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Vegetation change through glacial–interglacial cycles: a long pollen sequence perspective

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SUMMARY

A core recovered from a thick sedimentary sequence in the Ioannina basin, on the western flank of the Pindus Mountain Range, northwest Greece, presents the opportunity to observe multiple changes in vegetational communities at one locality through a series of glacial–interglacial Quaternary cycles. The Ioannina 249 record adds to the knowledge of vegetation history of areas of increased topographical variability and precipitation of the western Balkans and provides a complete stratigraphical record that can be compared with that of other long terrestrial sequences and with the marine record.

Pollen analytical results are presented as percentages and concentrations, the former providing information on the composition and structure of vegetation, while the latter is considered here to be a reliable indication of vegetation density when changes differing by an order of magnitude are documented. The record shows an hierarchical order of variation in the response of vegetation to environmental change. Higher order of magnitude changes are alternations between forest and open vegetation communities, a reflection of major climatic shifts from interglacial to glacial modes. Superimposed on these oscillations is a lower order variability associated with vegetation changes within interglacial and glacial periods. During forest periods a succession is recorded with *Quercus* and *Ulmus/Zelkova* expanding early, followed by *Carpinus betulus* and also *Ostrya carpinifolia/Carpinus orientalis*, and finally *Abies* often accompanied by *Fagus*. Although individual periods may be characterized by dominance of one or more taxa, the underlying pattern of differential expansion is usually distinct and consistent. Nine forested intervals are distinguished and are assigned local names to facilitate long-distance comparisons and correlations. During open vegetation periods a series of changes is also observed from transitional steppe–forest or forest–steppe vegetation, through grassland steppe communities, culminating in a discontinuous desert–steppe vegetation. In addition to the two ends of the spectrum (forest and desert–steppe), attention is drawn to the intermediate phases representing 'average' Quaternary conditions.

The Ioannina record is correlated with that of other long sequences from Europe and variation in the response of vegetation with site characteristics is considered. A strategy for long-distance correlations relying on the primary structure of vegetation and relative stratigraphical position of individual periods is described. The last interglacial period followed by two interstadials is recorded in much the same fashion in all records. Correlation of earlier periods was also in general agreement although only two continuous records that extend beyond the last interglacial are at present available for comparison. To minimize elements of circularity, similarities in the behaviour of individual taxa during particular periods are not part of the correlation criteria so that if their chronostratigraphical equivalence is independently corroborated their significance can be examined. On this basis, the importance of *Carpinus betulus* and the almost complete absence of *Fagus* on a subcontinental scale during the last interglacial are noted. Possible effects of climate, competition and disease are discussed. Cross-correlation with the deep-sea oxygen isotope record provides a tentative chronology for the Ioannina record. Based on this, the sequence down to a depth of 162.75 m is considered to represent a record of approximately the past 423 000 years. Aspects of land–sea correlations are discussed in the light of the Ioannina 249 record and the importance of long sequences in the development of European Quaternary stratigraphy is emphasized.

1. INTRODUCTION

Despite the rapidly increasing number of new sites being investigated on a global scale (e.g. COHMAP members 1988), there is still a clearly discernible pattern in the geographical distribution of palynological sites with the greatest concentrations occurring in the mid- to high northern latitudes, especially Europe and eastern North America. In Europe most palynological sites have been investigated in areas

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where lakes and mires developed on glacial deposits or on glacially scoured bedrock. The location of these sites within the southern limit of the last ice sheet or in an area of periglacial activity means that their histories do not extend earlier than the last glacial period. Thus, although detailed palynological studies of approximately the past 13 000 years have emerged (e.g. Huntley & Birks 1983), knowledge of the vegetation history of earlier interglacial periods has traditionally relied on evidence recovered from organic deposits interbedded within cold stage inorganic deposits. The chronostratigraphical position of these deposits is often uncertain and correlation across northwest Europe has relied on biostratigraphical similarities with the implicit danger of aggregating units of similar fossil contents but different ages. By comparison, the deep-sea sedimentary environment devoid of problems of stratigraphical discontinuities has provided a complete record of Quaternary climatic variability (e.g. Emiliani 1955; Shackleton 1967, 1969; Shackleton & Opdyke 1973, 1976; Imbrie *et al.* 1984; Martinson *et al.* 1987; Shackleton *et al.* 1990) that has become the standard against which fragmentary terrestrial records have been 'fitted', sometimes in the best Procrustean traditions. Cross-correlation of the terrestrial with the marine record has proved elusive and has been aggravated by the lack of an independent chronology. We still remain in ignorance as to how the 40–50 major climatic oscillations recorded in the marine record in the past 2.5 million years (Harland *et al.* 1990) translate to events on land.

In contrast to the situation in northern Europe, a concentration of deep Quaternary basins has been identified in southern Europe (see van der Hammen *et al.* 1971; de Beaulieu *et al.* 1991). Under favourable geological conditions, thick sequences have accumulated undisturbed by the glacial advances and periglacial processes that are so problematic in northern European stratigraphy. Such records provide an opportunity to observe shifts in vegetation communities over multiple glacial–interglacial cycles at single sites where background factors (e.g. bedrock, topography) can be assumed to have remained constant. In addition, the position of several interglacial periods within the same sequence defines their chronostratigraphical relationship and bypasses the problem of reconstructing a record by piecing together isolated interglacial deposits whose temporal relations may not always be clear. It thus becomes possible to obtain a complete continental stratigraphical record that can be compared with the marine record. Moreover, the multivariate nature of terrestrial sequences means that they contain greater detail than the univariate oxygen isotope signal. As such, they can provide an insight into the complexity of the response of terrestrial ecosystems to environmental changes.

In Greece, a thick sedimentary sequence accumulated under a régime of tectonic subsidence at Tenaghi Philippon, eastern Macedonia (41°10′N, 24°20′E; 40 m above sea level), has been the subject of palynological investigations over several years (Wijmstra 1969; Wijmstra & Smit 1976; van der Wiel & Wijmstra 1987*a*,*b*). Tenaghi Philippon has a continuous record of vegetation change that extends into the late Lower Pleistocene and has been the only long sequence from Greece studied hitherto. However, given a distinct east–west climatic gradient from the high precipitation areas of the western Balkan mountains to drier regions east of the mountains, vegetation in eastern Greece is generally less diverse than on the western flank of the Pindus mountains; such floristic differences have probably persisted during the Pleistocene and consequently the record from Tenaghi Philippon may not be representative of the areas of increased topographical variability and precipitation in the Balkans. Recent exploration by the Institute of Geology and Mineral Exploration (IGME) has identified the presence of additional thick sedimentary sequences that can provide a more complete account of Greek vegetational history. Of these, the Ioannina basin (39°40′N, 20°51′E; 470 m above sea level) on the western flank of the Pindus Mountain Range, in the interior of Epirus, northwest Greece, was considered particularly promising: (i) multiple coring by IGME had revealed the presence of a substantial Quaternary deposit (at least 300 m thick); (ii) earlier palynological work on the basin had been done by Bottema (1974), who obtained two cores (11.5 m and 5.65 m long), providing a record extending into the last glacial period. His results confirmed the presence of polliniferous sediments; and (iii) the site was located within a region where the presence of refugial populations of temperate trees during the last cold stage had been postulated (van der Hammen *et al.* 1971; Bottema 1974; Willis 1992*a*–*c*).

Of the several cores retrieved by IGME, core Ioannina 249 was selected for this study. Its original length was 230 m, but because of retrieval problems and extensive earlier subsampling by IGME, only the interval 10.20–186.00 m is considered here. It was assumed that correlation with Bottema's (1974) record could establish the chronostratigraphical position of the top of Ioannina 249.

The main aims of this paper can be summarized as follows: (i) to obtain a continuous record of vegetation change through multiple glacial–interglacial cycles; (ii) to examine and compare the nature of vegetational development of individual forest periods; (iii) to obtain a chronostratigraphical framework through cross-correlations with other pollen records and with the deep-sea oxygen isotope record; and (iv) to examine, once chronostratigraphical equivalence is independently established, the extent of variation in the response of vegetation with site characteristics and the behaviour of individual species by comparisons with other long pollen records from Europe.

The physical setting of Ioannina and the field and laboratory methods applied are described first. After a discussion of the zonation scheme employed, the Ioannina 249 data set is presented. Potential methodological problems and assumptions are considered before the interpretation of results is presented. Different levels of variation within the data set are described and similarities and differences between periods are outlined. A brief discussion on the nature of climatic changes involved is included. Before comparisons between Ioannina 249 and other long terrestrial records and the deep-sea record are presented, a strategy for correlations attempting to minimize elements of circularity is described. The behaviour of certain species on a European scale especially during the last interglacial is discussed and possible scenarios are invoked. Finally, the issue of land–sea correlations is considered in the light of the Ioannina 249 record.

Throughout this work vascular plant nomenclature follows Flora Europaea (Tutin *et al.* 1964–1980). The following abbreviations are used unless otherwise indicated: chenopod(s) for Chenopodiaceae–Amaranthaceae, *Ostrya* for *Ostrya carpinifolia*/*Carpinus orientalis* and *Carpinus* for *Carpinus betulus*. The terms 'cold stage', 'glacial period' or 'open vegetation period', and 'temperate stage', 'interglacial period' or 'forest period' are used informally to refer to Quaternary periods of relatively cold and/or arid, and warm and/or moist climates. Although the use of the terms glacial and interglacial in areas that have remained unglacierized has been discouraged (e.g. West 1984, 1988; Gibbard & Turner 1990), they are retained here on the basis that the effects of ice sheets are not limited to higher latitudes but extend on a global scale through changes of the general circulation of the atmosphere and planetary albedo. Dates and ages based on the radiocarbon method are given as uncalibrated radiocarbon years before AD 1950 (BP). Other dates and ages are given as years ago (e.g. ka for thousand and Ma for million years ago).

2. PHYSICAL SETTING

(*a*) *Geography*

The Ioannina plain is located on the west side of the Pindus Mountain Range, in the interior of Epirus, approximately 60 km from the Ionian coast (figure 1). The plain has an elevation of 470 m and is bordered to the east by the Mitsikeli Mountain (1810 m), an

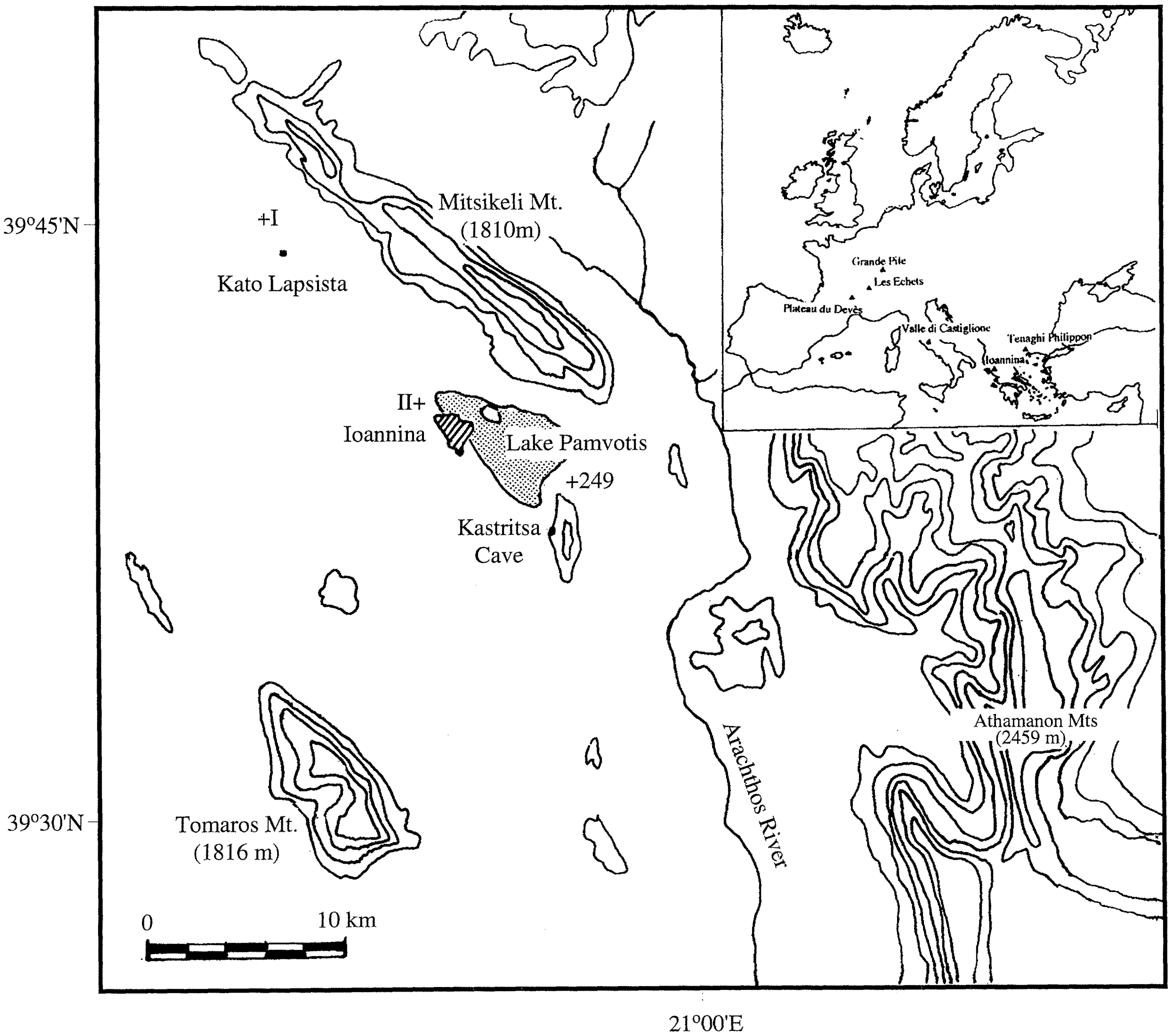


Figure 1. Topographical map of the Ioannina area. Elevation of the Ioannina plain is *ca.* 470 m. Location of borehole Ioannina 249 is shown as well as those of Ioannina I and II (Bottema 1974). Inset: locations of long sequences discussed in text.

anticline composed of limestones that have undergone extensive karst erosion. There is no significant runoff from Mitsikeli as surface waters disappear into sink holes and eventually appear as springs on the northern, eastern and southern coast of Lake Pamvotis (Conispoliatis *et al.* 1986). Lake Pamvotis occupies the east–central part of the basin and has an areal extent of 22.8 km^2 and maximum water depth of 9.6 m. The present surface area of the lake represents only part of its earlier extent prior to artificial drainage. The original size is not precisely known, although it is reported (Higgs *et al.* 1967; Conispoliatis *et al.* 1986) as having extended from Kato Lapsista to Kastritsa (figure 1). Alluvial valley deposits surround the eastern, western and southern periphery of the lake.

