

Deciphering Early Angiosperm Landscape Ecology Using a Clustering Method on Cretaceous Plant Assemblages

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1. Introduction

Fossils open up windows on past lives and evolutionary mechanisms inaccessible to other fields of biology. Palaeontology has highlighted five moments of major extinctions in the life history on Earth: Ordovician/Silurian, Late Devonian, Permian/Triassic, Triassic/Jurassic and Cretaceous/Tertiary (Sepkoski, 1986). These five crises shaped life (apparitions versus extinctions of species), as well as diversity, ecology, and landscape. So fossils are not objects only useful for taxonomy and systematics, but their ecological traits can be deciphered to reveal macro-evolutionary processes and landscape ecology.

Today, flowering plants or angiosperms include the greatest terrestrial plant diversity consisting of over 250,000 species. They constitute the most abundant and diverse plant group, and notably provide food and medicine to present-day animals and human beings. The sudden appearance of angiosperms in the fossil record, their mostly cryptic evolution during the Early Cretaceous (-145 to -100Ma), and their subsequent rise to dominance in all terrestrial habitats during the Late Cretaceous (-100 to -65Ma) remain one of the most puzzling mysteries in evolutionary biology. These events are often quoted in the literature as “Darwin’s abominable mystery”. The ascent to dominance by the new plant groups (i.e. angiosperms versus ferns and conifers) affected the whole terrestrial ecosystems, food chains, soil chemistry and atmosphere composition.

In order to better understand the chronology and mechanisms behind the considerable turnover from gymnosperm-dominated vegetation to angiosperm-dominated vegetation and their consequences, we have studied megafossil plant remains from the Barremian-Campanian of Europe. Because of the fossil record often provides incomplete and biased data, we have used the Wagner's Parsimony Method (WPM). It was developed in 1961 by Wagner who worked on the systematics of ferns. The WPM consists of a system of hierarchical classification; it is a classical clustering method now used in phylogeny, however it can be applied to fields other than cladistics (Masselot et al., 1997). In synecology, it can be used for classifying localities or samplings as a function of biological content. They

can also be related based on environmental conditions, so as to provide evidence of the relationship between palaeo-biocoenoses (known from fossils) and the palaeo-biotopes (known from sedimentology). Modern ecology concepts can be applied to a reconstruction of vegetation, and it is possible to relate ecological strategy and evolutionary history. We have applied the WPM for grouping localities by their megafossil plant content. For this study, we have run three successive WPM analyses using three time intervals: (1) Barremian-Albian, (2) Albian-Cenomanian and (3) Turonian-Campanian. The clusters obtained consist of seven types of depositional environments: (1) estuary mouth, (2) salt marsh, (3) freshwater swamp, (4) floodplain, (5) levee, (6) channel and (7) lacustrine deposits. They are each compared to independent sedimentological and palaeoenvironmental settings (e.g. crevasse splay deposits and lithographic limestones).

2. Geological setting

During the Cretaceous, oceanic accretion increased and wide volcanic provinces formed (such as the traps of Deccan) around the Cretaceous/Tertiary (K/T) boundary. The volcanic activity was associated with the releases of large volumes of CO₂ into the atmosphere, and consequently provoked greenhouse episodes in particular during the Cenomanian, which is considered to be the most recent warmest episodes of the Phanerozoic (Veizer et al., 2000). Also major perturbations in the carbon cycle occurred in the oceans. There were several oceanic anoxic events (OAEs) during which large quantities of organic-matter-rich black shales were deposited. These organic accumulations can have two origins (Leckie et al., 2002): (1) an increase in the concentrations of CO₂ or nutrients may have led to an increase in the marine production: production oceanic anoxic events (POAE); (2) an increase in rainfall precipitation may have led to an increase in detritic inputs: detritic oceanic anoxic events (DOAE).

In the last decades, palaeoclimate estimates were obtained from several marine and terrestrial proxies. For instance, oxygen isotopes were widely used to study palaeotemperature variations from marine animal shales (e.g. Bowen, 1961), while clay mineralogy provided information on conditions during formation of clays and therefore helped to reveal precipitation patterns (e.g. Ruffell & Batten, 1990). Plants were also used to infer palaeoclimates using leaf morphology (e.g., Climate Leaf Analysis Multivariate Program, CLAMP, Wolfe, 1993; Spicer & Herman, 2010 and reference therein) or pCO₂ (Retallack, 2001). On the basis of the data available for Western Europe, the time interval from the Barremian to the Santonian is divided into five climate stages: (1) Barremian - Early Aptian; (2) Late Aptian - Early Albian; (3) Albian; (4) Cenomanian - Early Turonian; (5) Late Turonian - Santonian.

