7. Cretaceous CO_2 Decline and the Radiation and Diversification of Angiosperms

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7.1 Introduction

Determining how a projected doubling of atmospheric CO_2 concentration by the end of this century (IPCC 2001) will influence species composition and biodiversity remains a major scientific and political challenge (Loreau et al. 2001). Long-term CO_2 experiments using FACE (free air carbon dioxide enrichment) now yield invaluable results on how forests and crops/grassland vegetation respond in terms of their biomass allocation, productivity, light use, water use, and nutrient use efficiency in elevated CO_2 (500–700 ppm) (DeLucia et al. 1999; McLeod and Long 1999; Oren 2001). Furthermore, related experimental approaches are increasing our understanding of plant reproductive responses (Hussain, Kubiske, and Connor 2001) and competitive interactions (Bazzaz et al. 1995) in high CO_2 conditions. However, the current spatial and temporal scale of these experiments ($<$10 years) are limited and cannot yet take into consideration the floristic changes that may result from continuing increases in anthropogenic CO_2 at the ecosystem or biome level. Such floristic and macroecological data are readily available from the plant fossil record on timescales of millions of years and on spatial scales spanning whole continents. In this chapter we investigate the effects of long-term fluctuations in atmospheric CO_2 concentration during the Cretaceous period (145–65 Ma) (Tajika 1998; 1999) on patterns of ecological dominance and taxonomic diversity in Cretaceous fossil floras. In particular, we test the hypothesis of Teslenko (1967) and Robinson

(1994) that "CO_2 starvation" during the Cretaceous contributed to the taxonomic diversification and ecological radiation of angiosperms.

7.2 Background

7.2.1 Angiosperm Radiation and Diversification

Unequivocal evidence for early angiosperms in the geological record is based on fossil pollen, which appears for the first time in lower Cretaceous (Valanginian and Hauterivian; ~140–130 Ma) sediments of Israel and Europe (Hughes 1994; Brenner 1996) with additional supporting evidence from fossil flowers (Friis, Crane, and Pedersson 1999), fruits (Dilcher 1989), and leaves (Hughes 1994) by the Barremian and Aptian (127–112 Ma) (Willis and McElwain 2002). However, the time of origin of angiosperms remains controversial due to the recovery of Triassic and Jurassic fossils that are enigmatic (Cornet 1986) or contain some, but not all, of the characteristics necessary for assignment to angiosperms (Cornet 1993; Cornet and Habib 1992). More recently, *Archaefructus liaoningensis*, a flowering plant fruiting axis, was described from the Yixian Formation in the Liaoning Province of China (Sun et al. 1998). Unfortunately the exact chronostratigraphic age of the formation is still under debate, with age assignments ranging from the early Cretaceous (Barrett 2000) to the late Jurassic (Sun et al. 1998; 2002).

Angiosperms then underwent a rapid ecological radiation and taxonomic diversification starting in the Aptian-Albian (121–99 Ma) into the Campanian (83.5–71.3 Ma) (Crane and Lidgard 1989; Lupia, Lidgard, and Crane 1999). An explosive angiosperm radiation, originating in the tropics (Crane and Lidgard 1989), is supported by an increase in continent-level species richness from average values of $<5\%$ to $>40\%$ within approximately 40 million years (Lidgard and Crane 1988; Crane and Lidgard 1990; Lupia, Lidgard, and Crane 1999) (Fig. 7.1).

Similarly, marked increases in the relative abundance of angiosperm fossil pollen in North American (Lupia, Lidgard, and Crane 1999) and Australian (Nagalingum et al. 2002) fossil floras during the same interval are indicative of the rise of angiosperms to ecological dominance. Earlier analyses of large-scale floristic trends through the Cretaceous indicated that angiosperms competitively replaced all gymnosperm groups (Gothan and Remy 1957). However, this is not supported by more recent analyses demonstrating a more selective replacement of some but not all gymnosperm groups (Lidgard and Crane 1988). In particular, a coeval decline in the relative abundances of free-sporing plants (broadly, pteridophytes) in lower latitudes (below 42°N) and Cheirolepidaceae (an extinct group of arid-adapted conifers) in North America as the angiosperms radiated suggests that these groups were competitively replaced by angiosperms (Lupia, Lidgard, and Crane 1999).

In contrast with these patterns of decline and extinction among nonflowering

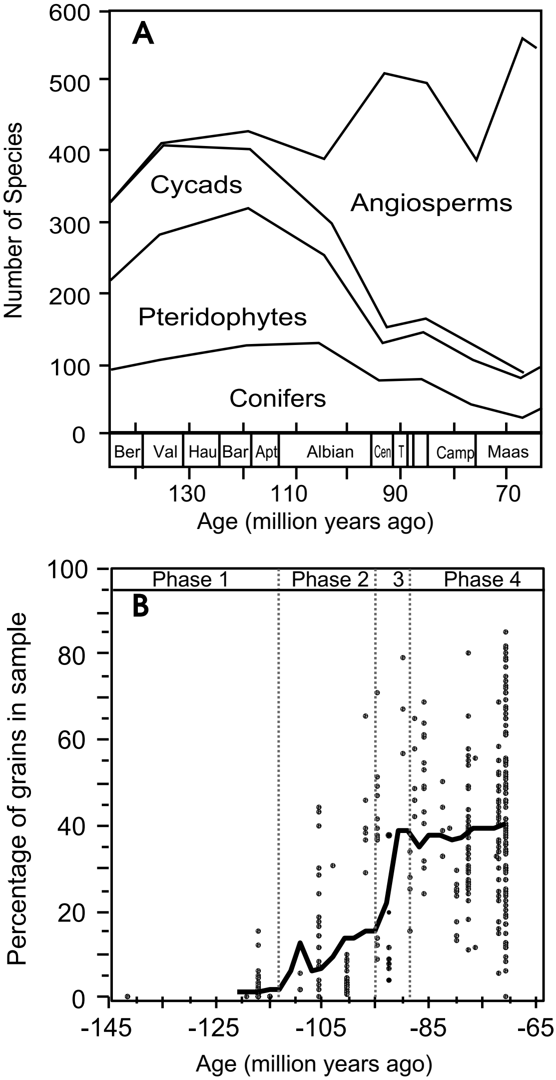


Figure 7.1. **(A)** Total species diversity changes during the Cretaceous illustrating the taxonomic radiation of angiosperms (redrawn from Lidgard and Crane 1988); **(B)** 7.5 million year moving average of angiosperm within flora relative abundance (providing an indication of ecological dominance) during the Cretaceous (redrawn from Lupia et al. 1999).

plant groups, fossil ephedroid (Gnetales) pollen diversity in lower latitudes increased synchronously with that of angiosperms (Crane and Lidgard 1989). This striking co-radiation of angiosperms and low latitude Gnetales during the early and middle Cretaceous led Crane and Lidgard (1990) to suggest that the evolution of both groups may have been strongly influenced or triggered by similar biological or abiotic factors. Unlike the angiosperms, however, the Gnetales did not continue to diversify and radiate into the late Cretaceous but underwent a precipitous decline in post-Cenomanian time (<90 Ma).

In summary, the Cretaceous period is characterized as a time of major floristic turnover and revolution, which in the case of North America (Lupia, Lidgard, and Crane 1999) and, in part, Australia (Nagalingum et al. 2002) can be divided into four distinct phases. In North America, the first phase, spanning from the Jurassic/Cretaceous boundary to the Aptian /Albian boundary (~145–112 Ma), gymnosperms (including conifers, cycads, bennettites, seed-ferns, and Ginkgos) and pteridophytes (all free-sporing plants) dominate the floristic diversity of Northern Hemisphere vegetation. The second phase is characterized by a gradual radiation and diversification of angiosperms between the early Aptian and mid to late Cenomanian (~95–93.5 Ma), followed by a third phase marked by a rapid rise to floristic and ecological dominance in the early Turonian (~93 Ma) to late Santonian (~84 Ma). A fourth macroecological phase is distinguished by an apparent stabilization of biome-level floristic composition to a new equilibrium with angiosperms making up over 40% of the floristic diversity and relative abundance; gymnosperms and pteridophytes shared the remaining 50 to 60%. This phase, however, is most probably an artifact of the data analysis, as the data series currently truncates at the boundary between the Cretaceous and the Tertiary. Extension of this type of analysis into the Tertiary would most likely reveal a continued radiation of angiosperms in the early Tertiary as demonstrated by previous largescale floristic studies (Lidgard and Crane 1990; Niklas, Tiffney, and Knoll 1983) and potentially by a second pulse of radiation in the latest Paleocene and earliest Eocene–a time when angiosperm-dominated forests extended beyond 60° paleolatitude in both poles (Upchurch, Otto-Bliesner, and Scotese 1999; Willis and McElwain 2002) and again in the Miocene, with the expansion of grass dominated ecosystems (Jacobs, Kingston, and Jacobs 1999, Willis and McElwain 2002). Owing to the lack of quantitative analysis of floral-level palynological and/or macrofossil records in the Tertiary, this chapter will focus on the Cretaceous record of angiosperm evolution only.

