Review of the Late Quaternary vegetation history of Epirus (NW Greece)

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Abstract. Based on data from the pollen analysis diagrams, an attempt has been made to represent in a synoptic manner the vegetation history of Epirus during the phases of Pleistocene and Holocene. In general, open steppe vegetation dominated during the glacial periods. Concurrently, though, forest vegetation was constantly present, especially in the mountainous regions of Epirus. Many woody species of the current temperate zone withdrew to and have survived in these regions. During the last interglacial, dense forest vegetation, which consisted mainly of mixed broadleaves, had developed, comprising many woody species that are now extinct. The vegetation development during the Early Holocene was influenced by the climate and resulted in the growth of forests in the plains as well as in the mountainous regions. Anthropogenic interference in Epirus has been traced back as early as the mid 6th millennium BC. Sooner or later, depending on the location, human interference, which mostly included pastoral activities, resulted in degradation and even extinction of the forest vegetation. Major events in the vegetation development of the last millennia were transformation of the deciduous oak forests to pseudomaquis or maquis vegetation mainly in the low and middle altitudes, and disappearance or withdrawal of the mountainous forest vegetation to lower altitudes, where forest limits have been formed as a result of human impact.

Key words: Epirus – Greece, Holocene, Pleistocene, pollen analysis, vegetation history

Introduction

Epirus is located in Northwest Greece. It is the most mountainous region of Greece, with a particularly intense and complex geomorphological anaglyph, starting from the Ionian Sea and ending at the Pindos mountain range. In combination with abundance of surface and ground waters associated with high precipitation, this anaglyph creates a plethora of alternating microenvironments and corresponding vegetation units of particular importance and interest.

In the western part of Epirus, starting from the seashore and up to 300–400 m a.s.l., the *Quercetalia ilicis* zone lies, dominated by phrygana and maquis. Above *Quercetalia ilicis* and up to 900 m, depending on the exposition, spreads the *Quercetalia pubescentis* zone. In the lower part of this zone (*Ostryo-Carpinion orientalis*) scrublands (pseudomaquis) or woodlands of *Quercus coccifera*, *Carpinus orientalis, Ostrya carpinifolia,* etc. occur, while in the higher part (*Quercion confertae*) there are forests of mainly deciduous *Quercus* spp. Extended *Pinus nigra* forests spread between *Querceta-*

lia pubescentis and *Fagetalia* zones. The *Fagetalia* zone covers the higher parts of the Pindos mountain range, where forests of *Abies borisii-regis* and mostly of *Fagus sylvatica* grow. In certain high-altitude parts of the Epirus mountains there are *Pinus heldreichii* woodlands, which belong to the *Vaccinio-Piceetalia* zone (*Pinion heldreichii*). Finally, the subalpine vegetation of the *Astragalo-Acantholimonetalia* zone at the mountain peaks comprises dwarf shrubs, e.g. *Juniperus communis* subsp. *nana*, and mainly grasses.

In many cases, the present vegetation has altered to such a degree that its past state cannot be inferred by its current appearance, as a result of the human presence and activity in this region throughout the centuries. According to Bailey (1997), humans have continually inhabited Epirus for 250 000 years and its natural environment has undergone the most intense changes as compared to any other part of Europe.

Information on the vegetation history of an area is provided potentially by palynological research and application of pollen analysis. In the present study an attempt has been made to represent synoptically the temporal vegetation development of Epirus on the basis of data obtained from pollen analysis at various sites of the area.

Methodology

Pollen diagrams present concisely the results from applications of pollen analysis and reproduce under certain conditions the successive stages of vegetation in an area. The study and interpretation of a pollen diagram allow not only a reconstruction of the vegetation history, but also provides characteristic information for conclusion-drawing on the factors that affect vegetation and its development (Faegri & Iversen 1989). Absolute dating of a pollen diagram can be achieved with the help of the radiocarbon (C^{14}) dating method.

In every pollen diagram the depicted vegetation development derives not only from the core-sampling area but also, more or less, from a wider region, depending on the 'openness' of the coring site, the existing geomorphological and climatic conditions, and the differential pollen production, dissemination and preservation (Prentice 1985; Spieksma & al. 1994; Sugita 1994). Obviously, data on vegetation development in a closer region to the coring site are more detailed and reliable.