(*b*) *Geology*

The physiography of the area is a result of tectonic movements that were initiated in the Tertiary and led to the development of a series of northwest–southeast trending synclines and anticlines, and subsequent faulting and sedimentation that continued in the Quaternary (e.g. Mountrakis 1985; Clews 1989). The geology of the immediate vicinity of the Ioannina basin is comprised of Mesozoic and Palaeogene limestones and Tertiary flysch (IGSR and IFP, 1966) (figure 2). Karst solution of the limestone basement led to the development of a closed depression or polje. Unpublished results by IGME suggest that a Late Pliocene–Early Pleistocene phase of fluvial deposition occurred which sealed the basin

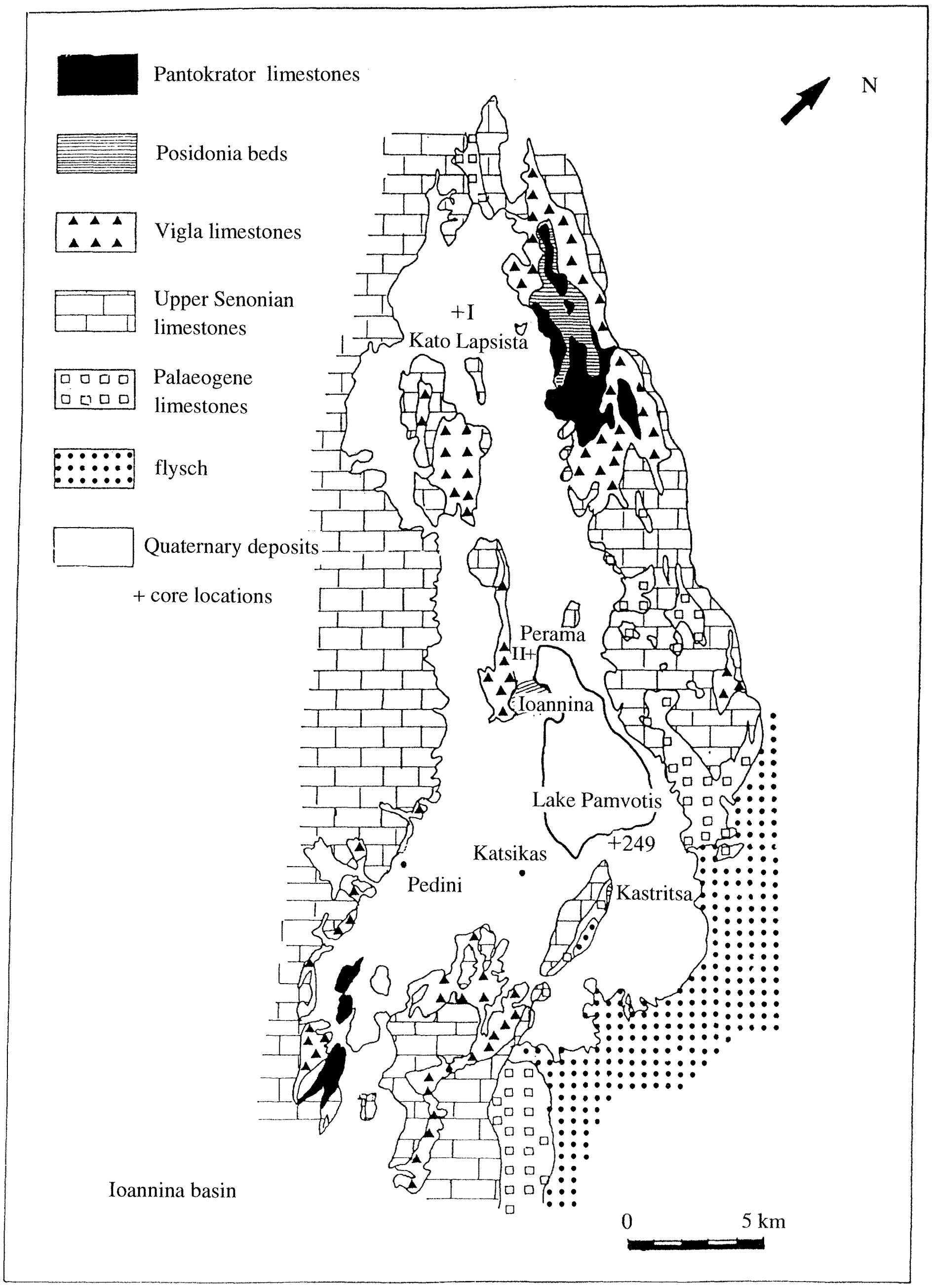


Figure 2. Geological map of the Ioannina basin and immediate vicinity (after IGSR and IFP 1966).

floor and was followed by continuous lacustrine sedimentation. The braided stream facies is overlain by a thick sequence of lacustrine sediments. Tectonic deformation of the area continued during the Quaternary. Correlation of stratigraphical markers throughout the basin has suggested that different parts of the basin have been moved vertically in relation to others and thus, smaller sub-basins might at times have existed independently of each other (IGME, unpublished results).

Mountain glaciation did occur during the last glacial maximum in the Pindus area (e.g. Denton & Hughes 1981), and presumably at earlier periods during the Quaternary. General extent of glacial sediments is mapped on certain geological sheets by IGME, but the age of the deposits is not always clear. In the Tsepelovon district, Voidomatis basin, approximately 26 km north of Ioannina, Woodward (1990) reports morphological and sedimentological evidence for 'recent Pleistocene glaciation'. Corries and hanging valleys, and a series of morainic lobes with associated glacio-fluvial landforms are mentioned, but no attempt has been made to correlate these deposits with others outside the Voidomatis basin. Systematic mapping of such deposits for the Pindus area is needed to assess the extent and number of local glacial events.

(*c*) ***Climate***

The Ioannina climate is considered 'Mediterranean' with a certain amount of continentality given its elevation and distance from the coast. Figure 3 presents a Walter type climate-diagram (Walter *et al.* 1975) based on climatic data recorded at the Ioannina meteorological station (39°40′N, 20°51′E; 484 m above sea level) for the period 1951–1981 (National Statistical Service of Greece). The most important features are the high levels of precipitation and the occurrence of a moderate summer drought. Annual precipitation levels (1200 mm) at Ioannina are amongst the highest recorded at stations in Greece, with maximum monthly precipitation occurring in December (176 mm) and minimum monthly precipitation in the summer months with August being the driest (29 mm). Mean annual temperature is 14.4°C, with mean temperatures for January and July being 4.9°C and 24.9°C, respectively. Absolute minimum and maximum temperatures recorded during the 1951–1980 period were −13°C (1966) and 41°C (1973).

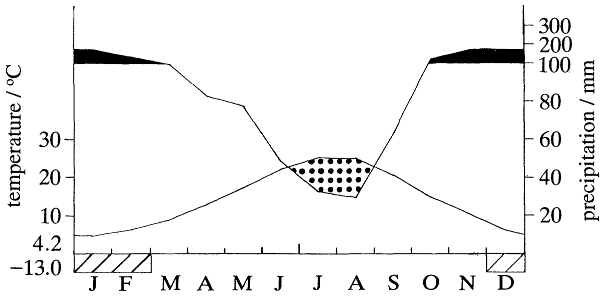


Figure 3. Walter-type diagram of Ioannina. Data recorded at the Ioannina meteorological station during the period 1951–1981 (National Statistical Service of Greece). The drought season is represented by the dotted field. Bars with angled hatching at base of diagram represent months with absolute minimum temperatures below 0°C. See text for further discussion.

(*d*) ***Vegetation***

Natural vegetation is virtually absent from the immediate vicinity, as the Ioannina plain is cultivated and nearby mountains are barren. On the Mitsikeli Mountain, Bottema (1974) recorded *Juniperus* cf. *oxycedrus* shrub along with *Carpinus orientalis*, *Cornus*, and *Amygdalus*. Further east, dense brushwood of *Carpinus orientalis*, *Juniperus* cf. *oxycedrus*, *Fraxinus*, *Acer*, *Quercus cerris*, *Q. pubescens*, *Colutea arborescens*, *Craetagus*, and *Phillyrea* occurs and there are a few *Quercus coccifera* patches on the plain. In the Metsovon area (30–40 km east–northeast of Ioannina), *Abies borisii-regis* and *Pinus nigra* (Strid 1986) and also *Fagus sylvatica* (Bottema 1974) are reported. Bottema (1974) suggested that the natural vegetation of the Ioannina plain would be deciduous with *Quercus coccifera*. Deciduous forest would grow on the slopes up to *ca.* 1000 m, while *Abies cephalonica* and *Pinus nigra* would be dominant higher up. *Fagus* would also occur in high elevations (1000–1700 m), probably on the higher parts of the Mitsikeli Mountain.

3. MATERIALS AND METHODS

(*a*) ***Field procedures***

Drilling of the Ioannina basin by IGME started in 1977 and was completed in 1989, forming part of a larger exploration programme. Stratigraphical information from approximately 280 cores assembled by IGME formed the basis of the selection process of the core for this study. Consideration of depositional régime, local tectonic setting and length of core formed the basis of selection. Areas of continuous sedimentation and subsidence that did not appear to show evidence of uplift or major disturbance in the depositional régime were given preference. The position of stratigraphical markers (e.g. top of upper lignite seam) relative to the thickness of the sediment column gave some indication of areas of higher sediment accumulation rates. The longer cores from such areas, presumably containing the most temporally extensive records in association with greater stratigraphical detail, were considered. Finally, cores had to meet requirements of good condition of storage. Under the guidance of IGME geologist Y. Brousoulis, core 249 (39°39′N, 20°55′E) was selected as fulfilling most criteria. It was collected from the area immediately southeast of Lake Pamvotis near Kastritsa, in the early part of 1987 (figures 1 and 2). Core recovery rates were 90% or better. Unpublished IGME information, based on the tracing of the upper lignite seam at increasing depths in different cores, suggests that core 249 was located in a local graben system.

(*b*) *Laboratory procedures*

(i) *Sediment analysis*

Samples used for pollen analysis were described in the laboratory using the Troels-Smith (1955) system of sediment classification. Sediment composition was examined under a light microscope at magnifications of ×100. Organic and carbonate content was determined gravimetrically by loss-on-ignition (Dean 1974). A drawback of the loss-on-ignition method is that it only gives total carbonate without indicating which carbonate minerals are present. For the present study, it is assumed that the results represent calcium carbonate. Magnesium carbonate (dolomite) could also be present, but no dolomite deposits were indicated in the geological map of the Ioannina area (IGSR & IFP 1966). Chemical processing of samples with HF (see next section) did not produce any violent reaction, suggesting absence of magnesium carbonate.

(ii) *Pollen analysis*

Standard chemical treatments (e.g. Berglund & Ralska-Jasiewiczova 1986, method B) were used to remove most of the sediment matrix and concentrate pollen grains in the residue. A known amount of exotic pollen in the form of tablets containing spores of *Lycopodium clavatum* (Stockmarr 1971) was added to each sample to enable estimation of fossil pollen concentration. Total pollen counts ranged from 200 to 1033 (mean 413) grains. Although a minimum count level was originally set at 300 grains, nine samples had counts between 200 and 300 because of low pollen concentrations.

Palynological identification of *Quercus* is usually to genus level but a further separation to evergreen and deciduous (and sometimes semi-evergreen) types is possible (e.g. Smit 1973; Colombo *et al.* 1983). In this study, however, differences between types did not always emerge clearly and poor preservation in certain samples made attempts to distinguish between different types difficult. Consequently, all *Quercus* pollen grains are grouped into one category; presence of evergreen type grains is noted only when it was felt that the distinction could be made unequivocally and as such it represents information of a qualitative nature. An attempt was also made to distinguish *Ulmus* from *Zelkova* pollen, but an intermediate type was also encountered, introducing uncertainties in the separation of the two taxa. Pollen frequencies of *Ulmus* and *Zelkova* species are therefore grouped into one category and presence of *Zelkova* is indicated qualitatively only when the distinction could be made unequivocally.

(iii) *Data analysis*

Pollen counts were expressed as percentages and concentrations. The calculation sum included pollen of terrestrial vascular plants. Unknown and indeterminable pollen, and the pollen and spores of aquatic vascular plants were excluded from the sum. Numerical zonation (Birks & Gordon 1985) was used to partition the pollen data. The method employed was optimal divisive analysis and zone variation was measured by information content deviations about a centroid. Only major taxa whose pollen or spore values had reached 5% or over at least once were included in the calculations. The results of numerical zonation were critically examined and where it was felt appropriate, boundaries of reduced numerical significance were also included in the final zonation scheme (Tzedakis 1991).

4. PRESENTATION OF RESULTS

(*a*) *Sediment stratigraphy*

In general, sediments can be described as grey silts having a high fine sand component in places and with varying calcium carbonate content. Lake marls characterized by high $CaCO_3$ content are the dominant sediment type in a few parts of the core. No distinct sedimentary surfaces representing unconformities were observed. All contacts were gradual with the exception of the interval between 166.00 m and 168.00 m where a sand slurry is recorded. This represents a sand lens which the drilling equipment had been unable to penetrate under normal procedures; water had to be pumped to that level producing a slurry and allowing drilling to continue. A dark coloured fine sand lens is recorded from 176.00 m to 177.00 m but presented no problems to drilling. Contrary to initial expectations, volcanic tephras were not detected.

The results of the loss-on-ignition analyses are given in figure 4*a*. The percentage organic matter, as determined by loss-on-ignition, generally tends to be low (approximately 5%) along most of the sequence, with intermittent short-lived peaks of just over 10%. The $CaCO_3$ content generally covaries with the organic matter content, albeit at higher values, reaching a maximum of 42% by dry mass. The origin of this carbonate material may be more difficult to assess. Microscopic examination of the carbonate-rich sediments from the Ioannina 249 sequence has suggested a precipitate origin.

