

## *Estimating latest Cretaceous and Tertiary atmospheric CO<sub>2</sub> from stomatal indices*

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### ABSTRACT

**A quantitative understanding of the levels of atmospheric CO<sub>2</sub> in the geologic past sheds light on the operation of the carbon cycle and the biosphere, and aids in the prediction of future climate change. Here I present a CO<sub>2</sub> reconstruction for the very latest Cretaceous to early Eocene and middle Miocene based on the stomatal distributions in fossil and extant *Ginkgo* and *Metasequoia* cuticles. Although both of these intervals are representative of globally warm climates, my CO<sub>2</sub> reconstruction indicates near present-day values (300–450 ppmV) for both times. Although these data do not cast doubt on the theory of the greenhouse effect, they do suggest that other thermal forcings were more important during these intervals than they are today.**

### INTRODUCTION

Globally averaged surface temperatures have risen sharply in the last century (~1 °C in the Northern Hemisphere) (Mann et al., 1998, 1999), concomitant with a 30% increase in the concentration of the greenhouse gas CO<sub>2</sub> (Friedli et al., 1986). It is now clear that CO<sub>2</sub> is largely responsible for this warming (Mann et al., 1998; Crowley, 2000; Barnett et al., 2001; Harries et al., 2001; Levitus et al., 2001; Mitchell et al., 2001). On the longer time scale of 10<sup>5</sup> yr, Antarctic air temperatures and atmospheric CO<sub>2</sub> have been tightly coupled for at least the last four glacial-interglacial cycles (Petit et al., 1999), and it appears that CO<sub>2</sub> has also been driving these temperature variations (Shackleton, 2000).

On multimillion year time scales, proxy- and modeling-based estimates of CO<sub>2</sub> over the Phanerozoic largely correlate with geologic indicators of continent-scale glaciations, which are the most reliable index for the presence of 'greenhouse' or 'icehouse' climates (Crowley and Berner, 2001). This correlation is not present, however, during certain intervals. CO<sub>2</sub> esti-

mates for the mid-Miocene thermal maximum (17–14.5 Ma), a brief interval of global warmth relative to today, suggest concentrations largely lower than the preindustrial value of 280 ppmV (Pagani et al., 1999; Pearson and Palmer, 2000). In addition, CO<sub>2</sub> estimates derived from multiple proxies for other time periods are not consistent. For example, early Tertiary (65–50 Ma) CO<sub>2</sub> estimates range from <300 ppmV to >3000 ppmV (Ekart et al., 1999; Pearson and Palmer, 2000).

Here I apply a CO<sub>2</sub>-calibrated set of stomatal indices from *Ginkgo biloba* and *Metasequoia glyptostroboides* to reconstruct paleo-CO<sub>2</sub> levels for the very latest Cretaceous to early Eocene (66–53 Ma) and the middle Miocene (~15.5 Ma). This study expands on the data presented by Royer et al. (2001b) and Beerling et al. (2002).

### THE STOMATAL INDEX METHOD

Most modern vascular C<sub>3</sub> plants show an inverse relationship between the partial pressure of atmospheric CO<sub>2</sub> and stomatal index (Woodward, 1987; Beerling, 1999; Lake et al., 2001;

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Royer, 2001). Stomatal index (SI) is the percentage of epidermal cells that are stomatal complexes (guard cells + stomatal pore), and is defined as the following (Salisbury, 1927):

$$SI = \frac{SD}{SD + ED} \times 100$$

where  $SD$  = stomatal density ( $\text{mm}^{-2}$ ) and  $ED$  = epidermal cell density ( $\text{mm}^{-2}$ ). The mechanism(s) linking  $\text{CO}_2$  to SI is not fully understood, but probably involves the strong selective pressure in plants to maximize carbon fixation per unit of water transpired (water-use efficiency) (e.g., Woodward, 1987). For example, in a rising  $\text{CO}_2$  regime plants can increase their water-use efficiency by reducing their stomatal conductance, thereby reducing water loss. Stomatal conductance is largely a function of stomatal pore area, which in turn is controlled by the size of individual stomatal pores and the density of those pores. On the time scale of several growing seasons or longer, stomatal density is typically more sensitive to changes in atmospheric  $\text{CO}_2$  than individual pore size (e.g., Royer, 2001). Furthermore, on multimillion year time scales stomatal density and SI across all plant taxa inversely respond to  $\text{CO}_2$  (Beerling and Woodward, 1997; McElwain, 1998; Royer, 2001).

In contrast to stomatal density, SI is area independent, which normalizes for the effects of cell expansion. Stomatal index is essentially a measure of the number of stomatal complexes that develop per unit number of epidermal cells. Plant water-potential strongly influences cell expansion (e.g., water stressed plants generally reduce the size of their epidermal cells [Royer, 2001]), but not the rate of stomatal initialization. Thus, changes in a plant's water budget can affect stomatal density, but not stomatal index. Both experimental and field studies show that SI is largely independent of water potential, irradiance, and temperature, and is primarily a function of  $\text{CO}_2$  (e.g., Kürschner et al., 1998; Beerling, 1999; Royer, 2001).

Stomatal indices (and stomatal densities) have been experimentally shown to respond to the partial pressure of  $\text{CO}_2$ , not concentration (as expressed as mole fraction, e.g., parts per million) (Woodward and Bazzaz, 1988). This finding is corroborated by a positive correlation in many plants between elevation and stomatal density (Körner and Cochrane, 1985; Woodward, 1986; Woodward and Bazzaz, 1988; Beerling et al., 1992) and SI (Rundgren and Beerling, 1999). It is important, therefore, to control for elevation when estimating  $\text{CO}_2$  from stomatal properties. The relationship between elevation and partial pressure in the lower atmosphere is roughly as follows (linear fit to equation 11.8 in Jones, 1992, p. 308):

$$P = -10.6E + 100$$

where where  $E$  = elevation in kilometers and  $P$  = the percentage of partial pressure relative to sea level. If one does not control for elevation (i.e., assumes concentration = partial pressure),  $\text{CO}_2$  concentration estimates will be underestimated by 3% for

plants growing at 250 m elevation, for example, and 11% for plants at 1000 m.