7.2.2 Environmental Trends and Events in the Cretaceous

The Cretaceous was the last entire period in Earth's history when a greenhouse climatic mode prevailed (Frakes 1999). Paleontological and geological indicators demonstrating significantly higher terrestrial and marine paleotemperatures than today are abundant (see Frakes 1999 for a review). Much higher paleotemperatures in the high polar latitudes are particularly striking in the Cretaceous. Both high greenhouse gas concentration (Arthur, Dean, and Schlanger 1985) and altered ocean circulation patterns (Herman and Spicer 1996) have been invoked to explain this phenomenon of Cretaceous polar warmth. However, despite a complete lack of evidence for polar ice throughout the entire period, the Cretaceous is no longer considered a period of uniformly warm climate (Barron and Washington 1984; Condie and Sloan 1998; Frakes 1999). Marked climatic variations, including short-term pulses of global cooling and warming, have been identified (Frakes 1999). In a recent climatic assessment of the Cretaceous based on a review of proxy evidence (e.g., Wolfe and Upchurch 1987; Parrish and Spicer 1988; Barrera et al. 1997), Frakes (1999) suggested that the early Cretaceous was generally cool, followed by a continuous warming through Albian to Cenomanian time, marked Cenomanian cooling, followed by even more marked Turonian warming, and then generally cooler global climates in the Santonian and Campanian (Fig. 7.2).

The Cretaceous period is also characterized as a period of substantial tectonic plate movements resulting in the final breakup of Pangea (Ziegler, Scotese, and Barrett 1982; Barron 1987; Scotese 1991). Most tectonic plate reconstructions show that breakup of major continental blocks—including Eurasia, Greenland, North America, South America, Africa, India, Australia, and Antarctica—had occurred by the end of the early Cretaceous (Ziegler, Scotese, and Barrett 1982; Barron 1987; Scotese 1991), but see Hay et al. (1999) for an alternative model, suggesting a late rather than early Cretaceous breakup. In particular, a period of rapid plate spreading was initiated in the Aptian (~124 Ma) until the Cenomanian (~83 Ma) (Sheridan 1997), resulting in changes in continental configuration and significantly increasing ocean crust production (Larson 1991; 1997). This period of enhanced ocean crust production and volcanic activity is thought to be primarily responsible for high global temperatures in the mid–Cretaceous, caused indirectly through increased volcanic release of greenhouse gases, such as CO_2 (Arthur, Dean, and Schlanger 1985) and possibly methane (Jahren et al. 2001). Large-scale changes in ocean circulation are also thought to have played an important role in the maintenance of high latitude polar warmth during the Aptian to Cenomanian interval (Herman and Spicer 1996; Zieglar 1998).

Three oceanic anoxic events (OAEs), characterized as intervals of enhanced organic carbon burial punctuated the Cretaceous period. These events are marked in the rock record by extensive deposits of black shale (Schlanger and Jenkyns 1976; Jenkyns 1980), which, based on stable carbon isotopic analysis, are interpreted to have resulted in major perturbations in the short-term (<1 million year) carbon cycle. Oceanic anoxic events are distinguished in the faunal record by major extinction events; although the causal mechanism or mechanisms for these events, as well as the extinctions that accompany them, are still hotly debated (Kaiho and Hasegawa 1994; Huber et al. 1999), there is a growing consensus that major perturbations in the composition of greenhouse gases (including methane and carbon dioxide) may be in some way involved (Kuypers, Pancost and Sinninghe-Damste 1999). Cretaceous OAE's occurred in the late Aptian to early Albian (OAE1), at the Cenomanian-Turonian boundary (OAE2)

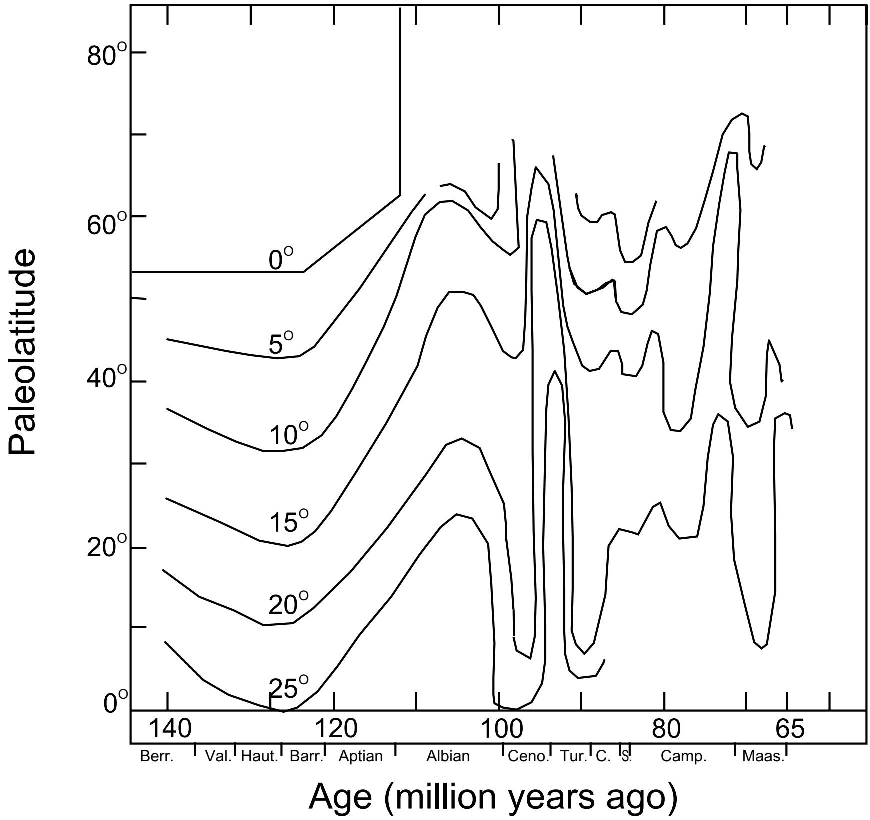


Figure 7.2. Cretaceous climate change (simplified from Frakes 1999) plotted as contours of marine paleotemperature on latitude versus age plot. Marked deviation of the paleotemperature contours into the higher latitudes indicate global warming intervals while deviations of the contours toward the lower latitudes provided an indication that cooler climates prevailed.

and during the Coniacian and early Campanian (OAE3) (Jenkyns 1980; Dean, Arthur, and Claypool 1986; Kauffman and Hart 1995; Arthur, Dean, and Pratt 1988). In summary, a combination of unusually high volcanic activity, large-scale changes in sea level and ocean circulation, with shorter term episodes of high organic carbon burial resulted in major atmospheric and climatic perturbations throughout the Cretaceous.

7.2.3 CO_2 Fluctuations and Trends in the Cretaceous

Biogeochemical models based on long-term processes influencing the carbon cycle (such as CO_2 production from volcanism and uptake from chemical weathering of silicate minerals, see Berner, this volume) predict that atmospheric CO_2

concentration underwent a long-term decline (Fig. 7.3) through the Cretaceous (Berner 1991; 1994; Berner and Kothavala 2001).

Estimates vary from 3.5 times to over 8 times preindustrial levels (300 ppm) for the early Cretaceous (Neocomian) and 1.8 to 4 times by the late Cretaceous (Senonian), according to the long-term carbon cycle models GEOCARB III (Berner and Kothavala 2001) and GEOCARB II (Berner 1994), respectively. In addition to solar and geological controls on the long-term carbon cycle, both models also take into account the role of such biological processes as the enhancement of chemical weathering by plants (see Berner this volume for further details).

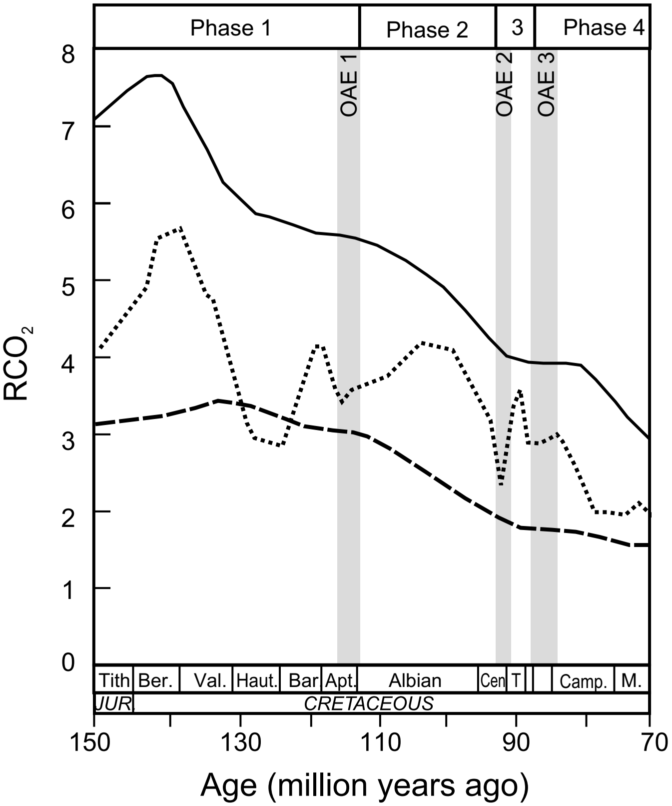


Figure 7.3. Compilation of Cretaceous CO_2 change and oceanic anoxic events. Solid (GEOCARB II, Berner 1994) and dashed (GEOCARB III, Berner and Kothavala 2001) lines represent estimates of CO_2 fluctuations from long-term models of the global carbon cycle. Dotted line represents CO_2 estimates from the carbon cycle model of Tajika (1998, 1999). Phase 1 to 4 represent distinct phases in angiosperms radiation and overall Cretaceous vegetation change as reflected in the data of Lupia et al. (1999) (see text for detailed description of phases).