2.1 Barremian - early Aptian arid phase

Ruffell & Batten (1990) identified an arid phase from the Barremian to the middle Aptian of Western Europe based on a review of climate indicators (e.g. evaporites and clay mineralogy). During the same time interval, Haywood et al. (2004), based on a climate computer simulation, suggested that England had mean annual temperature of 22-26°C and precipitation of about 1400-3000mm with a very marked drought season. A first OAE 1a (Fig. 1), with thin deposits of black shales occurred during the Early Aptian. It may be explained by changes (1) in the oceanic circulation, (2) in the hydrologic cycle with an increase of precipitation and erosion in a context of CO₂-induced global warming, and (3) in the oceanic fertilisation with an increase in iron of volcanic origin leading to higher oceanic

productivity and carbon burying (Leckie et al., 2002). Also there were an abrupt diminution of $^{87}\text{Sr}/^{86}\text{Sr}$ and a negative excursion of $\delta^{13}\text{C}$ that suggest a relation with the super panache (plume) of Otong-Java eruption (Fig. 1). These pikes may also be explained by volcanic light-isotope carbon inputs or by dissociation of methane hydrates (Leckie et al., 2002). After OAE 1a, the values of $\delta^{13}\text{C}$ values continued to decrease, suggesting that the carbon burying lasted during the middle Alptian in parallel with the sea-level rise.

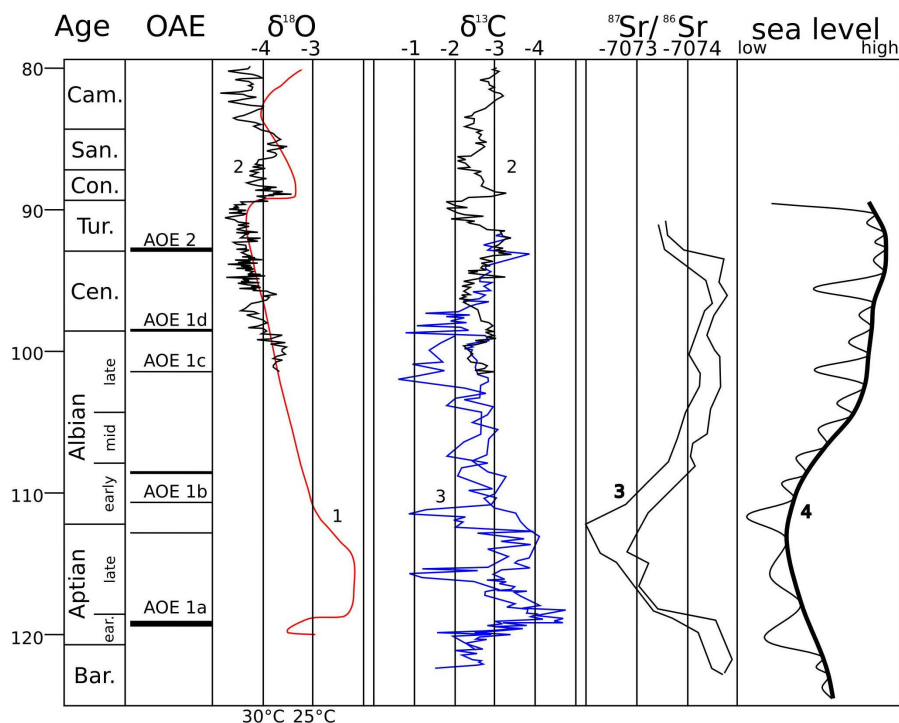


Fig. 1. Main proxies to estimate the Middle Cretaceous global changes (1, Steuber et al., 2005; Rudistes; 2, Stoll & Schrag, 2000, Foraminiferes; 3, Leckie et al., 2002; 4, Haq et al., 1988).

2.2 Late Aptian - earliest Albian humid phase

Negative excursions of $\delta^{13}\text{C}$ happened again during the upper Aptian and the Aptian/Albian (OAE 1b) (Fig. 1). Also, in Europe, there was a transition from an arid phase (Ruffell & Batten, 1990) to a humid phase as indicated by the deposits of detritic quartz at the bottom of the Vocontian trough (Wortmann et al., 2004). These changes were attributed to a positive retroaction, the carbon-burying during the OAE 1a and the level "Jacob" of OAE 1b resulting in lower atmospheric CO_2 concentration (Weissert & Lini, 1991). They are associated with a global cooling of about 5°C , a growth of polar caps, and a sea-level fall (Steuber, 2005). According to Erbacher et al. (1998), the black shales of level "Jacob" of OAE 1b may have formed because of the inputs of detritic organic matter (DOAE) related to an increase in the precipitation. In contrast, the level "Paquier" of OAE 1b is considered as a phase of warming (8°C according to Price et al., 2003) and wetting (Heerle et al., 2003).

