

Vegetation dynamics in Europe during the Neogene

Kovar-Eder, J., 2003 - Vegetation dynamics in Europe during the Neogene - in: Reumer, J.W.F. & Wessels, W. (eds.) - DISTRIBUTION AND MIGRATION OF TERTIARY MAMMALS IN EURASIA. A VOLUME IN HONOUR OF HANS DE BRUIJN - DEINSEA 10: 373-392 [ISSN 0923-9308] Published 1 December 2003

Based on the leaf, seed-fruit, and pollen record, the main trends of vegetational evolution in South and Central Europe are outlined. Paleoclimatic parameters are inferred partly from the comparison of the fossil assemblages with modern vegetation units and their climatic requirements and partly by summarizing the available data from the literature.

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Keywords: Europe, Neogene, vegetation history

INTRODUCTION

In Europe, the Neogene is characterized by paleogeographic reorganization due to the collision of the African with the Eurasian plate. Orogenic belts evolved in central and southern regions and large foredeep basins and wetland areas extended along the arising orogenes. Altitudinal vegetation zonation successively developed in the new orogenes, and increasing altitudinal differences ultimately constituted floristic barriers. In addition to the global climatic changes, the tectonic development and sea level changes severely influenced the climate in Eurasia; the annual course of precipitation, its quantity, and its regional distribution changed, thus also altering the temperature realm.

The Neogene European floral records are very rich and diverse (leaves, seeds-fruits, pollen, wood). However, they are not equally distributed over the continent but rather clustered in regions with appropriate sedimentation; some areas largely lack a fossil record. In certain regions, the latest investigations date to the 19th and early 20th century. The fossil record and its interpretation are typical-

ly restricted to only one of the plant organs (leaf or seed-fruit or pollen assemblages, respectively). As different plant organ assemblages are bound to specific taphonomic conditions, the derived interpretations may diverge considerably. Although the different plant organs often co-occur, they are only rarely evaluated jointly. In such cases, they offer a detailed and complementary rather than contradictory picture of the vegetation (e.g. Buzek *et al.* 1985, Kovar-Eder *et al.* 1998). Differences in preservation, investigation methods, reliability of age determination, and different "schools" of naming and treatment further complicate our profound large-scale understanding of the floristic and vegetational development.

THE MEDITERRANEAN

Early/Middle Miocene (Figs. 1-3)

Macrofloras of this interval are relatively scarce in the Mediterranean region. On the Iberian Peninsula, the leaf-floras from Martorell (Vallès-Penedès Basin, surroundings of Barcelona) have been assigned to the

Early and Middle Miocene (Sanz de Siria Catalan 1981a, 1982). The prevalence of nanophyllous and microphyllous leaf size classes (see Glossary) there is interpreted to document warm and possibly seasonally dry climatic conditions.

The record from former Yugoslavia is comparably richer. Dating of Early Miocene records has largely been based on their floristic composition due to the lack of objective correlation possibilities. Marine and brackish sedimentation offers better age control of the Middle Miocene floras, e.g. Pancevo Bridge near Beograd (Pantic & Mihajlovic 1977), or Radoboj, Croatia (Pantic 1992). The floras from the Balkan Peninsula and from Evia Island (Aliveri, Velitzelos *et al.* 1992; Kimi, Unger 1867) correspond physiognomically. Among these floras, the common presence of probably sclerophyllous (see Glossary) leaves

corresponding to the type *Quercus* sect. *Ilex* and/or *Suber* is a remarkable feature. The floras from Greece and former Yugoslavia also include relict taxa that were widespread in earlier periods in more northerly European regions, e.g. *Platanus neptuni* from Radoboj, Pancevo Bridge (Kovar 1982), or *Calocedrus* in Kimi (Kvacek 1999).

Floristic and leaf-physiognomical differences are clearly present between the Mediterranean and Central Europe. The main differences are in the abundance of taxa that fall into smaller leaf size classes (nano-, microphyllous) and in the abundance of entire-margined leaves (usually evergreen) versus non-entire margined (often deciduous) in the Mediterranean floras. However, floristic similarities may mask these differences at first glance, e.g. due to the presence of azonal (see Glossary) taxa such as *Liquidambar*,



Figure 1 The flora of Martorell, Vallès-Penedès Basin, Spain, Early Miocene (Sanz de Siria Catalan 1981), 0.8 X of the original plate size; composed of entire-margined small/narrow leaves, leaf-size class nano-/microphyllous.



Figure 2 The flora from the Martorell, Vallès-Penedès Basin, Spain, Middle Miocene (Sanz de Siria Catalan 1982), 1 X; composed of entire-margined small/narrow leaves, leaf-size class nano-/microphyllous.

Populus, and *Zelkova* in the Mediterranean and in Central Europe. Floristic and leaf-physiognomical differences are also present between the West and East Mediterranean. In this context, it is noteworthy that in the Early Oligocene, the physiognomical similarities between the Tard Clay flora (Hungary) and the Spanish record are closer than between the former and the Central European record. This indicates subxeric conditions for the Western Mediterranean and the Tard Clay flora (see chapter on Mediterranean vegetation), although the floristic correspondence of the Tard Clay flora is closer to Central Europe (Hably & Fernandez Marron 1998). Long-distance correlation based on floristic similarities as applied by Gregor (1990) is an unsuitable approach for age determination covering time-equivalent regional floristic differences. Consequently, Gregor is unable

to trace floristic and vegetational differences not only in the Mediterranean but also between the Mediterranean and Central Europe (Gregor 1990: 335).