(*b*) *Pollen stratigraphy*

The concept of superzone (*sensu* Tzedakis 1991, 1994) was routinely applied to a succession of pollen assemblage zones characterized by high arboreal pollen (AP) content. Although a number of zones were defined within periods of higher non-arboreal pollen (NAP) content, here they were not lumped into superzones because the element of hierarchical clustering did not always emerge clearly and uncertainty over the treatment of transitional periods of intermediate AP/NAP values. This does not invalidate the use of superzones as it is still theoretically possible to apply the concept to open vegetation periods, especially as more detailed information on the complexity of cold stages emerges

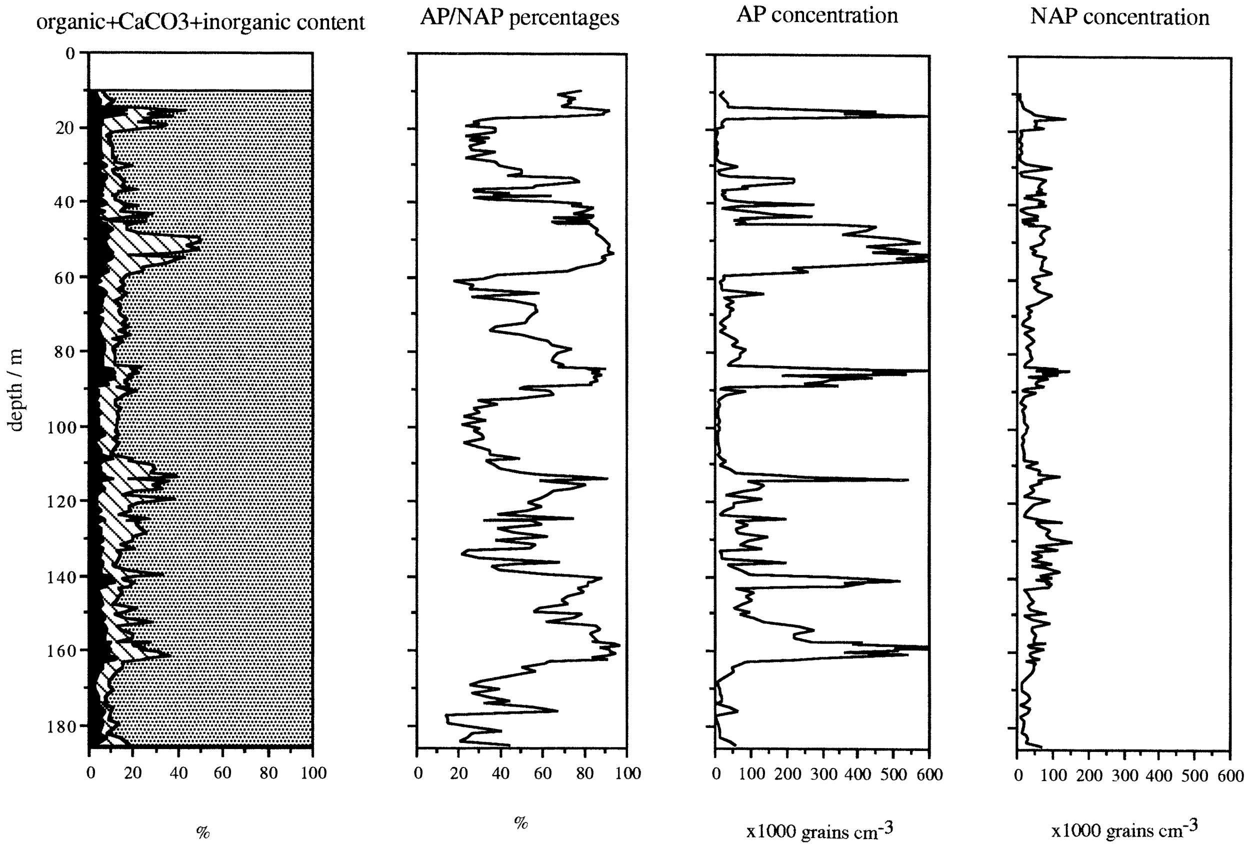


Figure 4. (*a*) Summary loss-on-ignition diagram: percent organic matter (black), calcium carbonate content (hatched) and inorganic matter (dotted) by dry weight of sediment; (*b*) AP/NAP percentage; (*c*) AP concentration; and (*d*) NAP concentration, plotted against depth.

in the future. In general, a hierarchical approach relying on superzones, zones and subzones appears to be better suited to the different levels of variation of the pollen data set.

The Ioannina 249 pollen data set was divided into 44 local pollen assemblage zones labelled IN and numbered from the base upwards. Of these zones 19 were nested under seven superzones labelled IN followed by a capital letter. In certain cases subzones were defined within zones; a total of eight subzones was defined and labelled using the zone numeral and a lower case letter. The pollen percentages and concentration diagrams for selected taxa are presented in figures 5 and 6, respectively. Summary diagrams of AP/NAP percentages and concentrations are given in figure 4*b–d*. Rare pollen and spore types (less than five grains at each level) are not included in the pollen diagrams, although those of vascular terrestrial plants have been included in the pollen percentage and concentration calculation sums.

For practical purposes, I have elected to avoid the usual practice of giving a zone by zone description of changes in pollen frequencies. Instead, a summary pollen zonation scheme with inferred vegetation character is presented in table 1. Mean pollen percentages and concentrations are given for each zone. Local names are assigned to forest periods to facilitate long-distance comparisons and correlations.

5. INTERPRETATION OF RESULTS

(*a*) *Methodological problems and assumptions*

Pollen concentrations (and subsequently pollen accumulation rates) can potentially provide independent information on the abundance of each taxon and by extension, a measure of population size. Attempts have been made to relate pollen influx to basal area for trees but, although a certain quantitative relationship was thought to exist, no clear statistical correlation emerged (Davis *et al.* 1973). In general, the degree of variability in both signal and noise in concentration data has meant that pollen percentages have been considered as statistically more reliable sources of information.

The situation is modified, however, if changes in total vegetation biomass are greater than the inherent variability of pollen concentration data (Prentice 1988). Davis (1969) drew attention to the important contribution of 'influx' values in comparing different stratigraphical zones in one sequence, when values can differ by an order of magnitude or more. It is this application of concentration values that is most useful to the Ioannina 249 pollen data, where total pollen concentrations can vary by as much as one order of magnitude from one zone to another. These changes must reflect changes in pollen production related to differences between major physiognomic vegetation types. Given the relevance of pollen concentrations to long pollen records, it is somewhat surprising that

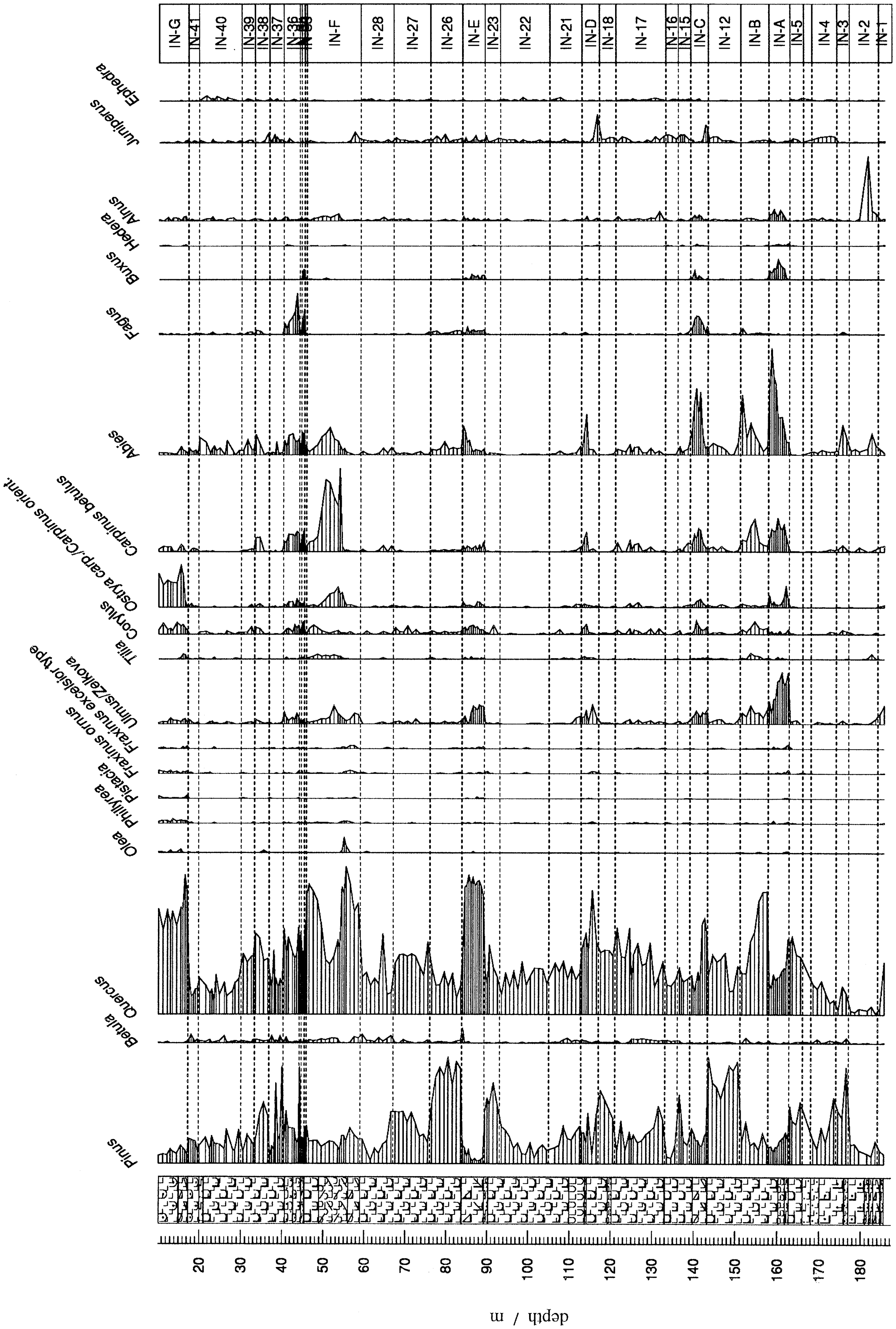


Figure 5. Pollen percentage diagram plotted against depth. Lithostratigraphic column is represented; symbols are based on Troels-Smith (1955).

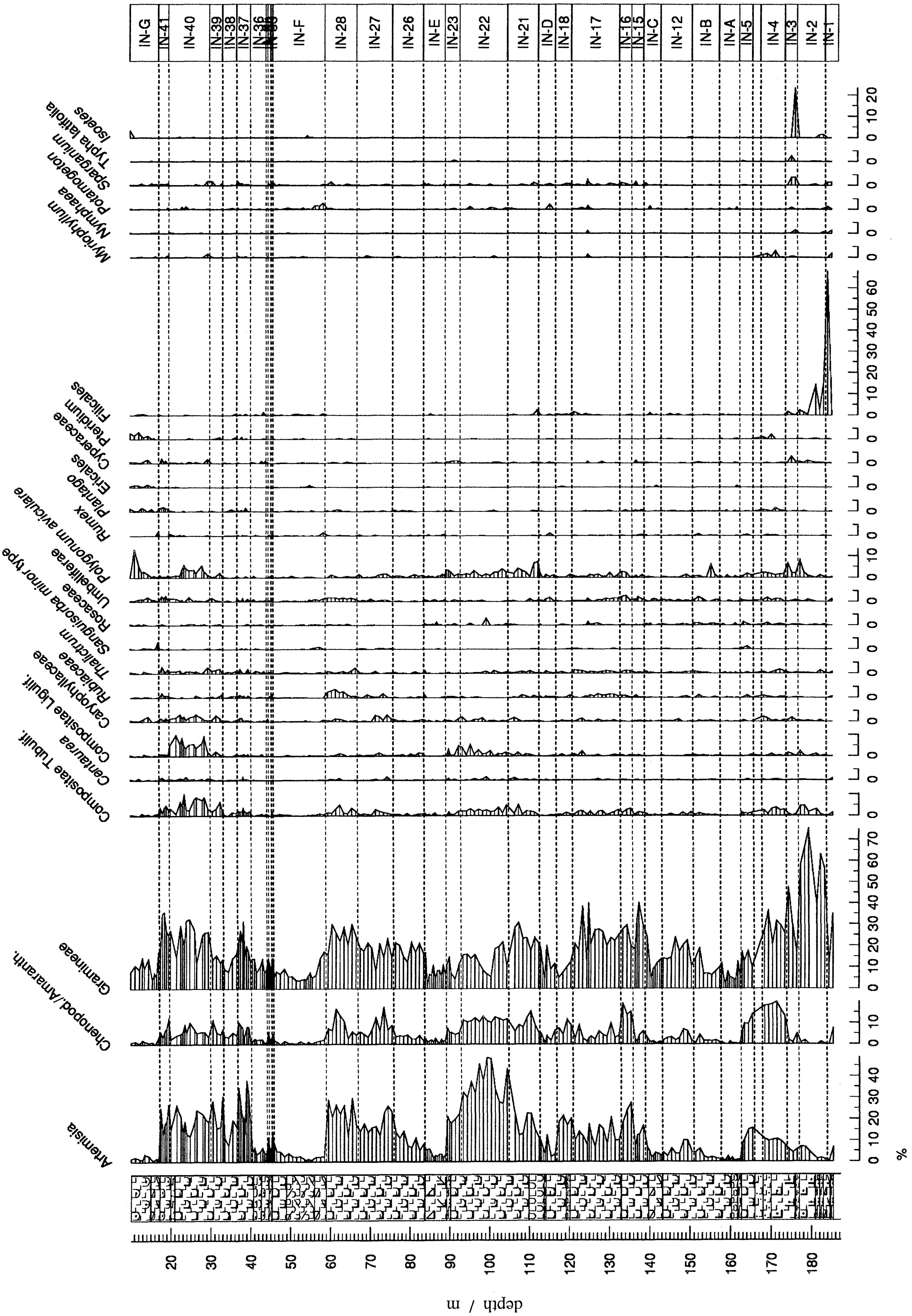


Figure 5. Continued.

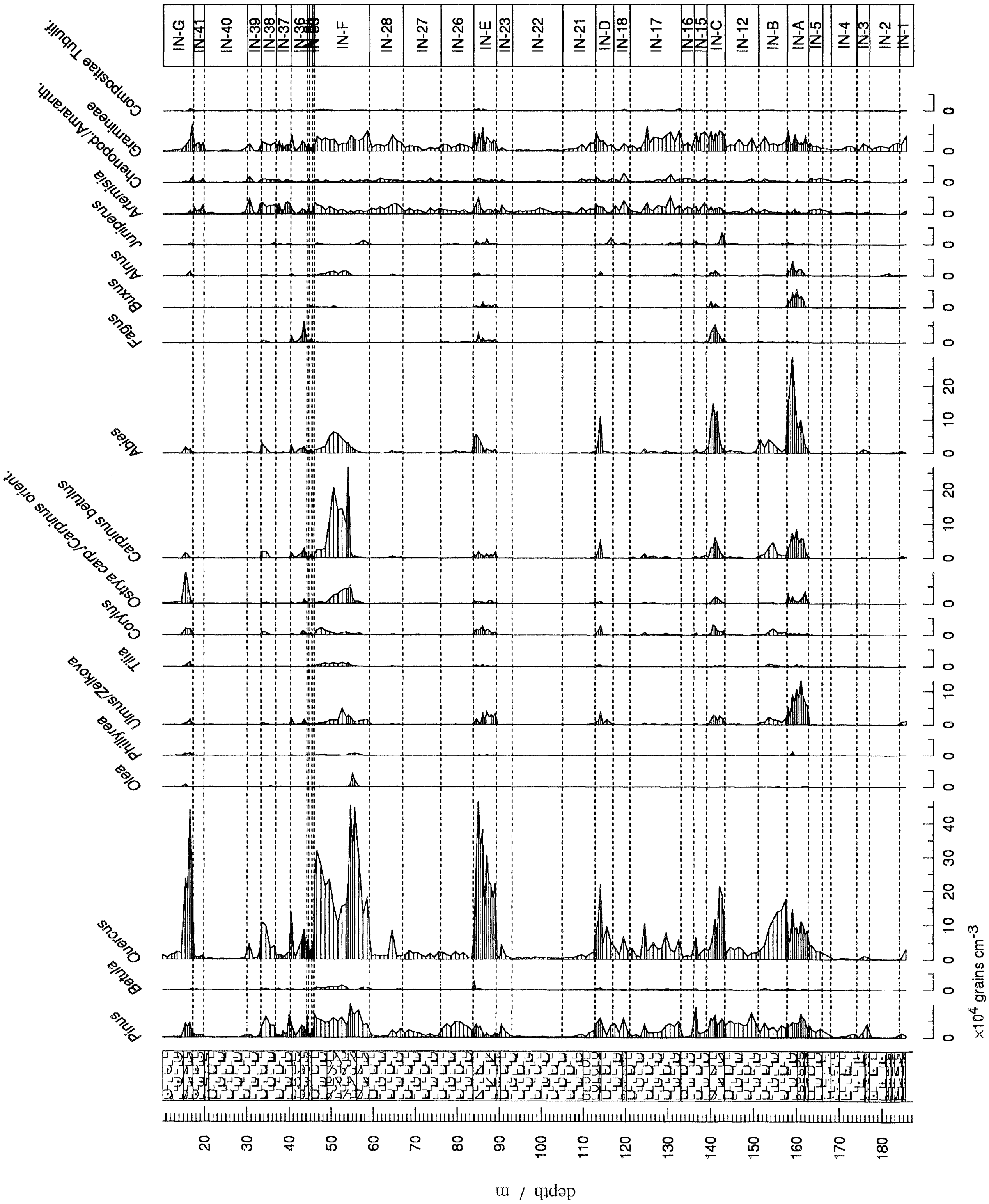


Figure 6. Pollen concentration diagram of selected taxa plotted against depth.