2.3 Albian warming

During the Albian, the oceanic accretion and the sea levels continuously increased (Fig. 1). Thus, more CO₂ entered into the atmosphere and Europe became an archipelago of islands (Fig. 2; Haq, 1988). This new input of CO₂ provoked a global warming phase with the temperatures rising from 12-14°C to 22-26°C in the North Atlantic (Fig. 1) (Leckie et al., 2002; Price et al., 2002). Also, clay mineralogy of sediments in northwestern Germany indicates a change to semi-arid conditions in Europe characterised by seasonal precipitations (Mutterlose et al., 2003).

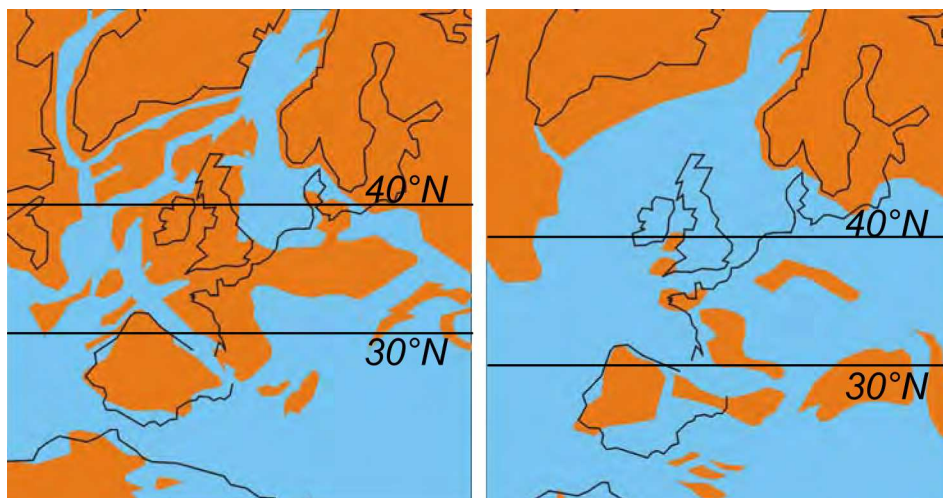


Fig. 2. Palaeogeography of Europe during low (Berriasian-Barremian) and high (Late Cenomanian) sea levels (modified from Ziegler, 1988).

During the lower Upper Albian, a new phase of oceanic anoxic event (OAE 1c) was produced by inputs of detritic organic matter (Leckie et al., 2002) and can be compared with the humid interval described by Fenner (2001) from clay mineralogy. The OAE 1c is followed by a warming of about 5°C (Fig. 1) (Stoll & Shrag, 2000) and seasonal precipitation (Fenner, 2001).

The Albian ended by another phase of oceanic anoxic event (OAE 1d; Leckie et al., 2002) related to input of detritic organic matter. The cyclicity of these OAEs might be due to a periodic change in the oceanic circulation favouring the upwelling of nutrient-rich waters and increasing the productivity (Leckie et al., 2002). Bornemann et al. (2005) also suggested oceanic circulation changes might be controlled by Monsoon-type climates. During OAE 1d, a new regression connected again to other islands in the European archipelago (Fig. 1-2) (Haq, 1988).

2.4 Cenomanian - early Turonian thermal maximum

The Cenomanian is considered the most recent warm time-interval of the Phanerozoic (Veizer et al., 2000). The Middle Cenomanian is, however, marked by a slight cooling and a

new regression (Fig. 1; Stoll & Shrag, 2000; Haq, 1988). CLAMP analysis of the megafossil leaf angiosperms from the middle Upper Cenomanian of Peruc-Koryčany indicated that the region of today's Czech Republic had a subtropical climate with a mean annual temperature of 17-20°C and precipitation of about 1400mm (Table 1; Kvaček, 2000).

Fossil flora	MAT (°C)	MAP (mm)	DSC (months)
Peruc-Koryčany Cenomanian	17-20	1400	9.5-10.5
Zliv, Klikov, Hluboká Senonian	14-17	1300	7.5-10

Table 1. CLAMPs from the Late Cretaceous of Europe (MAT, mean annual temperatures; MAP, mean annual precipitations; DSC, duration of the growth season).