Human activity in pollen diagrams

Human activity in the pollen diagrams is principally indicated by plants regarded as anthropogenic indicators and by the ratio of arboreal pollen to non- arboreal pollen (AP: NAP).

Anthropogenic indicators include pollen types directly or indirectly associated with human activity, such as pollen of cultivated plants, weeds and plants associated with grazing, overgrazing, as well as human activities for pasture creation (e.g. *Cerealia*, *Olea*, *Vitis*, *Humulus*/*Cannabis*, *Rumex*, *Plantago lanceolata*, *Asphodelus*). Other indicators are the plants characteristic of the destructive human impact on natural vegetation caused by fires, clear-cutting, etc. (e.g., *Artemisia*, *Chenopodiaceae*, *Juniperus*, *Pteridium*, *Poterium*/*Sanguisorba minor*), and species introduced through human activity (e.g. *Juglans, Castanea*) (Behre 1981, 1990; Bottema 1982; Bottema & Woldring 1990).

A decrease in the AP:NAP values reflects shrinking of the forest cover and, when associated with anthropogenic indicators, could be attributed to human activity. Conversely, an increase in the ratio usually indicates forest expansion, following either the lessening or ceasing of intense human interference in forest vegetation.

Palynological data from Epirus

In Epirus, the hydrologic conditions have formed sediments suitable for coring, mainly at low and middle altitudes. Currently, data was attained from a series of pollen diagrams from various sites in Epirus (Fig. 1), in order to present concisely the vegetation history of the area. Most of these diagrams cover a larger or smaller part of the Pleistocene. In fact, diagram É-249 (Tzedakis 1994) covers a period of 423 000 years, which is particularly significant for the vegetation history of the Pleistocene, and not only for Epirus but for a wider region of SE Europe in general. Chronologically, all diagrams extend to the Holocene, but in some of them the later part of that period was not covered, owing to the fact that the corresponding section of the sediment was either missing due to erosion, or did not contain preserved pollen grains. Table 1 shows the palynologically investigated sites in Epirus, the altitude, the zonal vegetation to which they belong according to Dafis (1975), their approximate basal age, and the authors. In Table 2 the pollen assemblage zones of the palynologically investigated sites in Epirus, are grouped in correspondence to the main stages of vegetation development.

Fig. 1. The palynologically investigated sites in Epirus.

Dating

The radiocarbon dating in the various pollen diagrams is in years BP. Along with this, data are given in years or time periods BC/AD, according to the curves of Stuiver & al. (1998a, b) so as to present the events in a more familiar time scale. In some cases a general chronological indication (e.g. centuries, millenia) was preferred, so as to associate the described events to particular historical periods.

Results and discussion

Pleistocene

The Pleistocene is characterized by intense climatic changes, since the glacial periods with their prevailing cold–dry climate alternate with the interglacial periods when the climate was warm and humid. In Southern Europe, the glacial–interglacial cycle had rather a dry–humid character than a cold–warm one. As a result, humidity in that area became the critical factor for the growth of plants (Bottema 1974; Willis 1997).

Table 1. The palynologically investigated sites in Epirus.

Site	Altitude (m a.s.l.)	Zonal vegetation	Approximate basal age (years BP)	Authors
Kalodiki	107	*Quercetalia ilicis* (*Quercion ilicis*)	24000	Ioakim & Christianis 1997
Ziros	50		16000	Turner & Sánchez-Goñi 1997
Gramousti	285	*Quercetalia pubescentis* (*Ostryo-Carpinion orientalis*)	14000	Willis 1992a
Tseravinas	450		16000	Turner & Sánchez-Goñi 1997
Ioannina I, II	500		> 46000	Bottema 1974
Ioannina, I - 284	500		25000	Lawson & al. 2004
Ioannina, I - 249	500		243000	Tzedakis 1994
Rezina	1800	*Vaccinio- Piceetalia* (*Pinion – heldreichii*)	10000	Willis 1992b

Table 2. Grouping of pollen assemblage zones of the palynologically investigated sites in Epirus in correspondence to the main stages of vegetation development.

