Latitudinal climatic gradients in the Western European and Mediterranean regions from the Mid-Miocene (*c*. 15 Ma) to the Mid-Pliocene (*c*. 3.5 Ma) as quantified from pollen data

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Abstract: In Europe and the Mediterranean region, the vegetation and climate of the Neogene is well understood, due to the abundance of pollen data, allowing the climate evolution at a time of global cooling to be described. This paper presents a climatic reconstruction of four key time-slices of the Neogene: the Mid-Miocene (*c*. 14 Ma), the Late Miocene (*c*. 10 Ma), the Early Pliocene (*c*. 5–5.3 Ma) and the Mid-Pliocene (*c*. 3.6 Ma). The results show that Neogene climate was warmer than today and that the transition from a weak latitudinal thermic gradient (around 0.48 °C/degree in latitude) to a gradient similar to that of today (0.6 °C/degree in latitude) took place at the end of the Miocene. The latitudinal precipitation gradient was more accentuated than today from the Mid-Miocene to the Mid-Pliocene, with higher precipitation than today in northwestern Europe and the northwestern Mediterranean but with conditions that were drier than or equivalent to today in the southwestern Mediterranean region.

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The Neogene is a period of intense climatic changes, from the 'greenhouse' climate of the Early to Middle Cenozoic to the 'icehouse' climate of the Late Cenozoic (Zagwijn 1960; Shackleton *et al.* 1995; Suc *et al.* 1999), and many factors, such as atmospheric CO_2, orbital parameters, ocean heat transport and palaeogeographical modifications, may have played a role in these changes.

The continental configuration of the world during the Miocene was similar to the present. However, plate tectonics led to intense palaeogeographical changes around the world during the Miocene, especially the Early and Middle Miocene. These changes contributed to fluctuations in the Neogene climate, in particular the opening of some ocean gateways (Drake Passage, Bering Strait) and the closure of others (the Atlantic-Pacific passage across Panama, the passage between the Indian Ocean and the Tethys) (Pagani *et al.* 2000; Hall *et al.* 2003). Changes in oceanic circulation at that time led to the establishment of the modern ocean circulation pattern (e.g. the Antarctic Circumpolar Current) that in turn affected the global climate. Ocean general circulation model simulations have shown the influence of ocean on global climate through changes in oceanic heat transport (e.g. Nisancioglu *et al.* 2003; Mikolajewicz *et al.* 1993). In addition, many atmospheric general circulation model (GCM) simulations have shown the influence of the uplift of mountain ranges and plateaus (Rocky Mountains, Andes, Himalayas, Alps, Tibetan Plateau) on global climate through changes in the atmospheric circulation (e.g. Ruddiman & Kutzbach 1989; Kutzbach *et al.* 1993; Ramstein *et al.* 1997; Fluteau *et al.* 1999; Kutzbach & Behling 2004).

Other authors have demonstrated that the Miocene climate variability was driven by fluctuations in the amplitude of obliquity and eccentricity (Westerhold *et al.* 2005). DeConto & Pollard (2003*a*, *b*) argue for a combination of atmospheric CO_2, orbital forcing and ice-climate feedbacks as the primary causes of climate transitions. Recently, Moran *et al.* (2006) have shown the dominance of greenhouse gases on climate control over tectonic forcing. The vegetation also had a significant influence on the Neogene climate. Climate model experiments demonstrate that the presence of high-latitude forests caused a warming in polar regions in the Miocene and, therefore, contributed to a weaker-than-present equator-to-pole temperature gradient (Dutton and Barron 1997; Micheels *et al.* unpublished data). Palaeovegetation changes, such as the evolution of grasslands during the Neogene (Retallack 2001), have an influence on the climate and must be considered when attempting to explain climatic fluctuations.

For Western European and Mediterranean regions, the Neogene vegetation history is well known as many pollen sequences have been studied during the last few decades. At present, more than 120 pollen records from the Early Miocene to the Early Pleistocene are available in this area (Zagwijn 1960; Suc 1980; Diniz 1984*a*, *b*; Bessedik 1985; Zheng 1986; Bertini 1992; 1994; 2001, 2003; Clet-Pellerin 1996; Bertini & Roiron, 1997; Bachiri-Taoufiq 2000; 2003; Jiménez-Moreno 2005), providing a reliable and accurate view of latitudinal and altitudinal vegetation change (Suc 1989; Suc *et al.* 1995*a*, *b*; Jiménez-Moreno & Suc 2007). The pollen-based descriptions of the palaeovegetation are supported by a number of macrofossils studies (Kovar-Eder *et al.* 2006).

In this paper, we reconstruct the evolution of climatic gradients in Europe and the Mediterranean region during the Neogene based on pollen data for four periods: the Middle Miocene, around 14 million years (Ma); the Late Miocene around 10 Ma (Tortonian); the Early Pliocene, around 5–5.3 Ma; and the Middle Pliocene, around 3.5 Ma. For each time-slice, the vegetation is briefly described based on the pollen records.

Methodology for climate reconstruction from pollen data

In order to produce comparable and homogenous results, the same transfer function was applied to all selected pollen sequences. The climate was estimated using the 'Climatic Amplitude Method' developed by Fauquette *et al.* (1998*a*, *b*) to quantify the climate of periods for which no modern analogues of the pollen spectra exist. The Neogene spectra contain a mixture of temperate, warm-temperate and subtropical plants (even tropical plants during the Miocene) that today live in different parts of the world. The past climate is estimated by transposing the climatic requirements of the maximum number of modern taxa to the fossil data. This method may be applied to the Neogene period as the pollen flora of the region has been defined following botanical nomenclature for many years now (Zagwijn 1960; Pons 1964; Elhai 1969; Suc 1976; Diniz 1984*a*, *b*; Bessedik 1985).

In contrast to other methods such as the best analogue method (Guiot 1990), this approach does not rely on the analysis of entire pollen assemblages, but on the relationship between the relative pollen abundance of each individual taxa and the climate. Presence/absence limits, as well as abundance thresholds, have been defined for 60 taxa from modern pollen spectra and the literature. This method takes into account not only the presence/absence criterion but also pollen percentages to provide more reliable reconstruction. Low abundances of some tropical and subtropical taxa

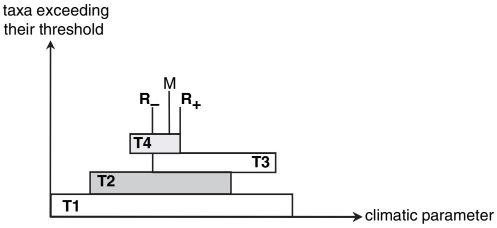


Fig. 1. Principle of the 'Climatic Amplitude Method' (Fauquette *et al.* 1998*a*, *b*). The most probable climate for a set of taxa exceeding their presence/absence and/or abundance thresholds in a pollen spectrum corresponds to the smallest climatic interval suitable for a maximum number of taxa [R−; R+]. A 'most likely value' (M) is then calculated (see text).

(e.g. *Microtropis fallax*, *Avicennia*) are meaningful and should be taken into account as these plants produce relatively small numbers of pollen grains. Conversely, low abundances of wind-pollinated taxa (e.g. *Quercus*, *Alnus*, *Corylus*) may reflect long-distance transport of these high pollen producers by air and water. In this case, very low pollen percentages are not significant.

With this method, the most probable climate for a fossil pollen assemblage is estimated as the climatic interval in which the highest number of taxa can exist (Fig. 1). The climatic estimate is presented as an interval [R−; R+] and as a 'most likely value' (M), which corresponds to a mean that is weighted according to the size of the climatic intervals of all taxa exceeding their presence/absence and/or abundance thresholds. As the precision of the information obtained from a taxon's climatic interval is inversely related to the breadth of this interval, the weights are greater for taxa with smaller intervals.

In this paper, we present reconstructions of two climatic parameters estimated from the pollen data: the mean annual temperature (Ta) and the mean annual precipitation (Pa).

High latitude/altitude taxa were excluded from the reconstruction process. The identification and exclusion of high latitude/altitude plants is based on numerous palynological studies (e.g. Suc *et al.* 1995*a*, *b*, 1999; Jiménez-Moreno, 2005) that show the Neogene vegetation zonation to follow a similar latitudinal and altitudinal zonation to that observed in present-day south-eastern China (Wang 1961), where most of the taxa that had disappeared from Europe by the late Neogene may be found. The estimates obtained, therefore, correspond to the climate at low to middle–low altitude (Fauquette *et al.* 1998*a*).

Pinus and non-identified Pinaceae (due to poor preservation of these disaccate pollen grains) have been excluded from the pollen sum of the fossil spectra (Fauquette *et al.* 1998*a*, 1999). The pollen grains of these taxa are often over-represented in the sediments due to their high production and over-abundance in air and water (fluvial and marine) transport (Heusser 1988; Cambon *et al.* 1997).

The climatic latitudinal gradient during the Middle Miocene (*c.* 14–15 Ma)

A number of new pollen samples covering this period have recently been published (Jiménez-Moreno 2005). The samples are located along a latitudinal range in western Europe, from 47° to 36° N. The Mid-Miocene palaeogeography, which is now well established (Rögl 1998; Meulenkamp & Sissingh 2003; Goncharova *et al.* 2004; Ilyna *et al.* 2004; Paramonova *et al.* 2004) has shown that these sites were (a) separated by around 12° in latitude at that time (instead of 11° today) and (b) situated a few degrees further south than today (Rögl 1998).