Aquitanian pollen profiles from southern France (Provence, Languedoc) are interpreted to reflect a littoral *Avicennia* mangrove; megathermic taxa are reported to infer seasonal tropical/subtropical conditions. The maximum development of the *Avicennia* mangrove along the coast of Languedoc and the best representation of megathermic taxa are recognized during the Langhian. In the Serravalian, the megathermic taxa and the *Avicennia* mangrove disappear, indicating climatic deterioration (Bessedik *et al.* 1984). The decrease in temperature and precipitation regime is assigned to the Antarctic glaciation and to changes in sea currents due to paleogeographic evolution (the isolation of the

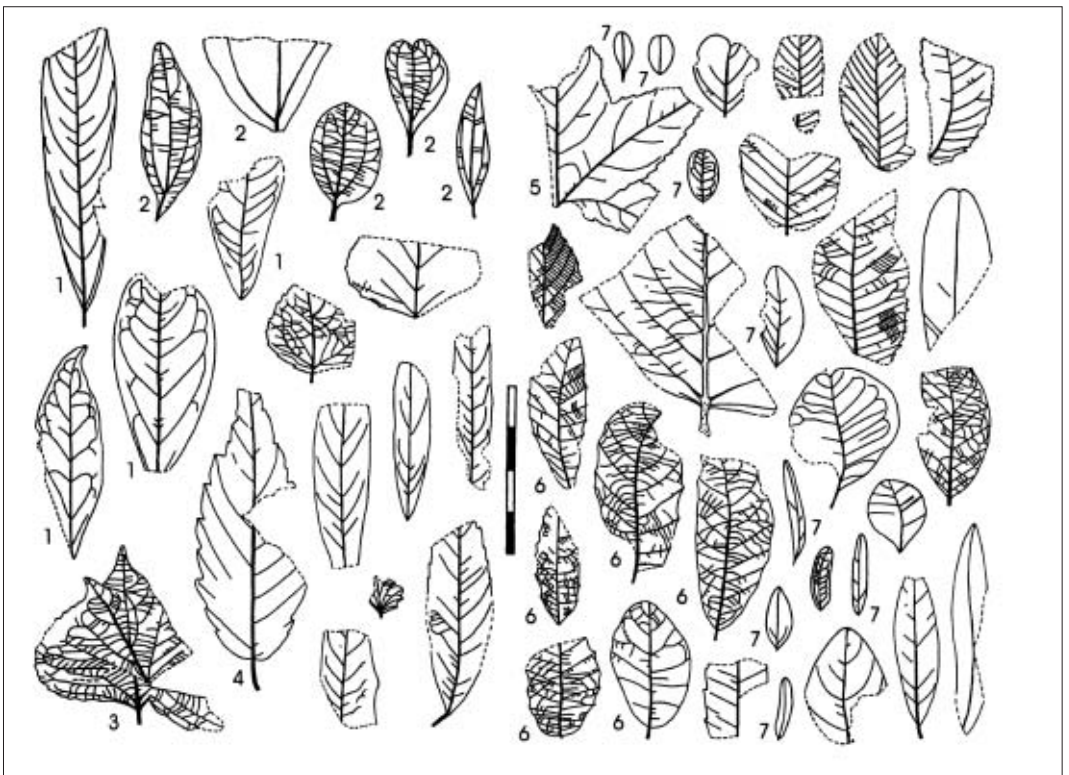


Figure 3 The flora of Kaludra, Serbia, Yugoslavia, Early Miocene (Mihajlovic 1988: pls. 1,2), composed of - broad-leaved (microphyllous), entire-margined, evergreen taxa: **1, 2** Lauraceae (2 *Daphnogene*), - broad-leaved (microphyllous/mesophyllous), non-entire-margined, deciduous taxa: **3** *Populus*, **4** *Zelkova*, **5** *Liquidambar* and - probably sclerophyllous taxa: **6** *Quercus* sect. *Ilex* and/or *Suber*; **7** entire-margined, small (nanophyllous) taxa of uncertain taxonomic affinity.

Mediterranean and Indian Ocean) (Suc 1986).

The pollen record from Middle/Late Miocene (Aragonian/Vallesian) deposits in the southeastern part of the Duero Basin in Spain is interpreted to indicate open woodland and steppe (Rivas-Carballo 1991).

Late Miocene (Figs. 4-6)

The floral record of this time interval is far richer throughout the Mediterranean than the previous one. Based on the floras of different Miocene age in the Vallès Penedès Basin, Sanz de Siria Catalan (1993) traced clear changes towards temperate climatic conditions in the Late Miocene. This is inferred from the appearance of broad-leaved deciduous taxa (leaf size class mesophyllous/microphyllous) such as *Acer tricuspidatum* and *Platanus leucophylla* in the Late Miocene (MN9) (Sanz de Siria Catalan 1981 b, 1993). The flora of Terrasse (MN10, Sanz de Siria Catalan 1997) yields also broad-leaved evergreen taxa (Lauraceae). In the lacustrine basin of La Cerdaña (Eastern Pyrenees), the Vallesian leaf and pollen flora of Vilella (Barrón 1999) supports this floristic and climatic interpretation. In the flora of Azambuja near Alenquer Tejo Basin (Lisboa region, Portugal, MN9), modern taxa (*Castanea sativa*, *Ulmus campestris*, *Quercus ilex*, *Quercus suber*) have been listed for the first time, thus indicating similarities to the modern European flora.

The Late Miocene (Tortonian) records from the Massif Central (Roiron 1991) and the plateau du Coiron (Ardèche, Tortonian, Brice 1965) give a species-diverse picture of broad-leaved, largely deciduous forests in which *Fagus*, roburoid oaks, and a variety of maple species are present. A floristic and physiognomical relationship to Messinian floras from northern Italy, e.g. Gabbro (Berger 1957, Bossio *et al.* 1981), and Late Miocene (?Pliocene) ones from Greece (Likudi, Vegora, Prosilion; Knobloch & Velitzelos 1987) is evident, although floristic differences also exist. The Central European broad-leaved deciduous floras of the latest Middle to

early Late Miocene (Sarmatian/Pannonian) correspond floristically as well. However, the characteristic presence of sclerophyllous *Quercus* sect. *Ilex* and/or *Suber*, for example, and of relicts such as *Engelhardia* and *Daphnogene* along with laurophyllous species in the Italian and Greek record indicate a closer relationship among the Mediterranean floras and climatic differences between the Mediterranean and more northerly European regions. Mai (1995) summarized the Italian and Greek floras as the Likudi-Vegora floral complex.