At the end of the Cenomanian, a new phase of oceanic anoxic event (OAE 2) is associated with a marine regression. The spike of more negative $\delta^{13}\text{C}$ is related to the burying of oceanic organic matter (Keller et al., 2001), while the fall in $^{87}\text{Sr}/^{86}\text{Sr}$ is induced by the strong oceanic accretion and the super panache of Kerguelen.

2.5 Late Turonian - Santonian cooling

From the Late Turonian to the Early Santonian a cooling and a regression occurred, and were related to a glaciation (Fig. 1; Stoll & Shrag, 2000; Miller et al., 2003). CLAMP analysis of the megafossil leaf angiosperms from the Senonian of Zliv, Czech Republic indicated that it was under a warm temperate climate, slightly cooler than that of the Cenomanian, with a mean annual temperature of 14-17°C and mean annual precipitation of about 1300 mm (Table 1; Hermann & Kvaček, 2002).

During the Cretaceous, climates varied greatly. In particular, during the Albian, the temperatures had reached plus 10°C in a few millions of years. These high climate variations came with wide fluctuations of climate zones and, subsequently, distant migrations of terrestrial plants. These global climate changes, in addition to eustatic oscillations (compartmenting terrestrial environments into isolated islands), created new niches and new evolutionary opportunities for the clades (e.g. development of extra-tropical megathermal forests).

3. Method

3.1 Synecological principle of the Wagner's Parsimony Method

The Wagner's Parsimony Method (WPM) consists of constructing one or more trees in which the objects (e.g. taxa in phylogeny, localities in synecology) are related to others based on their characters (e.g. nucleotides or morphology characters in phylogeny, presence/absence of a taxon in synecology). The tree(s) are dichotomous-branched trees (i.e. trees with each split forming two branches). The most parsimonious tree is that which minimises the number of changes in character states of each node on the whole tree. The total number of state changes of the whole character set for the same tree is called length of the tree. So this method consists of looking for the tree (or the trees) with the smallest length.

When several trees of minimal length (so-called most parsimonious) are created, it is possible to create a tree called the “strict consensus” that represents the existing groupings in all of the most parsimonious trees. When different solutions of grouping branches are possible, the consensus tree presents a polytomy that employs non-dichotomous branching. The most parsimonious trees are rooted with an external group to polarise the characters.

3.1.1 How are the data coded?

In the case of the palaeosynecology, the objects studied are the localities, and the characters used are the presence/absence of taxa, these data are obtained from the plant lists. With these data, we build a matrix with the localities as columns and the taxa as rows. Each box of the matrix takes the value 0 or 1 depending on whether the taxon is absent or present, respectively, in the locality. The taxa used must be identified at the species level and doubtful or uncertain data («cf.» or «aff.») can be coded by «?». The final treatment of these uncertain or missing data (or «?») can be made as in the classical cladistic analyses, by more parsimonious inference on the final trees. This treatment estimates whether or not the presence of particular taxa is consistent with the analysis.

3.1.2 Taphonomic biases and data collecting

Because taphonomic biases deeply constrain the contents of palaeontological assemblages, we compare the localities with similar biases. For instance, it would be absurd to compare insect assemblages of ambers with those of lacustrine lithographic limestones. Ideally, specimen collection would be verified to have been undertaken identically in all of the localities studied. The problem is the same and the solution is analogous to working on living organisms. The proportion of the (palaeo-)biological diversity collected must be estimated by establishing a curve of diversity per locality (Perochon et al., 2001). If the collection(s) are insufficient for one locality, then they must be completed in the field.

3.1.3 Differences between characters and attributes

In addition to the characters defined above, the localities studied include more information called attributes. The attributes are not used for building the parsimony trees. So, the trees obtained have no link to the attributes and the value of attributes can be tested. In our palaeosynecological case, the attributes most often consist of sedimentological and taphonomic data.

3.1.4 Why and how to choose the external group(s)?

To root a tree, we must define the states of primitive (plesiomorphic) and derived (apomorphic) characters (sensu Nel et al., 1998). Then, the characters constitute a so-called primary polarisation, since the latter is done before the WPM analysis.

According to Masselot et al. (1997) and Nel et al. (1998), the external group must be defined before the polarisation of the characters, that is before determining whether the state of a character is primitive or derived. The supposed primitive state of a character is thus that observed in the external group. This external group can correspond to one or more stations

or hypothetical of real samplings. The use of real ecological units (i.e. stations and samplings) is preferable because they introduce fewer a priori hypotheses.

In the particular case of a palaeosynecological study on the evolution of ecosystems through time, the time interval or the oldest locality studied can be chosen as the external group. With this choice, the presence of an “ancient” taxon within the external group is considered as primarily plesiomorphic and the presence of a “more recent” taxon as primarily apomorphic. Several external groups (i.e. more ancient time intervals or localities than all other localities studied in the internal group) can be used alternatively or simultaneously and their impact on the analysis tested.