It is noteworthy, however, that although the more recent and refined model, GEOCARB III, predicts lower concentrations in early and late Cretaceous CO_2 than does GEOCARB II, the general trends shown in both models are in good agreement and, in general, are well supported by independent proxy data (Chen et al. 2001; Robinson et al. 2002; Ekart et al. 1999). Long-term carbon cycle models do not take into account shorter scale processes influencing the carbon cycle, such as increased organic carbon burial at oceanic anoxic events, which may decrease concentrations of atmospheric CO_2 (Kuypers, Pancost, and Sinninghe-Damste 1999), or rapid methyle hydrate release, which hypothetically would increase CO_2 (Hesselbo et al. 2000; Jahren et al. 2001).

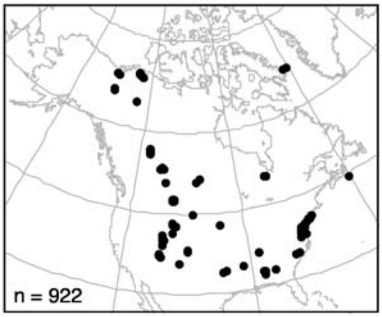
More recent advances in Cretaceous carbon cycle modeling now incorporate the influence of both long-term and short-term biogeochemical processes on atmospheric CO_2 (Tajika 1998; 1999). These higher resolution biogeochemical models predict a general pattern of declining CO_2 through the Cretaceous from an early Cretaceous high of nearly 6 times preindustrial levels (PIL) to concentrations in the region of 2 times PIL by the late Cretaceous (Tajika 1999), in good agreement with long-term CO_2 model estimates. Estimates of atmospheric CO_2 change from Tajika's model, as shown in Fig. 7.3, indicate relatively lower CO_2 levels in the Hauterivian (132–127 Ma), late Cenomanian (~95–93 Ma), and Campanian to Maastrichian (~85–65 Ma) in agreement with independent proxy CO_2 (Kuypers, Pancost, and Sinninghe-Damste 1999; Robinson et al. 2002; McElwain unpublished data) and climate (Frakes 1999) indicators for these times. Relatively higher CO_2 levels are estimated in the earliest Cretaceous (Tajika 1999). In the following sections we investigate how fluctuations in paleoatmospheric CO_2 concentration influenced the composition and macroecology of Cretaceous vegetation as reflected in North American fossil floras. In particular we present arguments and analyses in support of the original but as yet empirically untested hypotheses of Teslenko (1967) and Robinson (1994)—and noted by Beerling (1994) and Crane and Lidgard (1989)—that a reduction in atmospheric CO_2 concentration may have played an important role in the ecological radiation and taxonomic diversification of angiosperms (flowering plants) in the Cretaceous.

7.3 Material and Methods

Large-scale patterns of Cretaceous vegetation change were obtained from records of angiosperms, gymnosperms, and free-sporing plants and their relative floristic diversity and abundance in North American fossil floras (Fig. 7.4), compiled by Lupia, Lidgard, and Crane (1999).

This database contains pollen records from a total of 50 published papers incorporating 922 fossil pollen samples of relative floristic diversity (number of species in each group divided by total diversity, taken as an indicator of relative species richness) and 359 samples of relative abundance (number of specimens

A) Floristic diversity samples



B) Abundance samples

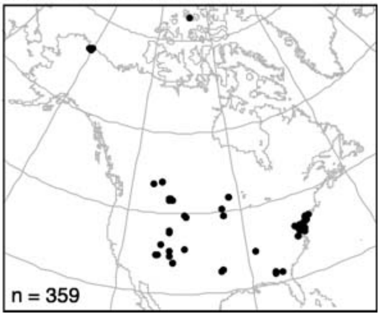


Figure 7.4. Maps of present-day locations of fossil pollen samples for **(A)** floristic diversity and **(B)** abundance in the North American Palynological Database (from Lupia, Lidgard, and Crane 1999, used with permission, The Paleontological Society).

of each group divided by number of specimens counted, taken as a measure of ecological dominance), spanning the entire Cretaceous period and covering 29°N to 84°N paleolatitude and 38° of paleolongitude. Further details on this database can be obtained from Lupia, Lidgard, and Crane (1999). In combination, the within-flora floristic diversity and abundance data serve as robust proxies for patterns of structure and ecological dominance within mainly local vegetation (see Lupia, Lidgard, and Crane 1999) thus enabling an assessment of the impact of CO_2 change on floristic composition through the Cretaceous period. Raw relative abundance and diversity data were then averaged per CO_2 concentration in order to investigate the role of CO_2 change in biome-level vegetation changes throughout the study interval. Long-term fluctuations in paleoatmospheric CO_2 concentrations were obtained from carbon cycle model predictions of Tajika (1998; 1999), GEOCARB II model (Berner 1994), and GEOCARB III (Berner and Kothavala 2001). Total relative floristic diversity and abundance data were regressed against atmospheric CO_2 concentration using simple linear and non-linear correlation-regression analysis in order to evaluate the potential role of CO_2 change in vegetation dynamics and particularly in the angiosperm radiation and diversification.

7.4 Results and Discussion

7.4.1 CO_2 and Cretaceous Vegetation Composition

Our results indicate that CO_2 fluctuations may have played an important role in both the relative diversity (Table 7.1, Fig. 7.5D,E,F) and abundance (Fig. 7.5A,B,C) of angiosperms, gymnosperms, and pteridophytes in Cretaceous fossil floras.

At the broadest level of comparison, it is noteworthy that the termination or initiation, or both, of all four macroecological phases in North American Cretaceous vegetation change are temporally coincident with three major Cretaceous oceanic events (see Fig. 7.3), each of which was associated with a carbon cycle perturbation and likely CO_2 and climatic fluctuations.

Significant inverse correlations are observed between atmospheric CO_2 and angiosperm species richness and abundance at both the local level (within-flora floristic diversity) and the biome level (mean North American relative diversity), as shown in Fig. 7.6.

In comparison, significant positive correlations were observed between North American pteridophyte species richness and atmospheric CO_2 and also gymnosperm species abundance and atmospheric CO_2 (see Fig. 7.5, 7.6). The significance of both correlations is, however, largely dependent on the patterns of change in gymnosperm abundance and pteridophyte richness in lower latitudes

Table 7.1. Relationship between the relative abundance and diversity of angiosperms, gymnosperms, and pteridophytes with alternative carbon cycle model estimates of CO_2 change during the Cretaceous

	Carbon Cycle Models			
Relative within flora floristic diversity (Lupia et al. 1999)	Geocarb I (Berner 1991)	Geocarb II (Berner 1994)	Geocarb III (Berner, Kothavala 2001)	Tajika (1999)
Angiosperms (n = 938)	(−) ($r^2 = 0.5803$) ***	(−) ($r^2 = 0.6142$) ***	(−) ($r^2 = 0.6467$) ***	(−) ($r^2 = 0.6269$) ***
Gymnosperms (n = 938)	(0) ($r^2 = 0.095$) n.s.	(0) ($r^2 = 0.1562$) n.s.	(0) ($r^2 = 0.152$) n.s.	(0) ($r^2 = 0.0402$) n.s.
Pteridophytes (n = 938)	(+) ($r^2 = 0.3596$) *	(+) ($r^2 = 0.1562$) n.s.	(+) ($r^2 = 0.3617$) *	(+) ($r^2 = 0.4033$) *