Was there an influence of the "Messinian salinity crisis" on the vegetation? Partly due to the relatively short time interval (less than 2 MA), the Messinian floral record is not very rich (macro: Murviel-lès Béziers,

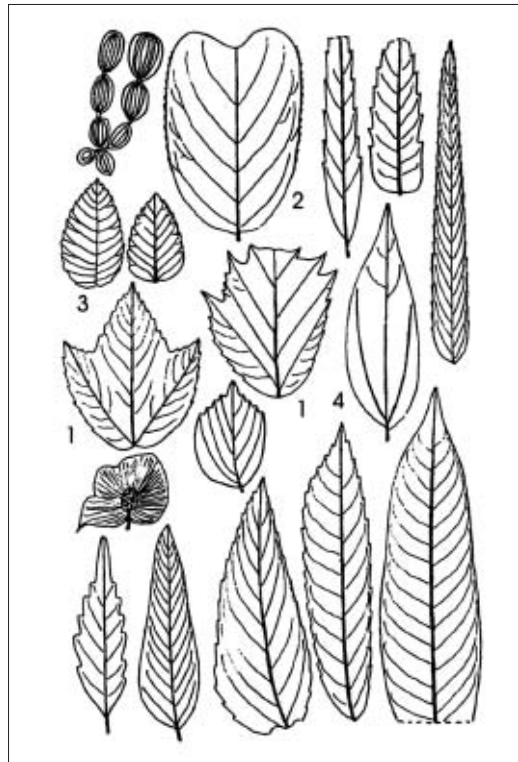


Figure 4 The flora of Bisbal, Vallès-Penedès Basin, Spain, Late Miocene (Sanz de Siria Catalan 1981), 0.8 X of the original plate size; broad-leaved deciduous (micro-/mesophyllous), non-entire-margined taxa prevail, among these: **1** *Acer*, **2** *Alnus*, **3** *Ulmus*; broad-leaved (microphyllous), entire-margined, evergreen taxa: **4** Lauraceae (*Daphnogene*).

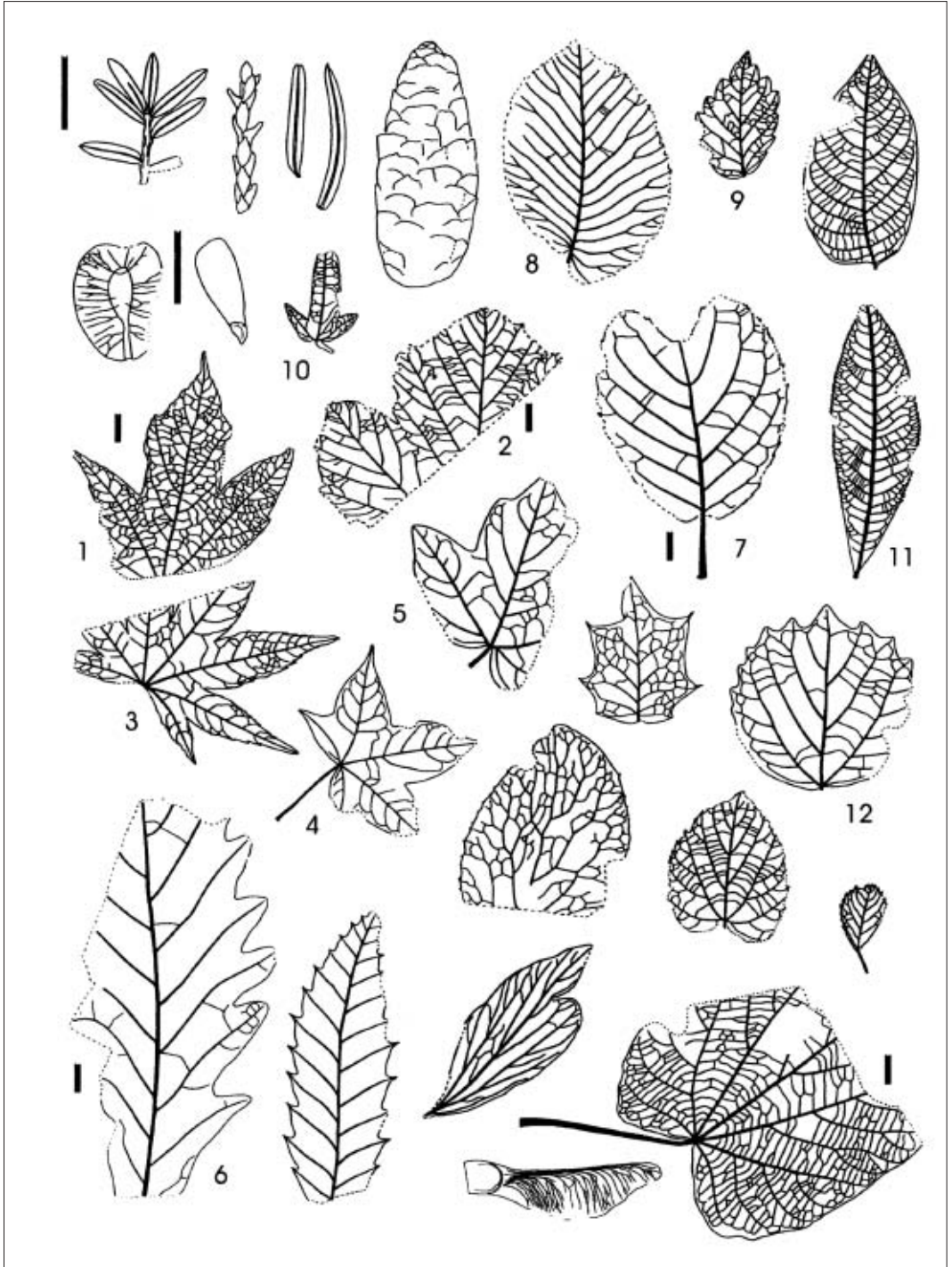


Figure 5 The flora of Murat, Massif Central, France, Late Miocene (selected from Roiron, 1991), all figures 0.6 X except where scale bar (10 mm); broad-leaved (microphyllous/mesophyllous), non-entire-margined, deciduous taxa prevail: **1-5** *Acer* div. sp., **6** roburoid oak, **7** *Alnus*, **8** *Ulmus*, **9** *Zelkova*, **10** *Carpinus*, **11** *Carya*, **12** *Populus*.