	Late Holocene	Early Holocene	Late glacial / Holocene	Late Glacial	Last Glacial (Würm)	Last Interglacial (Eem)	Earlier
Ziros	Z6	Z4	Z3	Z2	Z1		
Gramousti	GL5, GL6	GL4	GL3	GL1, GL2			
Rezina	RM5 to RM8	RM4	RM2, RM3	RM1			
Tseravinas	TS 5	TS 4	TS 3	TS 2	TS 1		
Kalodiki		E3	E2	E1			
Ioannina I	Y, Z	X	W / X	W	R to V		
Ioannina II	Y, Z	X				N, O	
Ioannina, I - 284	I-284-1 to I-284-4	I-284-5 to I-284-7		I-284-8 - I-284-10	I-284-11,12		
Ioannina, I - 249	IN-42 - IN-44		IN-33 - IN-41			IN-29 - IN-32	IN-1 - IN-31

The gradual changes in vegetation during the succession of glacial and interglacial periods can be paralleled to those in Northern Europe, with the significant difference that in Epirus, and more generally in Southern Europe, the various woody species "hibernated" in local refugia during the harsh periods, whereas the corresponding species in Northern Europe had to migrate to areas where they could survive (Bennett & al. 1991).

Glacial periods

According to the data of the pollen diagrams of Epirus, during the glacial periods open steppe vegetation generally prevailed, the dominant species being *Artemisia*, *Chenopodiaceae*, *Gramineae* and *Asteraceae*. The arboreal species were firmly present although generally with a limited appearance in the vegetation, especially in the lowlands where humidity was lower (Turner & Sánchez-Goñi 1997; Willis 1992a, b, c). However, in Epirus the available moisture even during glacial periods was higher than in the eastern regions of Greece (Tenaghi Philippon), where no arboreal taxa were recorded at the same time (Tzedakis 1994). In the mountainous regions, among certain microenvironments that developed due to the intense geomorphologic conditions, some were characterized by increased humidity and generally favourable conditions for the survival of the forest species, which withdrew there (Willis 1994a).

During the glacial periods, the mountainous regions of Epirus were areas where many species of today's temperate zone had found shelter and were able to survive for two main reasons. Firstly, the continuous mountain range of the Alps, which begins in Central Europe and runs all the way through to the Pindos Mountains, facilitated the migration of plants between the more northern parts of Europe and the southwest region of Epirus. Secondly, the fact that the cold north winds were blocked due to geomorphology, and especially the highly humid conditions of the Epirus mountain ranges established by the rain-bearing winds from the Ionian Sea, had favoured the appearance of microenvironments suitable for plant survival (Bottema 1974; Willis 1997; Lawson & al. 2004).

The pollen diagrams show very low or minimum values for forest trees (*Quercus*, *Abies*, *Pinus,* etc.) during the glacial periods, which reflect their very limited but nonetheless firm presence in the landscapes of open vegetation (Tzedakis 1993, 1994). Furthermore, during the Late Glacial, in the mountainous region of Rezina the trees that were preserved corresponded to at least ten taxa (Willis 1992b, 1994b). However, as previously mentioned, most species had a very limited presence. *Quercus* and *Pinus* prevailed during the glacial phases. Additionally, *Abies*, which evidently grew in mountainous regions too, had a significant presence; while in cases such as the final stage of the Riss Glacial Period, fir forests were dominant in the wider basin of Ioannina (Bottema 1974). Mention deserves the fact that in order to survive, the 'European' fir (*Abies alba*) withdrew to the Balkan Peninsula and in particular to inland Greece. After hybridisation with the Greek fir (*Abies cephalonica*) during the last glacial period, the species *Abies borisii-regis* developed, now dominating the mountain range of Pindos (Athanasiadis 1986).

Interglacial periods

During interglacial periods the vegetation was altering radically and forest vegetation prevailed. It consisted mainly of deciduous broadleaves appearing as mixed oak forests, where the dominant *Quercus was accompanied by Ulmus*, *Tilia*, *Fraxinus*, and *Corylus,* etc., while the mountainous vegetation was complemented by *Fagus*, *Pinus* and *Abies*. Along with this, the presence of certain species, such as *Pistacia* and *Phillyrea,* indicated that Mediterranean plant communities developed in certain localities (Turner & Sánchez-Goñi 1997). According to Tzedakis (1994), a distinct forest succession occurred progressively, which "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*".