r^2 = correlation coefficient

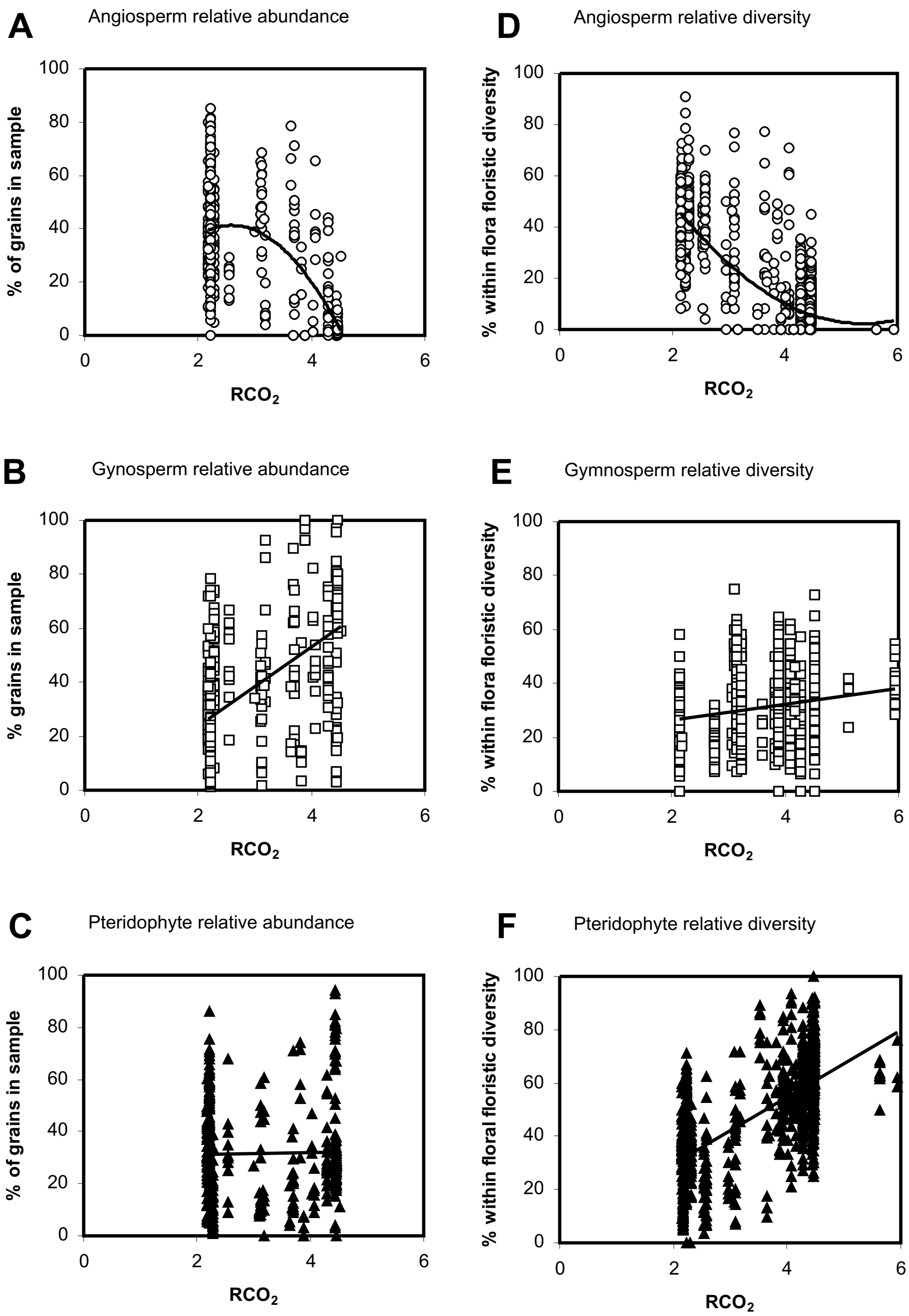


Figure 7.5. Relationship between relative abundance (dominance) and Cretaceous atmospheric CO_2 concentration for: **(A)** Angiosperms [$y = 4.1328x^2 - 44.503x + 122.1$ $r^2 = 0.6269$], **(B)** Gymnosperms [$y = 2.9474x + 20.369$ $r^2 = 0.0402$], and **(C)** Pteridophytes [$y = 12.547x + 4.5817$ $r^2 = 0.4033$]. Relationship between relative diversity (richness) and Cretaceous atmospheric CO_2 concentration for: **(D)** Angiosperms [$y=3.5689x^2 + 121.14$ $r^2 = 0.6513$], **(E)** Gymnosperms [$y= 2.0367x + 23.92$ $r^2 = 0.0466$], and **(F)** Pteridophytes [$y= -3.1461x^2 + 36.413x–40.195$ $r^2 = 0.5831$].

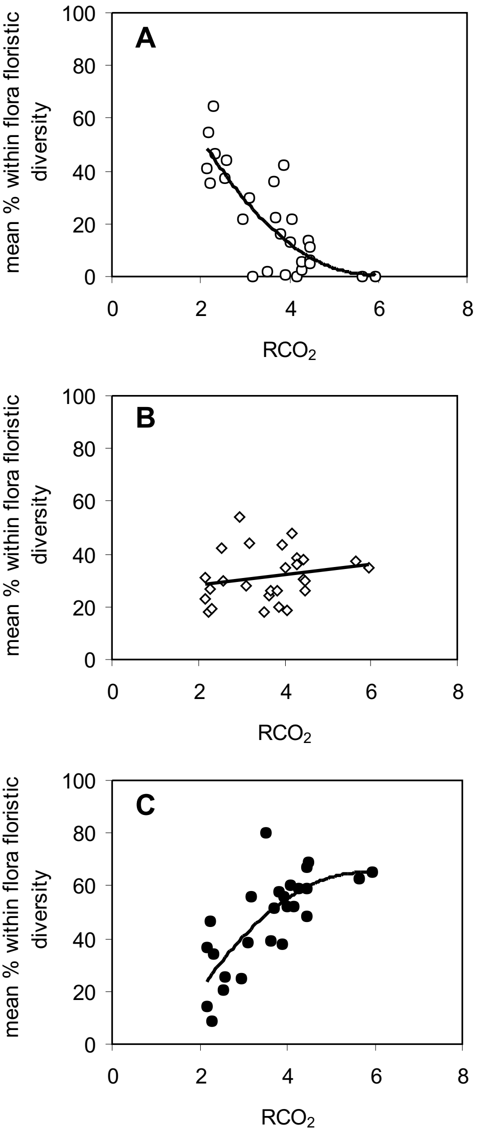


Figure 7.6. Relationship between mean relative diversity and Cretaceous atmospheric CO_2 concentration for: **(A)** Angiosperms [$y = -10.646x^2 + 55.092x–29.996$ R2 = 0.4506], **(B)** Gymnosperms [$y = 0.3769x + 30.553$ R2 = 0.0004], and **(C)** Pteridophytes [$y = 14.656x–5.5592$ $r_2 = 0.3188$].

of North America (below 42°N), suggesting that climatic and/or biogeographic factors, in addition to declining atmospheric CO_2, may have influenced the shifting pattern of gymnosperm diversity and ecology through the Cretaceous.

It has been suggested that key functional types rather than total biodiversity per se may exert the most important control on ecosystem functioning, including productivity, nutrient and water recycling, and so forth (Huston et al. 2000; Loreau et al. 2001). If this is the case, our observation that atmospheric CO_2 may have influenced the relative composition of angiosperms, gymnosperms, and pteridophytes in Cretaceous vegetation, particularly in the lower latitudes, may have extremely important implications for predicting the impact of future increases in atmospheric CO_2 on ecosystem functioning via its effect on large-scale compositional shifts in terrestrial vegetation.

Our results support the original but empirically untested hypotheses of Teslenko (1967) and Robinson (1994). These authors noted that a decrease in atmospheric CO_2 concentrations during the Cretaceous might have in some way triggered the remarkably rapid adaptive radiation of flowering plants. Although Teslenko (1967) had no way of testing his hypothesis, because no estimates of Cretaceous paleo-CO_2 concentration were available at that time, he speculated that angiosperms might have originated in higher elevations where they would have been accustomed and therefore pre-adapted to lower CO_2 partial pressures. The theory of high-elevation angiosperm origin (Axelrod 1952) has since been refuted due to both a lack of paleobotanical evidence (Doyle, Jardiné, and Doerenkamp 1982) and theoretical support from plant ecophysiological studies. Theoretical considerations, for instance, have shown that decreasing CO_2 partial pressure with elevation has little impact on overall carboxylation potential below 3000 meters, due to the counterbalancing effects of decreased O_2 partial pressure with elevation, resulting in reduced photorespiratory demand (Terashima et al. 1995) and the increased diffusivity of gases and hence conductance with elevation (Gale 1972).

By means of their rapid speciation rates—average speciation rates of > 0.35 $\triangle$s / Ma (new species per taxon per Ma) compared with <0.2 $\triangle$s / Ma for older mesophyte groups (Niklas, Tiffney, and Knoll 1983)—flowering plants, if not pre-adapted, likely would have been capable of rapidly evolving a suite of highly adapted vegetative characteristics, such as planate leaves with reticulate venation, fine-tuned stomatal regulation, highly efficient conductive tissue (vessels) that enabled them to optimize their physiology to the lowest CO_2 concentrations that had probably existed since the Carboniferous, approximately 100 million years earlier. Additionally, the almost unique ability of angiosperms to harness host-specific relationships with coevolving insects, may also have enabled angiosperm to survive as rarer species in isolated habitats, thereby reducing the high energetic cost associated with the manufacture of anti-herbivory toxins (Leigh and Vermeij 2002). Leaves that require a high investment of anti-herbivore defense compounds are more energetically expensive and therefore tend to have a longer leaf life span, which in turn is associated with lower maximum stomatal conductance and photosynthetic potential (Reich, Walters, and Ellsworth 1997)—traits that would not be favored under declining atmospheric CO_2.