Figure 6 The flora of Gabbro, Toscana, Italy, Late Miocene, Messinian (selected from Berger 1957), 0.6 x. - broad-leaved (microphyllous), evergreen taxa - "Central European relicts": **1, 2** Lauraceae (**2** *Daphnogene*), **3** *Tetraclinis salicornioides*, **4** *Engelhardia macroptera*-involucrum (fruit wing), **5** *Smilax*; - broad-leaved (microphyllous/mesophyllous), non-entire-margined, deciduous taxa: **6** *Alnus*, **7** roburoid oaks, **8** *Fagus*, **9** *Liquidambar*, **10** *Platanus leucophylla*, **11** *Populus*, **12** *Zelkova*; **13** *Carpinus*-involucrum (fruit wing) - probably sclerophyllous taxa: **14** *Quercus* sect. *Ilex* and/or *Suber*.

Ambert & Roiron 1990; Carbonara Scriveria, Balduzzi *et al.* 1980; Gabbro and Senigallia, Berger 1957, Bradley & Landini 1984, Massalongo & Scarabelli 1859, Principi 1908; pollen: Bertolani Marchetti & Cita 1975, Bertolani Marchetti 1984, Bertini 1994). Although the fossil documentation is largely restricted to the sediments deposited during the transgressive episodes one could expect some indications as of stress-induced higher percentages of sclerophyllous taxa or the disappearance of broad-leafed evergreen and deciduous taxa that are supposed to depend on high precipitation (atmospheric humidity). Palynological studies of cyclic sediments of the lower Komnina Formation (6.75-6.7 Ma and 6.33-6.28 Ma) at the lacustrine Lava section (Servia Basin, northwestern Greece) generally indicate continuously humid and warm climatic conditions. Correlations of the relative frequencies of *Pinus* versus *Cedrus* and *Fagus* versus *Abies* were interpreted to be indicative of superimposed subtle fluctuations in wintertime precipitation at higher altitudes related to precessional forcing (Kloosterboer-van Hove *et al.* 2000b). In comparison, the upper part of the Komnina Formation (5.44-5.21 Ma, Ptolemais Basin, northwestern Greece) includes the "Lago Mare" phase. Distinctly stronger precession-controlled precipitation fluctuations and lower temperature values of the cold season than for the underlying sequence are deduced. This was inferred from the pronounced cyclic increase in herbs characteristic of open vegetation (*Artemisia*, Chenopodiaceae, Compositae, Ephedra, Gramineae) and the periodical absence of Taxodiaceae there (Kloosterboer-van Hove *et al.* 2000a).

Concluding, there is yet no unequivocal proof of stronger effects of the salinity crisis on the flora and vegetation during the period of the salinity crisis than in other periods, however the discussion has not yet been settled satisfactorily. Distinguished discussions have been provided by Roiron (1984) and Suc (1986). Kloosterboer-van Hove *et al.* (2000a) have given a summary of most

recent interpretations.

Pliocene

A far-reaching consistency in the interpretation of the Early Pliocene plant record is evident compared to preceding periods. Especially the carpo-floras of the Turin surroundings (Italy, Martinetto *et al.* 1997) as well as the pollen record from the western Mediterranean (Fauquette *et al.* 1999) indicate the development of rich mixed mesophytic and evergreen broad-leafed forests. The Italian carpo-floras yield numerous "Central European relicts", subtropical taxa that were characteristic of the "Younger Mastixioid floras" *sensu* Mai (see chapter on central Europe: evergreen broad-leafed forests) in previous mainly Early/Middle Miocene floras of Central Europe (Germany, Poland, Czech Rep., Hungary, Austria). These include Mastixiaceae, evergreen Fagaceae-*Trigonobalanopsis*, Rutaceae, Symlocaceae, as well as members of the Hamamelidaceae and Juglandaceae. Although already traceable during earlier Miocene periods, the Mediterranean constituted a distinct refuge area for the Central European flora during the Pliocene. The Ca'Viettone floral complex introduced for the carpo-floras of Ca'Viettone and Sento by Martinetto *et al.* (1997) is included in the Lugagnano floral complex, which is stratigraphically bound to transgressive horizons of the Tabianian, NN12-13 (Mai 1995). This complex is furthermore characterised by "Mediterranean elements" such as *Quercus* sect. *Ilex* and/or *Suber*, *Olea*, and *Buxus* (compare Mediterranean vegetation) and by precursors of modern species of *Celtis*, *Fagus* ex gr. *orientalis*, *Juglans*, *Liquidambar*, *Pterocarya*, and *Zelkova*. The rich development of the Early Pliocene vegetation in the Mediterranean is connected to humid climatic conditions that are related to the earliest Pliocene transgressive phase (Suc 1986).

Based on the pollen record, Fauquette *et al.* (1999) and Suc *et al.* (1999) have presented vegetation maps for the western Mediterra-

nean region for the Early Zanclean. Fauquette *et al.* (1999) estimate temperature values of 1-4°C and annual precipitation of 400-700 mm higher than those of today for the European Mediterranean. The map of Fauquette *et al.* (1999) shows the Mediterranean region of France and Northern Italy as a warm and humid region suitable to host subtropical taxa ("Central European relicts"). However, the northern limit of the "broad-leaved/evergreen/warm mixed forests" on this map runs south of the Turin region with its famous relict rich floras. Therefore, the future use of different sources of the plant record (pollen/seeds-fruits/leaves) for vegetation modelling will lead to a higher resolution and probability of such models. According to the palynological investigations of Kloosterboer-van Hove *et al.* (2000a) in the Ptolemais Basin, the Greek continental record lacks optimal climatic effects of the Early Pliocene transgression on the vegetation.

The Late Pliocene of the Mediterranean is characterised by broad-leaved deciduous assemblages including *Fagus*, *Carpinus*, *Acer*, *Alnus*, and *Liriodendron*. "Central European relicts" are still present but their diversity decreases. Nano- and microphyllous taxa that might be interpreted as indicators of xeric conditions were rare. "Mediterranean taxa" are reported such as *Quercus* sect. *Ilex* and/or *Suber*, *Nerium*, *Cupressus*, or *Smilax*. The Pinaceae became richer both in taxa and abundances: *Pinus*, *Picea*, *Abies*, *Tsuga*, and *Cedrus*. *Taxodium*, *Glyptostrobus*, and *Sequoia* (all Taxodiaceae) were still present. The pollen record documents the disappearance of the Taxodiaceae from Catalonia during the Late Pliocene (Suc & Cravatte 1982), from southern Italy in the Early Pleistocene and from Georgia even later in the Pleistocene (Shatilova 1974). This clearly indicates the west/east heterochrony of floristic changes in addition to the north/south gradient. It is likely that the floristic west/east heterochrony is related to the west/east heterochrony of the tectonic and palaeogeographic evolution of southern European regions.