4. Results

The European Cretaceous plant record is well-constrained and dated stratigraphically and shows well-preserved angiosperms from the Barremian to the Maastrichtian. Furthermore, European palaeobotany provides many detailed studies of Cretaceous floras for analysis that encompass a full range of deposition environments. Three age intervals were studied in three successive WPM analyses: (1) Barremian-Albian, (2) Albian-Cenomanian and (3) Turonian-Campanian. The clusters obtained are compared to independent sedimentological and palaeoenvironmental settings for each age. The clusters consist of seven types of depositional environments: (1) estuary mouth, (2) salt marsh, (3) freshwater swamp, (4) floodplain, (5) levee, (6) channel and (7) lacustrine deposits (Coiffard et al., 2006, 2007, 2010). Plant taphonomy (i.e. the deductions of the characteristics of production, transport, burying, and fossilization based on the states of preservation of megafossil plant remains) strongly supports the close proximity between the living environments and the final depositional environments in all fossil assemblages retained for the WPM analyses. One may assume that plant communities living in similar biotopes fossilize in similar depositional environments. Thus the resulting cluster corresponds to communities that grew at or near the environment where they deposited and are recorded. The palaeo-vegetations or communities evolved in space and in time, and they may be interpreted in terms of landscape ecology. Thus each plant assemblage may reflect environmental mosaics juxtaposed in the same geomorphological unit (e.g. channel margins ranging from sandy banks to “hardwood” forests). Nowadays, such environmental mosaics take place within a few meters. All these factors together contribute to make a robust data set of the evolution of angiosperms from the Barremian to the Campanian that can be traced through various ecosystems and related to other plant groups occupying the same niches. These data sets produce a view of angiosperm radiation in three phases that reconciles the previous scenarios based on the North American record.

4.1 Phase 1: Barremian-Aptian freshwater lake-related wetlands

Worldwide, angiosperm megafossils from the Barremian are very rare, with the earliest records found in freshwater lake or wetland habitats of China and Spain (Sun et al., 1998, 2002; Gomez et al., 2006; Dilcher et al. 2007). In an aquatic community, these angiosperms competed with charophytes that dominated macrophytic associations since the Permian (Martín-Closas, 2003; Sun et al., 1998, 2002). In the Barremian of Europe, chloranthoid/*Afropollis* pollen indicates terrestrial angiosperms (Heimhofer et al., 2005), although matoniaceous fern thickets and open conifer woodlands in floodplains dominated the terrestrial vegetation. Such a vegetational physiognomy is consistent with the fact that

Western Europe underwent an arid phase from the Barremian to the Middle Aptian (Ruffell & Batten, 1990; Haywood et al., 2004). Aquatic angiosperm megafossil remains (Coiffard et al., 2007) and terrestrial chloranthoid, lauralean or magnolialean fossil pollen (Heimhofer et al., 2005) appear highly diversified in the Late Aptian. This diversification was accompanied by the closure of woodlands, conifers spreading over most environments, and near extinction of matoniaceous ferns. In contrast, terrestrial leaf megafossils are very rare except for *Quercophyllum* from the Aptian/Albian of Arnal (Portugal) that probably grew along freshwater lakes or pond margins. The Barremian-Aptian fresh waters and related wetlands are sketched at the bottom of Figure 3 (Fig. 3.1).