values have so far been calculated for only two sites, Valle di Castiglione (Follieri *et al.* 1988) and Clear Lake (Adam 1988). In interpreting the Ioannina 249 data set, pollen percentages are used as the main source of information on composition and structure of vegetation. Only significant variations in pollen concentrations are related to changes in vegetation biomass, density and cover (e.g. Follieri *et al.* 1988; Magri & Follieri 1992), although the reliability of the signal must be assessed beforehand. The discontinuous nature of vegetation during glacial periods may have contributed to increased levels of erosion and inwash into the basin as suggested by the higher inorganic component of the sediments (figure 4). The effect of this could be the dilution of the pollen concentration signal during glacial periods. Examination of the relative stratigraphical thickness of forest and open vegetation periods *versus* an approximation of the time represented by such periods may provide a test for the validity of the concentration signal. The length of interglacials appears to vary from 10 ka for the present interglacial to approximately 20 ka for the Hoxnian interglacial period (Turner 1975), and a figure of 15 ka is used here. The length of one complete cycle during the Brunhes Chron is taken as 100 ka (e.g. Ruddiman & Raymo 1988). Consideration of the last four cycles (excluding the Holocene), represented in the Ioannina 249 sequence from 162.75 m to 17.25 m (figure 4), shows that the ratio of the stratigraphical thickness of forest to open vegetation periods (1 : 4.2) exceeds the ratio of the duration of interglacial to glacial periods (1 : 5.6). This suggests that sediment accumulation rates are greater during interglacial periods (probably because of high authigenic production of $CaCO_3$) and hence relative dilution, if any, affects forest period pollen concentrations. Thus, the order of magnitude changes shown by the concentration data are not an artefact of sedimentation, and are considered to be a useful measure in the definition of open vegetation–forest period boundaries and in the assessment of vegetation density. In general, attention is focused on comparing average concentration values of zones and superzones (see table 1) and trends in the data, rather than variations recorded in isolated samples.

Despite the lack of surface pollen concentration data from modern open vegetation communities, the extent of glacial period vegetation cover and biomass can still be assessed (e.g. Cwynar & Ritchie 1980). In the Ioannina 249 sequence, pollen concentrations of herbaceous taxa in NAP-dominated zones (presumably reflecting glacial period vegetation) are equal to, or lower than herbaceous pollen concentrations recorded in AP-dominated (interglacial) zones (figure 4). Such NAP values coupled with order of magnitude lower total pollen concentrations indicate that abundance of herbs during the glacial periods were not more extensive than during the tree-dominated interglacial periods and suggest, therefore, a discontinuous vegetation cover. In this work, the term ‘desert–steppe’ is applied to pollen assemblages characterized by increased *Artemisia* or chenopod percentages and correspondingly low concentrations, as well as low total concentrations reflecting a discontinuous distribution of vegetation. The term ‘steppe’ is applied to pollen assemblages with increased Gramineae presence and relatively higher total concentration values reflecting a more continuous vegetation cover compared to desert–steppe. The terms ‘forest–steppe’ and ‘steppe–forest’ are here used informally to refer to pollen assemblages representing intermediate vegetation types between steppe and forest. The terms have been used by Bottema & Barkoudah (1979) and van Zeist & Bottema (1982) as follows: ‘steppe–forest’ to denote an open forest vegetation (woodland) and ‘forest–steppe’ to denote a steppe vegetation with sparse tree growth on local, suitable spots (Bottema & Barkoudah 1979). In this work, mean zone values of approximately 50–65% for AP and 100 000–200 000 grains cm^{-3} for total concentrations were taken to indicate a steppe–forest situation, while relatively lower AP percentages and total concentrations were associated with forest–steppe. It should be emphasized that such definitions are largely artificial in that they draw boundaries where a continuum of states actually exists, and that they are used here for purposes of description.

(*b*) *Evaluation of the Ioannina 249 record*

The results from the Ioannina 249 sequence show higher order of magnitude changes as open herbaceous vegetation and forest alternately dominated the landscape in response to glacial–interglacial conditions. Superimposed on these oscillations are lower order changes associated with forest succession and changes in the character of open vegetation.

The high order variations are shown by the AP percentage and total concentration curves (figure 4). Peaks in AP percentages indicate a forest period whereas corresponding peaks in total concentrations suggest a nearly complete vegetation cover. Peaks in NAP percentages, on the other hand, with corresponding low values in AP and total concentrations, suggest an open and at times discontinuous vegetation cover with variable presence of certain tree populations. The major fluctuations in vegetation composition and density depicted in these summary curves represent a record of biotic response to major climatic change. Examination of the results of sediment and pollen analyses shows that the organic and $CaCO_3$ contents of sediments covary with the AP percentage and concentration values (figure 4). Peaks in organic matter are thought to reflect an increase in macro- and microphyte activity in the lake during warmer/wetter periods and perhaps inwashing of plant debris at times of denser vegetation cover. The precipitate origin of the carbonate-rich sediments also points to warmer conditions.

The lower order variability is a reflection of the complex changes that are recorded within forest and open vegetation periods. Despite the individual character of each forest period recorded in the Ioannina 249 sequence, certain broad patterns emerge: a *Quercus* forest dominates the landscape at the early part of the period along with *Ulmus*/*Zelkova*,

Table 1. *Ioannina 249: summary pollen zonation scheme and inferred vegetation character. Local names are assigned to forest periods (see text for interglacial or interstadial status of different periods). Mean AP percentages and total pollen concentrations for entire periods are also shown. Concentration values in parentheses indicate possible problems with sediment accumulation rates*

local names	superzones/ zones/ subzones	depth/m	mean AP percentage	mean total concentration (grains cm^{-3})	inferred vegetation	characteristics
Holocene	G 44	10.20–15.00	77	(225 400)	forest	*Quercus* (+evergreen)-*Ostyra* forest; *Olea* presence
	43	15.00–16.25				*Quercus*—*Ostyra* forest. *Abies* populations at higher elevations
	42	16.25–17.25				*Quercus* (+evergreen)-*Ulmus* forest
	41	17.25–19.75	30	74 300	steppe	open Gramineae vegetation (*Quercus*, *Ulmus*, *Abies* present)
	40	19.75–30.00	30	11 800	desert–steppe	open, discontinuous Gramineae, *Artemisia* vegetation (*Quercus*, Abies)
	39	30.00–33.25	45	70 000	steppe	open *Artemisia*–Gramineae vegetation with presence of *Quercus*, *Abies* populations
Vikos	38b	33.25–35.00	76	287 500	forest	*Quercus* forest with *Ulmus* and *Carpinus; Abies* and *Fagus* at higher elevations
	38a	35.00–36.75	56	143 300	steppe–forest	*Quercus-Pinua* woodland; *Juniper* populations
	37	36.75–40.25	40	83 500	steppe	open Gramineae–*Artemisia* vegetation with *Quercus* and *Abies* populations
Pérama	36	40.25–44.12	79	257 600	forest	*Quercus*–*Ulmus*/*Zelkova*–*Carpinus* and *Fagus*–*Abies* forests
	35	44.12–44.62	70	156 100	steppe–forest	open *Quercus*–*Pinus* forest
Thyamis	34	44.62–45.38	79	(84 000)	forest?	*Quercus*–*Carpinus* and *Abies*–*Fagus* populations
	33	45.38–45.88	65	109 000	steppe–forest	open *Quercus* forest; *Abies* at higher elevations
Métsovon	F 32	45.88–49.00	86	527 000	forest	deciduous *Quercus* forest (*Carpinus*, *Corylus*)
	31	49.00–54.25				*Carpinus*–*Quercus* (+evergreen)–*Ulmus*/*Zelkova* forest; *Abies*at higher elevations
	30	54.25–57.00				*Quercus* (+evergreen)–*Olea*–*Ullmus*/*Zelkova* forest
	29	57.00–59.00				*Quercus*–*Ullmus*/*Zelkova* forest; open in character
	28	59.00–67.00	33	97 300	steppe	open Gramineae–*Artemisia*–chenopod vegetation. (*Quercus*, *Abies* present)
	27	67.00–76.00	49	57 600	forest–steppe	open Gramineae–*Artemisia* vegetation; *Quercus*, *Pinus*, *Corylus*, *Ulmus*/*Zelkova*, *Abies*
	26	76.00–83.75	65	87 800	steppe–forest	*Pinus* woodland with *Quercus* presence; *Abies* at higher elevations
Zitsa	E 25	83.75–85.75	83	453 000	forest	*Quercus* (+some evergreen); *Abies* populations at higher elevations
	24	85.75–89.25				*Quercus* (+evergreen) forest with *Ulmus* and *Zekova*
	23b	89.25–90.25	49	(34 600)	forest–steppe?	open *Artemisia*–Gramineae vegetation with *Pinus* populations

		23a	90.25–93.00	59	69 100	steppe–forest	*Pinus–Quercus* woodland
		22	93.00–105.50	28	23 600	desert–steppe	open, discontinuous *Artemisia*-dominated vegetation
		21	105.50–112.75	39	59 000	steppe	open Gramineae–*Artemisia* vegetation (*Quercus*, *Ulmus/Zelkova*, *Corylus*, *Abies*)
Katára	D	20	112.75–114.25	73	234 000	forest	*Quercus–Ullmus/Zelkova–Carpinus* forest. *Abies* forest at higher elevations
		19	114.25–117.00				*Quercus* (+evergreen)–*Ulmus/Zelkova* open forest
		18	117.00–121.00	60	145 000	steppe–forest	open *Pinus–Quercus* woodland
		17b	121.00–130.00	51	137 500	steppe–forest	*Quercus* woodland with *Carpinus*, *Ulmus/Zelkova*, *Corylus*. *Abies* populations
		17a	130.00–133.0	49	200 000	forest–steppe	*Pinus* and *Quercus* woodland with Gramineae–*Artemisia* open vegetation
		16	133.00–136.00	25	64 500	desert–steppe	open, discontinuous vegetation with *Artemisia*, Gramineae, chenopods
		15	136.00–139.00	47	169 000	forest–steppe	open Gramineae, *Artemisia* vegetation; *Pinus*, *Quercus*, *Abies* populations
Pamvótis	C	14	139.00–136.00	79	421 000	forest	*Abies-Fagus* forest *Quercus*, *Carpinus*, *Ulmus/Zelkova* populations
		13	136.00–143.25				*Quercus* (+some evergreen)–*Ulmus/Zelkova* forest
		12	143.25–151.00	69	115 000	steppe–forest	open *Pinus* woodland; *Quercus*, *Ulmus/Zelkova*, *Abies* populations
Dodóni II	B	11	151.00–153.00	80	256 000	forest	*Abies* forest. *Quercus*, *Ulmus/Zelkova*, *Carpinus* populations
		10	153.00–155.00				*Quercus*(+evergreen)–*Carpinus–Ullmus/Zelkova* forest. *Abies* at higher elevations
		9	155.00–157.75				*Quercus–Ulmus/Zelkova* forest
Dodóni I	A	8	157.75–159.75	90	485 000	forest	*Abies* forest
		7	159.75–161.75				*Ulmus/Zelkova–Quercus–Carpinus–Ostrya* forest. *Abies* forest at higher elevations
		6	161.75–162.75				*Ullmus/Zelkova–Quercus*(+evergreen) forest
		5	162.75–166.00	58	108 000	steppe-forest	open *Quercus–Pinus* woodland
		4	168.00–174.00	33	29 900	desert–steppe	open, discontinuous Gramineae, chenopod, *Artemisia* vegtation
		3	174.00–177.00	51	(56 700)	?	Gramineae-dominated spectra; *Pinus* and *Abies* recorded; possible erosional source
		2b	177.00–180.50	14	(15 600)	?	Gramineae-dominated spectra; *Abies* and *Alnus* recorded; mechanical damage and degradation of pollen grains along with changes in sediment stratigraphy suggest redeposition
		2a	180.50–184.00	29	(29 700)	?	
		1	184.00–185.50	32	93 100	forest–steppe?	end of a forested phase; reduced *Quercus* woodland in Gramineae open vegetation