The study sites are (from north to south): Le Locle outcrop (western Switzerland), Les Mées borehole (southern France), Bayanne outcrop (southern France), Farinole outcrop (Corsica, France), La Rierussa outcrop (northeastern Spain), Gor outcrop (southern Spain), Alborán A-1 borehole (southern Spain), Andalucía G-1 borehole (southern Spain) (Fig. 2). Le Locle locality is dated from the upper mammal unit MN16 (Kälin *et al.* 2001). The other sites are marine deposits and are generally dated by micropalaeontology Gor: calcareous nannofossil Zone CN-3 (Martín-Pérez & Viseras 1994); the time-interval taken from the Andalucia G1 borehole has been dated by planktonic foraminifera and ranges from zones N10 to N16 (Calandra in ELF 1984); the time-interval taken from the Alboran A1 borehole has been dated by planktonic foraminifera and ranges from zones N10 to N14 (Bailey *et al.* in CHEVRON 1986); La Rierussa: planktonic foraminifera (zone N4: Magné 1978) and calcareous nannofossil (zone NN4: C. Müller in Bessedik 1985); Farinole: planktonic foraminifera (zone N10) and calcareous nannofossils (zone NN6) (Ferrandini *et al.* 1998); Bayanne: planktonic foraminifera (zones N7 and N8: Besson *et al.* 2005). The Les Mées 1 borehole samples contain no micropalaeontological information. These samples have been allocated to the late Burdigalian as they correspond to the transgressive maximum according to the regional stratigraphy (Dubois & Curnelle 1978). Complete information is available in Jiménez-Moreno (2005).

Pollen taxa have been grouped following Suc (1989) and are detailed in Table 1.

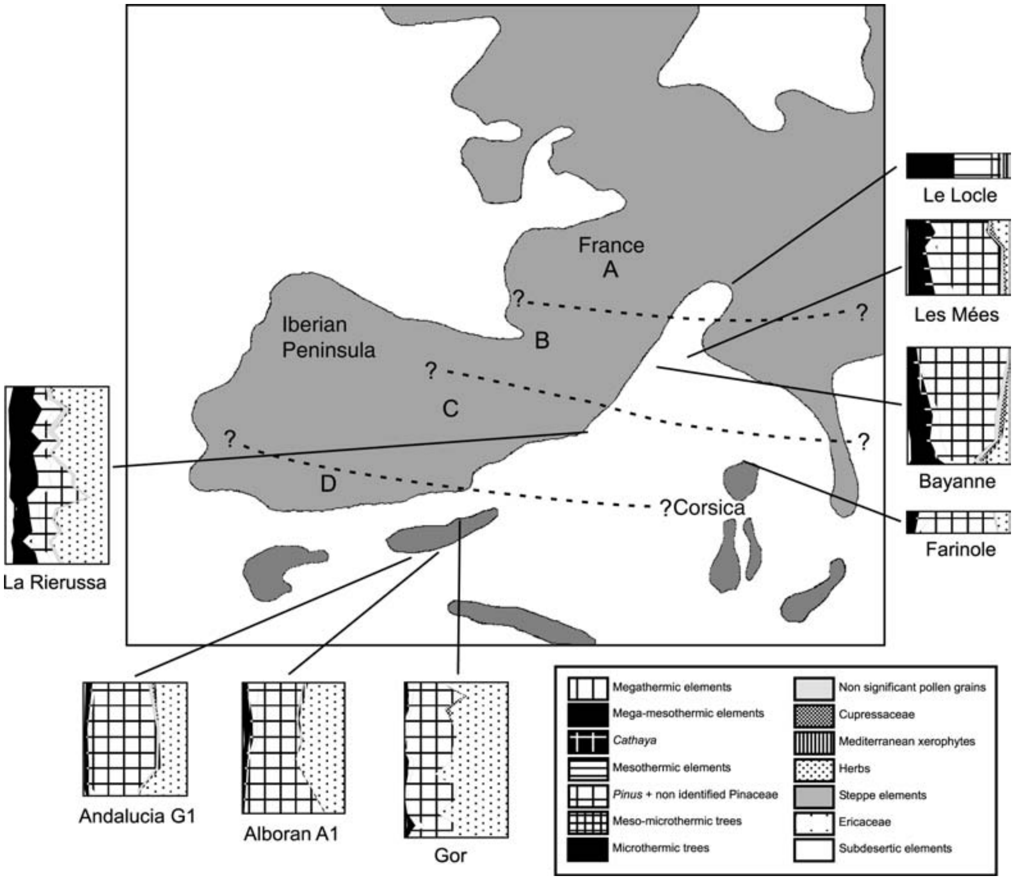


Fig. 2. Location of the studied sites covering the Middle Miocene and their synthetic pollen diagrams in the palaeogeographical framework of the early Serravallian (from Rögl 1998). Pollen localities (Jiménez-Moreno 2005): Le Locle-Combe Girard, Les Mées, Bayanne, La Rierussa, Farinole, Gor, Alborán A1, Andalucía G1. The four vegetational regions reconstructed from pollen data are indicated (A, B, C, D, see text for explanation).

The studied area can be subdivided into four vegetational domains from north to south on the basis of the pollen floras (Fig. 2) (Jiménez-Moreno 2005; Jiménez-Moreno & Suc 2007):

- In Western Switzerland (Fig. 2, zone A), the pollen flora is characterized by a high abundance of mega-mesothermic (= subtropical) elements, in particular *Taxodium* type and *Engelhardia*, and by high percentages of mesothermic (=warm-temperate) elements (mainly *Quercus* deciduous type). Some megathermic (= tropical) elements are present at low abundances. Percentages of herbs are very low.
- Southern France (Fig. 2, zone B) is characterized by the dominance of mega-mesothermic elements as well as temperate elements. *Avicennia*, a mangrove plant, is regularly present. Herbaceous percentages are higher, but do not dominate the pollen spectra. Semiarid taxa such as *Acacia*, Caesalpiniaceae or *Prosopis* are recorded at very low values.
- In northeastern Spain and Corsica (Fig. 2, zone C), pollen spectra are rich in herbs and shrubs. Caesalpiniaceae and *Acacia* occur at very low percentages in the pollen spectra. Mega-mesothermic and mesothermic taxa are highly abundant. Megathermic elements are abundant in all the samples. *Avicennia* plays an important role in this area, indicating the presence of an impoverished mangrove along the coast. Meso-microthermic and microthermic taxa (i.e. inhabiting middle and high altitudes, respectively), including *Cathaya*, a conifer living today in the subtropical mid-altitude forests of southern China (Wang 1961), occur infrequently in these samples.

Table 1. *Taxa groups*

Megathermic elements	Rutaceae, *Mussaenda* type, Acanthaceae, *Acacia*, *Sindora*, *Croton*, *Alchornea*, *Bombax*, *Buxus bahamensis* type, *Mappianthus*, Rubiaceae, Euphorbiaceae, *Avicennia*, *Phyllanthus* type, Melastomataceae, Simarubaceae
Mega-mesothermic elements	*Symplocos*, *Engelhardia*, Sapotaceae, *Platycarya*, *Distylium*, *Rhoiptelea*, Taxodiaceae, *Taxodium* type, Hamamelidaceae, *Rhodoleia*, Loranthaceae, *Microtropis fallax*, *Embolanthera*, *Corylopsis*, *Mallotus*, Celastraceae, *Parthenocissus*, *Leea*, *Myrica*, Menispermaceae, Theaceae, *Aesculus*
Mesothermic elements	*Quercus* deciduous type, *Fagus*, *Ostrya*, *Carpinus*, *Carya*, *Pterocarya*, *Juglans*, *Juglans cathayensis* type, *Parrotia* cf *persica*, *Liquidambar*, *Tilia*, *Castanea-Castanopsis* type, *Parrotiopsis jacquemontiana*, Restionaceae, *Buxus sempervirens*, *Ilex*, *Eucommia*, *Ligustrum*, *Populus*, *Ulmus*, *Zelkova*, *Celtis*, *Elaeagnus*
Meso-microthermic elements	*Cedrus*, *Tsuga*, *Sciadopitys*
Microthermic elements	*Picea*, *Abies*, *Keteleeria*
Mediterranean xerophytes	*Quercus ilex-coccifera* type, *Olea*, *Phillyrea*, *Ceratonia*, Cistaceae, *Pistacia*, *Nerium*
Herbs	Poaceae, Asteraceae Asteroideae, Asteraceae Cichorioideae, Centaurea, Convolvulaceae, *Plantago*, Ericaceae, Brasicaceae, *Helianthemum*, Geraniaceae, *Erodium*, Caryophyllaceae . . .
Steppe elements	*Artemisia*, *Ephedra*
Subdesertic elements	*Lygeum*, *Neurada*, *Calligonum*, *Nitraria*, *Prosopis*, Agavaceae

- Southern Spain (Fig. 2, zone D) is characterized by the dominance of herbs and shrubs in the pollen spectra; Poaceae and halophytes are repeatedly found at high values. Further, subdesertic elements, such as *Nitraria*, *Lygeum*, *Prosopis*, *Neurada* and *Calligonum* are very abundant. Significant amounts of megathermic elements, including *Avicennia*, occur in all samples. Mega-mesothermic and mesothermic are regularly present. Meso-microthermic and microthermic elements appear sporadically at very low values. These pollen spectra with high percentages of herbs are typical of an open environment.

The presence, all along this transect, of plants characterized by high thermic requirements such as *Engelhardia*, *Myrica*, *Taxodium*-type, *Mussaenda*-type and *Avicennia*, indicates that the latitudinal temperature gradient was lower than today. This is consistent with the presence in other pollen data, covering the Mid-Miocene of Central Europe, of thermophilous taxa at high latitudes (Jiménez-Moreno 2005; Jiménez-Moreno & Suc 2007). The occurrence of thermophilous plants at higher latitudes has also been observed in North America by Liu & Leopold (1994). These authors estimated a thermic gradient of 0.3 °C per degree of latitude for North America (between 35° N–65° N) during the Mid-Miocene.