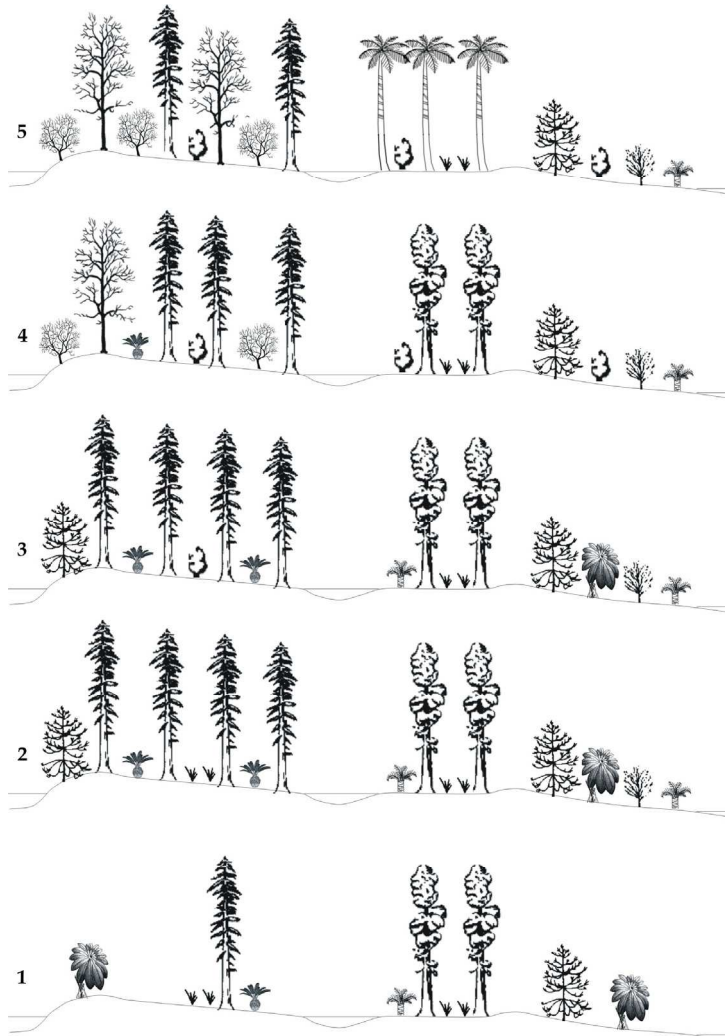


Fig. 3. Evolution of plant association through time and space. 1, Barremian; 2, Aptian/Albian; 3, Albian, 4, Cenomanian; 5, Campanian.

4.2 Phase 2: Aptian-Albian understory floodplains (excluding levees and backswamps)

The vegetation of Europe was highly diverse during the Albian (in floodplains, ca. 11 taxa per locality vs. 8 during the Barremian and 6 during the Aptian/Albian, Coiffard et al., 2007), probably forced by a warming period beginning in the early Albian (Leckie et al., 2002; Price & Hart, 2002). Angiosperms exhibited a wider ecological range during the Albian, occurring in significant numbers for the first time in floodplains and probably some became vines (e.g. *Menispermites* Lesquereux; Dobruskina, 1997). Also, angiosperms competed with Osmundaceae taxa (e.g. *Cladophlebis* Brongniart), which nearly disappeared during the Albian (see Fig. 3.2 and 3.3).

In contrast to the small-leaved, ramified angiosperm habit, ferns and gymnosperms that were replaced by angiosperms show a large-leaved, monocaule habit. The small-leaved, ramified habit is more resilient in case of limb fall: if the meristem of a monocaule plant is destroyed, it may die or recover slowly while a ramified plant can use many active meristems that will allow the plant to recover more easily. In closed forests of the floodplains, angiosperms occupied the understory, while conifers formed the canopy. In contrast, matoniaceous fern thickets were exclusive to open vegetation of floodplains. Most floodplain angiosperms belonged to core angiosperms (i.e. Eudicots and Magnoliids). The increase in Eudicots during the Albian could be due to a poleward migration driven by global warming. This migration is also supported by the poleward dispersion of tricolpate (Eudicots) pollen grains shown by Hickey & Doyle (1977).

4.3 Phase 3: Cenomanian-Campanian levees, backswamps and coastal swamps

At the beginning of the Cenomanian (Fig. 3.4), European angiosperms were already widespread, and inhabited most environments, except apparently estuary mouths (Coiffard et al., 2006). In backswamps, they replaced Cycadales, and to a lesser extent, matoniaceous and dicksoniaceous ferns. In coastal swamps, they competed with matoniaceous ferns (e.g. *Weichselia* Stiehler), and constitute the earliest record of halophyte angiosperms (Coiffard et al., 2006, 2009). Angiosperms exhibited clear tree habit, especially trees of Lauraceae and Platanaceae which inhabited disturbed channel margins. In such a niche, they may have displaced conifers due to a greater growth rate of seedlings in accordance with Bond's hypothesis (Bond, 1989; Becker, 2000; Coiffard et al., 2006). This may also have included the shorter life cycle of the angiosperms compared to the gymnosperms present in similar habitats.

From the Turonian (Fig. 3.4 and 3.5), various genera of the Platanaceae spread over more stable floodplain environments while Bennettitales and Dicksoniaceae decreased (Coiffard & Gomez, 2010). Palms competed with Cupressaceae (*Taxodium* affinities) in the backswamps. Thus, palm seedlings developed large leaf crowns that shade and impede weeds, whereas conifer seedlings must compete with weeds. During the later growth stage, palm monocaule habit represents a lower energetic cost than Cupressaceae trunks, resulting in either a faster growth or higher allocation to reproduction. Cupressaceae were maintained in cooler areas, while palms do poorly in cool and cold temperate climates.