7.4.2 Why Would a Decline in Atmospheric CO_2 Favor the Radiation and Diversification of Angiosperms?

7.4.2.1 Evidence from Comparative Plant Ecophysiology

From a photosynthetic perspective, although RUBISCO of most living angiosperm taxa today is saturated at CO_2 concentrations above 3 × PIL (preindustrial CO_2 level [PIL] taken as 300 ppm), i.e., ~900 ppm, it must be remembered that all gymnosperm and pteridophyte lineages in the early Cretaceous and the as yet unknown seed plant ancestor of basal angiosperms would have been photosynthetically adapted to much more elevated CO_2 concentrations (~>1500 ppm). Assuming therefore that Tajika's model estimates of paleo-CO_2 concentration are broadly correct, the sharp decline in atmospheric CO_2 concentrations from 5 × PIL in the Berriasian (144–137 Ma) to levels less than 3 times PIL by the Hauterivian (132–127 Ma) and perhaps as low as 1.67 times PIL by late Cenomanian time (Kuypers, Pancost and Sinninghe-Damste 1999) would have strongly selected plant anatomical, morphological, and physiological characteristics that enhanced water supply and improved water-use efficiency, while at the same time maintaining plant carbon balance. Plants maintain optimum photosynthetic efficiency by setting a constant CO_2 gradient of approximately 30% between the atmosphere and intercellular leaf space by increasing or decreasing their stomatal conductance (g_{max}) as CO_2 concentration decreases or increases, respectively (von Caemmerer and Evans 1991). Very high CO_2 gradients between atmosphere and leaf can be maintained with ease when atmospheric CO_2 concentration are very high, thereby enabling plants to improve their water-use efficiency (WUE) by either occluding the stomatal pore with papillae, decreasing stomatal density, or opening stomata only partially.

Plant stomata are kept open longer or wider, and/or stomatal number (density) increase (Beerling, McElwain, and Osborne 1998), when the concentration of atmospheric CO_2 decreases in order to maintain an adequate CO_2 gradient between the atmosphere and leaf. As a direct consequence of this, evaporative demand is increased and greater amounts of water are lost through transpiration. In a sense, therefore, reduced atmospheric CO_2 concentration imposes physiological drought (Street-Perrott et al. 1997). Significant long-term reductions in atmospheric CO_2 through the Cretaceous from typical levels of greater than 5 times PIL (Berner 1994; Ekart et al. 1999; McElwain 1998; McElwain, Beerling, and Woodward 1999), which had existed for the preceding approx 100 million years during the Triassic and Jurassic, would therefore select strongly for anatomical adaptations that enabled efficient transport of water to plant tissues and organs rapidly loosing water through increased evaporative demand.

The evolution of vessels in angiosperms from tracheids of a gymnospermous ancestor represents such an adaptation that would have readily enabled increasing conductive efficiency of xylem tissue as a whole (Table 7.2; Fig. 7.7).

Table 7.2. Generalized anatomical and morphological trends in the evolution of vessels in angiosperms from tracheids of a gymnospermous ancestor

Xylem Type	Type of bordered pit typically found in lateral xylem wall	Perforation plate	Taxa	First recorded occurrence of clade in fossil record	RCO_2
Simple tracheids (A) & (B) with circular bordered pits	Circular bordered pits of variable size and pit boarder thickness, complete pore membrane	Absent	Coniferales, Ginkgoales, Cycadales, Bennettittales	NA- predominant in Triassic and Jurassic (248 to 144 Ma)	>4 × PIL
Tracheids (C) with scalariform (ladder like) bordered pits on end walls only	Lateral wall bordered pits circular and alternately arranged	Absent	Winteraceae (eg Belliolum, Bubbia, Drimys, Tahkajania, Tasmania & Zygognum)	(121–99 Ma, Aptian-Albian)	3.62 to 4.43 × PIL
Tracheids (D) with scalariform bordered pits	Pits elliptical along horizontal axis pit membranes porous	Absent	[1]Trochodendron, [2]Tetracetron,	[1,2](118 Ma, Aptian),	4.47 × PIL
Vessels members with scalariform (E) or porous perforation plates of distinct morphology from some lateral pits	Some bordered pits of distinct morphology and porosity from perforation plates i.e. Nelumbo and some Nymphales lateral pits non porous	Present	[1]Chloranthaceae, [2]Illiciaceae [3]Nelumbo [1]Cornalean clade, [2]Ericalean clade, [3]Betulaceae, some [4]Saxifragaceae, [5]Caprifoliaceae,	[1](112–99 Ma, Albian), [2](? Aptian-Albian), [3](100 Ma, Albian), [4](69.5 Ma, Maastrichtian), [5](89.5 Ma, Turonian), [6](84 Ma, Santonian) [7](89.5 Ma), [8](53.2, Lwr. Eocene),	3.87 to 2.38 × PIL
Vessel members (F) with perforation plates intermediate between scalariform and porous	Multiple files of predominantly oppositely arranged bordered pits	Present	[1]Ericaceae, [2]Caprifoliaceae	[1](89.5 Ma Turonian), [2](53.2 Ma Lwr. Eocene)	3.07 to 2.38 × PIL

Table 7.2. *Continued*

Xylem Type	Type of bordered pit typically found in lateral xylem wall	Perforation plate	Taxa	First recorded occurrence of clade in fossil record	RCO_2
Vessel members (G) with simple perforation plates & strongly inclined end walls	Multiple files of opposite to alternately arranged circular bordered pits	Present	Boraginaceae, Rubiaceae, Oleaceae, Caprifoliaceae	(53.2 Ma Lwr Eocene)	2.38 × PIL
Wide (H) short vessel members with simple perforation plates & non inclined end walls	Multiple files of predominantly alternately arranged bordered pits	Present	[1]Proteaceae, [2]Capparales, [3]Rosaceae, [4]Myrtales, [5]Euphorbiaceae, [6]Polygalaceae, [7]Asteraceae, [8]Rubiaceae [9]Oleaceae, [10]Convolvulaceae, [11]Scrophulariaceae	[1](97 Ma, mid-Cretaceous), [2](89.5 Ma, Turonian), [3](44.3, Mid. Eocene), [4](84 Ma, late Santonian), [5,6](58.5 Ma, Upr. Paleocene), [7,8](29.3 Ma, Oligocene), [9,10](53.2 Ma, Lwr. Eocene), [11](37 Ma, Upr. Eocene)	4.27 to 2.07 × PIL

Xylem anatomy data sources (Bailey and Tupper, 1918; Carlquist and Schneider, 2002 and references therein;). RCO_2 = Range of estimated atmospheric CO_2 concentration for times of oldest occurrences of clades in fossil record (expressed as a ratio of past to pre industrial (PIL =300 ppm) CO_2 concentration (Cretaceous CO_2 data from Tajika, 1999, pre-Cretaceous CO_2 from Berner, 1994)

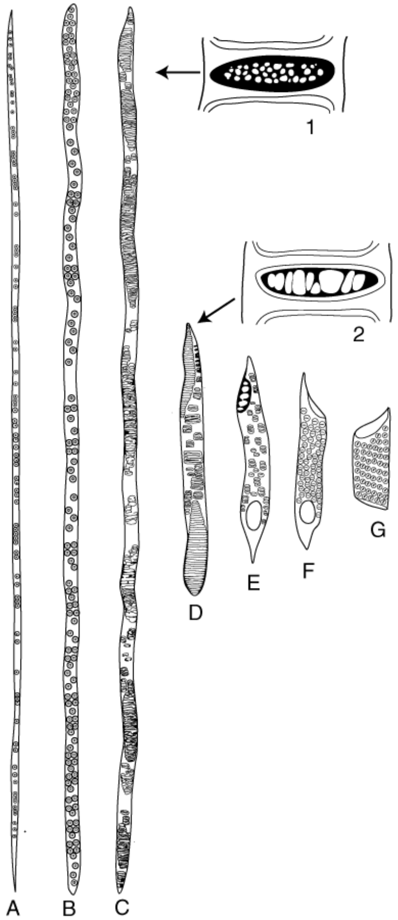


Figure 7.7. Diagrammatic illustration of the evolution of vessels from tracheids with simple bordered pits **(A, B)**, to elongated bordered pits in scalariform arrangement **(C)**, to vessel members **(D, E, F, G)** proposed by Bailey and Tupper (1918). **D** through **G** illustrate the proposed evolutionary trajectory from longer to shorter vessel members with reduced end-wall inclinations, from opposite to alternate pit arrangements, and a change from scalariform to simple perforation plates; **(A)** and **(B)** illustrate the evolutionary trajectory of increased porosity in the membranes of scalariform bordered pits in tracheids to those of scalariform perforation plates in primitive vessel members. See Table 7.2 for examples of living plant families possessing tracheid or vessel member anatomy illustrated as **A** through **G**. This xylem evolution model is broadly supported from observation of the plant fossil record of wood (Wheeler and Baas 1991). Redrawn from Bailey and Tupper (1918) with inset detail (1) and (2) from Carlquist and Schneider (2002).