While the Taxodiaceae disappeared completely from Europe and Asia Minor, the Hamamelidaceae, Platanaceae, and Juglandaceae have survived with a single genus/one species, respectively, in the Colchidic/Hyrcanian region (eastern coast of the Black Sea/southwestern coast of the Caspian Sea): *Liquidambar orientalis*, *Parrotia persica*, *Platanus orientalis*, *Pterocarya fraxinifolia*. Already during the Late Miocene/Pliocene this region was the richest among the probably already split refuge areas of southern Europe. The floristic changes partly reflect the reduction of wetlands (e.g. Taxodiaceae), but they doubtlessly also relate to global climatic deterioration (Suc 1986) as well as to more favourable climatic conditions in the Colchidic/Hyrcanian region than in other European regions. To some extent, these conditions last until today (higher/more equally distributed annual precipitation, relatively equable/higher temperatures).

The Late Pliocene pollen record from the Gulf of Lyon and southern Italy indicates that seasonal drought became stable only in the Late Pliocene (Bessedik *et al.* 1984). Low frequencies of arboreal pollen, except *Pinus*, and an increase of herbs point towards a reduced forest cover. The first appearance of herbaceous steppes (with *Artemisia* and *Ephedra*) has not taken place earlier than around 2.4 Ma (Suc 1984). This is consistent with the pollen data from the Bresse Basin (Rousseau *et al.* 1992).

Mediterranean vegetation

Modern natural Mediterranean vegetation in mesic habitats corresponds to evergreen sclerophyllous forests and scrubs under seasonally dry climate; frost is possible but usually not long lasting. The leaves of woody species are evergreen, drought resistant, their size ranging largely within nano- to microphyllous. Monodominant *Quercus ilex* forests or *Quercus coccifera* scrubs are characteristic in the main part of the Mediterranean region today. Neither is the shrub layer species

diverse nor is the herb layer well developed. Only in azonal or extrazonal communities of riparian and upland forests, deciduous woody elements (*Platanus*, *Fagus*, *Ostrya*, etc.) occur. Starting from the Eocene, in the Oligocene, and in the Neogene, sclerophyllous taxa repeatedly evolved under subtropical/warm-temperate climate. Generally, sclerophyllous leaves provide only evidence of water and/or nutrient deficit. However, high percentages of sclerophyllous taxa may also offer climatic information.

A primary source of sclerophyllous "Palaeomediterranean" species was supposedly the zonal vegetation of the Tethys/Paratethys region: broad-leaved evergreen/mixed mesophytic/deciduous forest communities (see chapter on Central Europe: zonal vegetation). Dry edaphic and microclimatic conditions probably favoured their development (Palamarev 1989). Subsequently they formed specific communities in different regions, e.g. on the Iberian Peninsula or southern France (Aix-en-Provence), Hungary (Tard Clay) in the Oligocene; on the Balkan Peninsula, e.g. Kimi, Aliveri, possibly also Parschlug (Styria, Austria, Kovar-Eder *et al.* 2004) in the Early/Middle Miocene, more commonly in the late Middle to Late Miocene, e.g. in Hungary (Tokaj); in the Pliocene they were rarer. Hably *et al.* (2000) state that due to climatic barriers xeromorphic elements of sclerophyllous subhumid vegetation were endemic in Europe during the Oligocene.

During the Neogene, most characteristic subxeric elements were, among others, mainly various sclerophyllous oaks, *Cedrelospermum*, *Tetraclinis brachyodon*, *Berberis* sect. *Wallichianae*, *Acer pseudodominans* = *pessulanum*, *Myrica*. However, these subxeric assemblages cannot be regarded as the direct precursors of the modern Mediterranean vegetation (Mai 1995). Based on the pollen record the modern Mediterranean vegetation zonation was first established in the latest Pliocene/earliest Pleistocene (Suc 1984). Nonetheless, the dis-

crepancies among different interpretations of the plant record should not be denied: Gregor (1990: 332) failed to discover "so-called Mediterranean elements", e.g. *Olea*, *Phillyrea*, *Pistacia*, in Late Neogene Mediterranean carpo-floras, while Mai (1995: 538) lists these and many more as being relevant in European subxeric/hemixerix forests.

CENTRAL EUROPE

The Miocene plant record is especially rich, and leaves, seeds-fruit, and pollen are well investigated (Germany, Czech Rep., Poland, Slovakia, western Ukraine, Hungary, Romania, Austria, Switzerland). Mai (1981, 1995) presented detailed summaries. In most cases it is possible to separate zonal from azonal vegetation.

Zonal vegetation

During the Neogene zonal vegetation underwent distinct floristic and physiognomical/structural changes. Generally, there was a tendency from evergreen broad-leaved and mixed-mesophytic forests to deciduous broad-leaved forests with an increasing component of dark conifers (Pinaceae). As oscillations and regional differentiation are well discernable this was not a linear development, but an overall general trend.

Evergreen broad-leaved forests (Fig. 7)

Predominantly in the Early to Middle Miocene, assemblages comparable to modern evergreen broad-leaved forests are documented. They were rich in species adapted to warm-temperate/subtropical, humid climatic conditions. Oligodominance of Lauraceae and evergreen Fagaceae (especially *Trigonobalanopsis rhamnoides/exacantha*) is most characteristic, as is the presence of Araliaceae, Mastixiaceae, Symplocaceae, Rutaceae, Theaceae, and others. Archaic taxa characteristic in the Palaeogene were absent. Living relatives show usually pan(sub)tropical, southeast Asiatic-neotropical or southeast Asiatic distribution/disjunction. Exotic conifers and



Figure 7 Warm-temperate evergreen broad-leaved forest, evergreen oak-laurel forest, leaf size class microphyllous prevailing; Wiesa near Kamenz, Lusatia, Germany, Early/Middle Miocene (Mai 1995: Abb. 144); **1, 2** Lauraceae (**1** *Daphnogene*), **3** *Trigonobalanopsis thamnoides*.

thermophilous, but probably deciduous species of largely temperate families such as Aceraceae, Hamamelidaceae, Juglandaceae, and Tiliaceae also constituted essential components of these forests. Leaves largely fall into the micro- to mesophyllous leaf size classes. Lianas and vines were diverse, belonging to angiosperm families such as Actinidiaceae, Menispermaceae, Smilacaceae, or Vitaceae, rarely to ferns. The herb layer is documented largely by ferns and probably was not well developed due to poor light conditions on the forest floor. These coenoses are known as the "Younger Mastixioid floras" sensu Mai.