The reconstruction of vegetation changes through the Cretaceous (Fig. 3) shows that angiosperm colonization happened in three stages: (1) during the Barremian-Aptian early angiosperms were restricted in water bodies of freshwater wetlands; (2) during the Aptian-

Albian angiosperms spread through understory floodplains (excluding levees and backswamps); and (3) during the Cenomanian-Turonian they finally colonized the natural levees, backswamps and coastal swamps.

These results show that the rise to dominance was not uniform and took place in space and time at different rates according to the environments.

5. Discussion

5.1 Usefulness of megafossil floras for palaeoecological studies

Plant taphonomy (i.e. the deductions of the characteristics of production, transport, burying, and fossilization based on the states of preservation of megafossil plant remains) strongly supports the close proximity between the living environments and the final depositional environments in all fossil assemblages analysed with the WPM. One may assume that plant communities living in similar biotopes fossilise in similar depositional environments. Thus the resulting cluster corresponds to communities that grew at or near the environment where they deposited and are recorded. This view is supported by the congruence between the clusters obtained with the WPM and the palaeoenvironmental data (i.e. each cluster corresponds to a single type of palaeoenvironment).

The palaeovegetations or communities evolved in space and time, and they may be interpreted in terms of landscape ecology. Thus each plant assemblage may reflect environmental mosaics juxtaposed in the same geomorphological unit (e.g. channel margins ranging from sandy banks to “hardwood” forests). Nowadays, such environmental mosaics take place within a few meters. Thus, if the palaeofloras chosen are parautochthonous (i.e. deposited close to the living place) the palaeovegetation can be reconstructed at the landscape scale.

5.2 Congruence with other northern mid-latitude record

A similar pattern of gradual rise to dominance of angiosperms is observed in the northern mid-latitudes of North America. However, gaps in the sedimentary record may be taken into account for explaining a few differences in the fossil record. The North American Potomac group succession was widely used to understand the early evolution of angiosperms. Doyle & Hickey (1976) and Hickey & Doyle (1977) suggested that fossil angiosperms from the Aptian-Lower Albian of Potomac Zone I were understory shrubs and grew on levees and in floodplains. Pinnately compound leafed platanoids (e.g. *Sapindopsis* Fontaine) from the Upper Albian of Potomac Zone IIB formed early successional shrubs in the same environments. These events may correspond to the phase 2 of our scenario. Platanoids (e.g. *Araliopsoides* Berry) evolved along disturbed channel margins from the Cenomanian of the Potomac Zone III and colonized floodplains from the Cenomanian-Turonian of the Potomac Zone IV. The latter two zones may be in agreement with our phase 3, mentioned above. However, Doyle & Hickey (1976) and Hickey & Doyle (1977) hypothesized that early angiosperms were riparian weeds before the Aptian, but had no fossil record to support their hypothesis.

Retallack & Dilcher (1981a) proposed a reconstruction of the Albian/Cenomanian Dakota Formation flora, and showed that angiosperms occupied a variety of environments.

Lauraceous trees/shrubs (e.g. *Prisca/Magnoliaephyllum*) occupied swampy woodlands and margins of coastal lagoons, angiospermous shrubs (e.g. "*Acerites*") colonized margins of tide-dominated deltas, platanoids were common around freshwater lakes, levees and swales of freshwater coastal stream sides (e.g. *Araliopsoides*), and conifers forested dry floodplains (Retallack & Dilcher 1981b). Closer inspection shows some differences with Europe (Kvaček & Dilcher, 2000) but overall the Dakota flora and their ancient environments fit well with the beginning of the third phase of our scenario mentioned above. The Magnoliales (e.g. *Liriophyllum* Lesquereux, *Didromophyllum* Upchurch et Dilcher) collected from North America were lacking in Europe, and the Laurales were represented by different taxa (e.g. *Pabiana* Upchurch et Dilcher in Northern America vs. *Cocculophyllum* Velenovský in Europe).

According to Crane (1987), North America apparently lacks early freshwater continental records compared to Europe. This situation led to the idea that early angiosperms were mainly present in disturbed floodplains such as the Potomac Zone I. However, we now know that European, Chinese, and North American records (Gomez et al., 2006; Sun et al., 1998, 2002; Wang & Dilcher, 2006) show that angiosperms occurred in aquatic environments from at least the Barremian. The occurrence of early aquatic angiosperms opens the way for reinterpretation of the North American records. The Aptian peltate leaves *Proteaephyllum reniforme* Fontaine was considered to be a step into aquatic environments (Hickey & Doyle, 1977), angiosperms having been temporarily helophytes that are flooded, before changing to become permanently flooded hydrophytes. However, it could be an early aquatic angiosperm that appeared in our phase 1.