Vessels are long ($\sim$10 mm to $>$15 feet) continuous water-conducting tubes made up of ‘vessel elements’ or ‘vessel members’ that are coalesced at their axial walls (Esau 1965; Zimmermann and Jeje 1981). Vessel members are elongated perforate cells with lignified secondary walls and no protoplast. They are characterized by the presence of perforated end walls, known as perforation plates, which enable water movement from member to member through the vessel. In contrast, tracheids, which is the only type of water-conducting cell found in most gymnospermous xylem (exceptions include Gnetales and Gigantopteridales, both of which have vessels), are imperforate cells. That is to say, tracheids do not have perforation plates in their end walls, and water flow from tracheid to tracheid occurs through the porous membrane of a pit depression in the secondary cell wall (Zimmermann 1983), which depending on the degree of porosity of the pit membrane, can moderately to greatly reduce water and solute flow, as shown in Fig 7.7A,B. In addition, tracheids are typically narrower in diameter and shorter in length than are vessels.

Such anatomical differences in the xylem of gymnosperms and angiosperms impact physiological function. For instance, comparative measurements of gymnosperm, angiosperm, and vessel-less angiosperm specific hydraulic conductive capacity (K_{sp}: conductivity per sapwood area) (Tyree and Ewers 1991; Becker, Tyree, and Tsuda 1999) and measures of whole plant conductivity (K_L stem hydraulic conductivity per unit leaf area) (Brodribb and Feild 2000) have demonstrated that conifers often have lower K_{sp} and K_L than do angiosperms or typically occupy the lowest ranges of angiosperm values but have similar or higher values than do vessel-less angiosperms (Brodribb and Hill 1999; Feild et al. 2001).

Although such comparative ecophysiological studies are rare and no such data are available for Pteridophytes (many of which, including most ferns, possess vessels), they suggest that the evolution of vessels in angiosperms and the evolutionary trajectory toward wider vessels (Bailey and Tupper 1918) with increased conductive area of vessel membrane end walls throughout the Cretaceous (see Table 7.2; Fig. 7.7D,G) (Carlquist and Schneider 2002) and on into the Tertiary (Wheeler and Baas 1991) would have enabled angiosperms to support greater leaf area and greater evaporative demand under progressively declining Cretaceous atmospheric CO_2, with relatively reduced investment in xylem tissue, compared to gymnosperms within the same communities and habitats. The work of Brodribb and Feild (2000) linking plant photosynthetic capacity with that of xylem conductivity also supports the suggestion that angiosperms may have been able to support greater photosynthetic capacity than gymnosperms within the same communities.

There is, however, a functional cost associated with increasing conductive capacity. The imperforate pit membrane of tracheids prevents movement of gas bubbles from tracheid to tracheid, thereby preventing the spread of air-filled, or embolized, tracheids. Air embolisms result in breakage of the water column within xylem tissue, and their spread can lead to catastrophic xylem dysfunction (Tyree and Sperry 1989). Air embolisms occur due to cavitations, which are sites, or nucleations, of vaporization within the water column. The main causes of cavitations in nature include: (1) air-seeding (Zimmermann 1983) due to water stress, where increasing negative pressure within the xylem can result in air being sucked into xylem through pores within the intertracheid or intervessel pit membranes—the larger the pores, the larger the bubbles (Tyree and Sperry 1989); (2) freeze-thaw cycles, where thawing of frozen water columns within xylem results in air bubbles being forced out of solution and nucleating a cavitation; and (3) sublimation of ice from frozen xylem leading to large bubbles on thawing (Tyree and Sperry 1989). Therefore, although the trajectory toward the evolution of vessel perforation plates in the axial walls of tracheids (see Fig. 7.7) would have enabled increased conductive capacity in basal angiosperm taxa (such as the scalariform bordered pits in the axial walls of *Trochodendron* and *Tetracetron*), by increasing the porosity of their pit membranes, total loss of pit membranes to form ever simpler perforation plates (see Table 7.2; Fig 7.7D,E,F,G transition) through the Cretaceous would have increased xylem vulnerability to both cavitation and spread of embolism in water-stressed and cold-stressed environments.

Taking these dual functions of xylem tissue into account, one would therefore expect the selection pressure for more efficient conductive tissue under declining Cretaceous atmospheric CO_2 to be greatest in seasonally dry but not permanently arid geographical areas of minimal temperature extremes with high evaporative demand (summer wet), and in light-limited habitats with ample water supply and limited temperature fluctuations, such as understory and subcanopy environments of tropical ever-wet forests. Plants in these habitats typically have lower maximum stomatal conductance (that is, they have higher resistance to CO_2 diffusion; Larcher 1995). In seasonally freezing climates (such as the cold temperate biome) and desert environments, retainment of tracheids or loss of vessels would provide protection against excessive cavitation and therefore embolism. An additional innovation that would have enhanced plant water supply under declining Cretaceous CO_2 was the evolution of high order reticulate venation with free-ending veinlets, which together with vessels evolved independently in Gnetales (*Gnetum*), early angiosperms, and Polypodiaceous ferns by the middle Cretaceous (Bailey 1944; Crane 1985; Trivett and Pigg 1996; Willis and McElwain 2002).

From a functional perspective, the models of Tyree and Sperry (1989) have demonstrated that xylem physiology and stomatal regulation must evolve as an integrated unit, as stomata play a vital role in the prevention of catastrophic xylem dysfunction from embolism. Robinson (1994) hypothesized that relatively lower CO_2 concentrations in the Cretaceous would also select strongly for plant groups with highly efficient stomatal control mechanisms and high potential maximum stomatal conductance (g_{max}). Although comparative statistics are few, the duration of stomatal opening and closing cycles is generally much faster in angiosperms than in gymnosperms and pteridophytes; angiosperms also tend to have higher maximum stomatal conductances than do gymnosperms and pteridophytes, respectively (see Robinson 1994 for review).

For instance, Gates (1968) has shown that the diffusive resistance in *Pteridium* is among the highest ever recorded. While Brodribb and Hill (1999) report typically stomatal opening times in excess of 2 hours for 16 Podocarpaceae and 7 Cupresaceae. Robinson (1994) argued therefore that angiosperms would be physiologically more optimized than gymnosperms and pteridophytes under conditions of "CO_2 starvation" as the more xerophyllous nature of gymnosperm leaves, which are often highly lignified and possess thick cuticle and lignified stomata, may have more inefficient stomatal control mechanisms since lignification may impede stomatal opening and closing responses (Robinson 1994). An alternative and perhaps more plausible explanation is that the degree of leaf lignification is positively correlated with leaf life span, which in turn is negatively correlated with leaf photosynthetic capacity (Reich, Walters, and Ellsworth 1997). The decline of overall gymnosperm diversity and abundance through the Cretaceous and perhaps the precipitous decline of Cheirolepidaceous conifers (many of which are characterized by xerophyllous leaves with deeply sunken stomata and overarching papillate epidermal cells) in post-Cenomanian time (Watson 1988) may be attributable to their inability to compete with higher photosynthetic efficiency among angiosperms under long-term declining atmospheric CO_2. By the middle Cretaceous, in marked contrast with gymnosperms, the leaves of angiosperms were larger and planate, relatively unlignified (based on comparative fossil anatomy), and presumably of shorter overall leaf life span, although this needs to be tested with fossil material using the leaf-life span method of Falcon-Lang (2000). Furthermore, angiosperm leaves were supported by a complex reticulate venation pattern and supplied with a highly conductive xylem tissue (vessels), which required less investment per unit leaf area than did their gymnospermous counterparts.

Estimates of maximum stomatal conductance of Cretaceous cheirolepidaceous conifer species range between 18.7 mmol m^{-2} s^{-1} (*Pseudofrenelopsis varians*) and 62.8 mmol m^{-2} s^{-1} (*Pseudofrenelopsis parceramosa*) (Cowie 1999). These are extremely low compared to values for modern angiosperm trees (^{150}–300 mmol m^{-2} s^{-1}; Larcher 1995) and herbs (150–700 mmol m^{-2} s^{-1}) and both deciduous and evergreen conifers, such as *Larix gmelinii* (365 mmol m^{-2} s^{-1}; Vygodskaya et al. 1997) and Pinaceae (200 mmol m^{-2} s^{-1}; Larcher 1995), respectively. The combination of potentially poor or slow stomatal control mechanisms and resultant lower stomatal conductance would be strongly selected against in a lower CO_2 world. Model and proxy estimates suggest that atmospheric CO_2 concentration may have reached levels of $2.5 \times$ PIL (Tajika 1999) and potentially as low as $1.67 \times$ PIL (Kuypers, Pancost, and Sinninghe-Damste 1999) due to high organic carbon burial flux at the C-T boundary. There is, therefore, a distinct possibility, although it remains to be tested, that CO_2 concentrations at the C-T boundary may have passed a critical lower threshold as a number of geographically widespread fossil taxa including numerous ephedroids, cheirolepidaceous conifers, and primitive clades producing the *Afropollis*-type pollen either suffered heavy extinctions or became extinct (Doyle, Jardiné, and Doerenkamp 1982; Crane and Lidgard 1989; Upchurch and Wolfe 1993).