### Choice of species

Stomatal responses to atmospheric  $\text{CO}_2$  are usually species-specific (Woodward and Kelly, 1995; Beerling and Kelly, 1997; Royer, 2001). For example, based upon genera represented by >1 species in the compilation of Royer (2001) ( $n = 7$ ), only one shows no significant intrageneric variation in SI ( $\alpha = 0.05$ ; chi-squared test). In order to quantitatively reconstruct paleo- $\text{CO}_2$ , then, the SI- $\text{CO}_2$  relationship in an extant species must be applied in the fossil record to the same species. This requirement has previously hindered the applicability of this method for fossil leaves predating the late Miocene (10 Ma) (van der Burgh et al., 1993; Kürschner et al., 1996). Here I use the lineages represented today by *Ginkgo biloba* and *Metasequoia glyptostroboides*, which greatly extends the temporal applicability of the method.

Morphologically indistinguishable forms of *G. biloba* extend back to the Early Cretaceous, leading many authors to consider the fossil and modern forms conspecific (Tralau, 1968; see Royer et al., 2003). This fossil form is most commonly identified as *G. adiantoides*, however many other designations are considered equivalent, e.g., *G. spitsbergensis* (Tralau, 1968). Similarity in the environment of growth of modern and Tertiary fossil *Ginkgo* also supports their conspecificity (Royer et al., 2003). *G. gardneri* is the only *Ginkgo* species of Tertiary age in the Northern Hemisphere sufficiently different from *G. adiantoides-biloba* to warrant a separate species (Manum, 1966; Tralau, 1968). *G. gardneri* occurs at one early Paleogene site on the Isle of Mull, Scotland (e.g., Boulter and Kvaček, 1989).

Chen et al. (2001) report that the SI in modern *G. biloba* is statistically independent of leaf size, long versus short shoots, and male versus female trees, and only minor differences (<5%) due to canopy position and the timing of leaf development are present. These results further suggest that stomatal indices in *Ginkgo* are reliable indicators of atmospheric  $\text{CO}_2$  concentration.

*Ginkgo* foliage is distinctive and readily identified. A *Ginkgo* leaf consists of a petiole and fan-shaped dichotomously veined lamina (Fig. 1). The veins only very rarely anastomose (Arnott, 1959). Vein spacing is typically ~1 mm. Stomata are found only on the abaxial side of the leaf (hypostomatous), and are distributed randomly in the intercostal regions. Subsidiary cells are moderately papillose and partially cover the stomatal pore. The leaf is usually divided into two lobes with wavy margins. The petiole contains two vascular strands, each of which vascularizes one of the lobes (Chamberlain, 1935; Gifford and Foster, 1989). Mucilage cavities are common and conspicuous, even in fossils. They are 1–5 mm in length, and are oriented parallel to venation (Chamberlain, 1935). The *G. adiantoides-biloba* form is differentiated from other ginkgo-forms (which largely occur earlier in the rock record) by its less dissected lamina (Tralau, 1968), however deeply lobed leaves do occur occa-

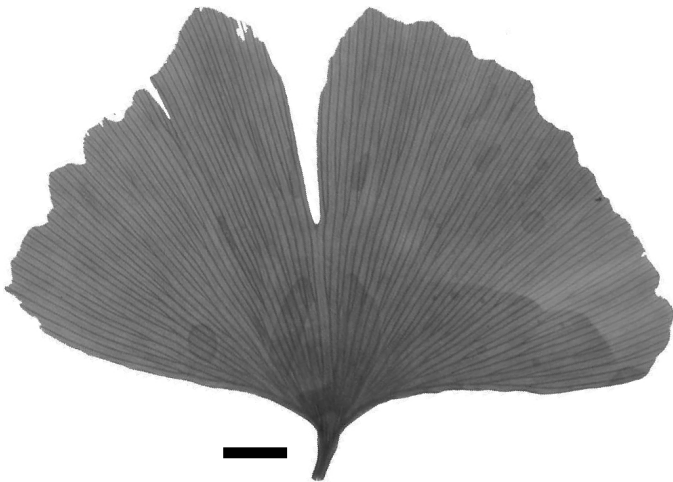


Figure 1. A leaf of *Ginkgo biloba*. Collected from New Haven, Connecticut (USA). Scale bar = 1 cm.

sionally in *G. biloba* (Critchfield, 1970). The only other plants with open dichotomizing venation and bilobed lamina are ferns such as *Adiantum* (e.g., Gifford and Foster, 1989). These can be distinguished from *Ginkgo* by the single vascular strand in their petioles, the presence of sori abaxially near the tips of their leaves, and their more closely spaced veins.

*Metasequoia* also has a long fossil record of morphologically similar forms back to the Late Cretaceous (Liu et al., 1999). Many workers consider this fossil form, *M. occidentalis*, closely related to, or conspecific with the modern *M. glyptostroboides* (Chaney, 1951; Christophel, 1976; Liu et al., 1999). *Metasequoia* needles are flat, ~15–20 mm long and ~2 mm wide. The leaf morphology of *Metasequoia* is very similar to *Sequoia* and *Taxodium*, however *Metasequoia* needles are opposite decussate while the needles in the other two genera are spirally alternate. *Metasequoia* also tends to have more rounded leaf tips, a higher angle of divergence between the leaf and shoot (~90°), and a more highly twisted base than *Sequoia* and *Taxodium* (Chaney, 1951).

The fossil records of *Ginkgo* and *Metasequoia* indicate that both were common components of mid- to high-latitude temperate forests (Tralau, 1967; Mai, 1994). In contrast to multi-story tropical forests, intracanopy CO<sub>2</sub> gradients are small in temperate forests and should not bias stomatal-based CO<sub>2</sub> estimates (Royer, 2001).

### Construction of training set

Leaves from dated herbarium sheets of *Ginkgo biloba* and *Metasequoia glyptostroboides* were used to assess the response of their SI's to the anthropogenic rise in atmospheric CO<sub>2</sub> concentration over the last 145 yr. Because both *Ginkgo* and *Metasequoia* have deciduous leaf habits, all leaves are assumed to have grown only during the year recorded on the sheets. The

CO<sub>2</sub> concentrations that the leaves developed in were taken from ice core derived (Friedli et al., 1986) and direct atmospheric (Keeling et al., 1995) measurements. The herbarium specimens came mostly from cultivated individuals in the United States, China, and Japan. All trees grew at <250 m in elevation, with 84% growing at elevations <75 m. Therefore, no correction is needed to convert CO<sub>2</sub> partial pressure to concentration. For each herbarium sheet, five mature leaves were randomly selected. Stomatal index was calculated for three fields of view (0.1795 mm<sup>2</sup> each) on every leaf. Measurements were made in the intercostal regions near the centers of the leaves, which in other species show the least variation in SI (Salisbury, 1927; Royer, 2001). Stomatal observations were made from acetate peels and cleared leaves (light microscopy), and unaltered leaf tissue (epifluorescence microscopy). No systematic variation in SI among the three preparation techniques was noted. During the growing season of 1999 (and 2000 for *Ginkgo*), SI was measured from trees growing in New Haven (Connecticut, USA), Ann Arbor (Michigan, USA), and London (UK). Sampling details are given in Table 1.