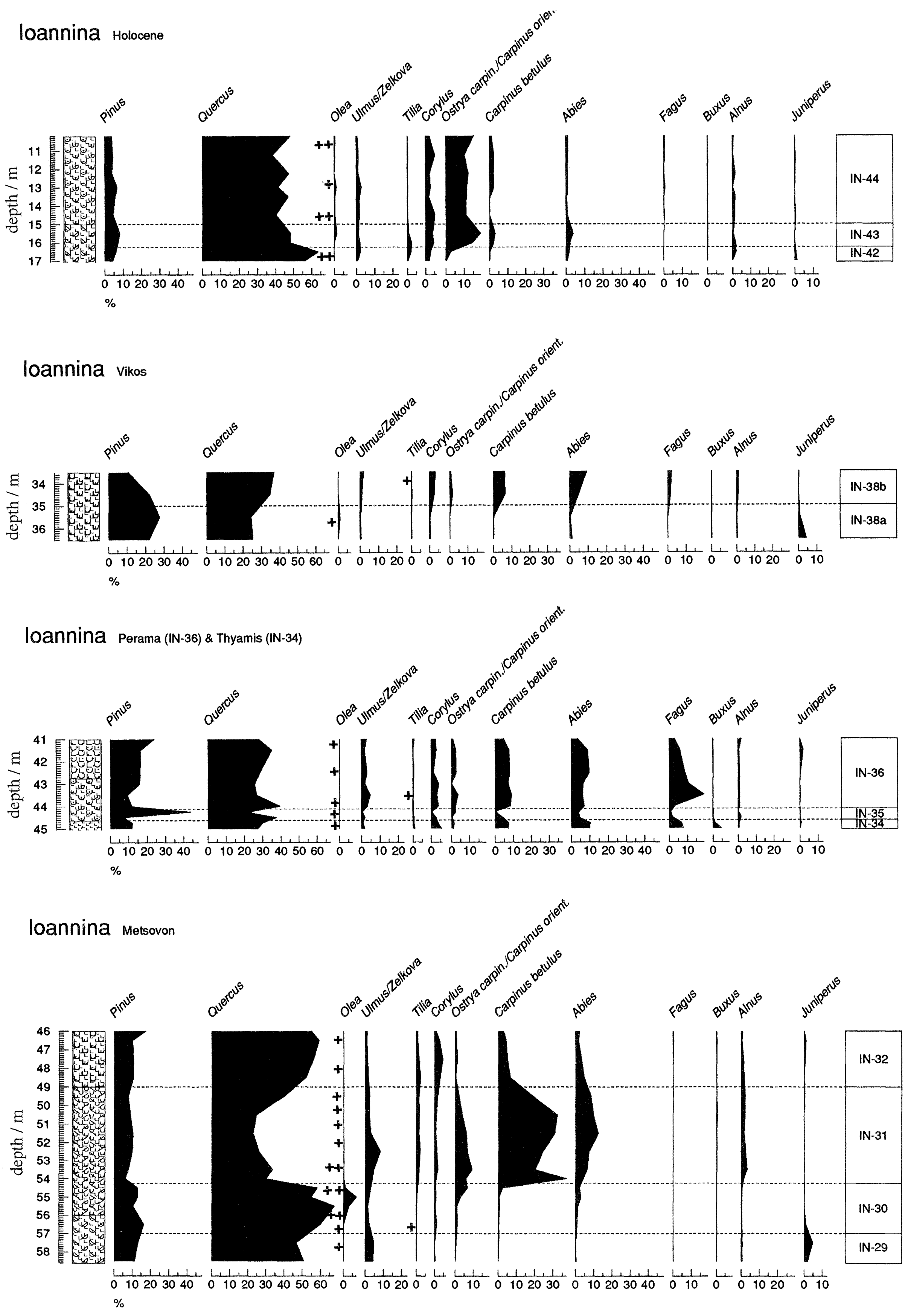
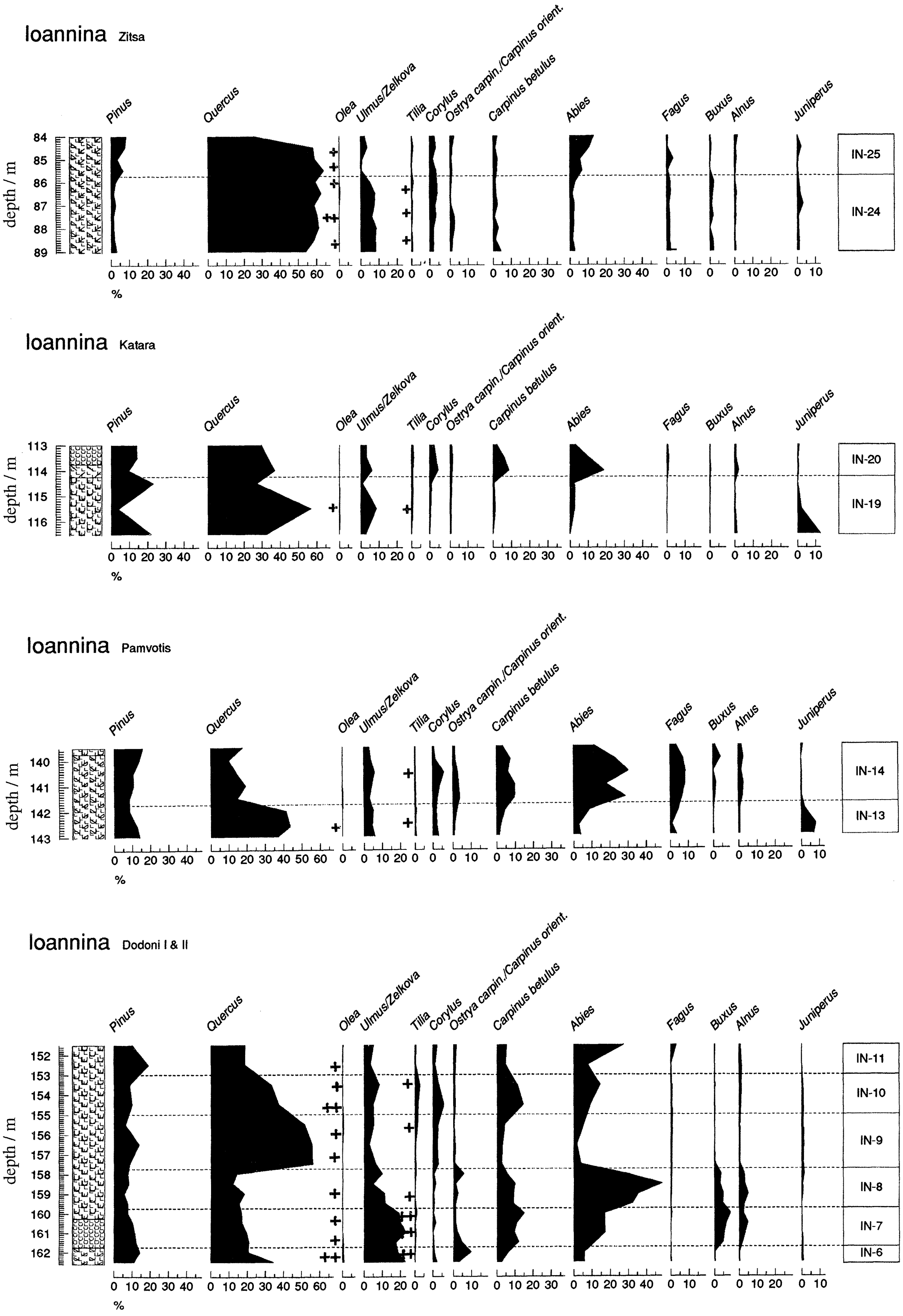


Figure 7. Summary pollen percentage diagrams of selected arboreal taxa of all forest periods of Ioannina 249. Presence of evergreen *Quercus* and *Zelkova* is indicated by a '+' sign; higher abundances by '++'.


Ioannina Zitsa

Ioannina Katara

Ioannina Pamvotis

Ioannina Dodoni I & II

Figure 7. Continued.

Fraxinus spp., *Pistacia*, *Olea* and *Phillyrea*; the *Quercus* forest is subsequently replaced (at least in part) by *Carpinus*, and to a lesser extent by *Ostrya*; an expansion of *Abies* populations occurs at the later stages of the period, sometimes accompanied by *Fagus*. Relatively open vegetation and presence of *Pinus* and *Juniperus* is usually associated with the opening and closing parts of the succession. The underlying pattern of differential expansion generally remains distinct and consistent, although particular taxa assume an overriding dominance over the assemblage during different forest periods. The following forest periods are distinguished (figure 7):

Dodoni (*151.00–162.75 m*): has two separate phases (I and II) of vegetational development, both characterized by high *Abies* values, a feature that sets them apart from all other forest periods. Distinct differences, however, exist between the two phases: dominance of *Ulmus/Zelkova* along with presence of *Ostrya*, a reduced role of *Quercus* and later expansions in *Buxus* and *Alnus* characterize Dodoni I; *Quercus* along with *Tilia* and *Corylus* expand in Dodoni II, while taxa important in the first phase have reduced presence.

Pamvotis (*139.00–143.25 m*): shows early expansion of *Quercus* and *Ulmus/Zelkova* followed by later increases in *Carpinus* and *Abies*. *Abies* is recorded at high abundances similar to those of Dodoni. Evergreen *Quercus*, however, is sparsely recorded, and *Ulmus/Zelkova* abundances are lower than those encountered in Dodoni, especially Dodoni I. Although *Fagus* appears sparingly during the Dodoni, it is recorded at relatively high abundances here. It is the presence of *Fagus* populations coupled with significant abundances of *Abies* that distinguishes the Pamvotis period.

Katara (*112.75–117.00 m*): appears as a relatively short period with no particular features (although this may have been caused by sediment accumulation irregularities). Despite its stratigraphical length, an early phase of *Quercus* and *Ulmus/Zelkova* followed by a later phase of expansions of *Carpinus* and *Abies* can be discerned.

Zitsa (*83.75–89.25 m*): starts with expansions of *Quercus* and *Ulmus/Zelkova* populations while *Carpinus* and *Fagus* populations persist at lower densities and *Abies* abundances increase towards the end of the period. The most distinguishing feature of Zitsa is the dominance of *Quercus*; once its populations expand early on they remain at high abundances, rather than the normal pattern of early increase and subsequent decline to more moderate abundances.

Metsovon (*45.88–59.00 m*): distinguished by (i) significant presence of evergreen *Quercus* and a peak in *Olea* abundances during the early phase of expansion of tree populations, (ii) a subsequent phase of *Carpinus* dominance, and (iii) a notable vegetation revertence expressed as a second peak in *Quercus* (mostly deciduous) during the later stages of the period. *Fagus* is absent throughout.

Thyamis (*44.62–45.38 m*): a brief episode of *Fagus* and *Abies* expansion as well as presence of *Quercus* and *Carpinus* populations.

Perama (*40.25–44.12 m*): shows persistence of taxa at moderate abundances but mostly without any specific tendencies for earlier or later increases. Its most distinctive feature is the expansion of *Fagus* populations early on, reaching the highest abundances recorded at any one period in Ioannina 249.

Vikos (*35.00–36.75 m*): shows moderate presence of temperate taxa with an early *Pinus* phase followed by *Quercus* and *Carpinus*, and finally *Abies*.

Holocene (*10.20–17.25 m*): not completely represented in Ioannina 249, but Bottema's (1974) pollen diagrams can be of assistance in considering its distinctive features. Despite the problems of distinguishing natural vegetational succession from man-related changes, it would appear that the expansion of *Ostrya* populations during the Holocene is its most characteristic feature. *Carpinus*, *Abies* and *Fagus* are present at low abundances without any signs of expansion, perhaps a reflection of anthropogenic influence.

Lack of an independent chronology precludes any attempt to compare the duration of individual forest periods and determine the rates of vegetational change, given possible variations in sedimentation rates. For the present time, the only statement that can be made with some certainty concerns the Dodoni complex which shows two complete cycles of vegetational development and may therefore represent double the length of time than the other forest periods.

The record of open vegetation periods is more difficult to assess. The complexity of cold (and/or arid) stages has become appreciated relatively recently (e.g. West 1988). The concept of cold stages as rather long periods of uniform steppe vegetation, interspersed with few interstadials is disappearing as evidence of a variety of climates and corresponding vegetation changes is emerging. Such changes are recorded in the pollen record of the Ioannina 249 sequence as shifts from one type of open vegetation to another and by the relative abundance of relict tree populations in the landscape. Thus, a series of changes is usually observed from transitional parkland (steppe–forest or a forest–steppe), through grassland steppe communities, to a discontinuous desert–steppe vegetation (with increased *Artemisia* and/or chenopod presence). This is often followed by a transitional steppe–forest or forest–steppe, before the onset of a forest period (figure 8). A distinctive feature of the Ioannina 249 pollen diagram is the presence of pollen of certain arboreal taxa (*Quercus*, *Abies*, *Pinus*, *Ulmus/Zelkova*, *Corylus*) during open vegetation periods. The levels and consistency of their representation suggest the occurrence of tree populations in the vicinity of the Ioannina basin (Tzedakis 1993). Populations of these taxa reach highest densities during interglacial periods but continue to persist at lower abundances during glacial periods. The matter of presence of refugial populations and the criteria devised for detecting such populations are discussed in detail elsewhere (Tzedakis 1991, 1993).

An aspect of the Quaternary record that has also recently become appreciated is that in between culminations of glacial and interglacial events

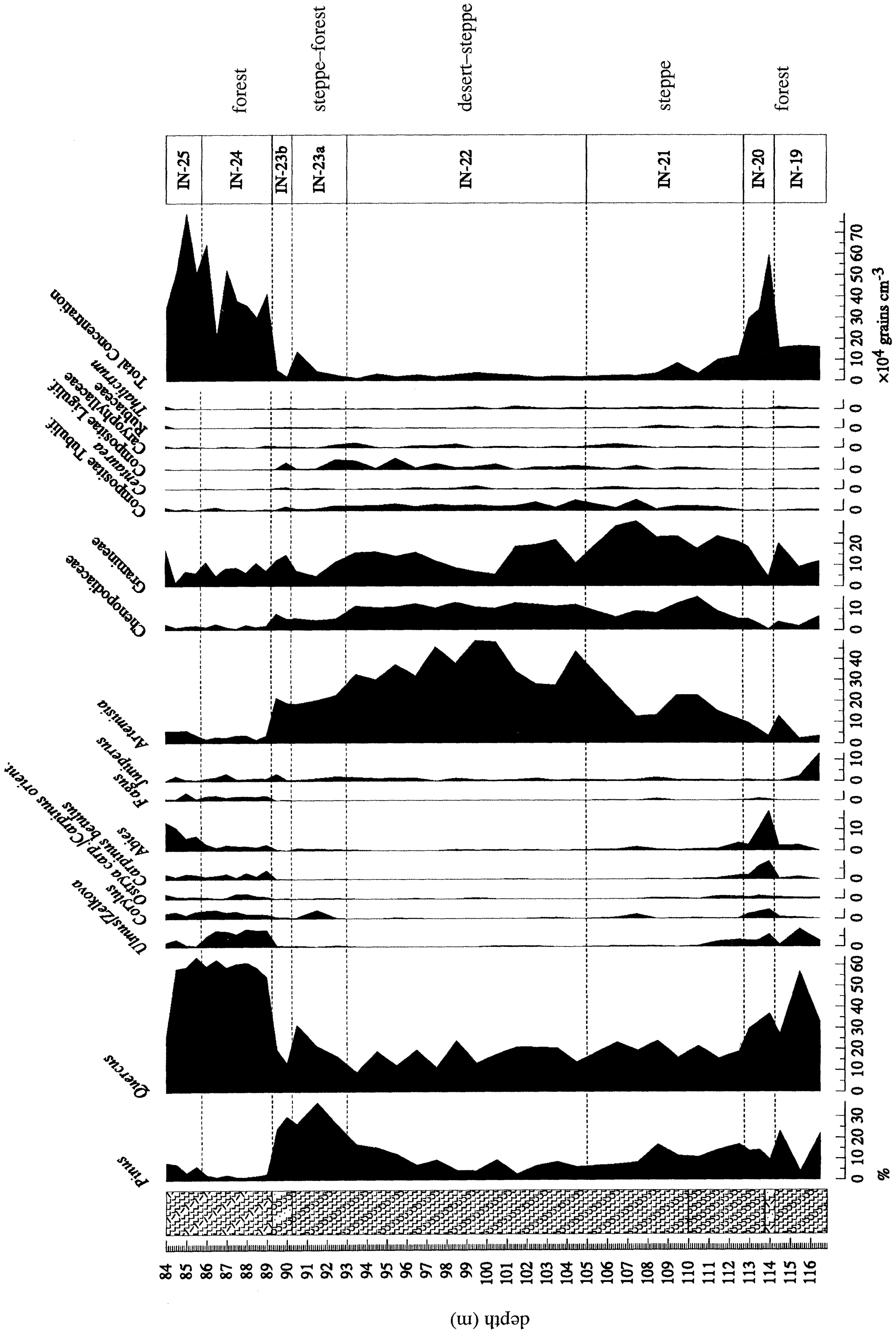


Figure 8. Pollen diagram of selected taxa showing representative series of changes in vegetation during a glacial period.

representing extreme conditions, are long periods which are intermediate in character (Porter 1989). Intermediate periods have been the norm for most of the Quaternary, representing 70–80% of the past 400 ka. Such 'average' conditions have had a significant effect in the evolution of Quaternary landscapes (Porter 1989). Average conditions in the Ioannina 249 record are represented by open vegetation periods defined as steppe–forest, forest–steppe and steppe. Extreme conditions, on the other hand, are represented by desert–steppe at one end of the spectrum, and forest periods at the other. Thus, the various vegetation phases depicted in this palynological record can be thought of as forming a continuum, one end of which is represented by closed forest and the other by open, discontinuous vegetation with possible presence of scattered trees. In between the two extremes a number of transitional types occur, which can be conceptualized either as open vegetation interspersed with tree populations of varying abundance and density, or as woodland with varying degrees of open vegetation, representing 'average' (*sensu* Porter 1989) conditions.