The observation that both extinction (Cheirolepidaceae) and marked declines in relative abundances (*Afropollis* and ephedroid taxa) at the C-T boundary was most prevalent among xerophyllous taxa, as indicated by xeromorphic anatomy and morphology or by their association with arid indicators, such as evaporite sediments, is consistent with the prediction that low CO_2 would be more detrimental to plants of arid adapted habitats (Robinson 1994). A transient CO_2 drawdown for a total duration of approximately 100 K to 150 K years (Meyers, Sageman, and Hinnov 2001) at the Cenomanian-Turonian boundary, which is supported by geochemical proxy data (Kuypers, Pancost, and Sinninghe-Damste 1999) and by a biogeochemical model (Tajika 1999), may have conferred further competitive advantage to angiosperm clades since the North American pollen database (Lupia, Lidgard, and Crane 1999) shows the steepest increase in both relative richness and abundance during this interval. The same pattern of steeply increasing angiosperm abundance occurs synchronously in the Southern Hemisphere in Australian fossil floras (Nagalingum et al. 2002), again strongly supporting the role of a global abiotic trigger such as CO_2 change. High-resolution independent proxy CO_2 data, together with independent paleoclimate estimates spanning the Cenomanian-Turonian oceanic anoxic event, are now required in order to constrain the possible threshold CO_2 concentration or climatic perturbation that contributed to the rapid competitive replacement of cheirolepidaceae and ephedroids by flowering plants.

7.4.2.2 Supporting Evidence from the Plant Fossil Record

Reticulate venation has arisen independently and repeatedly in many different phylogenetic groups throughout the history of land plants (for a detailed review, see Trivett and Pigg 1996). At first view, therefore, there appears to be little adaptive significance of reticulate venation in relation to abiotic factors; it has instead been interpreted purely as an indicator of biological complexity or evolutionary status (Trivett and Pigg 1996). Highly ordered tertiary and quaternary reticulate venation does not appear in the fossil angiosperm record until the late Aptian and Cenomanian, as indicated by the classic work of Doyle and Hickey (1976), a time according to model estimates when paleo-CO_2 concentrations were declining sharply from >4 times to <3 times PIL. The only pre-Cretaceous occurrences of large compound or simple planate leaves with tertiary or quaternary reticulate venation and free-ending veinlets are restricted to two unique genera *Gigantoclea* and *Delnortea*, both of which belong to a group of extinct Permian seed ferns: Gigantopterids (Trivett and Pigg 1996). More importantly, Gigantopterids are the only pre-Cretaceous seed plants that possess true vessels within xylem tissue (Li, Taylor, and Taylor 1996; Li and Taylor 1999). It is noteworthy that the early Permian was the only other pre-Cretaceous time in Earth's history according to proxy CO_2 (McElwain and Chaloner 1996; Ekart et al. 1999) and model estimates (Berner and Kothavala 2001) when CO_2 concentrations reached levels lower that 3 times PIL. The number of shared vegetative characteristics between angiosperms, gigantopterids (Fig. 7.8), and

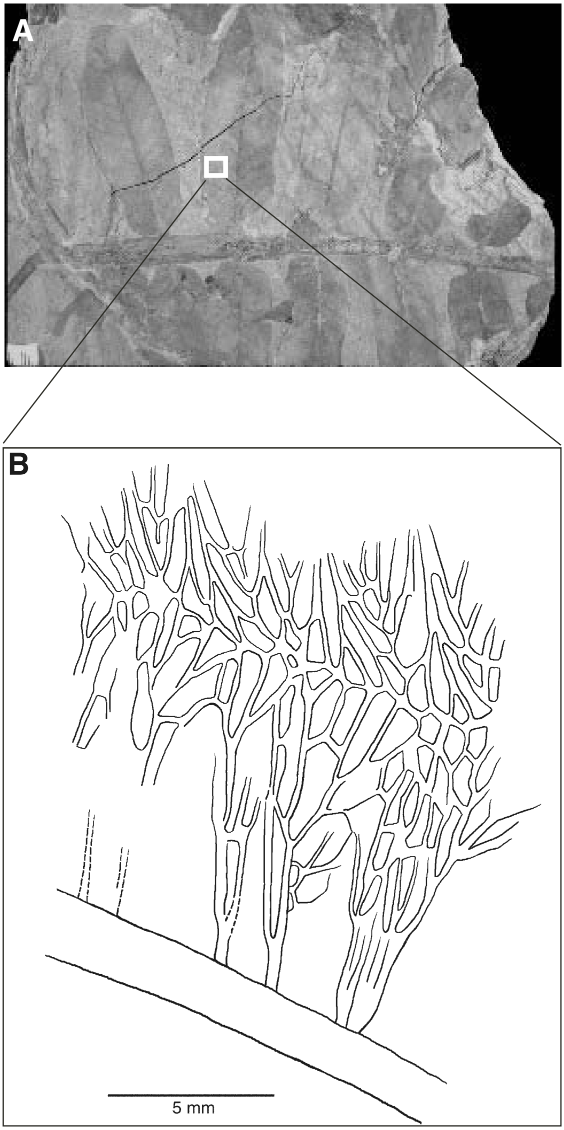


Figure 7.8. **(A)** Details of leaf morphology, and **(B)** venation of *Gingantoclea guizhouenensis* (PP34440), a Permian Gigantopterid seed fern from China.

Gnetum with respect to their venation and xylem are remarkable and may therefore represent functional convergence of morphology and anatomy to relatively lower atmospheric CO_2 concentrations.

However, similar patterns are not observed in spore-bearing plants as a number of pteridophytes, including lycopods (such as *Sellaginella,*), equisetum, and many ferns possessing both reticulate venation (Trivett and Pigg 1996) and true vessels in their rhizomes, roots, and/or stems (Carlquist and Schneider 2001) are not restricted to times of relatively low atmospheric CO_2 in Earth's history.

If the evolution of xylem vessels by angiosperms was a key innovation enabling them to competitively replace gymnosperms and pteridophytes in a lower CO_2 world, as we have argued, why have vessel-less angiosperms both persisted (e.g., Amborellaceae: Feild et al. 2001) and been secondarily derived (e.g., Winteraceae: Herendeen, Wheeler, and Baas 1999; Feild, Zwieniecki, and Holbrook 2000)? Recent comparative ecophysiological work has demonstrated that neither the presence of tracheids in primitive angiosperms nor the absence of vessels in conifers always imposes higher limitations on water transport than do plants with xylem vessels in the same environment (Feild and Holbrook 2000). In a recent review, Carlquist (1996) noted that "a reason for the persistence of primitive character states in wood may be the tendency for other aspects of the vegetative apparatus to evolve more readily, offering compensation." Carlquist (1996) argued that because leaf size and morphology are so plastic, xeromorphic leaf structure compensates readily for a primitive xylem configuration (e.g., microphylly) in Bruniaceae and Grubbiaceae, both of which have primitive wood and needle or scale leaves more typical of conifers. The evolution of true vessels, therefore, likely enabled angiosperms to attain much greater leaf sizes, which together with the structural support afforded by reticulate venation would have reduced the necessity for strongly xeromorphic leaf characteristics in angiosperms. As the high lignin content and structural rigidity of xeromorphic leaves may impede fine-tuned stomatal control (Robinson 1994) and tends to be associated with longer leaf life spans and lower photosynthetic capacity (Reich, Walters, and Ellsworth 1997), this in turn may have enabled the development of enhanced conductive capacity and photosynthetic potential in angiosperm leaves.

7.4.3 Role of Other Abiotic Triggers in the Angiosperm Radiation

Many competing hypotheses have been proposed for the remarkable radiation of angiosperms (see Taylor and Hickey 1996). It has long been held that global increases in aridity were the most probable trigger for the flowering plant radiation as angiosperms possess a number of innovations that may have made them more drought resistant and therefore competitively superior to other plants. These innovations include tough leathery leaves, a tough resistant seed coat that protected the young embryos from drying out, xylem vessel providing much more efficient water-conducting cells than in previous groups, and a deciduous habit. However, these traits are not unique to angiosperms. In fact, it seems paradoxical that cheirolepidaceous conifers, which were perhaps the most prominent fossil taxa found in association with aridity indicators, such as evaporite deposits, throughout the early and mid Cretaceous, became extinct if the trigger was increased aridity. Furthermore, the presence of tracheid elements rather than vessels is the preferred conducting tissue for plant taxa of the most extremely water-deficient environment because tracheids afford better protection from catastrophic embolism (Carlquist 1996) than do vessels. The possession of tracheids as well as vessels in many angiosperm evergreen shrubs of the Mediterranean region prevent embolism during the hottest part of the year when water availability reaches an annual minimum (Carlquist 1996). Also, the deciduous habit was not first invented by angiosperms. Indeed, supporting evidence suggests that many Paleozoic and Mesozoic gymnosperm taxa were deciduous (e.g., Glossopteridaceae, Ginkgoales, Taxodiaceae, and Cycadales) particularly in higher latitudes where seasonal climatic extremes and light limitation were more prevalent (Falcon-Lang 2000; Rees, Ziegler, and Valdes 2000). Finally, a gymnospermous seed would have afforded the same protection from desiccation that an angiospermous seed would have provided, and the foliage of gymnosperms, such as *Brachyphyllum* and *Pagiophyllum* (representing cheirolepidiaceous conifers at least in part), was eminently adapted to aridity.