There are, however, important changes in the vegetation from north to south in Western Europe, occurring gradually between Switzerland and southern Spain (between 36° N and 47° N). The vegetation becomes more and more open from north to south with the presence of subdesertic taxa in southern Spain, reflecting a latitudinal gradient in precipitation.

The results of the climatic quantification (Fig. 3) show, from north to south, increasing annual temperatures but decreasing annual precipitation. The reconstructed most likely values show higher mean annual temperatures than today all along the gradient (*c*. 2 to 8 °C higher) and higher mean annual precipitation than today in Southern France, Corsica and northeastern Spain (between 400 mm and 700 mm higher). In southwestern Europe, the mean annual precipitation is almost equivalent to modern values (maximum 200 mm higher). This is also the case at Le Locle, where little change in mean annual precipitation values is shown. The thermic gradient is weaker than the modern one as the differences between the Miocene and the modern temperatures are between *c*. 2 °C in southern Spain, *c*. 4 °C in northern Spain, *c*. 5/6 °C in southern France and *c*. 8 °C in western Switzerland. On the basis of the most likely value reconstructed from pollen data, the thermic gradient in Western Europe was around 0.48 °C per degree in latitude whereas it is around 0.6 °C today (Ozenda 1989). This result is in agreement with the estimations obtained by Bruch *et al.* (2004) from fossil floras of Europe where they find a lower latitudinal temperature gradient than today.

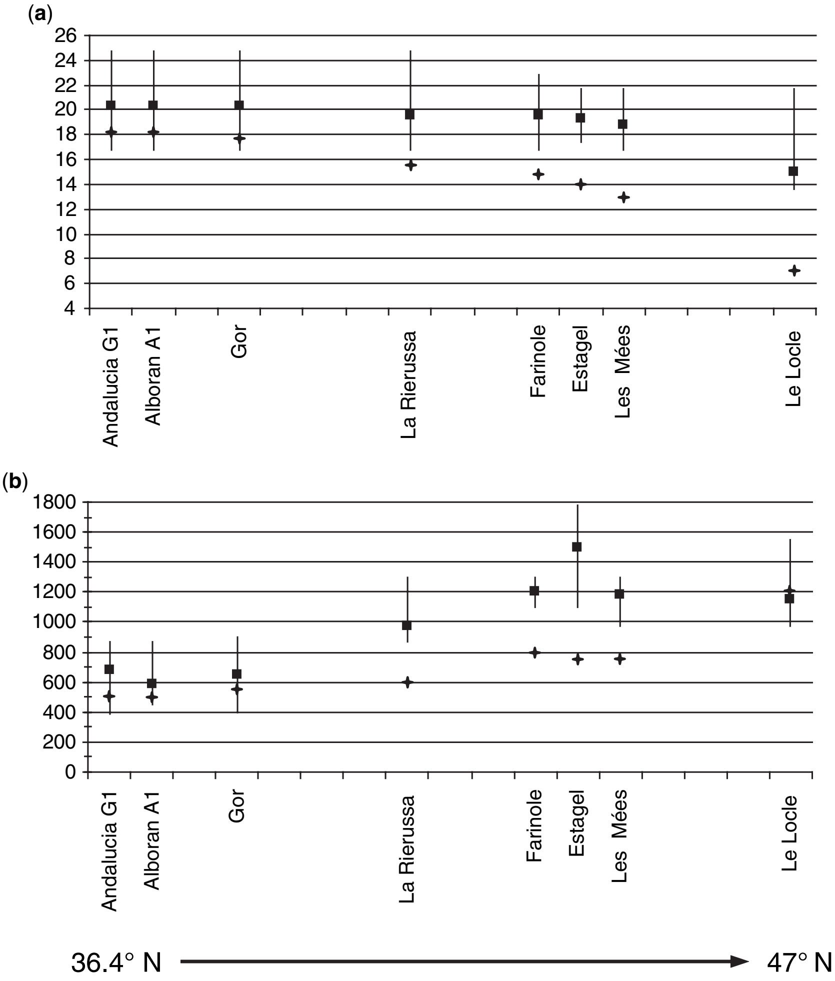


Fig. 3. Climatic reconstruction from pollen data (climatic interval and most likely value) in Western Europe and Mediterranean region showing (**a**) the gradient of temperature (mean annual temperature in °C) and (**b**) precipitation (mean annual precipitation in mm) for the Middle Miocene. Modern values are indicated by a cross to show the differences between modern and Miocene latitudinal gradients. Pollen data of Le Locle-Combe Girard, Les Mées, Bayanne, La Rierussa, Farinole, Gor, Alborán A-1, Andalucía G-1 (Jiménez-Moreno 2005) have been used.

The latitudinal climatic gradient at the end of the Miocene (Tortonian, *c*. 10 Ma)

For this period, pollen spectra from the sites of Ambérieu (Farjanel & Mein 1984), Mirabel (Naud & Suc 1975), Sanabastre and Sampsor in Cerdanya (Bessedik 1985), Zaratan (Rivas-Carballo *et al.* 1994), Capodarso in Sicily (Suc *et al.* 1995*c*) and MSD 1 borehole in Morocco (Bachiri-Taoufiq 2000) have been used to estimate the climatic gradient (Fig. 4). The palaeogeography has been established by Paramonova *et al.* (2004). The Cerdanya sites (Agusti & Roca 1987), Zaratan (Rivas-Carballo *et* al. 1994) and Ambérieu (Farjanel & Mein 1984) were assigned to the Tortonian on the basis of mammal biochronology. The site of Mirabel belongs to the volcanic Coirons area and has a radiometric age (Naud & Suc 1975). Planktonic foraminifera are available for the MSD1 borehole for zones N16 and N17 (Barhoun 2000). The Capodarso section covers the late Tortonian to early Messinian according to planktonic foraminifera and calcareous nannofossils (Cita *et al.* 1973; Suc *et al.* 1995*c*). Only the lower part of this section is considered here.

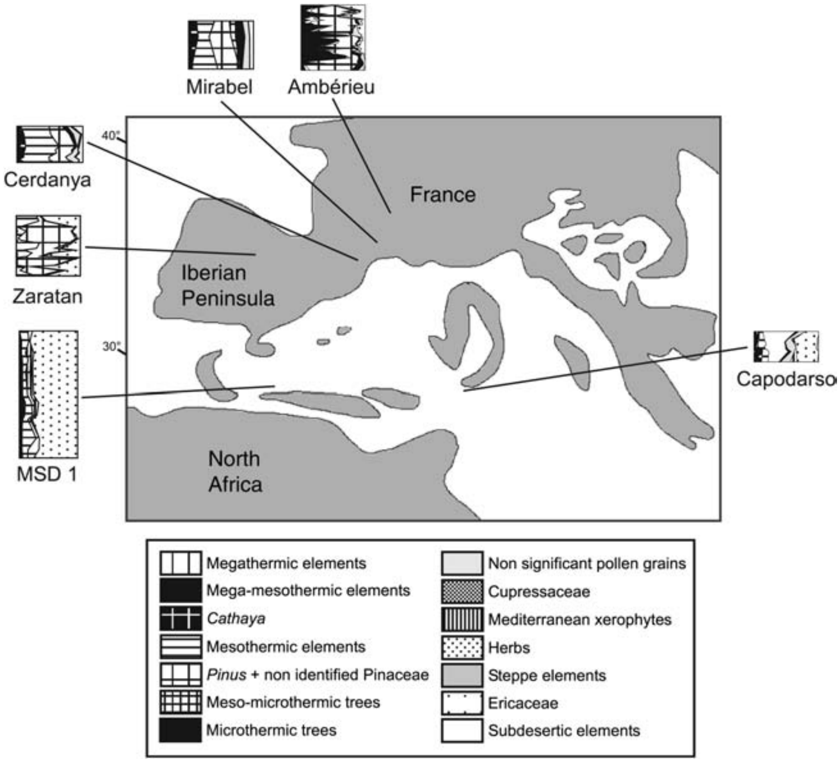


Fig. 4. Location of the studied sites covering the Tortonian around 10 Ma in Western Europe and Western Mediterranean region and their synthetic pollen diagrams in the palaeogeographical framework of the Late Tortonian (Paramonova *et al.* 2004). Pollen localities: Ambérieu (Farjanel and Mein 1984), Mirabel (Naud & Suc 1975), Sanabastre and Sampsor sites in Cerdanya (Bessedik 1985), Zaratan (Rivas-Carballo *et al.* 1994), Capodarso in Sicily (Suc *et al.* 1995*c*) and MSD 1 borehole in Morocco (Bachiri-Taoufiq 2000).

Although less pollen data exist for this period, a clear latitudinal gradient is observed for both temperature and precipitation. In northwestern Europe (Ambérieu, Mirabel sites), pollen data indicate forested environments, characterized by taxa growing under a wet climate (Taxodiaceae, *Engelhardia*, *Symplocos*, *Platycarya* . . .). Forested environments are also indicated in the northwestern Mediterranean region (Sanabastre/Sampsor sites in Cerdanya, Bessedik 1985), where arboreal pollen dominates with low values of herbaceous taxa. The microflora is characterized by the dominance of *Quercus, Fagus, Alnus* and conifers (*Cathaya, Pinus*, Taxodiaceae), reflecting the presence of mixed deciduous forests. Pollen grains of *Abies* are also recorded. Only few megathermic plants are present at low values. However, the presence, in the Cerdanya Basin, of plants such as evergreen *Quercus* (in the microflora) or even *Cassia, Mahonia, Cinnamomum, Banksia*, Combretaceae (in the macroflora, Menendez Amor 1955) indicates a warmer climate than today. At Zaratan, the pollen assemblages are similar to those found today in the southwestern Mediterranean region with sclerophyllous woods of *Quercus* and pines associated with species characteristic of open vegetation as Cistaceae, Cupressaceae, Ericaceae, Geraniaceae and *Plantago*. The presence of deciduous taxa indicates a warm-temperate climate in this region (Rivas-Carballo *et al.* 1994). Finally, in the southwestern Mediterranean region (Capodarso in Sicily and MSD 1 borehole in Morocco), the pollen spectra are largely dominated by herbaceous taxa, indicating dry open environments with the presence of subdesertic herbs such as *Lygeum*. However, pollen data also indicate the presence of forests on the surrounding uplands. The record of *Avicennia* in the MSD 1 borehole (Bachiri-Taoufiq 2000) indicates an impoverished mangrove along the south Mediterranean shoreline during the Tortonian.