Today, forests of similar composition thrive above all in China and Taiwan, mainly between 20-30° northern latitude (Wang 1961). They are also present in central and southern Japan (Hara 1959). Representative plant assemblages are documented for example from the Cypris Shale, Czech Republic (Buzek *et al.* 1996); Köflach-Voitsberg Formation, Austria (Kovar-Eder *et al.* 1998, Meller 1998), both Early Miocene; Wackersdorf, Bavaria (Knobloch & Kvacek 1976, Gregor 1978); and Wiesa near Kamenz, Oberlausitz, Germany, both late Early/early Middle Miocene. Their variability reflects the climatic range of these forests. Starting from the late Middle Miocene and the subsequent Late Miocene, records of evergreen broad-leaved forests are restricted to refuge areas, such as the Rhenish embayment (van der Burgh 1987) or the Colchidic region (Kodor, Abchasia, Kolakovskij 1964). Characteristic taxa as *Trigonobalanopsis rhamnoides/exacantha*, laurels, *Tetraclinis salicornioides*, or *Engelhardia orsbergensis/macroptera* get increasingly confined to south(eastern) parts of Europe (Italy, Romania, Balkan Peninsula) (Kovar-Eder *et al.* 1994).

Mixed mesophytic forests An overall characteristic feature is a decrease in evergreen woody taxa and an increase in deciduous ones, resulting in associations comparable to modern mixed mesophytic forests. Taxa

whose relatives are mostly evergreen and/or thermophilic are common, for example: *Ailanthus*, *Engelhardia*, *Quercus*, and *Symplocos*. In modern mixed mesophytic forests the uppermost layer of the multi-storied canopy is composed of deciduous species and polydominance prevails, while evergreen woody taxa are restricted to the lower stories of the canopy and the shrub layer.

Deciduous broad-leaved forests Further reduction of the evergreen component is documented in Late Miocene /Pliocene plant assemblages. *Acer*, *Betula*, *Carpinus*, *Carya*, *Fagus*, *Fraxinus*, *Ginkgo*, *Juglans*, *Liquidambar*, *Liriodendron*, *Quercus*, *Tilia*, *Ulmus*, and *Zelkova* are among the most important representatives. Prevailing leaf size classes are mesophyllous to microphyllous. Their modern relatives show panholarctic, east Asiatic-European-North (east) American, east Asiatic-North (east) American, Eurasiatic, east Asiatic, or North American distribution patterns. Evergreen taxa were rare and largely confined to the shrub layer, e.g. *Myrica*, *Buxus*, *Ilex*. These assemblages, such as Laaerberg, Moravska Nova Ves, Vienna Basin, Late Miocene, Pannonian (Berger 1955; Knobloch 1969), may be compared to modern, species-diverse, broad-leaved largely deciduous forests. Due to gradual impoverishment polydominance is replaced by oligodominance. Especially in Late Miocene/Pliocene assemblages, *Fagus* is sometimes dominant. To express more precisely this process, a further subdivision of the Neogene forest communities is necessary (Carpino-Fagetea/ Quercetea, Mai 1995). Climatic requirements of modern evergreen broad-leaved forests, mixed mesophytic forests and broad-leaved deciduous forests in China (after Wang 1961) offer approximative details of the climatic changes in Central Europe during the Neogene (Table 1).

Mixed coniferous and broad-leaved forests/boreal conifer forests Late Pliocene Central European records are generally rare. The

Table 1 Comparison of climatic data from observation stations within the modern broad-leaved deciduous, mixed-mesophytic and evergreen broad-leaved forests in China (summarized after Wang 1961). Values without brackets from observation stations < 500 m N.N.; values in brackets from climate stations > 1000 m N.N. MAT – mean annual temperature, MAP – mean annual precipitation.

	deciduous broad-lea fed forest	mixed mesophytic forest	evergreen broad-lea fed forest
latitude of the observation stations	34-41° N	29-32° N	25-28° N
MAT	10-15° C	15-16 (11) ° C	18,5-19 (15-16)
No. of months with mean temp < 0° C	1-3	0	0
No. of months with mean temp > 10° C	7	8-9 (6-7)	9-11
No. of months with mean temp. > 22° C	3-5	4 (1-2)	5-6 (0)
mean temp. of the warmest month	26-28° C	27-28 (23-24) ° C	27-29 (20-21) ° C
mean temp. of the coldest month	-9 to -1 ° C	2-4,5 (-3-1) ° C	5-9 (8,5-9,5) ° C
MAP	550-720 mm	1000-1500 (2000)	(1300) 1400-1950
No. of months with precipitation <10 mm	2-5	0	0 (1)

Vildstejn floristic complex (North Bohemia, Czech Republic, Buzek *et al.* 1985) documents mixed forests rich in broad-leaved deciduous woody species with a high admixture of dark conifers such as *Abies*, *Picea*, *Pinus*, *Tsuga*. The estimated MAT is 12-14°C, the warmest monthly mean about 25°C (comparable to New York or Washington today). Sensitive taxa indicate that the mean temperature of the coldest month was not below 1°C. The ultimate disappearance of such sensitive taxa, e.g. Taxodiaceae, *Liriodendron* or *Symplocos*, indicates climatic deterioration resulting in Pinaceae-dominated forests. Modern climatic data from Montreal and Halifax serve for comparison: MAT 6.3°/7.0°C, coldest monthly mean -14.2°C/-9.4°C.

In the Lower Rhine embayment (opencast mine Hambach, Germany) the floral record documents climatic deterioration from the Reuverian to the Praetiglian. The pollen spectra from the seams wedged within the Reuverian clay show a continuous decrease in characteristic warmth requiring taxa, such as *Nyssa*, *Pterocarya*, *Sequoia*, and *Taxodium*. An impoverished flora with high *Pinus* and herb values is characteristic of the superimposed sediments (Heumann 2001, Heumann & Litt 2002).