It therefore appears highly unlikely that aridity alone, if at all, was an important driving influence on the radiation of angiosperms. We support the alternative (or at least complementary) explanation of Doyle and Donoghue (1986) that dramatically accelerated speciation rates, which are characteristic of angiosperms, simply led to an overwhelming diversity of adaptive morphologies (Lupia, Crane, and Lidgard 2000). However, we propose that a marked decline in atmospheric CO_2 through the Cretaceous imposed severe physiological limitation on gymnosperms and pteridophytes, particularly those of understory and seasonally dry habitats. Owing to the suite of adaptive vegetative characteristics (high potential stomatal conductance, high stomatal control, vessels, and reticulate venation), which in combination but not separately are unique to angiosperms, the reduction in CO_2 may have provided an essential abiotic trigger for the rapid evolutionary and ecological radiation of flowering plants.

7.4.4 Which Came First: Angiosperm Radiation or CO_2 Decline?

It has been proposed that the evolution of deciduous angiosperms in the Cretaceous played a significant role in the long-term decline in atmospheric CO_2 by accelerating chemical weathering of calcium and magnesium silicate rocks more than did the previous gymnosperm-dominated vegetation (Knoll and James 1987; Volk 1989). Because calcium and magnesium silicates are ultimately precipitated as carbonates in the oceans, silicate chemical weathering represents one of the most important sinks of atmospheric CO_2 in the long-term carbon cycle (see Berner, this volume). There are, however, very little comparative data on the relative weathering potential of angiosperms and gymnosperms, and based on the available studies to date, Volk's assumption that angiosperms have a higher chemical weathering potential remains controversial. For instance, studies in Iceland show that angiosperms have a significantly greater weathering potential on a per unit biomass basis than do gymnosperms (Berner 1997; Moulton, West, and Berner 2000; Berner and Kothavala 2001); the only other available study, however, shows the opposite (Quideau et al. 1996). Despite this uncertainty, it is important to consider whether declining atmospheric CO_2 may have led to the radiation and diversification of angiosperms as we have argued (see Table 7.1; Fig. 7.5), or whether the reverse is true: that the proliferation of angiosperms resulted in enhanced chemical weathering and Cretaceous CO_2 drawdown.

In order to address the problem of which came first, we have plotted the raw angiosperm relative abundance data from Lupia, Lidgard, and Crane (1999) on the same temporal scale as three paleo-CO_2 models (Fig. 7.9). It is clear from

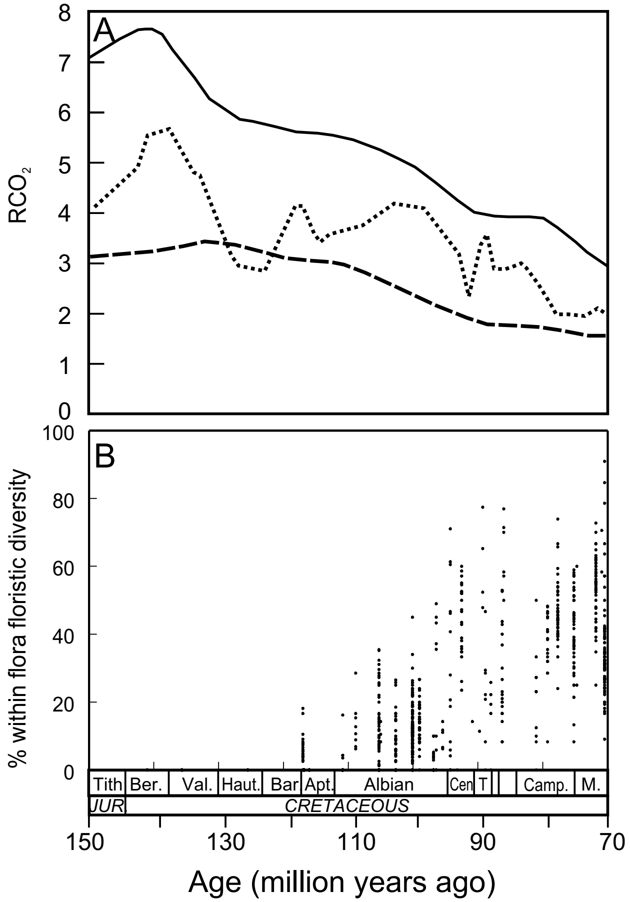


Figure 7.9. Illustrating a decline in atmospheric CO_2 in the Berriasian and Valaginian before the taxonomic radiation of angiosperms in the Aptian and Albian.

these comparisons that although angiosperms originated during an episode of high atmospheric CO_2, their taxonomic radiation and, more importantly, their rise to ecological dominance within Cretaceous fossil floras clearly followed an initial steep decline in CO_2 from $>5 \times$ PIL to $3 \times$ PIL in the Valanginian (137–Ma) (Tajika 1999). It is likely, therefore, that a long-term trend of CO_2 decline through the Cretaceous period may have played an extremely important role in the diversification of angiosperms, leading to their ecological dominance in almost every biome with the exception of the high latitude boreal realm by the Maastrichian.

7.5 Summary

The evolution of megaphyll leaves (Beerling, Osborne, and Chaloner 2001) and the C4 photosynthetic pathway (Ehleringer et al. 1991; Ehleringer, Cerling, and Helliker 1997) were both strongly influenced by declines in atmospheric CO_2 concentration in the Paleozoic and Cenozoic, respectively. In this chapter we present evidence that a long-term decline in atmospheric CO_2 concentration through the Cretaceous ($\sim$ 140–65 Ma) significantly influenced the floristic composition of Cretaceous vegetation. Highly significant inverse relationships are observed between both the relative abundance and the richness of angiosperms in Cretaceous fossil floras and estimated atmospheric Cretaceous CO_2 concentrations (Tajika 1998, 1999). In contrast, significant positive correlations are shown between paleo-CO_2 concentration and gymnosperm relative abundance and pteridophyte relative species richness. We propose that a combination of vegetative innovations, including high order reticulate venation, xylem vessels, and rapid stomatal control mechanisms enabled angiopserms to maintain high maximum stomatal conductance and CO_2 assimilation rates in a significantly lower CO_2 world. This combination of characteristics would have conferred a competitive advantage to angiosperms over gymnosperms and pteridophytes, particularly in seasonally but not permanently arid environments and light-limited habitats of the tropics, where adaptations to water and light limitations, respectively, likely severely impacted plant carbon balance. The ecophysiological differences among angiosperms, gymnosperms, and pteridophytes provide a mechanistic explanation for the observed relationships in the diversity and dominance patters of the three reproductive grades. Our results suggest that adaptation to CO_2 starvation, in addition to any advantages resulting from advanced reproductive biology in flowering plants, may have been an important trigger in the ecological radiation and taxonomic diversification of flowering plants through competitive replacement of less physiologically optimized gymnosperm and pteridophyte clades.

Our results indicate that an overall trend of declining CO_2 concentration through the Cretaceous differentially influenced each reproductive grade, favoring angiosperms over gymnosperms and pteridophytes in terms of their abundance and taxonomic diversity, respectively. It has been suggested from photosynthetic modeling studies on extant plants that angiosperm photosynthetic responses may be more optimized to low CO_2 concentrations than are gymnosperms and pteridophytes (Beerling 1994; Beerling and Woodward 1997). We propose that declining CO_2 concentrations during the Cretaceous may have provided a competitive physiological edge to angiosperms, which possessed reticulate veined leaves, vessel members, and sensitive stomatal control, thus contributing, along with their advanced reproductive strategy, to the competitive replacement of less physiologically optimized gymnosperm and free-sporing plant groups. However, the Gnetales remained an exception within the gymnosperms. Unlike all other gymnosperm clades, they show no significant reductions in relative diversity within Cretaceous fossil floras until post-Cenomanian time (Crane and Lidgard 1990), a point at which a critical minimum CO_2 threshold may have been reached resulting in widespread extinction of arid adapted clades. The fact that Gnetales, unlike all other Mesozoic gymnosperms, independently evolved two of the three key adaptations to optimize photosynthesis under relatively lower atmospheric CO_2 (planate leaves with high order reticulate venation and true vessels) helps to explain their initial co-radiation with angiosperms in response to declining CO_2 before the Cenomanian-Turonian OAE2. An explanation for the demise of many Gnetalean taxa at the C-T boundary, however, remains an interesting avenue for further research.

Our results, although preliminary and requiring further support from modern comparative plant ecophysiological studies, may have profound implications for projecting future effects of rapidly rising CO_2 on global plant biodiversity and the floristic composition of natural ecosystems. The predicted future doubling of CO_2 by the end of this century (IPCC 2001), based on our results, may significantly alter the percentage composition of angiosperms gymnosperms and pteridophytes in the world's biomes. Further work will aim to quantify CO_2 change throughout the Cretaceous period using the stomatal method (McElwain 1998) in order to define the critical threshold CO_2 level at which significant changes in vegetation composition occur, as current model estimates lack the precision to address this critical issue.

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