5.3 Evolutionary implications

Darwin's "abominable mystery" about the sudden appearance of rather modern genera of flowering plants can now be understood. What most questioned Darwin was "the sudden appearance of so many extant taxa of flowering plants in the Upper Chalk (Darwin, 1875). At that time, he was using a very limited Cretaceous plant record compared to present knowledge. Thus, in the last decades numerous Lower Cretaceous localities containing earlier angiosperms have been described as extinct angiosperm leaf morphotypes. Our scenario supports the view by Darwin (1875) that "the presence of even one true angiosperm in the Lower Chalk makes inclined to conjecture that plant of this great division must have been largely developed in some isolated area, whence owing to geographical changes, they have last succeeded in escaping, and spread quickly over the world". So the rise to dominance of angiosperms was a process that lasted over more than twenty million years.

During the last twenty years, the development of phylogenies has led to two main hypotheses. A posteriori, these were, however, only supported by the fossil records of North America and especially the adequacies with Doyle and Hickey's scenario (Doyle & Hickey, 1976, Hickey & Doyle, 1977).

Taylor & Hickey (1996) suggested that early angiosperms were perennial rhizomatous plants resembling herbaceous Magnoliids such as Piperaceae and competed with ferns and sphenopsids in disturbed areas such as stream margins. These angiosperms then invaded

the aquatic niche in the early Cretaceous thanks to their rhizomatous growth habit and efficient seedlings, thus creating a stable environment.

Feild et al. (2004) hypothesized a disturbed forest understory and/or streamside shrubby ecology similar to the ecology of extant basal angiosperm lineages (i.e. Amborellaceae, Nymphaeales, Austrobaileyales, and Chloranthaceae). Taylor and Hickey's "paleoherb" (Taylor & Hickey, 1996) and Feild et al.'s "dark, damp and disturbed" (Feild et al., 2004, 2009) hypotheses are supported by the occurrence of angiosperms in disturbed floodplain environments from the Aptian (e.g. lower zone I of the Potomac group, USA; Hickey & Doyle, 1977; Hochuli et al., 2006). This early angiosperm ecology may fit our phase 2, but is unlike our phase 1. However, Feild et al. (2004) suggest that the colonization of aquatic environment occurred early in angiosperm evolutionary history. If so, one may question whether earliest angiosperms were shade tolerant as proposed by the "dark, damp and disturbed" hypothesis (Feild et al, 2004).

In a recent study of the evolution of angiosperm vein density during the Cretaceous, Feild et al. (2011) showed that the leaf hydraulic capacities of angiosperms escalated several steps during the Cretaceous. This change occurred in three phases. During the first phase (Lower Cretaceous), angiosperms are not significantly different from gymnosperms. The second phase (Mid-Cretaceous) witnesses an increase above gymnosperms but still below living angiosperms. Finally, angiosperms reached their modern value during the Upper Cretaceous. Those can be paralleled with the three phases observed in the ecological widening of angiosperms.

However, angiosperms were not the only clade that experienced a diversification during the Cretaceous: core Leptosporangiate ferns, Pinaceae, Gnetaceae and Podocarpaceae also underwent extensive diversification (Crane & Upchurch, 1987; Kelch, 1998; Rydin et al., 2003, 2006; Schneider et al., 2004; Wang et al., 2000). So, there is an underestimation of the turnovers of the whole vegetation. Thus, most researchers have worked on innovative features in angiosperms, whereas when dealing with angiosperm evolution we should also think and work upon angiosperm evolution in time and space as they occupied changing environments through times.

6. Conclusion

The survey of the megafossil plant remains from the Barremian to the Campanian of Europe reveals that the rise to dominance of angiosperms in the environments was non-synchronous. Thus, the early ecological evolution of angiosperms that shaped the Cretaceous landscapes was a gradual diversification in space and time of taxa and of their ecology. In contrast to the famous quote by Darwin, the appearance of angiosperms was not sudden, but it lasted from the Barremian (or earlier) to the Cenomanian, that is at least 30 million years.

The evolution of angiosperms at the local scale of Europe mirrors the gradual spread at a global scale previously reported from low latitudes to high latitudes during the Early Cretaceous by Hickey & Doyle (1976). More recently, Coiffard & Gomez (2012) suggested that angiosperm rise to dominance was probably driven by the climates, and especially the

rather continuous global warming from the Barremian to the Cenomanian favoured the spread of eudicots to high latitudes and the establishment of megathermal forests.

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