable that some herb taxa actually decline during the deforestation event, especially Umbelliferae and Ranunculaceae, both of which are typified by taxa that favour unwooded ground but may be affected by grazing. The deforestation coincides with an increase in Cereal-type pollen, especially well recorded at Kp-4 and, while this curve does not exclude every wild grass species in Greece, it suggests that an increase in grazing at high altitudes occurred alongside an increase in arable cultivation, presumably at low- to mid-altitudes.

The data from Nisi concord with data from existing sites in Greece in suggesting that the major deforestation event in northern Greece occurred well after the beginnings of agriculture. Although the chronology is not well constrained, the age model suggests a date of 5000 cal. BP at Nisi – almost a millennium earlier than suggested by Bottema for his Edessa record but in line with data from other dated mid-altitude sites in northern and northwest Greece, including Giannitsa. At Bor-3 and Kp-4 the evidence for deforestation is less marked, but a gradual decline in AP occurs at Bor-3 above the date of 3770 ± 80 ^{14}C BP (4410–3920 cal. BP; the data from Kp-4 are perhaps too equivocal to draw firm conclusions). As noted by other authors, the onset of the Neolithic period, with the appearance of domesticated crops and animals in archaeological contexts, occurs much earlier than this in Greece, around 9000–8000 cal. BP (Willis and Bennett, 1994, 1996; Magri, 1996; Edwards *et al.*, 1996). The reason for the delay between the initiation of farming and widespread woodland clearance

has not yet been resolved. One possible explanation is that the late clearance was due to the introduction of iron-working and improved ploughs capable of supporting large-scale arable farming (Willis and Bennett, 1994). Our data suggest, however, that clearance occurred relatively late in the high mountains, as well as in the low and middle altitudes, an event that is clearly not directly caused by forest clearance for arable cultivation at high altitudes. Intensified grazing, perhaps as a secondary effect of increased population pressure brought about by more intensive cultivation at lower altitudes, could be responsible. As with all Holocene vegetational changes, however, the deforestation is quite possibly overdetermined, with some combination of climatic change, succession, pedogenesis and human impact all playing a partial causative role.

Despite the significance of the deforestation event recorded in our records in the formation of the modern landscape, it is perhaps worth pointing out that, in comparison with some other parts of Greece, the north remains relatively well-wooded. In general, the amplitude of the mid/late Holocene deforestation varies spatially with precipitation within Greece (as does the timing of its onset; Magri, 1996), such that sites towards the drier southeast such as Xinias (Bottema, 1979; Digerfeldt *et al.*, 2000) and Kopais (Greig and Turner, 1974; Allen, 1990) show a larger and faster fall in AP. It may also be that the topography of a site's pollen catchment has an impact on its sensitivity to this event. Compared with Nisi, Kastoria (Bottema, 1974) shows a much stronger signal. As noted above, Kastoria is surrounded by a much greater expanse of flat land suitable for cultivation than Nisi. This suggests that another explanation for the relatively subdued anthropogenic signal in sites from northern Greece in general is that there was simply little opportunity for extensive arable cultivation in the hilly terrain. This observation is supported by the distribution of known early Neolithic sites, which tend to occur on low-lying plains (Halstead, 1994; Bailey, 2000; Tringham, 2000).

Conclusions

(1) *Within-basin palynological comparisons and taphonomy.* Consistent variations in the proportions of pollen taxa between the five analysed cores from Nisi support the view that facies changes can cause changes in pollen taphonomy. Rapid stratigraphic changes in Gramineae and Cyperaceae observed at Nisi and other shallow-water sites in Greece are probably attributable to stratigraphic facies shifts. In these situations, inclusion of Gramineae (*Phragmites*) in the pollen sum can give a false impression of the past regional vegetation.

(2) *Limited evidence for woodland expansion during the Lateglacial.* Like other sites in northern Greece, Nisi shows only a small expansion of *Pinus* during the Lateglacial Interstadial, and only subtle vegetation change during the Younger Dryas chronozone. This weak expression of Lateglacial environmental change may be a consequence of site-specific factors rather than an indication that Lateglacial climate changes in northern Greece had a smaller amplitude than elsewhere in Europe.

(3) *Warm, dry summers 10 500–7500 cal. BP.* Sclerophyllous taxa expanded in northern Greece during the period of peak summer insolation, although to a lesser degree than at more southerly sites.

(4) *Middle Holocene woodland diversification.* Two major shifts in the composition of temperate woodland occurred during the middle Holocene, the first an expansion of *Ostrya carpinifolia/Carpinus orientalis* and *Abies* around 7500 cal. BP, the second an expansion of *Fagus* at *c.* 5000 cal. BP. The cause of this diversification remains unresolved. Migration is unlikely to be an explanation, given that these taxa had glacial refugia within the Balkans (Bennett *et al.*, 1991); intrinsic ecological/population dynamical processes, soil development, climatic change and/or human agency could all be involved (Willis, 1994).

(5) *Late Holocene deforestation and farming.* Despite archaeological evidence for the introduction of farming to Greece around 9000–8000 cal. BP, no clear evidence for human impact can be seen in the data until around 5000 cal. BP when a major decrease in tree cover occurred around Nisi. A similar decline in tree cover, although less well dated, occurred at high altitudes in the Boras mountains. Although some climatic involvement cannot be ruled out, the expansion of crops and ruderal taxa immediately following this deforestation points to human agency.

(6) *Spatial patterns of Lateglacial and Holocene vegetation change.* Comparisons between sites across northern Greece yield much useful information on spatial, and especially altitudinal, patterns of vegetation change. Without macrofossil data it is not possible to state definitively that the moderate percentages of *Ostrya*-type, *Corylus* and *Betula* pollen in the lowermost samples of Kp-4 represent local, high-altitude populations, but pollen and macrofossil evidence from Bulgaria (e.g., Tonkov, 2001, 2003; Stefanova and Ammann, 2003) supports the conclusion that mixed deciduous woodland in the region had a greater altitudinal range in the first half of the Holocene than at present. The data from Kp-4 and Bor-3 also show that *Fagus* and *Abies* came to dominate the upland forests around the mid-Holocene, and suggest that the late-Holocene decline in tree cover, so marked in low- and mid-altitude pollen sites, also extended to the high mountains, probably as a result of human activity. Pollen data from Kastoria (Bottema, 1974), where the degree of deforestation in the late Holocene was greatest, support the reasonable assumption that forest clearance was concentrated in areas of flat, cultivable land. Data from Vegoritis (Bottema, 1982), where the size and bathymetry of the basin mean that a major contribution by *Phragmites* to the Gramineae counts is unlikely, give an indication of the limited extent to which trees were removed from the landscape as a whole: here, AP remains above 35% even after the deforestation. It seems likely that the mountainous terrain of northern Greece retained its woodland to a much greater extent than in many other parts of Europe during the second half of the Holocene.

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