The climatic reconstruction based on these pollen sequences shows that temperatures were higher than today during the Tortonian, in particular in the northwestern Mediterranean area. The climate was warm and humid in Western Europe (most likely values 4 to 9 °C and annual precipitation rainfall 100 to 600 mm higher than today), and warm and dry in the south Mediterranean region (most likely values of 3 to 4 °C higher and less than 200 mm higher than today). The difference between the Tortonian and the modern annual temperature is larger for the site of Sampsor. Indeed, this site is currently situated at about 1000 m above sea level but was at lower altitude during the Tortonian (Mauffret *et al.* 2001).

The climatic estimates show that the north–south climatic gradient that existed during the Tortonian was similar to today, with increasing temperature and decreasing precipitation, but with higher temperatures (Fig. 5). On the basis of the most likely values reconstructed from pollen data of MSD 1 borehole and Ambérieu section, the thermic gradient is around 0.6 °C per degree in latitude. This does not agree with the estimated reduction of about 50% in the thermic gradient calculated by Bruch *et al.* (2006) from fossil floras of Central and Eastern Europe.

The climatic latitudinal gradient for the Early Pliocene (*c*. 5.0–5.3 Ma)

During this period, the palaeogeography was similar to today, with the exception of the existence

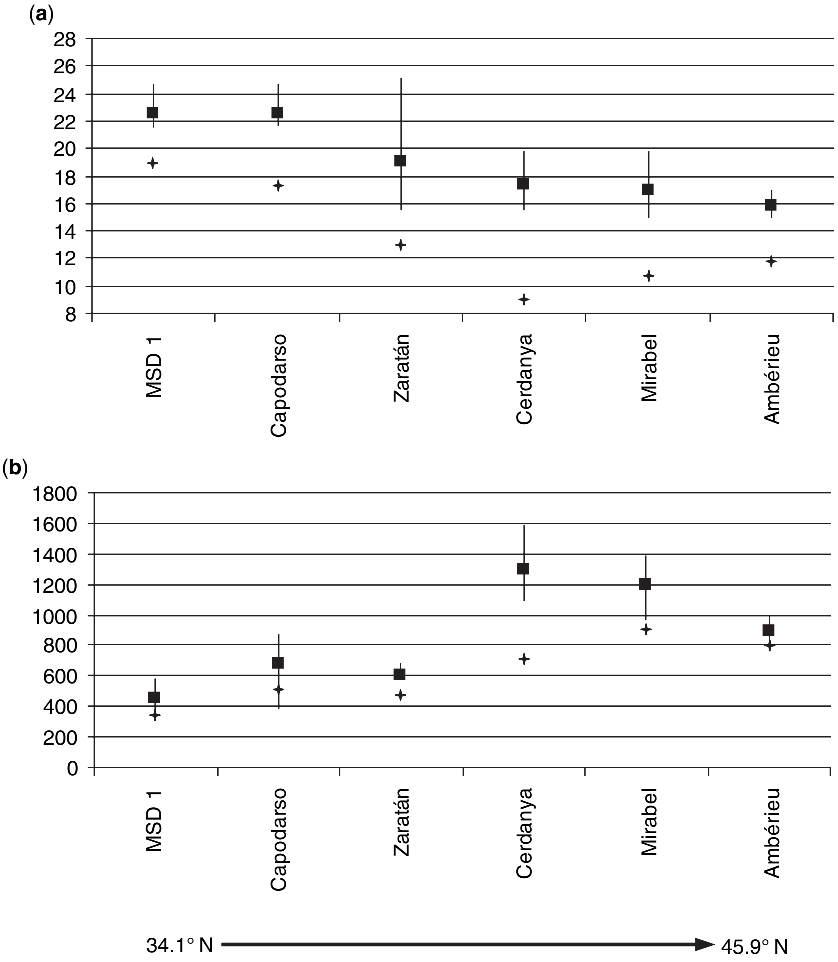


Fig. 5. Climatic reconstruction (climatic interval and most likely value) from pollen data covering the Tortonian in Western Europe and the Mediterranean region showing (**a**) the temperature gradient (mean annual temperature in °C) and (**b**) the precipitation gradient (mean annual precipitation in mm). Modern values are indicated by a cross.

of rias (corresponding to the excision of deep canyons by rivers during the desiccation of the Mediterranean Sea margins at the time of the Messinian Salinity Crisis), which penetrated lands (Clauzon *et al.* 1995). During the earliest part of the Pliocene (5.33 Ma), the reflooding of the Mediterranean basin by Atlantic waters (to about 70–80 m above the present-day sea level, Haq *et al.* 1987) resulted in the accumulation of terrigenous sediments in a large number of areas. As a result, this period is rich in pollen sites. Here, we have used pollen spectra from the sites of Susteren 752/72 (Zagwijn 1960), Stirone (Bertini 1994, 2001), Saint-Martin du Var (Zheng 1986), Cap d'Agde 1 (Suc 1989), Le Boulou (Suc *et al.* 1999), Garraf 1 (Suc & Cravatte 1982), Tarragone E2 (Bessais & Cravatte 1988), Rio Maior F16 (Diniz 1984*a*, *b*), Capo Rossello (Suc *et al.* 1995*c*), Andalucia G1 (Suc *et al.* 1995*a*), Oued Tellil (Suc *et al.* 1999), Nador 1 (Fauquette *et al.* 1999), Habibas 1 (Suc *et al.* 1999), to estimate the climatic gradient during the Early Pliocene. All sites (except Susteren and Rio Maior F16) are marine deposits belonging to the Mediterranean earliest Pliocene and are well-dated by both planktonic foraminifera (zones MPl1-3) and calcareous nannofossils (zones NN12-13) (Suc *et al.* 1995*b*). In addition, the lowermost layers of these sequences directly overly the Messinian erosional surface, providing a synchronous chronological marker at 5.33 Ma (Clauzon *et al.* 1996). The lower part of the Susteren borehole belongs to the Brunssumian climatic phase (Zagwijn 1960). The lower part of the Rio Maior F16 borehole has been correlated to the Brunssumian climatic phase on the basis of a similar evolution of the vegetation to the Early Pliocene changes recorded in the Garraf 1 borehole (Suc & Zagwijn 1983; Suc *et al.* 1995*b*).

Three main vegetation domains in Western Europe and the Mediterranean region (Fig. 6) have been described by Suc (1989) and Suc *et al.* (1995a), during the Early Pliocene, with a clear latitudinal zonation of vegetation. Sites on the Atlantic coast of Western Europe (Fig. 6, zone A, Susteren and Rio Maior sites) show forested vegetation dominated by Taxodiaceae, Ericaceae and mesothermic deciduous trees *(Quercus, Carya, Pterocarya, Acer, Carpinus, Fagus, Liquidambar, Parrotia persica)*. In the north Mediterranean region (Fig. 6, zone B), the forests were dominated by Taxodiaceae (*Taxodium*/*Glyptostrobus* or *Sequoia* dependent on local environment conditions, respectively swamps and slopes), accompanied by mega-mesothermic plants such as *Engelhardia*, *Symplocos* and *Platycarya*. These latter taxa were reduced later, in the Mid-Pliocene. The South Mediterranean region (Fig. 6, zone C) was characterized by Mediterranean xerophytic ecosystems ('matorral' composed by *Olea*, *Phillyrea*, *Pistacia*, *Ceratonia*, evergreen *Quercus*, *Nerium*, *Cistus*) and, to the south, by open environments dominated by subdesertic plants like *Lygeum*, *Neurada*, *Nitraria*, *Calligonum*, Geraniaceae and Agavaceae.

The climatic reconstruction shows that temperatures at the beginning of the Pliocene at around 5.0–5.33 Ma were higher than today, particularly in the northwestern Mediterranean area. The average climate was warm and humid in Europe and the north Mediterranean region (most likely values 1 to 4 °C and precipitation 400 to 700 mm higher than today), and warm and dry in the south Mediterranean region (most likely values equal to or 5 °C higher and drier than or equal to today) (Fauquette *et al.* 1998*b*, 1999; Fauquette & Bertini 2003; this study). A north–south climatic gradient existed at the beginning of the Pliocene, with, as today, increasing temperatures and decreasing precipitation (Fig. 7). The thermic gradient calculated on the 'most likely values' of mean annual temperatures of Susteren and Habibas sites is around 0.65 °C per degree in latitude.

The climatic gradient reconstructed for the West European Pliocene, both for temperatures and precipitation, seems to be very similar to that observed today in northwestern North America and in particular in western California and Lower California. This gradient may be summarized as follows. The climate of northern California is particularly humid, with annual precipitation from *c*. 1000 to more than 2000 mm, especially in the Coast Ranges to the north of San Francisco (summer is the drier season). Mean annual temperatures range from 9 °C to 14 °C. To the south, in central California, the climate is less humid with precipitation ranging from *c*. 600 to 1500 mm/year. This region is characterized by decreasing humidity and an increasing summer drought from north to south. Mean annual temperatures are between 10 and 18 °C. In southern California, mean annual temperatures are between 14 and 24 °C and mean annual precipitation between 400 and 800 mm. Finally, in Lower California, the climate is arid with annual precipitation from *c*. 100 to 500 mm (Walter 1979; Thompson *et al.* 1999). Mean annual temperatures are comprised between 17 and 30 °C.