According to Dorofeev (1970), dark conifers first appeared during the Oligocene, in the Altai, Mugodshary, and Ural mountains. Mainly documented by pollen, they were already present during the Miocene in the

European mountain ranges. Palynological evidence of Oligocene and Late Miocene boreal dark conifer forests derives from the Greenland Sea, Hovgard ridge, beyond the Arctic Circle. *Picea*, *Pinus*, *Tsuga*, and *Taxodium* were associated with a minor element of angiosperms and common ferns (Boulter & Manum 1996).

Azonal vegetation

Extended regions of diversified wetland vegetation are documented by fluvial/lacustrine and brackish sediment complexes. Principally, the taphonomic conditions for the preservation of plant remains from azonal coenoses are better than these from zonal ones, resulting in a better understanding of azonal habitats. Most of these associations were relatively species-poor, characterized by oligo- or monodominance of single species; they constituted unstable stages in vegetation succession.

Conifer-laurel associations Mai (1995) distinguishes, among others, laurel-conifer forests, open pine-laurel forests, and bog-laurel scrubs. They developed on nutrient-poor, often sandy and therefore edaphically dry soils. *Pinus* and different Taxodiaceae were usually associated with Cupressaceae, Ericaceae, Myricaceae, Symplocaceae, Theaceae, palms, and others. During the Neogene these associations underwent a decline in diversity.

Swamps and swamp forests (Fig. 8) They developed on wet and organically rich soils, constantly below or close to the groundwater table. The monodominance of *Taxodium* or *Glyptostrobus* was characteristic; they were associated with *Alnus*, *Myrica*, *Nyssa*, *Quercus rhenana*, and *Salix*. Common accessories constituted *Acer*, *Cephalanthus*, *Fraxinus*, and *Magnolia*. Plants whose photosynthetically active parts tolerate long periods of submergence or floating (helophytes) were characteristic in the herb and shrub layer, e.g. Cyperaceae, Lythraceae,

Zingiberaceae. Puddles along with herbaceous and woody habitats were intermingled in a mosaic-like manner. The variability of swampy associations is well documented in the numerous Neogene coal-bearing sequences. Thorough floristic comparison of Early/Middle Miocene associations in eastern Austria, Bohemia, and eastern Bavaria showed distinct differences in peat-forming vegetation, possibly partly related to edaphic factors (Kovar-Eder *et al.* 2001).

Modern *Taxodium-Nyssa* swamps in Florida, Georgia, Louisiana, and Mississippi as well as swampy lowlands with *Glyptostrobus pensilis* in Kwangtung, Kwangsi, and Hainan Island (Wang 1961) are comparably close. In the late Middle and Late Miocene (Sarmatian, Pannonian) a peculiar swamp association developed in the area of the Pannonian Basin, e.g. Givulescu (1992), Hably & Kovar-Eder (1996), but is also known from the Transcarpathian region (Il'nica, Ukraine, Iljinskaja 1968). There, *Glyptostrobus* and *Byttneriophyllum tiliifolium* (probable systematic affinity to Malvales) were the only dominants associated by *Alnus*. The few other taxa reported constituted mere accessories, e.g. *Osmunda* or *Salix*.

Riparian forests (Fig. 9) Riparian forests had comparatively high species diversity; however, diversity and variability in composition depended on the location within a fluvial system. Oligodominance was characteristic of the probably stratified canopy. Throughout the Neogene, deciduous species of *Acer*, *Alnus*, *Carya*, *Celtis*, *Fraxinus*, *Glyptostrobus*, *Juglans*, *Liquidambar*, *Platanus*, *Populus*, *Pterocarya*, *Quercus*, *Salix*, *Taxodium*, *Ulmus*, and *Zelkova* prevailed. The shrub layer, lianas, and the herb layer were well developed. While some species such as *Liquidambar europaea*, *Alnus gaudinii*, *Acer tricuspdatum*, and *Zelkova zelvokifolia* are documented in these associations starting from Oligocene time throughout the Miocene into the Pliocene, Neogene floristic changes are reflected at the infrageneric



Figure 8 *Glyptostrobus*-*Byttneriophyllum* swamp forest, Il'nica, Transcarpathia, Ukraine, Late Miocene/Pliocene (Mai 1995: Fig. 158), 0.6 X; 1 *Byttneriophyllum tiliifolium*, 2 *Glyptostrobus europaeus* (twigs, cones, seeds), associated mainly by 3 *Alnus*, 4 *Salix*, 5 *Osmunda*, 6 *Populus*.



Figure 9 Riparian forest association, Schrotzburg, Baden, Germany, late Middle/Late Miocene (Mai 1995: Fig. 228); largely consisting of broad-leaved (micro-/mesophyllous) deciduous, non-entire-margined taxa: 1 *Platanus leucophylla*, 2 *Liquidambar europaea*, 3 *Ulmus*, 4 *Salix*, 5 *Populus*, 6 *Fraxinus*, 7 *Juglandaceae*, 8 *Acer*, 9 Lauraceae (*Daphnogene*), a representative of the already impoverished evergreen broad-leaved component.

level: The first reliably dated, Central European records of *Acer aegopodifolium*, *Acer vindobonensis*, *Alnus ducalis*, *Platanus leucophylla*, and *Quercus pseudocastanea*/roburoid oaks derive from the late Middle Miocene (Kovar-Eder *et al.* 1994, 1996).

TAXODIACEAE

Members of the swamp cypress family (partly evergreen/partly deciduous trees) constituted important components, mostly in azonal vegetation. *Cunninghamia*, *Glyptostrobus*, *Sciadopitys*, *Sequoia*, *Taiwania*, and *Taxodium* partly co-occur in the Neogene European record. *Sequoia* is known until the Late Pliocene from Central Europe. In the Mediterranean the heterochronous disappearance from west to east is documented by pollen. In the Colchidic refuge area, eight

genera were reported from the Early Pleistocene (Chochieva 1990) prior to their complete extinction there (see also chapter on the Mediterranean: the Pliocene). The modern Taxodiaceae are relicts, geographically isolated from each other (*Glyptostrobus*, *Sciadopitys*, *Cunninghamia*, *Taiwania* - Southeast Asia, *Sequoia* - southwest North America, *Taxodium* - southeast North America). *Glyptostrobus*, *Sciadopitys*, *Taiwania*, and *Taxodium* are commonly regarded as essential components in peat-forming vegetation. The role of *Sequoia* in different azonal and zonal associations is sometimes disputable (Kovar-Eder *et al.* 2001). This refers to the fact that modern relicts often do not occur at their physiological optimum today, but rather where they are still successful competitors.