Consideration of the principal vegetation changes from forest to open vegetation in response to shifts from interglacial to glacial modes recorded in southern Europe and of the relation between modern vegetation and climate in the Near East and further afield has suggested that moisture availability has been the critical ecoclimatic variable, while temperature may have played a supporting role (e.g. Follieri *et al.* 1988; Bottema, 1992; Rossignol-Strick *et al.* 1992). As such, fluctuations in the AP:NAP ratio showing changes in the primary structure of vegetation at Ioannina may be regarded as an approximate measure of variations in the moisture supply. *Artemisia*, chenopod and Gramineae-dominated pollen spectra have thus been considered indicative of increased aridity during glacial periods. This is in agreement with evidence from Tenaghi Philippon where results of scanning electron microscopy on chenopod pollen from the last glacial period established the occurrence of xerophytic species with present distributions in steppe and semi-desert environments (Smit & Wijmstra 1970). It may, however, be in apparent conflict with geomorphological evidence from the Kastritsa cave, south of Lake Pamvotis (figure 1) where beach deposits representing higher lake levels (maximum at 6.4 m above present lake level) have been identified and assigned a last glacial maximum (LGM) age (Higgs *et al.* 1967; Bailey *et al.* 1983). The cave was associated with evidence for human occupation beginning at or shortly before 20 000 BP. The upper beach deposits were bracketed by hearths which provided radiocarbon dates between 20 000 and 21 000 BP. Bailey *et al.* (1983), taking into account the pollen evidence for arid vegetation during the glacial maximum, attributed raised lake levels to reduced evaporation rates due to lower temperatures. It must be emphasized, however, that the tectonic setting of the area, especially given IGME's stratigraphical evidence of relative movements of different parts of the basin, may complicate attempts to decipher past lake level fluctuations. Examination of stratigraphical logs from several boreholes in the vicinity show that the top of the upper lignite layer is encountered at increasingly shallower depths (229 m to 40 m) moving from the present-day lake shores to the Kastritsa cave (IGME, unpublished results), indicating Pleistocene tectonic uplift of the area. Thus, the possibility that vertical movements have continued to affect the block of Senonian limestones where the Kastritsa cave is situated also within the past 20 ka must be given serious consideration. It appears therefore that although the evidence of a high lake level stand at Ioannina during the last glacial maximum has hitherto permeated the literature, additional sediment stratigraphical examination and micro/macrofossil analysis on a spatial array of cores (e.g. Digerfeldt 1986) along with careful evaluation of tectonic information are required before the matter is settled. Be that as it may, pollen-inferred aridity during glacial periods is also in conflict with results from palaeoclimatic modelling of the LGM that show a steep January temperature decline and little change in precipitation (Kutzbach & Guetter 1986) or even increased seasonality of precipitation (Broccoli & Manabe 1987). To address this apparent paradox, increased cloudiness and reduced evaporation rates in summer have been invoked coupled with lowered winter temperatures and precipitation levels (COHMAP members 1988). Recently, a series of sensitivity experiments with varying winter and summer temperature and precipitation values coupled with water-balance and biome models were applied to LGM conditions at Ioannina (Prentice *et al.* 1992). Of the different scenarios examined the one involving cold winters, intense winter precipitation and summer drought was thought to reconcile most of the apparently conflicting observations: increased winter precipitation would account for greater runoff and higher lake levels, while at the same time growing season soil moisture deficit and low winter temperature would have maintained an open vegetation (Prentice *et al.* 1992). The increased seasonality of precipitation was attributed to a southward displacement of the jet stream over the Mediterranean in winter bringing increased precipitation along its track, as predicted by palaeoclimatic modelling (Kutzbach & Guetter 1986; Harrison *et al.* 1992). Nonetheless, the results of Prentice *et al.* (1992) will have to await independent confirmation from studies of evaporation/precipitation changes (e.g. trace element geochemistry of ostracod shells (Chivas *et al.* 1986)) along with a definitive statement on lake level stand at the LGM. In the meantime, the relative importance of temperature versus moisture availability remains unclear given the available evidence.

6. COMPARISON OF IOANNINA 249 WITH OTHER RECORDS

An attempt is made to compare the Ioannina 249 sequence with other established records of vegetational and environmental change. The purpose of the proposed comparisons is threefold: (i) to determine regional differences and similarities in the response of vegetation to major climatic changes; (ii) to gain an insight into the behaviour of individual species through consideration of a larger spatial scale; and (iii) to provide a chronostratigraphical framework for the Ioannina 249 record. Spectra below 166.00 m are not considered because of possible problems of redeposition and discontinuities.

(*a*) *Comparison with Ioannina I and Ioannina II*

Bottema (1974) obtained two cores from the Ioannina basin, Ioannina I and II (see figure 1 for locations). Ioannina I contained a record of the last glacial period, characterized by high values of Gramineae, *Artemisia* and chenopods and pollen of arboreal taxa present at generally low abundances, and similar to the record contained in Ioannina 249. An interstadial was recorded (zone T) with alternating high pollen frequencies of *Pinus* (reaching 40%), bracketed by high values of *Quercus*, and significant presence of *Abies* (values reaching 30%), while *Carpinus* (up to 20%) and *Fagus* (5%) also have a significant presence. Two radiocarbon dates of 37 660 ± 930 BP (GrN 6529) and 40 000 ± 1000 BP (GrN 4793), in reverse stratigraphical order, were obtained for this interstadial. Bottema (1974) proposed that the former sample may have been contaminated with younger material and considered the possibility that the other date was also too young. Examination of the forest phases recorded during the last glacial cycle in Ioannina 249 reveals a lack of obvious candidates for correlation with the interstadial of Ioannina I, mainly because of the combination of high *Abies* and *Pinus* frequencies in Bottema's (1974) sequence, although Zone IN-38 (Vikos) of Ioannina 249 represents the most plausible choice given its peaks in corresponding taxa (but at lower values) and its stratigraphical position. Assuming that the correlation is correct, the position of these phases (zone T and Vikos) within the last glacial period is still unclear as they may represent an interstadial earlier in the glacial interval than suggested by the radiocarbon dates. The late glacial–postglacial transition, represented by a decline in *Artemisia* and chenopods and an increase in *Quercus* frequencies, is dated at 10 190 ± 90 BP (GrN 4875) at Ioannina I. The corresponding transition in Ioannina 249 is found at a depth of 17.00 m. As stated earlier, the top 10.20 m of the Ioannina 249 core is missing, but despite that, the uppermost forest phase recorded in Ioannina 249 bears distinct similarities to the Holocene record of Ioannina I, in distinguishing the early rises in *Ulmus*, *Corylus* and *Tilia* associated with the rise in *Quercus* values and the later increase and maintenance of significant *Ostrya* pollen frequencies.

Ioannina II contained a basal interval (565–460 cm) initially with high *Abies* frequencies (72.9%) followed by high frequencies of deciduous *Quercus* and also *Ostrya*, *Ulmus*, *Tilia*, *Buxus*, *Celtis* and *Parrotia*. The upper part of this interval was characterized by an increase in *Pinus* and *Quercus* values. The sediment section 460–425 cm was devoid of pollen and was followed by the Holocene sequence described above. The presence of *Celtis* and *Parrotia* and the distinct character of the pollen stratigraphy of the basal section, led Bottema (1974) to propose an 'Eemian' (last interglacial) age for the base of Ioannina II. No correlation of this section has been proposed with any of the forest phases of Ioannina 249 on the basis of the biostratigraphy. The fact that such high *Abies* frequencies and the presence of *Celtis* and *Parrotia* have not been recorded in Ioannina 249 suggests that the base of Ioannina II belongs to a much earlier interglacial. Given the tectonic setting of the basin and the different behaviour of separate sub-basins, discussed earlier, this is entirely possible.

(*b*) *Strategy for long-distance correlation with terrestrial sequences*

Long-distance correlations based on pollen content require good stratigraphical control in addition to knowledge of regional vegetation history (West 1981). This is especially significant when attempting to correlate fragmentary records corresponding to individual stages or parts of stages, as has been the case in northwest European Quaternary stratigraphy. In the case of long continuous sequences the problem of the relative stratigraphical position of various stages is directly resolved, but attention to lithostratigraphy becomes vital in determining the completeness of the record. Breaks in a sequence, however, may be difficult to identify in one borehole, especially if sedimentary boundaries appear gradational. The firmest evidence can be provided by litho- and biostratigraphical examination of an array of boreholes from the same region, but this may represent an ideal situation not usually attained. In the absence of any lithological evidence for hiatus(es), the Ioannina 249 core is considered to be complete (at least the upper 166.00 m). As such, it is compared in detail only with established records from other long and continuous (rather than fragmentary) sequences in Europe, that contain a record extending at least back to the beginning of the last interglacial: Tenaghi Philippon, northeast Greece, Valle di Castiglione, central Italy and La Grande Pile, Les Echets and Plateau du Devès, France. A record of regional vegetation, unobscured by local changes, is considered of greater value for purposes of correlation, and all sequences considered here appear to fulfil this criterion. The region under consideration is sufficiently non-uniform in physiographic, climatic and floristic terms, to see wide-ranging variation in response of vegetation to environmental change. Nonetheless, first order changes associated with major climatic events should be adequately recognizable in different pollen records, given the scale and magnitude of the events. Lower order changes may or may not be represented in individual sequences or may appear sufficiently modified for direct comparisons to be made. Parallel behaviour of the same species from sequence to sequence is not necessarily expected, given the geographical variation discussed above. If it is observed, caution should be exercised in ensuring that the synchroneity of the event is corroborated by independent evidence. If such distinct similarities do belong to the same chronostratigraphic stage, then it may be useful to consider the reasons for such a widespread event. In proceeding with correlations a 'counting backwards' method in matching individual peaks or troughs in AP values is avoided. Rather, emphasis is placed first on those periods that appear to display comparable primary characteristics (e.g. extent of vegetational development) and share similar stratigraphical positions.

Examination of the forest phases in the Ioannina 249 sequence shows that an hierarchical differentiation did occur and the terms 'interglacial' and 'interstadial' are retained (see also Wijmstra & Smit 1976. cf. West 1984; Follieri *et al.* 1988). The criteria used here to define an interglacial are: (i) development of a vegetational succession where an early phase of *Quercus* (including evergreen) and *Ulmus*/*Zelkova*, followed by a phase of *Carpinus*, *Ostrya* and finally *Abies*, are discerned; (ii) total pollen concentrations reached consistently high values (over 200 000 grains cm^{-3}; mean values for the entire period exceeding 400 000 grains cm^{-3}). It should be emphasized that such criteria are for local use only in assigning hierarchical status to different forest periods of the Ioannina 249 sequence. Periods thus evaluated may be directly comparable to periods of similar status in other sequences although this may not always be the case. The Pamvotis, Zitsa, Metsovon and Holocene are assigned interglacial status, while Dodoni I and II are considered together as one interglacial (complex). The Katara along with Thyamis, Perama and Vikos phases are assigned interstadial status. Of the above mentioned periods, the Pamvotis represented the least straightforward case showing generally lower arboreal values and reduced presence of evergreen *Quercus* than the other periods of interglacial status. Problematic is also the status of Dodoni II which shows complete vegetation development with presence of evergreen *Quercus* but has mean pollen concentration values of 256 000 grains cm^{-3}. On its own it may have been assigned an interstadial status but with Dodoni I is taken to represent an interglacial complex. These decisions underline the difficulties of drawing artificial boundaries where a continuum of states is represented.

(*c*) *Tenaghi Philippon*

The Tenaghi Philippon sequence, eastern Macedonia, Greece (41°10′N, 24°20′E; 40 m above sea level), is the longest palynological record in Europe extending back to the late Lower Pleistocene (Wijmstra 1969; Wijmstra & Smit 1976; van der Wiel & Wijmstra 1987*a*,*b*) and has its own independent chronology (Wijmstra & Groenhart 1983). This and its proximity to the Ioannina area, make it the obvious standard for correlation. The proposed correlation scheme appears in table 2. Specific points where correlations are tentative are discussed in Appendix 1*a*. In general, despite differences in the character of vegetation, higher order changes are apparent in both the Tenaghi Philippon and Ioannina 249 sequences making possible the correlation of interglacials and interstadials. The effect of an east–west gradient in available moisture at the two sites was evident, not only during interglacial periods when a richer vegetation occurred at Ioannina, but also during glacial periods when arboreal taxa were generally not recorded at Tenaghi Philippon in contrast to the situation at Ioannina.

(*d*) *Valle di Castiglione*

A 250 ka pollen record is available from Valle di Castiglione (41°53′30″N, 12°45′35″E; 44 m above sea level), in central Italy (Follieri *et al.* 1988). Pollen concentration values are available from Valle di Castiglione and facilitate comparisons with Ioannina 249. Comparison of the two sequences is to some extent pre-empted by the correlations already made between Valle di Castiglione and Tenaghi Philippon (Follieri *et al.* 1988). The correlation scheme between Ioannina 249 and Valle di Castiglione (table 2) developed here appears to be in general agreement with that of Follieri *et al.* (1988), apart from one difference discussed in Appendix 1*b*.

Table 2. *Proposed terrestrial correlations*

Grande Pile/ Les Echets/ Plateau du Devès	Valle di Castiglione	Ioannina 249	Tenaghi Philippon
Holocene	Holocene	Holocene	Holocene
St Germain II	VdC-14	Vikos	Elevtheroupolis
St Germain Ic	VdC-12c	Perama	Drama
St Germain Ia	VdC-12a	Thyamis	Doxaton
Eemian	Eemian	Metsovon	Pangaion
	Roma III	IN-26	H2-3 Symvolon
	Roma II	Zitsa	H1 Symvolon
		IN-23a	Strymon
	Roma I ?	Katara	Kavalla
		IN-17b ?	Krimenes
		Pamvotis	Litochoris
		Dodoni I and II	Lekanis

(*e*) *Grande Pile, Les Echets and Plateau du Devès*

Two extensively studied sequences from France have provided a continuous record of vegetation change of the period from the end of the penultimate glacial to the Holocene in Europe: Grande Pile located in the southern Vosges Mountains (47°44′N, 6°30′14″E; 330 m above sea level) (Woillard 1978, 1979; Woillard & Mook 1982; de Beaulieu & Reille 1992*a*) and Les Echets, northeast of Lyon in the southwestern part of the Dombes Plateau (45°48′30″N, 4°55′20″E; 267 m above sea level) (de Beaulieu & Reille 1984*a*,*b*). Recently a composite record from the plateau du Devès has also emerged incorporating results from Lac du Bouchet (44°55′N, 3°47′E, 1200 m above sea level) and the ancient lake of Ribains (1070 m above sea level) (Reille & de Beaulieu 1990; de Beaulieu & Reille 1992*b*; Pons *et al.* 1992).

Correlations of the sites have been presented (de Beaulieu & Reille 1984*a*,*b*; Pons *et al.* 1992) and despite differences in the behaviour of individual taxa, the records appear remarkably similar, reinforcing the validity of the results. In view of the close correspondence amongst the records they are here discussed together. Generally accepted correlations of the sequences with other long records have already been proposed: Grande Pile with Tenaghi Philippon by Woillard (1978) and both Grande Pile and Les Echets with Valle di Castiglione by Follieri *et al.* (1988). Fitting of the Ioannina 249 record into this framework of the Upper Pleistocene is relatively straightforward (table 2). The last interglacial period followed by two interstadials is recorded in much the same fashion at Ioannina as in the French sites. Zone IN-35 may be the equivalent of the Montaigu event (Reille *et al.* 1992). As with other sequences, correlations with middle glacial interstadials is not attempted because of insufficient resolution of the Ioannina 249 record.