The vegetation zonation imposed by the latitudinal/altitudinal climatic gradients in this region is also similar to that of the European and Mediterranean Pliocene (Fig. 8). Humidity, as either rainfall or fog, allows the installation of dense *Sequoia* forests in Northern California in the littoral plain as well as in the Coast Ranges (Quézel & Barbero 1989; Thompson *et al.* 1999). These forests occur at up to 900 m a.s.l. on the

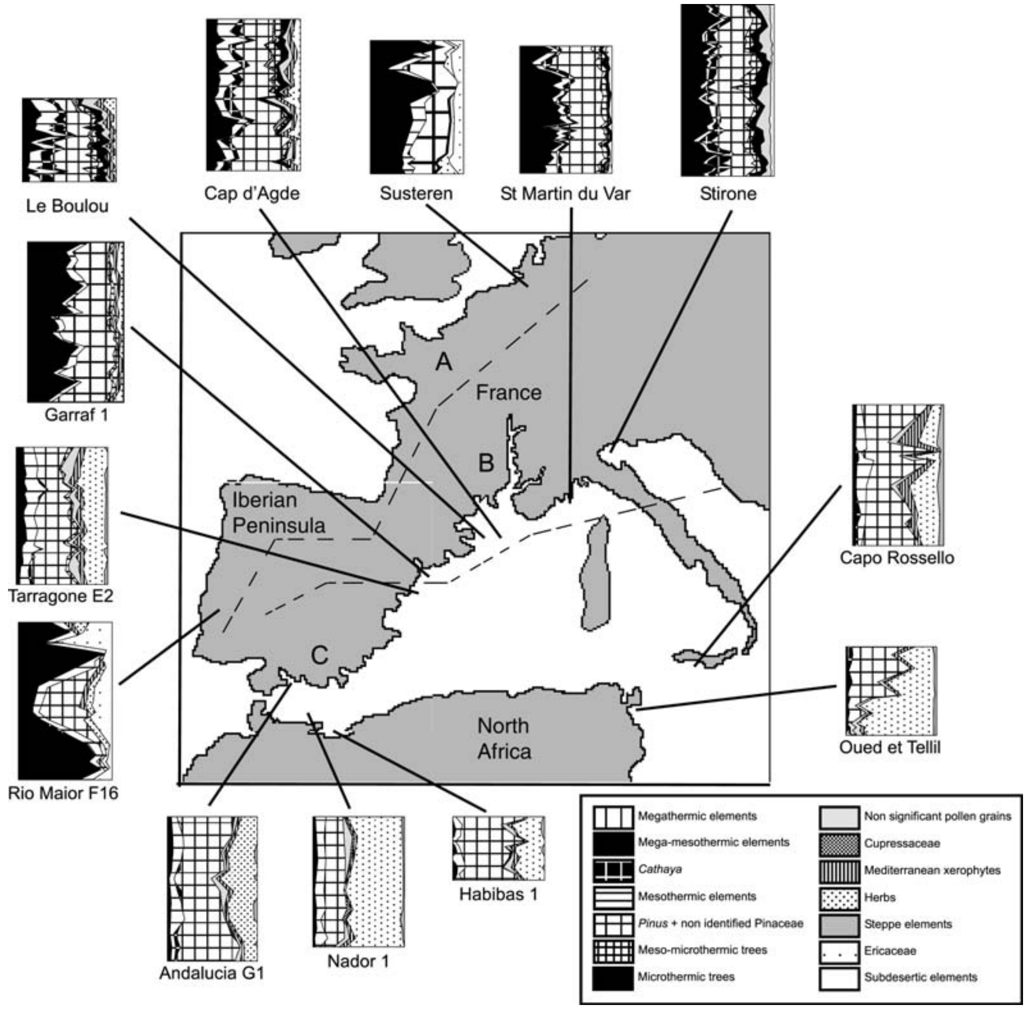


Fig. 6. Location of the studied sites covering the Early Pliocene, at around 5–5.3 Ma, and their synthetic pollen diagrams in the palaeogeographical framework of the Early Pliocene (Clauzon *et al.* 1995; Clauzon 1996; Jolivet *et al.* 2006). Pollen localities: Susteren 752/72 (Zagwijn 1960), Saint-Martin du Var (Zheng 1985), Stirone (Bertini 1994, 2001), Cap d'Agde 1 (Suc 1989), Rio Maior F16 (Diniz 1984), Andalucia G1 (Suc *et al.* 1995*a*), Le Boulou (Suc *et al.* 1999), Nador 1 (Fauquette *et al.* 1999), Habibas 1 (Suc *et al.* 1999), Tarragone E2 (Bessais & Cravatte 1988), Garraf 1 (Suc & Cravatte 1982), Oued et Tellil (Suc *et al.* 1999), Capo Rossello (Suc *et al.* 1995*c*).

Coast Ranges to the north of San Francisco. To the south, the occurrence of sequoias in the uplands becomes sparse (Quézel & Barbero 1989). This vegetation zone closely resembles the Europe and northwestern Mediterranean area dominated by Taxodiaceae and other taxa growing under a wet climate during the Early Pliocene.

Central and southern California are dominated by the chaparral vegetation type (Walter 1979), which resembles the Mediterranean 'matorral' *s.s.* defined by Quézel & Barbero (1989). This vegetation type developed in Europe during the Pliocene with the appearance of the summer drought (Axelrod 1973; Thompson 1991; Thompson & Fleming 1996). The very low precipitation in Lower California prevents the installation of forests, and only a subtropical desert vegetation type may develop in this arid zone (Walter 1979). This zone may be compared to the subdesertic vegetation reconstructed for the Pliocene in North Africa (Suc *et al.* 1995*b*; Fauquette *et al.* 1999).

In California, therefore, the vegetation zonation imposed by the latitudinal climatic gradient along the Pacific coast shows very strong similarities to

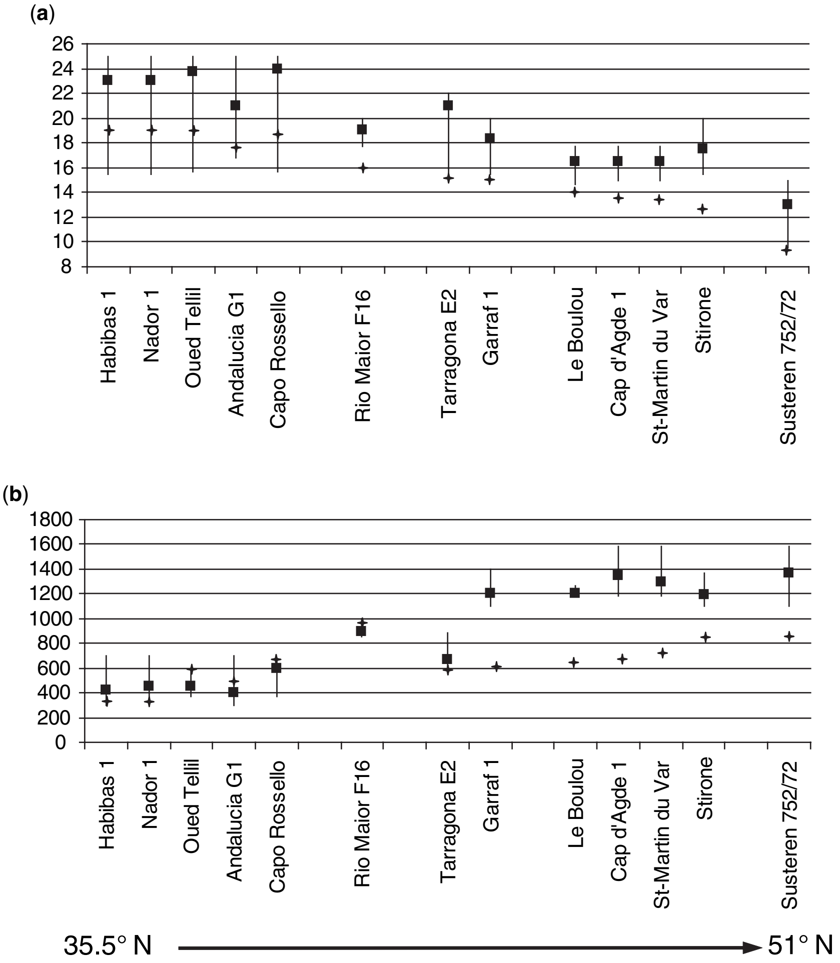


Fig. 7. Climatic reconstruction (climatic interval and most likely value) from pollen data covering the Early Pliocene (*c.* 5–5.3 Ma) in Western Europe and the Mediterranean region showing (**a**) the temperature gradient (mean annual temperature in °C) and (**b**) the precipitation gradient (mean annual precipitation in mm). Modern values are indicated by a cross.

the Pliocene in European and the Mediterranean region, with a development from dense humid forests in the north to subdesertic/desertic vegetation in the south. Changes in vegetation types to the north and south of the region considered also support this comparison. Today, the desertic zone is replaced to the south by intertropical forest in Central America (Walter 1979); a pollen sequence obtained from a borehole in the Guinea Gulf shows a similar change during the Pliocene in Central Africa, to the south of our study area (Suc *et al.* 1995*b*). In northern California, *Sequoia* forests are replaced to the north by forests composed of *Tsuga* in association with other conifers and some deciduous trees such as *Alnus* (Walter 1979); during the Pliocene in Europe, *Tsuga* forests replaced *Sequoia* forests at higher altitudes and latitudes.