Stomatal indices were also measured on saplings growing in greenhouses at four discrete CO<sub>2</sub> concentrations. For each CO<sub>2</sub> treatment, three potted saplings were placed in each of four independent greenhouses (see Beerling et al., 1998, and Beerling and Osborne, 2002, for details). For the 430/445 ppmV and 790/800 ppmV treatments, SI was measured after CO<sub>2</sub> exposure times of both one and two growing seasons. The *Metasequoia* saplings were one-year-old after their first season of CO<sub>2</sub> treatments. Two sets of *Ginkgo* saplings were used, aged one- and six-years-old after their first season of CO<sub>2</sub> treatments. For the 350 and 560 ppmV treatments, SI was determined from three-year-old *Ginkgo* saplings after a CO<sub>2</sub> exposure time of two growing seasons (Beerling et al., 1998). Sampling details are given in Table 1.

### Application to fossil cuticles

Stomatal indices were calculated from 28 very latest Cretaceous to middle Miocene-aged *Ginkgo* cuticle-bearing sites and three middle Miocene-aged *Metasequoia* cuticle-bearing sites. As with the training set material, SI was determined for three fields of view on each fossil leaf. At least five leaves were measured per site (see Table 2). This ensures that at least as many leaves per site were used to reconstruct paleo-CO<sub>2</sub> as were used per herbarium sheet to establish the training sets. This contrasts with other studies, where <5 fossil leaves are commonly measured per fossil site (e.g., Retallack, 2001). For *Ginkgo*, epifluorescence microscopy on unaltered cuticle was employed. Fossil *Metasequoia* cuticle failed to fluoresce, and so leaves were first cleared using 1% sodium hypochlorite (bleach) and then analyzed using light microscopy. For voucher specimen information for both the training and fossil data sets, consult Royer (2002).

The paleoelevations of all regions sampled in this study are most likely <1000 m. For example, the Late Cretaceous Hell

TABLE 1. DETAILS OF SAMPLING FOR TRAINING SETS

A. Historical Collections						
Species	Year(s) collected	CO <sub>2</sub> (ppmV)	Mode of preparation	Trees <sup>†</sup>	Leaves <sup>†</sup>	Field of views <sup>†</sup>
<i>G. biloba</i>	1856–1996	288–361	E	1	5	15
	1999	367	A	6	13	46
	2000	369	C	3	10	30
<i>M. glyptostrobooides</i>	1947–1980	310–338	A, C	1	5	15
	1999	367	A	4	21	46
B. Greenhouse Experiments						
Species	Exposure to CO <sub>2</sub> (years)	CO <sub>2</sub> (ppmV)	Mode of preparation	Trees <sup>†</sup>	Leaves <sup>†</sup>	Field of views <sup>†</sup>
<i>G. biloba</i>	2	350 <sup>§</sup>	A	8	16	160
	1	430 <sup>#</sup>	C	8	16	48
	1	430 <sup>**</sup>	C	8	8	24
	2 <sup>‡</sup>	445 <sup>#</sup>	C	8	8	24
	2 <sup>‡</sup>	445 <sup>**</sup>	C	8	8	24
	2	550 <sup>§</sup>	A	8	16	160
	1	790 <sup>#</sup>	C	8	16	48
	1	790 <sup>**</sup>	C	7	7	21
	2 <sup>‡</sup>	800 <sup>#</sup>	C	8	8	24
	2 <sup>‡</sup>	800 <sup>**</sup>	C	8	8	24
<i>M. glyptostrobooides</i>	1	430 <sup>**</sup>	C	8	16	48
	2 <sup>‡</sup>	445 <sup>**</sup>	C	7	7	21
	1	790 <sup>**</sup>	C	8	16	48
	2 <sup>‡</sup>	800 <sup>**</sup>	C	8	8	24

Note: A—acetate peels (light microscopy); C—cleared leaves (light microscopy); E—unaltered leaves (epifluorescence microscopy).  
<sup>†</sup>Total number per CO<sub>2</sub> value or herbarium sheet.  
<sup>§</sup>From Beerling et al. (1998). Three-year-old saplings.  
<sup>#</sup>Six-year-old (for 430 and 790 ppmV treatments) and seven-year-old (for 445 and 800 ppmV treatments) saplings.  
<sup>\*\*</sup>One-year-old (for 430 and 790 ppmV treatments) and two-year-old (for 445 and 800 ppmV treatments) saplings.  
<sup>‡</sup>Includes the exposure time from the previous growing season (either 430 or 790 ppmV).

Creek Formation in the Williston Basin contains marine and brackish facies (Frye, 1969; Murphy et al., 1999), indicating paleoelevations near sea level. In the Bighorn Basin, which produced the largest number of fossil cuticle sites, there are few constraints on paleoelevation (see discussion in Chase et al., 1998). The highest estimates for the basin during this time range from 1500 to 2500 m (Chase et al., 1998), however other workers consider these estimates to be too high because they think it unlikely that climate at these higher elevations would be warm enough to support the large number of subtropical and frost intolerant plants that are known from basinal deposits (S.L. Wing, 2001, personal commun.). Also, estimates of mean annual temperature for the low-lying Williston Basin during this time are similar to estimates for the Bighorn Basin (15–17 °C) (Hickey, 1977; Wing et al., 2000). Since both basins are at similar paleolatitudes, the most parsimonious solution is a similar low paleoelevation for the Bighorn Basin. Due to the lack of reliable estimates for the Bighorn Basin and the inferred low paleoelevations for the other

sites used in this study, no corresponding corrections were applied to the CO<sub>2</sub> estimates.

Most (88%) *Ginkgo*-bearing sites used in this study have been interpreted as representing streamside and crevasse splay environments (Royer et al., 2003). These highly disturbed environments usually support well-watered, open-canopy forests. Mesic conditions should improve the fidelity of the SI-CO<sub>2</sub> signal, while open canopies should remove any potential intracopy CO<sub>2</sub> gradients and provide a closer analog to the open grown trees used to construct the training set.