(*f*) *Emerging broad-scale differences and similarities*

In general, all sequences considered appear to record similar changes in the primary structure of vegetation, associated with major fluctuations in global climate. The extent and character of forest development served as the main points for correlation, while the nature of open vegetation was less helpful in this respect. These palynological records can be considered a reflection of major climatic changes related to the reorganization of general atmospheric circulation under the influence of changes in insolation and extent of ice sheets. Vegetation changes, however, are a function of not only how global events are translated into local climatic terms, but also of the pool of plant taxa available at a site, the climatic tolerances and internal biotic factors of taxa, and the state of soils in the area. One would thus expect to see differences from one area to the next as the same large-scale event is expressed in variable vegetational terms.

In Greece, *Quercus* and *Pinus* dominate forest periods, although in northwest Greece *Abies*, *Carpinus*, *Ulmus*/*Zelkova* and *Fagus* assume a significant role during certain periods. In central Italy, *Quercus* is again important but other taxa such as *Fagus* and *Carpinus* share the same role, while *Abies*, *Ulmus* and *Zelkova* show periods of high abundances less consistently. In France, different taxa expand at different times during the same forest period, rather than having one or two that appear at high abundances during all or most of the period. Thus a temporal sequence of changing dominance (rather like a relay) is recorded: *Pinus–Betula*, *Quercus–Ulmus*, *Corylus*, *Taxus*, *Carpinus*, *Abies–Picea*. The main features particular to the French sites are the peaks in *Corylus* abundances and the presence and expansions of *Picea* and *Taxus*. Periods of open vegetation are generally characterized by high Gramineae–*Artemisia*–chenopod values although a general trend of decreasing *Artemisia* and chenopod abundances from south to north can be discerned. The highest values of chenopods are recorded at Valle di Castiglione. This may be a reflection of increased aridity in the Valle di Castiglione area during glacial periods. The high chenopod values may also represent increased presence of halophytes, a reflection of local saline conditions.

Given the factors influencing the character of local vegetation, it is interesting to consider similar tendencies of the same taxa in different regions. Such tendencies are even intriguing when they appear to occur approximately at the same time throughout the region.

An expansion of *Olea europaea* populations during the early part of the last interglacial is recorded at both Valle di Castiglione and Ioannina 249. They are associated at both sites with an increase in evergreen *Quercus* and indicate Mediterranean conditions with frost-free winters and summer drought. Presence of *Olea* pollen is recorded at the high altitude site of Ribains (Plateau du Devès) and although attributed to long-distance transport it was considered indicative of presence of Mediterranean-type vegetation at the margins of the region (de Beaulieu & Reille 1992*b*).

High abundances of *Zelkova* have been recorded at Valle di Castiglione, especially during the last interglacial, but also during the subsequent interstadials. As *Zelkova* has not been recorded outside Italy in Upper Pleistocene sediments before (Follieri *et al.* 1986, 1988) the presence of (albeit few) pollen grains of *Zelkova* during chronostratigraphically equivalent periods at Ioannina is worth noting. Although today the only *Zelkova* species in Europe is restricted to Crete (*Z. abelicea*), the number of species involved remains unclear as the possible presence of another *Zelkova* species (*Z. carpinifolia*) has been reported from earlier interglacials in Italy (Follieri *et al.* 1986) and pollen of intermediate (*Ulmus–Zelkova*) morphology was encountered at Ioannina. Given such uncertainties in identification, the history of *Zelkova* in northwest Greece and how it compares to the record in Italy will have to await additional studies on pollen morphology and also pollen analysis of other long sequences.

Carpinus betulus is the species that has the most impressive common pattern. It is present during the last interglacial at all sites and shows high peaks in the Ioannina 249, Les Echets, Grande Pile and Plateau du Devès records. This pattern appears to be in agreement with the prevailing view of a *Carpinus betulus* zone as a characteristic feature of the last interglacial (e.g. Phillips 1974; Turner 1975; Watts 1988). This is documented throughout Europe to the extent that fragmentary records from interglacial deposits are often assigned to the last interglacial period on the basis of presence of the *Carpinus betulus* zone. Such practice of biostratigraphical correlation without sufficient emphasis on lithostratigraphical relations may in fact be responsible for certain records being assigned to the wrong temperate stage. *Fagus* is the other taxon that has a common pattern on a wide scale. With the exception of occasional grains, it is virtually absent throughout the last interglacial at all sites except Valle di Castiglione where it persists at low abundances; the *Fagus* values at the Italian site, however, are the lowest recorded during a forest period within that sequence. Examination of the Ioannina 249 record shows that the last interglacial is the only forest period where *Fagus* is absent; although *Fagus* may not always be a significant feature of the other forest periods, it is nonetheless recorded at higher and more consistent frequencies than the last interglacial. The almost complete absence of *Fagus* throughout the last interglacial is also supported by the palynological record from central and western Europe (e.g. Watts 1988) where generally, apart from sporadic occurrences in some deposits (e.g. Środoń 1950; Šergcelj 1966), *Fagus* pollen is generally not encountered. Exceptions to this rule have been reported in certain cases with *Fagus* reaching significant values, but they are derived from fragmentary records (e.g. Pop 1957; Božilova & Djankova 1976; Gremmen *et al.* 1984) where the chronostratigraphical position of the deposit is far from clear, or from soils formed on loess (e.g. Frenzel 1964) where additional problems of pollen taphonomy and provenance may arise. In contrast to its Eemian condition, *Fagus* reaches significant values during the ensuing interstadial period at Valle di Castiglione, Les Echets and Ioannina (up to 40%, 30% and 20%, respectively) and is even recorded during the Drama interstadial at Tenaghi Philippon, where it is absent in most forest phases. What emerges, therefore, is the uniformity of the last interglacial vegetation with regard to the occurrence of high values of *Carpinus betulus* throughout Europe (even in areas beyond its modern geographic range) and also the virtual absence of *Fagus*. This suggests that an explanation for the distinctive features of the Metsovon interglacial of Ioannina 249 may lie with factors whose influence extends to a continental scale and a climatic interpretation appears plausible. The climatic influence must have been extreme to the extent that it overrode local variability and led to the establishment of a *Carpinus betulus* forest in Europe, while *Fagus* populations never expanded but continued to survive at low abundances restricted to few sites (e.g. Valle di Castiglione?). Independent non-biological evidence, such as calculated insolation values, generally indicate that the last interglacial period was characterized by higher summer temperatures than the Holocene. This is largely related to July solar radiation being 12% higher at 125 ka than today, a function of greater orbital eccentricity during the last interglacial (Berger 1978*a*,*b*). The greater radiation would have led to increases in sensible and latent heat. Results from a sensitivity experiment to astronomical forcing at 125 ka and 115 ka using a spectral general circulation model (Royer *et al.* 1984), show higher summer temperatures and lower winter temperatures at mid-latitudes than today at 125 ka, and a cooling in surface temperatures along with an increase in soil moisture at 115 ka compared to 125 ka. It is possible that high temperatures and reduced available moisture were responsible for the vegetation changes observed during the last interglacial in Europe.

As low precipitation and high temperatures are limiting factors for *Fagus* today (Jahn 1991), it is possible that the climatic conditions of the last interglacial reduced the competitive vigour of *Fagus* or contributed to direct drought damage. It is difficult, however, to envisage a climatic scenario on a European scale that only affected a species of such wide climatic amplitude as *Fagus* (e.g. Ellenberg 1988; Jahn 1991), while other trees were not influenced. It may be that the actual damage occurred during the preceding cold stage, when particular climatic conditions led to the virtual extermination of the refugial *Fagus* populations; frost damage may have been critical in this case. The problem with a climatic explanation, however, still remains, namely why other taxa sharing the same glacial stations were not affected. Competition for limited resources may have played a role, and low temperatures and water deficiency may have put *Fagus* at a disadvantage. An alternative explanation for its virtual absence in Europe during the last interglacial may be disease through a forest pathogen specific to *Fagus*. Bark disease associated with the fungus *Nectria coccinea* (Phillips & Burdekin 1992) may provide a modern analogue. Drought or extreme frost have also been considered important causes of bark disease. Outbreaks of tree epidemics have been observed in the pollen record as in the case of the documented *Castanea dentata* blight in North America this century (Anderson 1974) and have been inferred for *Tsuga* in North America at 4700 BP (Davis 1981; Webb 1982). These events are more or less synchronous (within 50 years) on a subcontinental scale and appear in pollen records as a sudden collapse in values. As such decline for *Fagus* is not observed in Eemian records because its populations never expanded in the first place, it may be that an epidemic spread during the population contraction phase of the preceding cold stage. However, the lack of enough pre-Eemian records coupled with problems of palynological detection of small tree populations preclude the detection of such an event. If indeed an epidemic spread during the cold stage, then *Fagus* populations remained suppressed for a considerably longer period compared with the 1000-year period for *Tsuga* in N. America (Davis 1981); this, in turn, may suggest that when finally *Fagus* developed a resistance, or the pathogen lost its virulence, a restoration to original abundances did not occur because of adverse climatic conditions and competition that continued into the Eemian. Perhaps new and possibly more robust populations developed by the time of the early Weichselian interstadial which were able to compete successfully and expand their range. For the present, however, it remains unclear as to whether climatic conditions, competition, disease, or a combination of the above inhibited the expansion of *Fagus* populations during the last interglacial in Europe.

(*g*) *Correlation with the marine oxygen isotope record*

The oxygen isotope record from benthonic or planktonic foraminifera has assumed the importance of a global stratigraphical correlation standard not only for deep-sea sediments, but also for continental sequences (see discussion in Shackleton 1989; West 1984). Correlation of continental events with the marine record for the period *ca.* 130 ka to present is generally established (e.g. Mangerud 1989). Correlation of earlier stages, however, has not been very successful, mainly frustrated by uncertainties of independent dating on terrestrial sediments and general lack of sufficiently long terrestrial sequences to provide a stratigraphical framework.

The univariate nature of the oxygen isotope curve means that the only diagnostic features available for correlation are the degree of change recorded and the general shape of the curve. As the summary AP percentage and concentration curves of Ioannina 249 appear to convey the higher order changes in vegetation, they are considered an adequate record for the attempted correlations. Despite the fact that the oxygen isotope and pollen curves are a direct representation of entirely different parameters, they are both considered proxy indicators of climate. It is on this basis that stratigraphical correlation can be attempted, through the definition of geological-climate units. However, visual inspection of the curves and assignment of units to specific isotope stages on general similarity of individual peaks or troughs and relative stratigraphical position, is not an entirely satisfactory approach, especially when considering that the AP curves contain a local climatic signal which may or may not coincide with the global one. The solution comes from the Tenaghi Philippon record, which has been correlated with the oxygen isotope record on the basis of its independent chronology. Wijmstra & Groenhart (1983) developed an age model derived from radiocarbon dates from the upper part of the sequence, a generally accepted approximation of 120 ka for the last interglacial and the age of the Brunhes–Matuyama magnetic reversal boundary. A time–depth relation curve made possible the calculation of the age of the major pollen zone boundaries. These independently derived results were compared with the age of oxygen isotope stage boundaries from core V28-239 (Shackleton & Opdyke 1976). The comparison of the ages of major boundaries showed good agreement and a correlation scheme was proposed (Wijmstra & Groenhart 1983). Given the established correspondence of primary events of the Ioannina 249 and Tenaghi Philippon records discussed above (table 2), an attempt has been made to cross-correlate the Ioannina 249 record with the isotope record using Tenaghi Philippon as a 'stepping stone' in the process (Tzedakis 1993). Since the correlation between the two terrestrial records is not entirely complete nor perfect, direct comparisons between summarized pollen curves and the oxygen isotope curve can be of assistance.

Following Shackleton (1989), correlation is attempted here with a physical marine sediment sequence rather than with an idealized and averaged curve. Instead of core V28-239 (Shackleton & Opdyke 1976) used for correlations by Wijmstra & Groenhart (1983), two sequences of improved resolution and chronostratigraphical control obtained from the Panama Basin in East Pacific are considered here: core V19-30 (3°21′S, 83°21′W) (Shackleton & Pisias 1985) and core V19-28 (2°22′S, 84°39′W) (Ninkovich & Shackleton 1975). In this study, the oxygen isotope record of core V19-30 was used for the interval 340 ka to present, while that of V19-28 was used for the earlier part.

The proposed correlation between the Ioannina 249 record and that of (V19-30 + V19-28) appears in figure 9. Specific points of the correlation scheme are presented in Appendix 1*c*. Interglacials and interstadials are assigned to odd-numbered isotope stages and substages according to their correlation with the equivalent periods at Tenaghi Philippon. As pollen zones or superzones of Ioannina 249 may correspond to specific intervals within an isotope stage, substages are also used in correlations. Substages are here taken to represent an interval within a stage containing a local maximum or minimum in isotope values (i.e. an isotope event *sensu* Pisias *et al.* (1984) and Prell *et al.* (1986)), so that, for example, substage 9c contains event 9.3. Substages informally defined here are designated in lower case letters.