The diagram Ioannina II (Bottema 1974) provides significant data about the last interglacial (Eem). The onset of this stage saw a rapid reduction in fir, while there was an increase in deciduous broadleaved mixed oak forests consisting of *Quercus*, *Ulmus, Tilia*, *Carpinus betulus, Fraxinus excelsior, Carpinus orientalis,* and/or *Ostrya carpinifolia*, *Alnus*, *Celtis, Buxus,* and *Parrotia*. The appearance of the last three and the increased presence of *Buxus* (up to 10%) and *Parrotia* (up to 11%) indicate that during that particular phase, as well as the last interglacial in general, the dominant vegetation at low and intermediate altitudes was different from what it was in the Holocene. By comparing the pollen diagram data, Bottema (1974) argued on the similarities between the vegetation of the last interglacial to that existing today in the Hyrcanian forests in Northern Iran. These forests are referred to the class *Zelkova-Parrotietea* and several of their elements such as *Zelkova*, *Albizia*, *Gleditsia*, *Diospyros,* etc. are considered to have participated in the composition of the interglacial forest vegetation in Epirus. In addition, Bottema (1974) pointed out that, given the fact that *Buxus* is generally under-represented in the pollen diagrams, its relatively high percentage values at this particular stage could be explained only by the intensive presence of another tree species, rather than it being the shrub *Buxus sempervirens*. The occurrence of arboreal species during the last interglacial, which disappeared during the subsequent glacial, is supported by the presence of *Parrotia*. Along with this, it is evident that climatic conditions during the last glacial were particularly harsh, since some species that had managed to survive during the previous glacial periods had disappeared that time. Finally, considering the current climatic conditions in the Hyrcanian forests, it appears that during the last interglacial in Epirus, precipitation was higher and the dry period was shorter than it is today.

Late Glacial / Holocene transition

The last glacial (Würm) was characterized by the harshest conditions for plants. While it lasted, a fair number of species, which managed to survive during the preceding glacial periods of the Pleistocene, actually disappeared. More specifically, during the last glacial maximum climate dryness increased a fact which was reflected in the changes of floral composition of the steppe vegetation. Namely, there was an increase in the presence of *Artemisia* and *Chenopodiaceae*, while at the same time *Asteraceae* and *Fillipendula* had decreased (Turner & Sánchez-Goñi 1997). Towards the end of the Pleistocene and prior to the improvement in the climatic conditions, an increased presence of more thermophilous-hygrophilous forest species was observed. The spread of *Quercus* at the expense of *Pinus* and *Artemisia*, and of *Chenopodiaceae* at the expense of *Gramineae* points to a temperature increament. The spread of the thermophilous species, however, shows that the improvement in climatic conditions was of limited duration (Lawson & al. 2004). That stage was paralleled to the corresponding Allerød stage in Northern Europe. The end of the glacial period was characterized by a new deterioration in conditions, a short stage paralleled to the Younger Dryas period in Northern Europe. During that period there was a temporary spread in steppe vegetation as well as a simultaneous increase in the presence of pine and decrease in oak.

The vegetation evidence for the Late Glacial/ Holocene transition varies highly between the Greek sites and suggests that response of the vegetation to the Late Glacial climatic changes in Greece was localized (Willis 1992c). According to Willis (1997), the Late Glacial/Holocene transition had occurred in both sites of Gramusti and Rezina around 9800–9300 BP (9270–8600 BC). That time interval could be considered valid for the entire region of Epirus. During that transition a rapid spread of forest vegetation that replaced the steppe vegetation was observed. Almost pure oak forests grew at the low-altitude sites (Ziros, Kalodoki), whereas in the intermediate and higher altitudes (Tseravinas) the broadleaved forests were mixed, with *Quercus* as dominant species, but also with the presence of *Ulmus, Tilia*, *Fraxinus, Corylus,* etc. (Turner & Sánchez-Goñi 1997, Ioakim & Christianis 1997). At the highest sites (Rezina) there was also an intense presence of conifer forests, with prevalence of pine (Willis 1992b).