SOURCES OF THE DECIDUOUS ELEMENT IN THE CENTRAL EUROPEAN FLORA AND REGIONAL FLORISTIC DIFFERENTIATION

A regional floristic differentiation is indicated in the earlier documentation of temperate (largely deciduous) representatives in northern versus southern parts of Central Europe (as of the Oligocene), their more pronounced presence in the east versus west (Mai 1981), as well as in the longer persistence of archaic elements in the Paratethys region. Invasion waves of deciduous woody taxa are evident since the late Palaeogene. *Acer*, *Liquidambar*, *Populus*, and *Salix* are among the early appearing examples (late Early Oligocene) known from the Weissensteiner Basin (Leipzig region, Germany; Mai & Walther 1978). The thorough investigation of selected Neogene Central European taxa, e.g. *Acer aegopodifolium*, *Quercus pseudocastanea*/robust oaks, indicated in some cases their and their ancestors' earlier appearance in eastern regions of Europe and Kazakhstan (Kovar-Eder *et al.* 1994, 1996). The increase of deciduous woody taxa in the Neogene European flora, however, may not only be a result of invasions: climatic oscillations may also have stimulated their autochthonous development (Mai 1981).

CONCLUSIONS

During the Early/Middle Miocene physiognomical and floristic differences are discernable within the Mediterranean and between the Mediterranean and Central Europe. On the Iberian Peninsula small, slender, entire-margined leaves prevail. On the Balkan Peninsula and Evia Island the small, entire-margined component is also well developed; additionally, broad-leaved evergreen taxa, and broad-leaved non-entire margined, probably deciduous ones are documented, as well as regularly leaves of sclerophyllous oaks. On the Balkan Peninsula and Evia Island "Central European relicts" - taxa that were present in Central Europe in preceding periods - are documented, as *Platanus neptuni* and

Calocedrus. Broad-leaved evergreen forests known as "Younger Mastixioid floras" are well documented in Central Europe during the Early/early Middle Miocene.

In the Late Miocene/Pliocene broad-leaved, non-entire margined taxa were widespread in the Mediterranean from the Iberian to the Balkan Peninsula and Central Europe. The Mediterranean constituted increasingly a refuge for "Central European relicts". Broad-leaved evergreen forests got restricted to climatic favourable regions as the Rhenish embayment and parts of the Mediterranean. Finally they got confined to the Colchidic/Hyrcanian region.

In addition to the north/south gradient a west/east heterochrony in floristic changes is traceable in Central Europe and in the Mediterranean. In the Mediterranean the west/east heterochrony is likely related to the west/east advancing tectonic and palaeogeographic evolution.

ACKNOWLEDGEMENTS

I would like to thank Z. Kvacek for critically reading the manuscript.

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Received 19 May 2001

Accepted 8 September 2003

GLOSSARY

Latin and popular names of taxa (taxa lacking popular names not listed):

Abies-fir, *Acer*-maple, *Alnus*-alder, Araliaceae-ivies and ginseng, *Artemisia*-wormwood, *Avicennia*-black mangrove, *Berberis*-barberry, *Buxus*-box, *Carpinus*-hornbeam, *Carya*-hickory, Chenopodiaceae-goosefoot family, Compositae-sunflower family, Cupressaceae-cypress family, *Engelhardia*-member of the walnut and hickory family (Juglandaceae), Ericaceae-heather, Fagaceae-beech, oak and sweet chestnut family, *Fagus*-beech, *Fraxinus*-ash, *Glyptostrobus*-water pine, Gramineae (alternatively Poaceae)-grasses, Hamamelidaceae-witch hazels and sweet gums, Juglandaceae-walnut and hickory family, *Juglans*-walnut, Lauraceae-laurels, *Liquidambar*-amber tree, *Liriodendron*-tulipe tree, Lythraceae-cupheas, lythrums and henna, *Magnolia*-magnolia, Mastixiaceae-now included in the Cornaceae-dogwoods as mastixioid-nyssoid clade, Menispermaceae-curare, *Nerium*-oleander, *Nyssa*-tupelo tree, *Olea*-olive, *Parrotia*- member of the witch hazels and sweet gums family (Hamamelidaceae), *Picea*-spruce, Pinaceae-pine family, including dark conifers (*Picea*, *Abies*, *Tsuga*), *Pinus*-pine, *Populus*-poplar, *Platanus*-plane tree, *Pterocarya*-wing nut, *Quercus*-oak, *Quercus ilex*-holm oak, holy, Rutaceae-citrus fruit family, *Salix*- willow, *Sciadopitys*-umbrella pine, *Sequoia*-red wood, Taxodiaceae-swamp cypress family, *Taxodium*-swamp cypress, Theaceae-tea and camellias, *Tilia*-lime or linden, *Trigonobalanopsis*-fossil genus related to evergreen oaks, *Smilax*-smilax, *Tsuga*-hemlock spruce, *Ulmus*-elm, Vitaceae-grapevine and virginia creeper

Vegetation units:

zonal vegetation: Large-scale vegetation developing under mesic soil conditions (no extremes). The climatic factors have stronger influence than the edaphic ones. Therefore, high relevance for climate reconstruction. Largely synonymous in use are the terms upland and hinterland vegetation.

azonal vegetation: the development of plant communities is more severely influenced by edaphic factors than by climate (alluvial, wetland vegetation), therefore relatively low relevance for climate reconstruction.

extrazonal vegetation: due to more extreme climatic conditions at the geographic limits of their natural distribution area the vegetation may change its habitat (e.g. from lower to higher elevation).

Leaf size classes:

nanophyllous 0.25-2.25 cm²

microphyllous 2.25-20.25 cm²

mesophyllous 20.25-182.25 cm²

Climate parameters:

MAP - mean annual precipitation

MAT - mean annual temperature

Miscellaneous:

megathermic plants require a MAT $\geq 24^{\circ}\text{C}$

sclerophyllous - leaves with low surface area, usually coriaceous, evergreen

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