The following sources were used to date the fossil sites: Williston Basin (Hell Creek Formation)—Hicks et al. (2002); Bighorn Basin (Fort Union and Willwood Formations)—Wing et al. (1995) and Age Model 2 in Wing et al. (2000); Denver Basin (Dawson Formation)—Raynolds et al. (2001, p. 25); Spitsbergen (Firkanten Formation)—Manum (1963) and Kvaček et al. (1994); Hanna Basin (Hanna Formation)—Higgins (2000); Alberta (Paskapoo Formation)—Fox (1990); Isle of

**TABLE 2. SAMPLING DETAILS AND CO<sub>2</sub> RECONSTRUCTION FOR FOSSIL DATA**

<b>A. GINKGO ADIANTOIDES*</b>						
Site	Location <sup>†</sup>	Depository <sup>§</sup>	Age (Ma)	<i>n</i> <sup>#</sup>	SI (%)	CO <sub>2</sub> (ppmV)
DMNH 566	WB	DMNS	65.5	31	8.32	385
LJH 7423	BHB	USNM	64.5	5	9.48	339
LJH 7659	BHB	YPM	64.5	15	9.32	344
DMNH 2360	DB	DMNS	64.1	5	9.90	329
Basilika**	S	PMO	64.0	8	9.42	341
DMNH 2644	HB	DMNS	61.0	5	10.93	313
Burbank	A	UA	58.5	7	7.55	451
Joffre Bridge	A	UA	58.5	5	7.96	409
SLW 0025	BHB	USNM	57.3	7	9.01	353
LJH 7132	BHB	YPM	56.4	5	8.75	363
SLW 991	BHB	USNM	55.9	5	10.97	312
SLW 992	BHB	USNM	55.9	8	10.80	314
SLW 993	BHB	USNM	55.9	8	11.43	307
LJH 72141—1	BHB	USNM,YPM	55.8	12	10.63	317
SLW 9155	BHB	USNM	55.7	10	11.21	309
SLW 9411	BHB	USNM	55.6	8	11.50	306
SLW 9434	BHB	USNM	55.4	7	12.23	299
SLW 9715	BHB	USNM	55.3	12	8.23	390
SLW 9050	BHB	USNM	55.3	5	12.18	300
SLW 9936	BHB	USNM	55.3	15	11.77	303
SLW 8612	BHB	USNM	55.3	7	12.41	298
Ardtun Head <sup>††</sup>	M	BNHM, PMO,YPM	55.2	13	6.54	826
SLW 9812	BHB	USNM	55.1	22	8.53	373
SLW 9915	BHB	USNM	54.8	8	8.83	360
SLW LB	BHB	USNM	53.9	5	9.29	345
SLW H	BHB	USNM	53.5	9	10.22	323
LJH 9915	BHB	YPM	53.4	15	9.38	342
Juliaetta (P6)	I	YPM	16.5	14	8.14	396
<b>B. METASEQUOIA OCCIDENTALIS</b>						
Clarkia (P33a)	I	YPM	15.3	6	11.59	310
Clarkia (P33b)	I	YPM	15.3	10	10.94	316
Emerald Creek (P37a) I		YPM	15.2	10	10.95	316

\*Unless noted otherwise.  
<sup>†</sup>WB—Williston Basin (North Dakota, USA); BHB—Bighorn Basin (Wyoming and Montana, USA); DB—Denver Basin (Colorado, USA); S—south-central Spitsbergen (Norway); HB—Hanna Basin (Wyoming, USA); A—south-central Alberta (Canada); M—Isle of Mull (Scotland, UK); I—north-central Idaho (USA).  
<sup>§</sup>Depository for cuticle preparates: DMNS—Denver Museum of Nature & Science; USNM—National Museum of Natural History, Smithsonian Institution; YPM—Yale Peabody Museum; PMO—Oslo Paleontological Museum; UA—University of Alberta; BNHM—British Natural History Museum.  
<sup>#</sup>Number of leaves measured for calculation of SI.  
\*\**Ginkgo spitsbergensis* used for stomatal counts, which is considered conspecific with *G. adiantoides* by Tralau (1968).  
<sup>††</sup>*G. gardneri* used for stomatal counts.

Mull (Staffa Group)—Royer et al. (2001b); Idaho (Latah Formation)—Reidel and Fecht (1986).

### THE STOMATAL RATIO METHOD

An alternative, semiquantitative, stomatal-based CO<sub>2</sub> proxy compares the SI in a fossil species to its nearest living equivalent (NLE) (McElwain and Chaloner, 1995, 1996; McEl-

wain, 1998; McElwain et al., 1999). NLE's are defined ecologically and structurally, not taxonomically. The stomatal ratios of the extant:fossil species are directly translated into CO<sub>2</sub> estimates in a linear fashion, such that a stomatal ratio of three equates to a CO<sub>2</sub> estimate of 900 ppmV if the leaves of the extant trees grew in a 300 ppmV CO<sub>2</sub> atmosphere. This method is not species-specific, and so can be applied to sediments dating back to the Early Devonian (McElwain and Chaloner, 1995),

however it assumes that the SI's in the related sets of species respond to  $\text{CO}_2$  in the following hyperbolic fashion:  $\text{CO}_2 \propto (\text{SI})^{-1}$ .

To provide an independent check on the early Paleogene *Ginkgo*-derived  $\text{CO}_2$  estimates, the stomatal indices in *Platanus guillelmae* from the *Ginkgo*-bearing site SLW H were compared to its NLE's, *P. occidentalis* and *P. orientalis* (and their hybrid *P. × acerfolia*), using the stomatal ratio method. *P. occidentalis* and *P. orientalis* are morphologically similar to the broadly trilobed *P. guillelmae*, and both the modern and fossil species are most commonly found in disturbed streamside environments (Royer et al., 2003).

## RESULTS AND DISCUSSION

The stomatal indices in both *Ginkgo* and *Metasequoia* show a strong linear response to the anthropogenic increases in atmospheric  $\text{CO}_2$  over the last 145 yr ( $r^2 = 0.98$ ,  $P < 0.001$  for *Ginkgo*;  $r^2 = 0.68$ ,  $P < 0.001$  for *Metasequoia*). For  $\text{CO}_2$  concentrations above present-day levels, the responses are nonlinear (Fig. 2; Table 3). This nonlinear response is predicted by plant physiological principles (Kürschner et al., 2001) and supported by recent genetic work (Gray et al., 2000). Overall, both nonlinear regressions are highly significant (Fig. 2).