Generally, in the mountainous regions there was a diversity of forest trees and the various tree species that survived throughout that transitional period gradually spread, as shown by the difference in the AP:NAP ratio between the middle (1:1) and high (3:1) altitudes (Willis 1997).

Holocene

After the onset of the Holocene, the climate continuously warmed up, thus accelerating the spread of forest vegetation over steppe vegetation. Throughout the first millennia, the development and growth of the vegetation was determined almost exclusively by abiotic factors, especially the climate. The first indications of human interference in the natural vegetation appeared in the 6th millennium BC (Turner & Sánchez-Goñi 1997). Subsequently, the anthropogenic impact on the natural environment had become ever more intense and consequently humans played a major role in shaping out the vegetation. The indications of anthropogenic impact on the vegetation had set the criterion for dividing the Holocene into two phases: Early and Late (Willis 1997, Lawson & al. 2004). However, these indications did not appear at the same time in all pollen diagrams, and therefore the determination of the temporal transition from Early to Late Holocene was based on a rough estimate. Generally for Epirus, it was estimated that transition occurred around the mid 6^{th} millennium BC (5550 BC), considering the age (6635 BP) provided by Turner & Sánchez-Goñi (1997).

Early Holocene (8600–5500 BC)

At low and intermediate altitudes mixed oak forests dominated, which gradually gained larger density, as the diversity of broadleaved woody species increased. Except *Quercus,* which dominated at first but then showed a gradual decrease, other species of significant presence were *Ulmus*, *Tilia*, *Fraxinus*, *Acer*, *Carpinus orientalis* and/or *Ostrya carpinifolia*, *Corylus,* etc. During the first millennia of the Holocene, the maximum values of *Pistacia* pollen, in conjunction with the abundance of Gramineae and the presence of *Sanguisorba minor* indicated that the mixed deciduous oak forests were fairly open, facilitating the growth of these species. *Pistacia terebinthus* must have been the dominant species during that period, since the absence of macquis vegetation elements indicated that the climatic conditions, besides being relatively dry, were too cold to allow the growth of *Pistacia lentiscus* (Bottema 1974; Lawson & al. 2004). The subsequent withdrawal of *Pistacia* and *Sanguisorba minor* and the expansion of broadleaved trees could be attributed to a change in the climatic conditions and in particular to an increase in precipitation.

During the first millennia of the Holocene, ca 8600 to 6400 BC (9300–7500 BP), dense mixed oak forests dominated the mountainous regions of Epirus, increasing the AP: NAP ratio to 10:1 as shown in the Rezina diagram (Willis 1992b, 1997). By the mid 7^{th} millennium BC (7500 BP), fir showed a significant increase and became the main component of forest vegetation (Willis 1992b, c). That fact, along with the presence of other species, such as *Fagus*, *Carpinus betulus,* etc., was also related to the climatic changes mentioned above.

Late Holocene (5500 BC – Present)

In spite of the fact that the development of vegetation was largely determined by the impact of abiotic factors, especially the climate, during the first millennia of that period (5500–2000 BC) human presence and interference in vegetation was ever more frequently traced out in the pollen diagrams. In fact, there were specific cases where the actual results of that interference determined the development of vegetation. As a rule, however, these events tended to have a local effect. As from the mid 3^{rd} millennium BC and thereafter, human impact on the vegetation of Epirus and generally across Greece had not only gradually intensified but occurred on a larger scale (Gerasimidis 1995). Moreover, anthropogenic disturbance in the majority of cases formed in the Balkan regions the present-day landscape during the three millennia BC (between 4500 and 2000 BP) (Willis 1994a).

Around the mid 6^{th} millennium BC (6635 BP), there appeared to have been a significant decrease in *Quercus,* along with forest vegetation in general, as shown in the Tseravinas diagram. The simultaneous increase of certain herbs, such as *Artemisia*, *Plantago* and in particular of *Pteridium*, was associated with intense grazing activity in the area. In the corresponding sediment section, the abundance of charcoal indicated that the vegetation in the area was extensively burnt out, most likely for creation of pastures. This is the earliest indication of an anthropogenic impact on the natural environment in Greece and generally in the Balkans. Open vegetation continued to mark the landscape and around 2500 BC (about 4000 BP) became ever more pronounced (Turner & Sánchez-Goñi 1997).