The climatic latitudinal gradient for the Middle Pliocene (*c.* 3.5 Ma)

The climatic gradient in Western Europe at around 3.5 Ma has been estimated using pollen spectra from the sites of Susteren (Zagwijn 1960),

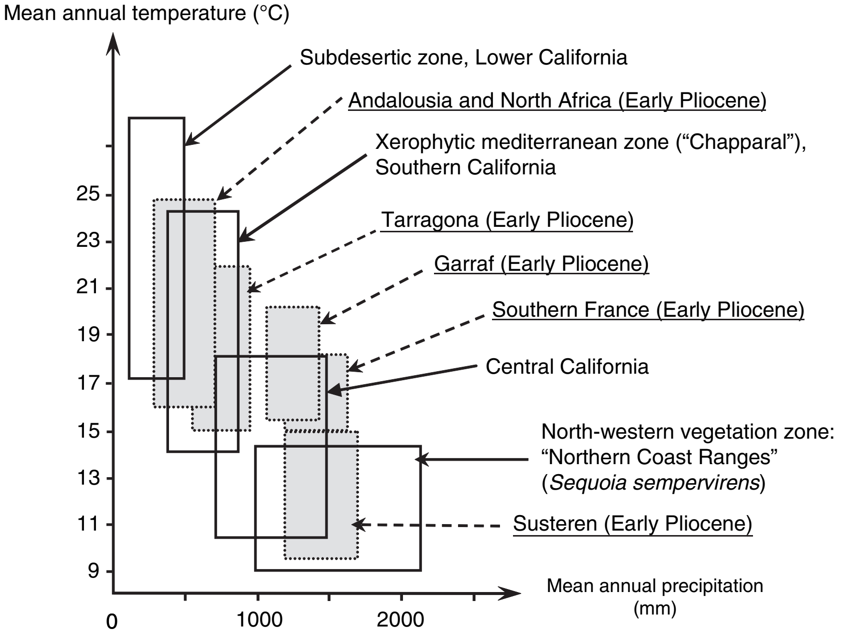


Fig. 8. Comparison between modern climate/vegetation structures of California and those of the Mediterranean Pliocene defined from pollen data and climate reconstruction.

La Londe (Clet & Huault 1987), Saint-Isidore (Zheng 1986), Garraf 1 (Suc & Cravatte 1982), Tarragona E2 (Bessais & Cravatte 1988), Andalucia G1 (Suc *et al.* 1995*a*), Habibas 1 (Suc *et al.* 1999) and Oued Galaa (Suc 1989) (Fig. 9). All sites, except Susteren, La Londe and Rio Maior F16, are marine deposits dated using planktonic foraminifera (zone MPl4): Saint-Isidore (Zheng & Cravatte 1986), Garraf 1 (Suc & Cravatte 1982), Tarragone E2 (Bessais & Cravatte 1988), Andalucia G1 (Suc *et al.* 1995*b*), Habibas 1 (J. Cravatte, unpublished information), Oued Galaa (J. Cravatte, unpublished information). The section of the Susteren borehole sequence used here belongs to the Reuverian climatic phase (Zagwijn 1960) and has been climatostratigraphically correlated to the upper part of the Rio Maior F16 pollen diagram (Suc *et al.* 1995*b*). The same method has been used to attribute uppermost part of the La Londe pollen diagram to the Praetiglian climatic phase (Clet & Huault 1987). The lower part of this section therefore belongs to the Reuverian climatic phase, correlated to the Mediterranean Piacenzian Stage (Suc & Zagwijn 1983; Suc *et al*. 1995*b*).

These pollen data show a clear climatic latitudinal gradient for both temperature and precipitation. In northwestern Europe, along the Atlantic coast (Fig. 9, zone A), the vegetation was characterized by taxa growing under a wet climate, as during the Early Pliocene, but with a reduction in mega-mesothermic taxa (Suc *et al.* 1995*a*). In the northwestern Mediterranean region (Fig. 9, zone B), mega-mesothermic taxa are still well represented but there is a general increase in deciduous mesothermic taxa, especially at Saint-Isidore (southern France) where microthermic plants, which developed at higher altitudes, also increase. In the southwestern Mediterranean region (Fig. 9, zone C), pollen spectra have the same composition as those of the Early Pliocene, characterizing open steppe-like vegetation and dry and warm environments.

As during the Early Pliocene, the climate reconstructed from these pollen data show higher mean annual temperatures than today along the entire gradient (most likely values 3 to 6 °C higher than modern values) and mean annual precipitation that is higher than today in northwestern Europe (most likely values 400 to 700 mm higher), but equivalent to modern values in southwestern Europe (maximum 200 mm higher) (Fig. 10).

The difference in the climate reconstructions between the Early and Middle Pliocene is negligible despite notable variations in pollen assemblages between these two periods (e.g. decrease in pollen percentages of some mega-mesothermic trees but increase in pollen percentages of some mesothermic trees at Garraf in Catalonia, at Saint-Martin du Var and Saint-Isidore in southern France). These

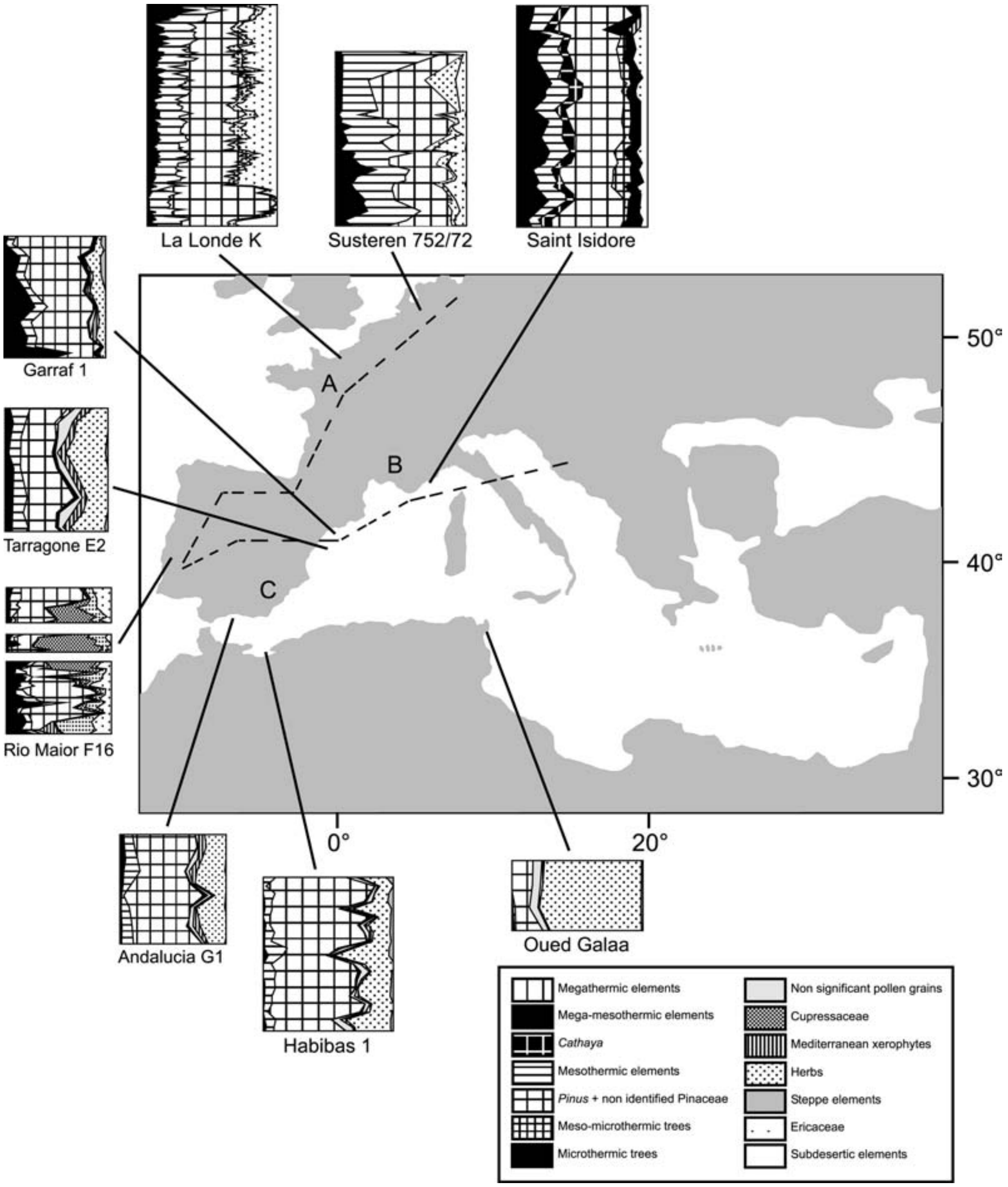


Fig. 9. Location of the studied sites covering the Middle Pliocene, at around 3.5–3 Ma in Western Europe and the Western Mediterranean region and their synthetic pollen diagrams in the palaeogeographical framework of the Middle Pliocene (Khondkarian *et al.* 2004). Pollen localities: Susteren 752/72 (Zagwijn 1960), La Londe (Clet & Huault 1987), Saint-Isidore du Var (Zheng 1985), Garraf 1 (Suc & Cravatte 1982), Tarragona E2 (Bessais & Cravatte 1988), Andalucia G1 (Suc *et al.* 1995*a*), Oued Galaa (Suc unpublished) and Rio Maior F16 (Diniz 1984).

variations in pollen records are often too slight to result in changes in the reconstructed climate. This result indicates the sensitivity limit of the ‘Climatic Amplitude Method’ and of all the methods based on the principle of co-existence intervals.