The correlation of the Ioannina 249 record with the oxygen isotope record provides a provisional chronostratigraphical framework. Ages of boundaries of isotope stages are only transferred to the equivalent boundaries of contrasting vegetational episodes of the Ioannina 249 record when their correlation is considered reasonably secure. Thus, the boundaries most accurately placed are the glacial-to-interglacial transitions corresponding to the 'terminations' of Broecker & van Donk (1970). Given that the lower boundary of Dodoni is considered to correspond to the Stage 12 to Stage 11 transition (Termination V), it is proposed that the sediment sequence of Ioannina 249, down to a depth of 162.75 m represents a record of the past 423 ka. Since the correlation of different periods of the Ioannina 249 record represented varying

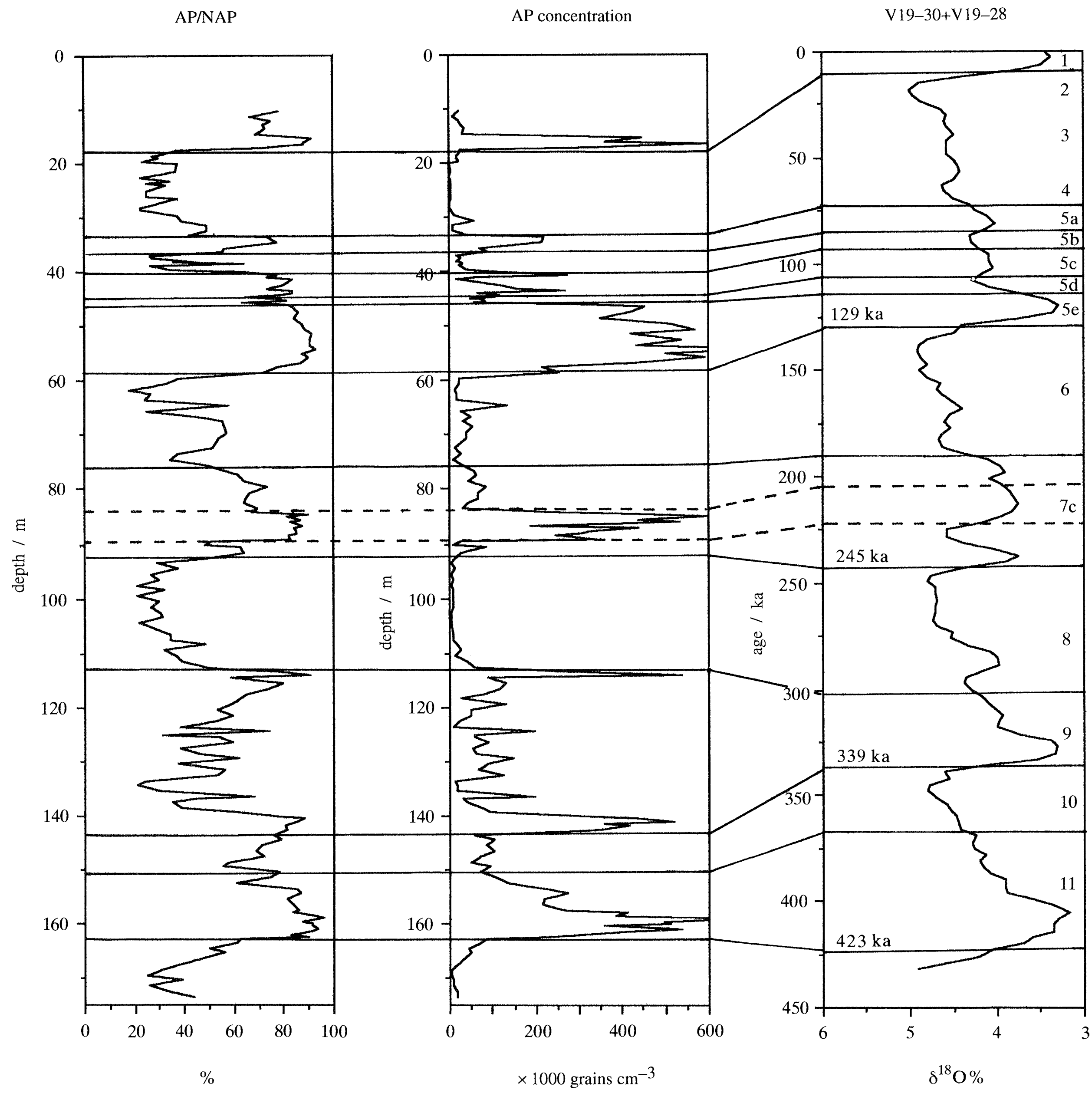


Figure 9. Ioannina 249 AP/NAP percentage and AP concentration curves plotted again depth (10.20–174.00 m) and composite oxygen isotope record of V19-30 (for 0–340 ka) and V19-28 (for 340–432 m) plotted against time. Proposed correlations between Ioannina 249 and the marine record are presented. See text for further discussion.

degrees of uncertainty, there has been no attempt to assign ages to all pollen zone boundaries.

It is important to bear in mind that in 'borrowing' the marine chronology, the operative assumption is the synchroneity of events in the oxygen isotope record and in the terrestrial vegetation record. This may be a reasonable assumption when dealing with transitions from glacial to interglacial conditions which are relatively rapid and large-scale events. The transition from interglacial to glacial conditions, however, is temporally a more diffuse event as ice sheet growth tends to be slower in comparison to ice sheet decay (Weertman 1964; Imbrie & Imbrie 1980). It is possible that the assumption of synchroneity may not be correct in this case, as vegetation may respond to a different set of climatic variables and at different rates than the process of ice build up as recorded in the oxygen isotope curve. The oxygen isotope record can serve as a valuable stratigraphical tool in land–sea correlations but assessment of leads and lags between vegetation and different components of the climate system can only be achieved when an independent terrestrial chronology of sufficient accuracy and detail becomes available.

Examination of figure 9 suggests that the primary structure of the AP percentage curve mirrors that of the isotope record. Peaks in the AP concentration curve, on the other hand, appear to correspond to specific events within isotope stages. To illustrate this, the way that the equivalent period of isotope Stage 7 is represented in the terrestrial curves is considered. The percentage curve shows generally high values over a broader area than the concentration curve but the intervals of local maximum values for both curves coincide. The interval is defined as the Zitsa interglacial and the pollen evidence suggests a dense *Quercus*-dominated forest. Adjacent to this interval are transitional phases of high *Pinus* percentages and low total concentrations, indicating an open *Pinus* woodland. These intervals taken together (IN-23 + Zitsa + IN-26) have been correlated with Stage 7, considered to represent a time span of 59 ka (Martinson *et al.* 1987). The more extreme conditions of dense forest associated with maximum AP values must then be equivalent to a specific isotope substage (probably that of 7c: duration of 12 ka).

This example draws attention to the definition of interglacial in the terrestrial record. As discussed earlier, 'interglacials' or 'temperate stages' in palynological records are usually defined by extent and length of forest development and their duration is approximately 10–20 ka; the lower boundary of a temperate stage is defined as the point where AP frequencies consistently exceed those of NAP (Zagwijn 1957), while the reverse definition is used for the temperate-to-cold stage boundary. The lower boundary of a cold stage (and by extension the top of a temperate stage) may be difficult to place given the diffuse nature of the transitional period, as discussed above. By comparison, boundaries of deep-sea stages represent inflection points in the isotope curve from intervals of higher values to those of lower values and vice versa, with glacial-to-interglacial transitions more clearly defined as they represent rapid events (terminations). Most odd-numbered isotope stages in the past 450 ka are approximately 50–60 ka in length. The obvious conclusion is that a terrestrial temperate stage that is not compound in character but contains only one forest period may not be chronologically equivalent to an odd-numbered deep-sea stage but rather to an interval within a stage, as their boundary definitions (especially the upper boundaries) may not necessarily represent the same event. Thus, the last interglacial period in northwest Europe (Eemian) is generally considered as the equivalent of isotope Substage 5e rather than the whole of Stage 5 (e.g. Mangerud 1989). In the fragmentary record of glaciated regions, an interglacial deposit found sandwiched between cold stage inorganic deposits may indeed contain the upper (temperate-to-cold) terrestrial stage boundary but the later transitional interval including the stratigraphical level equivalent to the marine odd-to-even stage boundary may be missing because of erosion, lack of lake sedimentation etc. Thick and continuous terrestrial sequences on the other hand, present the opportunity to determine the entire length of the period equivalent to an odd-numbered isotope stage by consideration of the transitional periods (e.g. steppe–forest and forest–steppe periods) and the choice of correlating them *en bloc*. As such, long sequences can make a significant contribution to the land–sea correlation scheme, not least through the evaluation of the completeness of the terrestrial stratigraphical record.

7. CONCLUSIONS

1. A core recovered from a thick sedimentary sequence in the Ioannina basin provided a continuous record of vegetational dynamics spanning several glacial–interglacial cycles. Correlation with the deep-sea oxygen isotope curve led to the assignment of an age of 423 ka to the earliest glacial-to-interglacial transition recognized in the Ioannina 249 record. The Ioannina sequence thus presented an opportunity to observe changes in vegetational communities at one location through a series of Quaternary climatic modes where background factors (bedrock, topography) can be considered constant.
2. The results of pollen analyses of Ioannina 249 showed an hierarchical order of variability embedded in the data set. Higher order of magnitude changes in vegetation were alternations between forest and open vegetation communities. These changes reflected the response of vegetation to major climatic shifts from interglacial to glacial modes. Superimposed on these oscillations was a lower order variability reflecting transient vegetational development within interglacial and glacial periods. During forest periods a distinct succession occurred which was complex and progressive: succession began with expansion of *Quercus* and *Ulmus*/*Zelkova*, followed by *Carpinus* and to a lesser extent *Ostrya*, and finally *Abies* populations increased often accompanied by *Fagus*. Although particular taxa assumed an overriding importance and modified the character of different periods, the underlying pattern of differential order of expansion usually remained discernible. A series of changes was also observed during the course of open vegetation periods starting with a steppe–forest or a forest–steppe vegetation, followed by a grassland steppe community and finally a discontinuous desert–steppe vegetation. In general, the progression to desert–steppe vegetation was reflected by increased importance of *Artemisia* and chenopods over Gramineae, diminished presence of relict tree populations, and reduced vegetation cover.
3. Long-distance comparison of Ioannina 249 with other continuous sequences from Greece, Italy and France showed that, despite certain differences, a correlation scheme among the records could be established. The emergent good correspondence, especially with the Tenaghi Philippon record, provided further support for the absence of any major stratigraphical discontinuity at the Ioannina sequence. Proposed correlations were based on the primary structure of vegetational development and relative stratigraphical position. Distinct features relating to a taxon's dominance during particular periods did not form part of the correlation criteria, so that once chronostratigraphical equivalence was established their

significance could be assessed. The emergent similarities in the behaviour of individual taxa during the same period on a European scale were linked to processes operating at a continental scale and able to override local variability.

4. Correlation of Ioannina 249 with the marine record has highlighted differences between terrestrial and deep-sea stages. The length of time represented by the two types of stages may be significantly different and a terrestrial temperate stage that is not compound in nature is normally equivalent to an interval (substage) within a deep-sea stage.
5. Examination of additional long pollen sequences from Greece, and generally from southern Europe, can provide an improved insight into long-term vegetation dynamics and contribute to the evaluation of the completeness of the records hitherto available and the degree to which events represented in one area are of local or regional significance. The variation of response of vegetation with site characteristics can thus be assessed, leading to the emergence of a large spatio-temporal scheme of vegetation change that can be compared with the marine record and with independent palaeoclimatic information from General Circulation Models (e.g. Royer *et al.* 1984; Prell & Kutzbach 1987), or with estimates of insolation values (e.g. Berger & Loutre 1991).

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APPENDIX 1

CORRELATIONS OF IOANNINA 249 WITH OTHER RECORDS: SPECIFIC POINTS

(*a*) *Tenaghi Philippon*

There are two areas in the Tenaghi Philippon and Ioannina records where correspondence is somewhat tentative and alternative scenarios could be invoked. The first regards the proposed correlation between Doxaton and Thyamis (table 2). This is complicated, by the somewhat ambiguous nature of Thyamis: the increased inorganic content of the sediments, associated with presence of *Abies*, *Fagus*, *Carpinus* and *Buxus*, may point to redeposited pollen. However, lack of *Fagus* in the preceding interglacial makes redeposition less likely. Another plausible interpretation is that the early part of the interstadial (with relatively higher values of *Quercus* and *Ulmus/Zelkova*) is missing because of erosion. In that case an alternative correlation may be proposed where Thyamis is equivalent to Drama and Perama to Elevtheroupolis, leaving Vikos to represent a middle glacial interstadial at Ioannina, which is not represented at Tenaghi Philippon. Nevertheless, in the absence of any direct evidence (e.g. erosional contact) the most parsimonious explanation remains the first correlation scheme as presented in table 2.

The second area where correlation presents certain difficulties is the interval between the Strymon and Lekanis periods of Tenaghi Philippon where three interstadials (Kavalla, Krimenes and Litochoris) are represented (table 2). The lowermost of the three (Litochoris) displays the most complete vegetational development, which is similar to the vegetational development observed at the Pamvotis forest period of Ioannina 249, the difference being the considerably more significant expansion of *Abies* associated with *Fagus* populations at Ioannina. A correlation between Litochoris and Pamvotis is proposed. Although Kavalla is characterized by deciduous *Quercus* forest with *Pinus* dominating the landscape, while the Katara forested interstadial of Ioannina 249 shows a sequence of deciduous and evergreen *Quercus* forest with *Ulmus/Zelkova* followed by expansion of *Abies* populations, a correlation is suggested between the two periods. This is based partly on relative stratigraphical position but also on the fact that upon closer examination a sequence of vegetational development can in fact be discerned at Kavalla with an early *Ulmus* presence followed by *Abies* expansion. Correlation of Krimenes is more difficult as no major forested phases are recorded at Ioannina between Pamvotis and Katara. Krimenes is characterized by deciduous *Quercus* forest with *Pinus* and a possibly equivalent period is represented by subzone IN-17b showing increased presence of *Quercus* woodland in an open forest–steppe vegetation. A tentative correlation between Krimenes and subzone IN-17b is suggested.

(*b*) *Valle di Castiglione*

The main difference between the correlation scheme of Follieri *et al.* (1988) and the present one, regards the treatment of Roma I (VdC-3) which was originally correlated with the Strymon interstadial of Tenaghi Philippon. This solution, however, appears to disregard the fact that whereas Roma I is characterized by a complete vegetational development with significant values of *Carpinus* (over 40%) and presence of *Ulmus*, evergreen *Quercus*, *Fagus* and *Abies*, and high pollen concentration values, Strymon is solely represented by an expansion of deciduous *Quercus*. Moreover, the steppe period of VdC-4 appears to be longer and, judging from the low concentration values, more extreme than zone G of

Tenaghi Philippon. In Ioannina 249, the Katara forested interglacial shows a vegetational development with *Quercus* (including evergreen), *Ulmus/Zelkova*, *Abies* and *Carpinus*, and generally high concentration values. On the basis of the vegetational development and high concentration values correlation of Roma I with Katara is proposed. This means that by extension Roma I becomes indirectly correlated with the Kavalla interstadial of Tenaghi Philippon, which, must be admitted, is not fully satisfactory either. Nevertheless, Kavalla appears to be of greater length and have somewhat higher presence of other arboreal elements than the Strymon interstadial.

(*c*) *V19-30 + V19-28*

The following points in the correlation scheme between Ioannina 249 and the marine record deserve attention.

The Dodoni interglacial complex is correlated with isotope Stage 11. Dodoni I is taken to correspond to substage 11c.

Examination of Stage 10 reveals that it is less extreme than Stages 12, 6, and 2 (Shackleton 1987) and of relatively short duration (approximately 23 ka (Imbrie *et al.* 1984)) which can account for the moderate character of zone IN-12. In keeping with the Tenaghi Philippon correlation scheme, the interval including the forest periods Pamvotis and Katara along with the intervening periods of fluctuating conditions have been correlated *en bloc* with isotope Stage 9. The Pamvotis period is taken to correspond to isotope substage 9c.

A point of departure from the Tenaghi Philippon oxygen isotope correlations concerns the end of Stage 7. Pollen zone H3 of Tenaghi Philippon was assigned to Stage 6 by Wijmstra & Groenhart (1983). In the present account, however, zones H2 and H3 of Tenaghi Philippon were correlated with zone IN-26 of Ioannina 249 which along with Zitsa and zone IN-23 are considered here to belong to the complex represented by isotope Stage 7. The Zitsa interglacial is probably the chronostratigraphical equivalent of substage 7c.

Metsovon, Perama and Vikos periods are correlated with Substages 5e, 5c and 5a, respectively. In keeping with the Tenaghi Philippon correlations with the oxygen isotope record (Wijmstra & Groenhart 1983), the Thyamis interstadial (correlated with Doxaton of Tenaghi Philippon) together with zones IN-33 and IN-35 are assigned to Substage 5d. It should be pointed out that this, by extension, is in disagreement with proposed correlations between Grande Pile (and by extension Les Echets and Plateau du Devès) with Tenaghi Philippon, on one hand, and with the oxygen isotope record, on the other: St Germain Ia was considered equivalent to Doxaton by Woillard (1978) (see table 2), while St Germain Ia, Ib and Ic were considered together as equivalent to Substage 5c, and Melisey I equivalent to 5d by Guiot *et al.* (1989). Zone IN-37, correlated with zone T of Tenaghi Philippon, is assigned to Substage 5b.

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