The Gramousti diagram shows similar events (Willis 1992a, c). Already since the end of the 5^{th} millennium BC (5200 BP) there was a significant decrease in all woody species and a substantial increase in herbaceous vegetation. The severe limitation of forest vegetation caused erosion and soil degradation, as indicated by the influx of allochthonous material in the sediment accumulated during that phase, as well as the increase in Compositae. Deterioration of soil conditions was partly irreversible. That can be seen in the following phase from ca 3800 to 2500 BC (from ca 5000 to 4000 BP), when despite the large re-expansion of woodland vegetation (AP:NAP=7:1), species diversity was quite limited. Moreover, it is likely that part of the AP values originated from kermes oak scrub, which developed as a result of grazing*. During the last millennia, vegetation resembling pseudomaquis

* In the Gramoustis and Rezina diagrams no distinction was made between evergreen and deciduous oaks, according to the two types of pollen – *Quercus ilex*-type and *Quercus robur*-type – which include the pollen of the evergreen and deciduous oaks respectively.

remained relatively stable, with *Quercus* (possibly *Q. coccifera*), *Carpinus orientalis* and/or *Ostrya carpinifolia* as dominant species (Willis 1997).

The decisive role of human impact on the development of vegetation can be traced clearly out in the diagrams of the region of Ioannina. Their data do not coincide chronologically with those of Tseravina and Gramousti diagrams, thus making difficult any generalizations about the temporal vegetation development in Epirus. Nevertheless, the vegetation in the various regions appeared to have evolved differently as a result of early human activity, which was manifested differently from area to area.

In Ioannina, forest vegetation decreased during the period 4500–2400 BC (5700–3900 BP), while the taxa associated with animal husbandry and agriculture increased (Lawson & al. 2004). Since 2400 BC (3900 BP) and until 250 BC (2220 BP), however, the area seemed to have experienced an exceptional re-expansion of woodland vegetation, considering the extreme soil erosion that occurred previously. While mixed deciduous forests of similar composition with those of the Early Holocene had developed, the conifers, and especially *Abies,* did not fully recover, perhaps due to the fact that the ecosystems at high altitudes were more susceptible to soil erosion. Along with this, there was an increase in the ratio of evergreen/deciduous oaks, most probably as a result of grazing pressure, while the abundance of cereals indicated intensification of the agricultural activity in the Ioannina basin. The traced out agricultural and pastoral activity was puzzling, considering the observable re-establishment of the forest. Most likely, anthropogenic activity was limited to low altitudes. The transfer of these activities to the mountainous regions appeared often in the pollen diagrams of Greece and was associated with the historical events that forced the inhabitants of the lowlands to seek refuge in the mountains (Gerasimidis 1995; Gerasimidis & al 2002). A second and final deforestation in the wider region of Ioannina during the period 250 BC– 450 AD (2220–1500 BP) reduced the AP values to the levels of the glacial phase. Of the forest plants, only the obviously cultivated *Olea* and *Phillyrea* (maquis element) showed increased values. An increase in cereals and weeds (*Plantago*, Apiaceae) revealed simultaneous expansion of cultivation.

Data from the pollen diagrams of the middle altitude regions referred to above (Tseravinas, Gramousti, Ioannina) make it possible to present the historical development of the vegetation in a wider area. Furthermore, important data on the vegetation development in the plains and mountainous regions were derived from the diagrams of the low-altitude Ziros site (Turner & Sánchez-Goñi 1997) and high-altitude Rezina (Willis 1992b, 1997).

In the lowlands, the cover of mixed oak forests, which developed during the Early Holocene, was significantly affected by the appearance or spread of *Carpinus orientalis* and/or *Ostrya carpinifolia,* as well as of such evergreen broadleaves as *Quercus coccifera* and/or *Q. ilex*, *Phillyrea* and *Olea*. The latter, in combination with *Pistacia*, *Spartium* and *Cistus* indicated the development of Mediterranean vegetation (maquis) similar to the present-day vegetation in the region at altitudes up to about 400 m.

A further decline in oak woodlands and a subsequent increase in the indicators of open vegetation (*Taraxacum*-type and *Centaurea nigra*-type) were associated with the increase of cultivated plants plants, which were mainly cereals and to a lesser extent vineyards, olives and walnut trees (Turner & Sánchez-Goñi 1997).