The West European climatic gradients during the Middle Pliocene, in particular the thermic gradient, appear to be very similar to that observed today, i.e. around 0.6 °C per degree in latitude (Fig. 10).

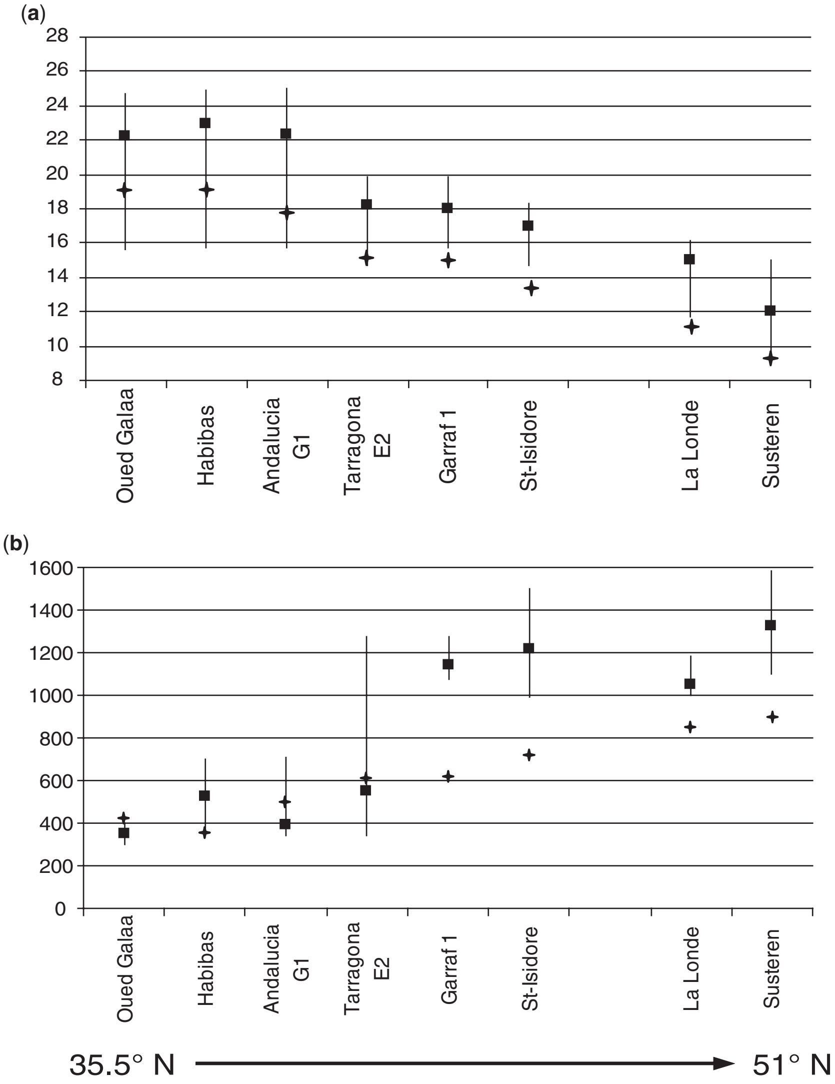


Fig. 10. Climatic reconstruction (climatic interval and most likely value) from pollen data covering the Middle Pliocene in Western Europe and Mediterranean region showing (**a**) the temperature gradient (mean annual temperature in °C) and (**b**) the precipitation gradient (mean annual precipitation in mm). Modern values are indicated by a cross.

Discussion

During the Middle Miocene, the reconstructed thermic gradient was approximately 0.48 °C per degree of latitude. Whilst this estimated value is certainly not the exact value as it is calculated using solely the most likely values, the weakening of the gradient is supported by changes in the entire climatic intervals. A weaker gradient during this period has also been suggested by other studies based on macro- and microfloras of the circumalpine region and Central Europe (Bruch *et al.* 2004) and also in North America (Liu & Leopold 1994).

From the end of the Miocene (Tortonian) to the mid-Pliocene, the vegetation and climatic latitudinal gradients (in particular the thermic one) differ from those of the Middle Miocene. Temperatures were higher than today, as during the Mid-Miocene, but the difference between the north and the south was greater than during the Mid-Miocene, resulting in a similar gradient in temperature and vegetation to today.

Our results place the transition, for mid-latitude regions, from the weak thermic gradient of the Mid-Miocene to the modern-like gradient of the Pliocene during the Middle–Late Miocene, before or during the Tortonian.

Simulations with the AGCM ECHAM4 coupled to a slab ocean model have been made in order to study the climate response during the Tortonian to a generally low palaeo-orography, a weaker-than-present palaeo-oceanic heat transport and a changed palaeovegetation (Steppuhn *et al.* 2006; Micheels *et al.* unpublished data). Climate trends in the Tortonian model simulations show an overall reduction of the meridional temperature gradient (Steppuhn *et al.* 2006; Micheels *et al.* unpublished data). For the Mediterranean region, the simulated climate is slightly warmer and drier than today (Micheels *et al.* unpublished data), which agrees with our data from southwestern Europe (Sicily, Central Spain). In northern Africa, the Tortonian model simulates warmer and less-arid conditions than today (Micheels *et al.* unpublished data). Our evidence for subdesertic herbs and forest elements in Morocco supports the climate modelling results. However, it should be noted that these two groups of plants certainly developed at different altitudes that may not be adequately resolved by the climatic model. The pollen flora of the Ambérieu and Mirabel sites indicate forest environments that developed under a warm and wet climate. The Tortonian simulation indicates an increased precipitation over Central Europe. Although this simulation tends to be too cool at higher latitudes (Micheels *et al.* unpublished data), our data from Europe largely agree with the model simulation.

On the basis of fossil floras of Central and Eastern Europe, Bruch *et al.* (2006) indicate a much weaker thermic gradient than today during the Tortonian, with a reduction of approximately 50%. Whilst the ECHAM model is unable to reproduce this weak temperature gradient, our results show higher mean annual temperatures than the simulated zonal average temperature for land surfaces but agree with the thermic gradient simulated (Fig. 11).

Simulations have been made of the Mid-Pliocene climate by Haywood *et al.* (2000*a*) using the HadAM3 version of the UK Meteorological Office's (UKMO) general circulation model and by Jost (2005) using the LMDz (Laboratoire de Météorologie Dynamique, zoom, Institut Pierre Simon Laplace) atmospheric general circulation model.

Boundary conditions of the models are those established by the Pliocene Research, Interpretation and Synoptic Mapping group of the US Geological Survey (PRISM 2, see Cronin & Dowsett 1990; Dowsett *et al.* 1994, 1999). Jost (2005) confirms the increase in global temperatures compared to the present (Fig. 12a), previously shown by Haywood *et al.* (2000*a*). This increase is greater at mid- to high latitudes than at the equator.

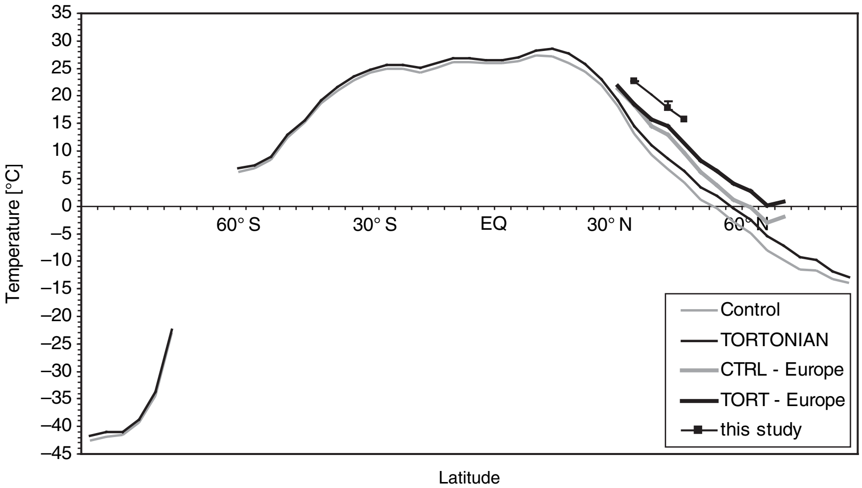


Fig. 11. The zonal average temperature (in °C) for land surfaces of the Tortonian simulation (black line), the present-day control simulation (grey line) and terrestrial proxy-data (squares and reconstructed interval). In order to obtain the zonal averages of proxy-data, the data locations are transformed into the grid point resolution (3.75°) of the model ECHAM4. For Europe, the zonal average temperatures of the model runs are shown separately.