A discontinuity exists in the *Ginkgo* training set between the experimentally derived SI measurements at elevated  $\text{CO}_2$  (>370 ppmV) and the rest of the training set (which includes one experimentally derived measurement at 350 ppmV) (Fig. 2). Plants often require >1 growing season for their SI's to respond to  $\text{CO}_2$  concentrations above present-day levels (Royer, 2001), and indeed, the stomatal indices in *Ginkgo* exposed to  $\text{CO}_2$  treatments for two growing seasons are lower than the same plants from the first growing season (Fig. 2; Table 3). In the case of the 440 ppmV  $\text{CO}_2$  treatment, the difference is significant [ $F(1, 118) = 10.61$ ;  $P < 0.001$ ; one-way ANOVA]. This suggests that the discontinuity is an artifact of insufficient  $\text{CO}_2$  exposure time.

The  $\text{CO}_2$  reconstruction based upon 31 *Ginkgo*- and *Metasequoia*-bearing fossil sites is shown in Figure 3 and Table 2. Except for one estimate near the Paleocene-Eocene boundary, all reconstructed  $\text{CO}_2$  concentrations (300–450 ppmV) are close to present-day values. Estimates based upon <5 cuticle fragments are less reliable (Beerling and Royer, 2002a), however in general they conform with their more reliable coeval estimates (Table 4).

There is some stratigraphic evidence that the site associated with the one high  $\text{CO}_2$  estimate (Ardtun Head, Isle of Mull, Scotland) dates to the Initial Eocene Thermal Maximum (IETM; previously known as LPTM) (Royer et al., 2001b; cf. Jolley et al., 2002). The IETM was brief ( $\sim 10^5$  yr; Kennett and Stott, 1991; Bains et al., 1999; Norris and Röhl, 1999) but significant (global mean surface temperatures rose  $\sim 2^\circ\text{C}$  [Huber and Sloan, 1999]). Concomitant with warming, there was a worldwide negative excursion in  $\delta^{13}\text{C}$ , ranging in magnitude from  $-2.5\text{‰}$  in the benthic marine record (Kennett and Stott, 1991; Bains et al., 1999) to  $-6\text{‰}$  in the terrestrial record (Koch et al., 1992; Sinha

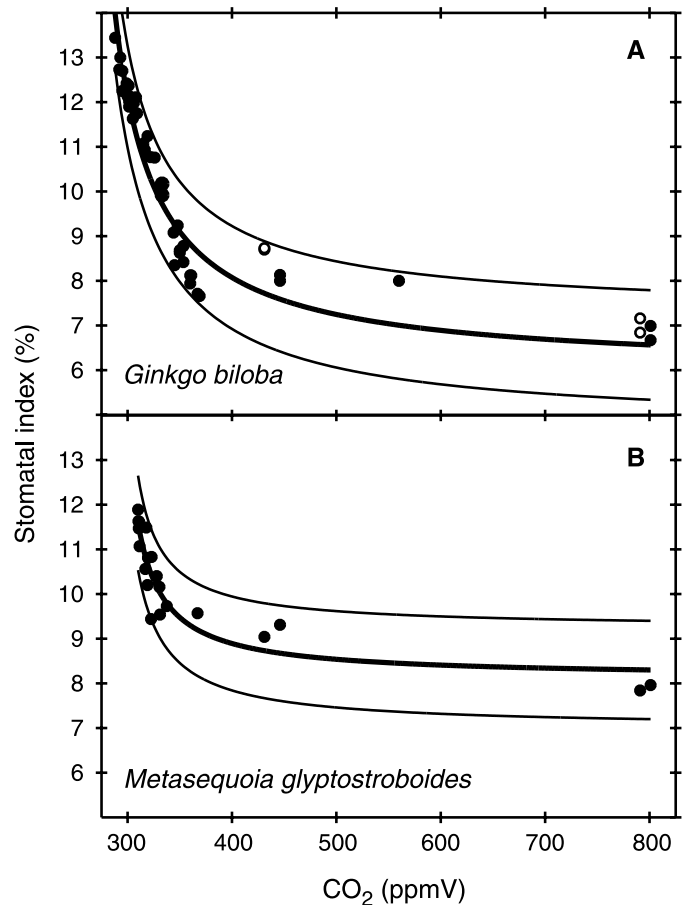


Figure 2. Training sets for (A) *Ginkgo biloba* ( $n = 44$ ) and (B) *Metasequoia glyptostroboides* ( $n = 20$ ). Thick lines represent regressions [*Ginkgo*:  $r^2 = 0.93$ ,  $F(1, 37) = 243$ ,  $P < 0.0001$ ,  $\text{SI} = 2000 \times [\text{CO}_2 - 196.1] / [333.7 \times \text{CO}_2 - 83000]$ ; *Metasequoia*:  $r^2 = 0.86$ ,  $F(1, 17) = 54$ ,  $P < 0.0001$ ,  $\text{SI} = 10000 \times [\text{CO}_2 - 273.7] / [1230.1 \times \text{CO}_2 - 350000]$ ]. Thin lines represent  $\pm 95\%$  prediction intervals. For *Ginkgo*, experimental results based upon a  $\text{CO}_2$  exposure time of one growing season ( $\circ$ ) were not used in regression (see text).

and Stott, 1994; Bowen et al., 2001). The leading hypothesis to explain this event involves the dissociation of isotopically light ( $\sim -60\text{‰}$ ) methane hydrates along continental margins (Dickens et al., 1995; Bains et al., 1999; Katz et al., 1999) and their subsequent oxidation to carbon dioxide. However, all previous attempts to discern this hypothesized atmospheric  $\text{CO}_2$  spike using other  $\text{CO}_2$  proxies have failed (Koch et al., 1992; Stott, 1992; Sinha and Stott, 1994). Although it is tempting to correlate Ardtun Head and its corresponding 500 ppmV spike in atmospheric  $\text{CO}_2$  to the IETM, further stratigraphic work is required to resolve this issue. If it is not of IETM age, then it is recording another high- $\text{CO}_2$  event. Alternatively, Ardtun Head is the one site where *G. gardneri* was used (see Table 2), and this species may respond to  $\text{CO}_2$  differently than *G. adiantoides*.