With the onset of the Late Holocene, forest vegetation began to withdraw in the mountainous regions, resulting in a AP:NAP value of 2:1. The shrinking of forests could be attributed exclusively to sustained soil erosion because of increased precipitation, but mainly to anthropogenic destruction of the forest vegetation, considering the indication of anthropogenic interference in the vegetation of the lower regions, as well as the increased input of allochthonous material in the sediments accumulated during that period (Willis 1997). That hypothesis was supported by the simultaneous increase of the herbaceous species diversity, a feature which marks the beginning of the anthropogenic interference in an area (Birks 1986). The absence of cultivation indicators points to clear-cuttings for the purposes of animal husbandry rather than agriculture. In fact, the modern clearing of low and high areas supports the hypothesis of seasonal movement of herds also in the past; i.e. in winter the livestock was kept in the lowlands and in summer it was moved to the mountainous pastures (Willis 1997).

Around 2500 BC (*ca.* 4000 BP), another deforestation made the AP:NAP ratio decrease further to 1:1, a value corresponding to the last glacial phase. The shrinking of mountainous forest vegetation in conjunction with intense grazing caused strong soil erosion and created conditions for the development of herbaceous vegetation consisting of such taxa as *Chenopodiaceae*, *Artemisia*, *Rumex,* etc. The Rezina diagram indicates that the downward movement of the tree line, the degradation of forest vegetation, and the final shaping out of vegetation to its present state had started already about 2000 BC. (Willis 1992b).

Despite all this, the development of pine forests in the period between ca 0-800 AD (ca 1990–1200 BP) showed that preconditions still existed for the growth of forests, which, however, lacked the diversity of the mixed forests of the first millennia of the Holocene. The expansion of pine forests was attributed to either a rise in precipitation or to a decline in human activity in the mountainous regions during that period (or even perhaps to combination of the two). However, since the beginning of the last millennium, open grasslands caused by grazing pressure have been the dominant elements in the vegetation of the mountainous regions until now. Willis (1997) pointed out that current vegetation is in conflict with what it was in the past, prior to human impact. The result was that the mountainous regions were deforested, while oak forests grew abundantly in the lowlands, even though they consisted mainly of kermes oak scrub, which have replaced the grazing-degraded mixed deciduous oak forests.

Conclusions

According to the palynological data, the general conclusions about the vegetation history of Epirus are the following:

Pleistocene. During the **glacial periods** open steppe vegetation generally prevailed. However, arboreal species were firmly present, although with a generally limited occurrence in the vegetation. In the mountainous regions, certain microenvironments characterized by favourable conditions, were cited as refugia for temperate taxa. During the **interglacial periods** the vegetation altered radically and forest vegetation prevailed. It consisted mainly of deciduous broadleaves appearing as mixed oak forests, while the mountainous vegetation was complemented by *Fagus*, *Pinus* and *Abies*.

Late Glacial/Holocene transition. A rapid spread of forest vegetation replaced the steppe vegetation. At low altitudes almost pure oak forests grew, while at the intermediate altitudes there were mixed oak forests. At high altitudes conifer forests developed, in which pine prevailed.

Holocene. The Holocene is divided into Early and Late Holocene. This division is based on the first palynological data on the anthropogenic impact on the vegetation, which for Epirus dates back to about the mid 6^{th} millennium BC: the earliest data in Greece and generally in the Balkans.

Early Holocene. Throughout that period, the development and growth of the vegetation was determined almost exclusively by abiotic factors, especially the climate. At low and intermediate altitudes pure oak forests gradually gained larger density and diversity and expanded to higher places. At high altitudes, in the beech and coniferous forests, fir became the main component of the forest vegetation.

Late Holocene. That last period was characterized by the anthropogenic impact on natural vegetation. The first indications of these events in Epirus appeared in the mid 6th millennium BC. Subsequently, anthropogenic disturbance of the natural environment became ever more intense and consequently humans played a major role in shaping out the vegetation. The most important changes in natural vegetation were degradation of the mixed oak forests at low and medium altitudes into macquis and pseudomaquis, as well as formation and gradual downward movement of the mountain treeline at the highest altitudes.

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