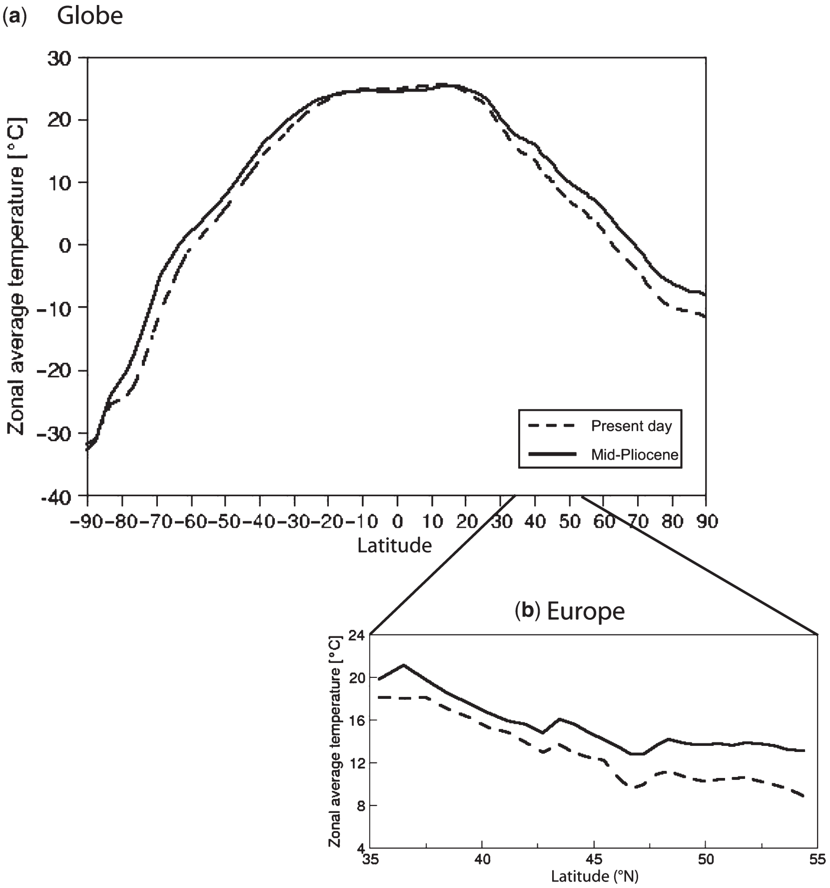
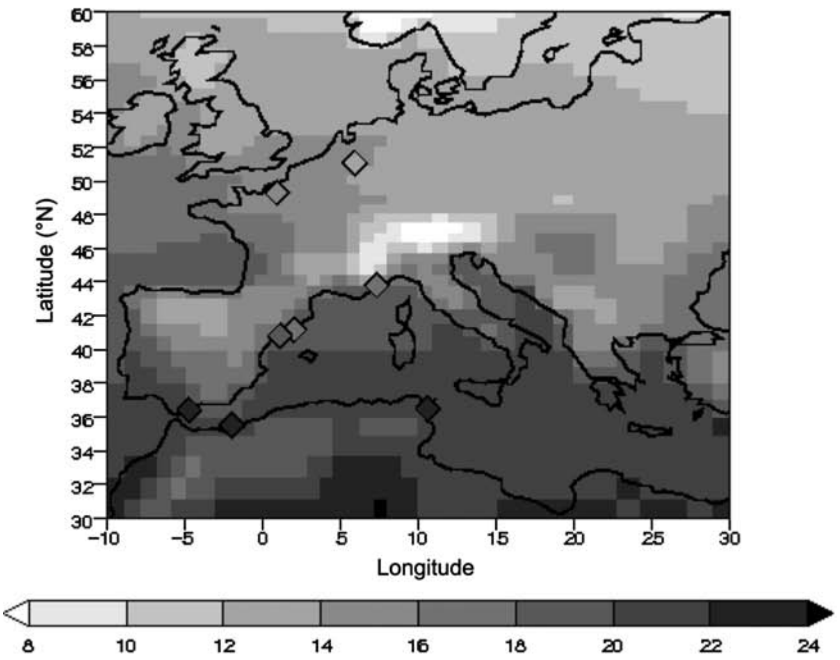


Fig. 12. The zonal average temperatures (in °C) for land surfaces of the Middle Pliocene simulation (bold line) and the present-day control simulation (dotted line), (**a**) for the globe, (**b**) for Europe (from −10 to 20° East and 35 to 55° West), from the LMDz AGCM (modified from Jost 2005).

However, despite this weakened pole-to-equator thermic gradient, the simulation shows similar changes of temperature at mid-latitudes of the Northern Hemisphere between the Middle Pliocene and today (Fig. 12b), suggesting that, for this region, the latitudinal thermic gradient was close to the modern one (i.e. around 0.6 °C/degree in latitude). This pattern is completely consistent with our reconstructed climate and vegetation distribution. The mean annual temperatures of the simulations cited above are in good agreement with the reconstructed climate (Fig. 13a) with temperatures that are clearly higher than today in the study region.

There are, however, some important differences between the reconstructed annual precipitation and changes simulated by the AGCM LMDz (Fig. 13b). Pollen data indicate in western Europe and in the western Mediterranean higher annual precipitation than the LMDz model.

On the contrary, the pollen-based precipitation estimates are in better agreement with the simulations by Haywood *et al.* (2000*a*, *b*). As shown on Figures 7 and 10, the precipitation gradient, whilst still decreasing from north to south, was more accentuated, with a larger difference between the Pliocene and today in the north than in the south. Haywood *et al.*'s simulations (2000*b*) show annual zonal average precipitation similar to modern values between around 30 and 42° N and higher than today between 42 and 51° N. This pattern is particularly true in Western Europe and western Mediterranean and has been explained by the authors by an increased arrival of southwestern air masses. During the Mid-Pliocene, the enhancement of the Icelandic low- and Azores high-pressure systems and the stronger pressure gradient in the North Atlantic caused an intensification of annual westerly wind strength. Combined (**a**) Mean annual temperatures (°C)



(**b**) Mean annual precipitation (mm)

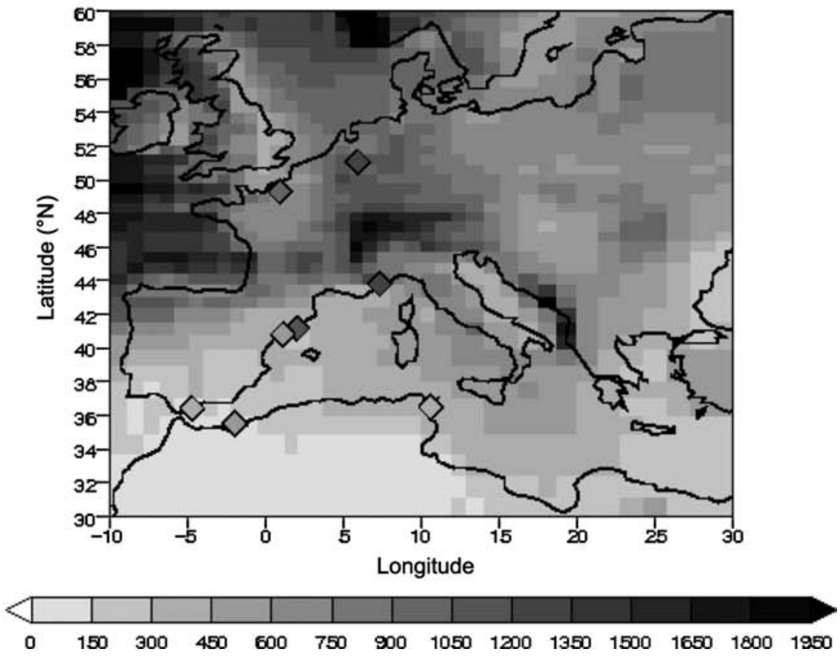


Fig. 13. Comparison for the Mid-Pliocene (3.5–3 Ma) between (**a**) mean annual temperatures and (**b**) annual precipitation simulated by the LMDz atmospheric general circulation model (modified from Jost 2005) and the values obtained from pollen data (diamonds).

with warmer sea-surface temperatures, the atmospheric transport of heat and moisture over Europe and the Mediterranean region was increased (Haywood *et al.* 2000*a*). This pattern is in agreement with the development of Ericaceae moors along the European Atlantic coast that suggest an enhanced westerly wind pattern (Suc *et al.* 1995*a*, *b*).

New simulations realized by Haywood *et al.* (2002) with the HadAM3 AGCM coupled with the BIOME 4 vegetation model (Kaplan 2001) show that, due to higher temperatures and higher precipitation, Europe and the Mediterranean region were dominated by forest biomes during the Mid-Pliocene. This agrees with the pollen data, especially in higher latitudes where forests extended into what is now tundra. This confirms the good agreement between our pollen data and the HadAM3 AGCM.

Conclusion

A thorough review of existing pollen data has allowed us to present a regional climate synthesis for the Neogene, from the Middle Miocene (*c*. 14–15 Ma) to the Middle Pliocene (*c*. 3.5 Ma).

In Western Europe and the Mediterranean region, from the Middle Miocene to the Middle Pliocene, the vegetation cover reflects a clear latitudinal gradient. In all of the considered periods, the quantitatively reconstructed climate shows, in comparison to today, higher mean annual temperatures along the gradient and increases in mean annual precipitation in northwestern Europe and the northwestern Mediterranean, but similar precipitation to today in the southwestern Mediterranean region. The results also show a clear latitudinal gradient of temperature and precipitation, increasing for temperatures but decreasing for precipitation from north to south.

The results show that the thermic gradient has evolved in time. During the Middle Miocene, the presence of mega-mesothermic taxa in pollen spectra at all sites, even in Switzerland, shows that the thermic latitudinal gradient was weaker than the modern one. Based on the climate reconstructed from pollen data, the thermic gradient was around 0.48 °C per degree of latitude whereas it is today around 0.6 °C degree in Western Europe. This result is in agreement with estimations obtained from fossil floras of Europe (Bruch *et al.* 2004) and America (Liu & Leopold 1994). During the Tortonian and the Pliocene, the vegetation distribution and the climate reconstruction show the thermic latitudinal gradient to have been close to the modern one. The transition from the weak thermic latitudinal gradient of the Mid-Miocene to the modern-like gradient of the Pliocene appears to take place during the Middle–Late Miocene, before or during the Tortonian.

The precipitation gradient was more accentuated than today from the Mid-Miocene to the Mid-Pliocene: the precipitation anomalies between the Neogene and today are larger in the north than in the south. The transition from this pattern to the modern latitudinal gradient took place after the Mid-Pliocene, at time of the first glacial–interglacial cycles.

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