TABLE 3. RAW DATA FOR TRAINING SETS

<b>A. GINKGO</b>				
Date	CO <sub>2</sub> (ppmV)	SI (%)	Herbarium*	Source
1856	288	13.44	YPM	N.D.
1880	292	12.73	YPM	Hartford, Connecticut
1883	293	13.00	MBG	Botanic Garden, Cambridge, Massachusetts
1900	295	12.25	NA	Washington, D.C.
1900	295	12.70	YPM	Yale Forestry School, New Haven, Connecticut
1910	299	12.42	BBG	Orange, New Jersey
1915	300	12.13	MBG	Hannibal, Missouri
1918	301	12.37	BBG	Arnold Arboretum, Boston, Massachusetts
1920	302	11.90	MGB	Nanking, Kiangsu Province, China
1921	302	12.02	MGB	Missouri Botanical Garden, St. Louis, Missouri
1922	302	12.13	BBG	Purdys, New York
1928	304	11.93	NA	Maymont Park, Richmond, Virginia
1932	305	11.63	MA	Arnold Arboretum?, Boston, Massachusetts
1937	306	11.98	MBG	Japan
1942	308	12.11	NA	Berkeley, California
1943	309	11.75	MBG	Japan
1958	315	11.07	MBG	Tower Grove Park, St. Louis, Missouri
1960	317	10.93	MBG	Peking, China
1965	319	11.24	MA	Arnold Arboretum, Boston, Massachusetts
1968	322	10.77	NA	Arnold Arboretum, Boston, Massachusetts
1971	326	10.76	MA	Knox College, Galesburg, Illinois
1977	333	9.92	NA	U.S. Capitol, Washington, D.C.
1977	333	10.17	NA	Blandy Experimental Farm, Boyce, Virginia
1984	344	9.08	MBG	China (Yellow Plateau Team)
1985	345	8.35	BBG	Brooklyn Botanical Garden, New York City, New York
1987	348	9.24	NA	Morton Arboretum, Lisle, Illinois
1988	350	8.68	MBG	Clemson University, Clemson, South Carolina
N.A.	350	8.63	Exp	3-year-old saplings in greenhouses <sup>†</sup> (2 <sup>§</sup> )
1990	354	8.42	MBG	Missouri Botanical Garden, St. Louis, Missouri
1990	354	8.78	MBG	Oomoto Kameyama Botanical Garden; Kyoto, Japan
1995	360	7.94	YPM	Yale Peabody Museum, New Haven, Connecticut
1995	360	8.12	MBG	Missouri Botanical Garden, St. Louis, Missouri
1996	361	8.12	MBG	Oomoto Kameyama Botanical Garden; Kyoto, Japan
1999	367	7.71	Modern	New Haven, Connecticut
2000	369	7.66	Modern	New Haven, Connecticut
N.A.	431	8.70	Exp	6-year-old saplings in greenhouses (1 <sup>§</sup> )
N.A.	431	8.73	Exp	1-year-old saplings in greenhouses (1 <sup>§</sup> )
N.A.	446	8.13	Exp	7-year-old saplings in greenhouses (2 <sup>§</sup> )
N.A.	446	8.00	Exp	2-year-old saplings in greenhouses (2 <sup>§</sup> )
N.A.	560	8.00	Exp	3-year-old saplings in greenhouses <sup>†</sup> (2 <sup>§</sup> )
N.A.	791	7.16	Exp	6-year-old saplings in greenhouses (1 <sup>§</sup> )
N.A.	791	6.84	Exp	1-year-old saplings in greenhouses (1 <sup>§</sup> )
N.A.	801	6.99	Exp	7-year-old saplings in greenhouses (2 <sup>§</sup> )
N.A.	801	6.67	Exp	2-year-old saplings in greenhouses (2 <sup>§</sup> )
<b>B. METASEQUOIA</b>				
1947	310	11.89	UC	E Szechuan / NW Hubei, China
1948	310	11.63	UC	E Szechuan / NW Hubei, China
1949	311	11.47	UC	Berkeley, California
1950	311	11.62	UC	Bar Harbor, Maine
1953	312	11.07	UC	San Rafael, California
1961	317	10.56	UC	Tallahassee, Florida
1962	318	11.49	YPM	Bethany, Connecticut
1964	319	10.20	MA	Pennsylvania
1965	320	10.81	UC	Washington, D.C.
1968	323	9.44	UC	Fukuchiyama-city, Japan
1969	323	10.83	BBG	Brooklyn Botanical Garden, New York

continued

TABLE 3. continued

B. METASEQUOIA				
Date	CO <sub>2</sub> (ppmV)	SI (%)	Herbarium*	Source
1973	328	10.40	NA	Turlock, California
1975	331	10.16	UC	University of Oregon, Eugene, Oregon
1976	331	9.54	UC	University of Oregon, Eugene, Oregon
1980	338	9.73	UC	Western Hubei, China
1999	367	9.57	modern	New Haven, Connecticut; London, UK
N.A.	431	9.04	exp	1-year old saplings in greenhouses (1 <sup>§</sup> )
N.A.	446	9.31	exp	2-year old saplings in greenhouses (2 <sup>§</sup> )
N.A.	791	7.84	exp	1-year old saplings in greenhouses (1 <sup>§</sup> )
N.A.	801	7.96	exp	2-year old saplings in greenhouses (2 <sup>§</sup> )

Note: N.D.—no data; N.A.—not applicable.

\*YPM—Peabody Museum of Natural History (Yale University); MGB—Missouri Botanical Gardens; NA—U.S. National Arboretum; BBG—Brooklyn Botanic Gardens; MA—Morris Arboretum (University of Pennsylvania); UC—University Herbarium (University of California, Berkeley); modern—collections of fresh leaves; exp—collections from greenhouses. All cuticle prepreparates deposited at YPM.

<sup>†</sup>From Beerling et al. (1998).

<sup>§</sup>Number of growing seasons saplings were exposed to CO<sub>2</sub> treatments.

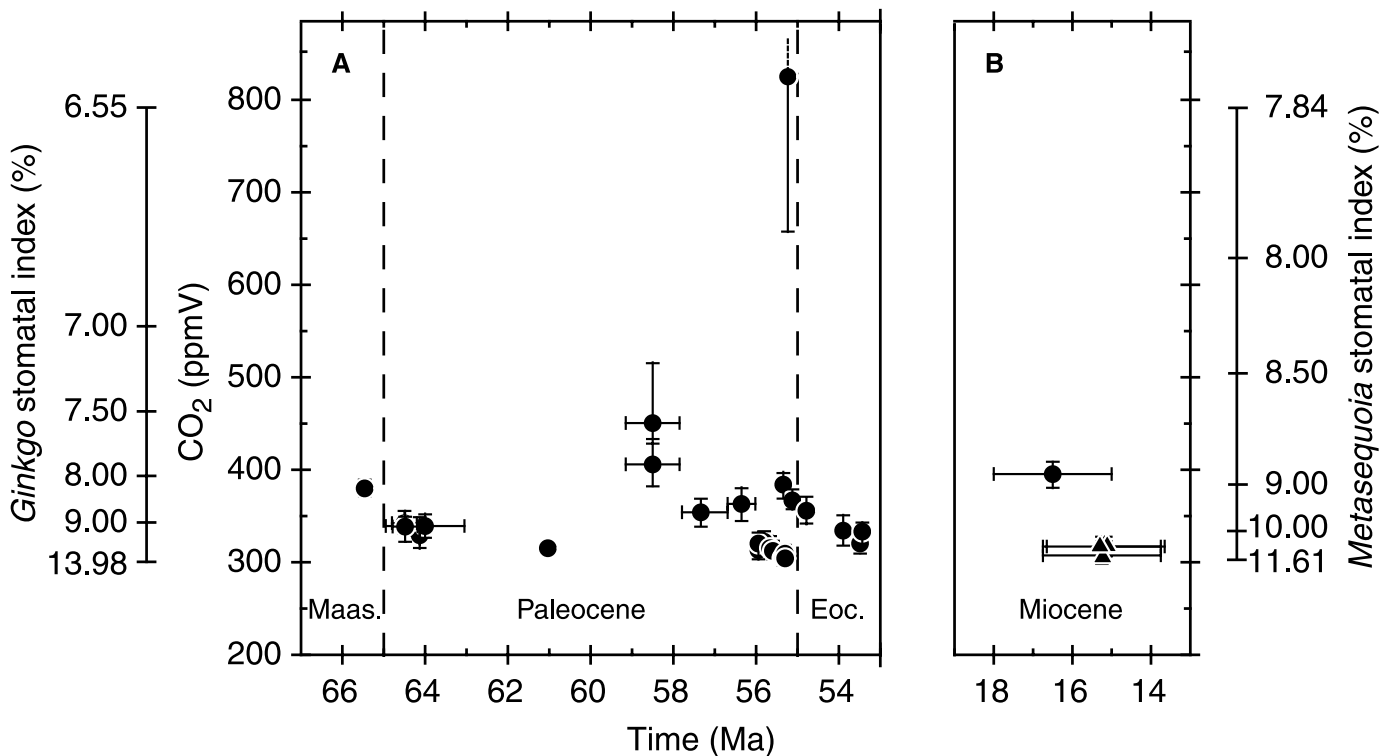


Figure 3. Reconstruction of paleo-CO<sub>2</sub> for the (A) very latest Cretaceous to early Eocene and (B) middle Miocene based upon SI measurements of *Ginkgo* (●) and *Metasequoia* (○) fossil cuticles. Errors represent ±95% confidence intervals. Regressions used to solve for CO<sub>2</sub> were rewritten from the training set-derived regressions (*Ginkgo*:  $CO_2 = 2000 \times [415 \times SI - 1961] / [3337 \times SI - 20000]$ ; *Metasequoia*:  $CO_2 = 70000 \times [50 \times SI - 391] / [12301 \times SI - 100000]$ ).



**TABLE 4. SAMPLING DETAILS AND CO<sub>2</sub> RECONSTRUCTION FOR FOSSIL GINKGO DATA BASED UPON SITES WITH <5 CUTICLE FRAGMENTS**

Site	Location*	Depository <sup>†</sup>	Age (Ma)	<i>n</i> <sup>§</sup>	SI (%)	CO <sub>2</sub> (ppmV)
DMNH 571	WB	DMNS	65.9	1	7.03	554
KJ 87134	WB	YPM	65.8	3	7.09	536
DMNH 1489	WB	DMNS	65.4	2	8.42	379
N.D.	BHB	YPM	~63	3	8.60	370
UF 18255	PRB	FMNH	~58	3	11.24	309
DMNH 907	WB	DMNS	56	2	8.89	358
LJH 8411	E	YPM	55	2	8.29	386
Klärbecken	G	BNHM	~2	3	12.29	299

Note: N.D.—no data.

\*WB—Williston Basin (North Dakota, USA); BHB—Bighorn Basin (Wyoming and Montana, USA); PRB—Powder River Basin (Wyoming, USA); E—Ellesmere Island (Canada); G—Germany.

<sup>†</sup>Depository for cuticle preparates: DMNS—Denver Museum of Nature & Science; YPM—Yale Peabody Museum; FMNH—Florida Museum of Natural History; BNHM—British Natural History Museum.

<sup>§</sup>Number of leaves measured for calculation of SI.

### Ginkgo and Metasequoia cuticle as reliable recorders of atmospheric CO<sub>2</sub>

There are numerous factors indicating that the CO<sub>2</sub> reconstruction presented here is accurate. As discussed above, both genera are restricted in the fossil record to mid- and high-latitude temperate forests, and, in addition, *Ginkgo* is preferentially found in disturbed riparian settings. These characteristics should strengthen the applicability of the fossil cuticles to their respective training sets. Also, both *Ginkgo* and *Metasequoia* are highly conservative phylogenetically, and, in the case of *Ginkgo*, the slope of the SI-CO<sub>2</sub> relationship derived from modern *Ginkgo* (Fig. 2) is similar to the SI-CO<sub>2</sub> relationship derived from a multimillion year sequence of fossil SI measurements and coeval pedogenic carbonate-derived CO<sub>2</sub> estimates (Beerling and Royer, 2002b). This suggests that (1) the SI-CO<sub>2</sub> relationships in *Ginkgo* and *Metasequoia* have remained unchanged throughout the Cenozoic; and (2) the short-term (largely phenotypic) responses captured in the training sets are similar to the long-term (largely genotypic) responses reflected in the fossils.

As a cross-check on the early Paleogene *Ginkgo*-derived estimates, I compared the SI's of *Platanus guillelmae* from site SLW H with the SI's of its nearest living equivalents *P. occidentalis* and *P. orientalis* using the stomatal ratio method (see above). Although this method can only generate semiquantitative estimates of CO<sub>2</sub>, all of the estimates for this site fall between 350 and 390 ppmV (Table 5). This range compares favorably with the *Ginkgo*-derived CO<sub>2</sub> estimate from the same site (323 ppmV), indicating, again, that *Ginkgo* faithfully records CO<sub>2</sub>.

The SI's of nearly all the measured fossil material fall within the range of high CO<sub>2</sub> sensitivity in the training sets (Fig. 2; Table 2). This contrasts with the study of Retallack (2001),

where the stomatal indices in 82% of the fossil sites fall outside the total range captured in his training set, and so these CO<sub>2</sub> estimates are less reliable. In addition, I have intensively sampled several intervals, for example 12 sites from the last 1 m.y. of the Paleocene. These characteristics allow for more precise determinations of paleo-CO<sub>2</sub> relative to other CO<sub>2</sub> proxies, and, because SI's respond to CO<sub>2</sub> on the time scale of 10<sup>0</sup>–10<sup>2</sup> yr, the ability to discern rapid shifts in atmospheric CO<sub>2</sub> (Royer et al., 2001a).

A few of the fossil SI's fall outside the densely sampled regions in the training sets. This suggests that the SI's in *G. biloba* and *G. adiantoides* are not constrained to a limited range (8%–12%) irrespective of atmospheric CO<sub>2</sub> levels. Additional evidence that the SI's in *Ginkgo* are highly adaptable comes from Mesozoic studies where SI's in *Ginkgo* are as low as 2.6% (McElwain and Chaloner, 1996; McElwain et al., 1999; Chen et al., 2001; Retallack, 2001).

The only possible confounding factor that I have discerned in my fossil data set is latitude (Fig. 4). Except for the Spitsbergen site, there is a negative correlation between latitude and the SI in *Ginkgo*. Even within the densely sampled Bighorn Basin, there is a small (slope = –2.2 using SI as the dependent variable) but moderately significant (*r*<sup>2</sup> = 0.43; *P* = 0.002) correlation. Differences in irradiance (Lake et al., 2001) or temperature (Wagner, 1998) may be driving this response, however more data are required before any firm conclusions can be drawn.

### Paleoclimatic implications

Fig. 5 is a compilation of most published proxy- and modeling-based CO<sub>2</sub> estimates for the last 66 m.y. There is very good agreement among the methods for the Neogene, strongly indicating that CO<sub>2</sub> levels were not much different from the present

TABLE 5. CO<sub>2</sub> RECONSTRUCTION FROM STOMATAL RATIOS IN *PLATANUS*

A. FOSSILS						
Species	Site	Age (Ma)	<i>n</i> *	SI (%)		
<i>P. guillelmae</i>	SLW H	53.5	7	12.89		
B. NEAREST LIVING EQUIVALENTS						
Species	Site	Date	<i>n</i> *	SI (%)	Stomatal ratio <sup>†</sup>	Paleo-CO <sub>2</sub> (ppmV) <sup>§</sup>
<i>P. occidentalis</i>	North Carolina, USA	1891	6	15.35	1.19	350
<i>P. orientalis</i>	Iraq	1975	5	15.22	1.18	390
<i>P. × acerfolia</i>	Connecticut, USA	2001	5	13.28	1.03	381
<i>P. occidentalis</i>	Connecticut, USA	2001	6	13.44	1.04	386

\*Number of leaves measured for calculation of SI.  
<sup>†</sup>Stomatal ratio—SI<sub>modern</sub> / SI<sub>fossil</sub>  
<sup>§</sup>CO<sub>2</sub> reconstructions for site SLW H. These estimates should be considered semi-quantitative only. Values calculated by multiplying the stomatal ratio by the corresponding CO<sub>2</sub> concentration in which the leaves developed (see text for details).

day. CO<sub>2</sub> reconstructions for the Paleogene, however, are inconsistent, ranging from <300 ppmV to >3000 ppmV. These inconsistencies are largely stratified by method, with the highest CO<sub>2</sub> estimates derived from the boron proxy and the lowest from this stomatal study (Fig. 5).

What do these CO<sub>2</sub> reconstructions mean in terms of paleoclimate? Assuming that we understand the role of CO<sub>2</sub> as a greenhouse gas in regulating global temperature, it is possible to convert a given concentration of atmospheric CO<sub>2</sub> into a prediction of global mean surface temperature (GMST). I have done this for the Late Cretaceous to early Paleogene (69–50 Ma) and middle Miocene (19–13 Ma) CO<sub>2</sub> reconstructions, the two intervals for which I have stomatal data, using the CO<sub>2</sub>-GMST

sensitivity study of Kothavala et al. (1999). This general circulation model study was calibrated to present-day conditions. Although it may be instructive to use sensitivity studies calibrated to early Paleogene and middle Miocene conditions, the CO<sub>2</sub>-GMST relationship is most accurately known for present-day conditions, and applying a sensitivity study calibrated to the present day allows testing the sole effects of CO<sub>2</sub> on GMST. In other words, if the CO<sub>2</sub>-derived GMST predictions do not match the geologic indicators of GMST for a given period, then factors in addition to CO<sub>2</sub> (e.g., paleogeography, vegetative feedbacks) are required to explain the GMST for that period.

The CO<sub>2</sub>-derived GMST predictions are shown in Figure 6. As with the raw CO<sub>2</sub> data, there is general agreement for the middle Miocene, with most predictions within 1 °C of the present-day GMST. Predictions for the early Paleogene are not consistent, ranging from near present-day values to >10 °C warmer than the present-day GMST.

Both the early Paleogene and middle Miocene are intervals of global warmth relative to today. The physiognomic characters of early Paleogene fossil floras indicate temperatures much higher than today at mid and high latitudes (e.g., Hickey, 1980; Spicer and Parrish, 1990; Wing and Greenwood, 1993; Wolfe, 1994; Greenwood and Wing, 1995; Wilf, 2000). The comparison of these fossil plants with their Nearest Living Relatives (NLRs) also indicates warmer temperatures (e.g., Hickey, 1977; Spicer and Parrish, 1990). For example, frost intolerant palms occur at paleolatitudes up to 20° north of their current northern limit in North America (Greenwood and Wing, 1995). The early Paleogene distributions of large tortoises (Hutchison, 1982) and crocodylians (Markwick, 1994, 1998) in the United States also indicate temperatures warmer than the present day.

Although the above data constrain continental temperatures, δ<sup>18</sup>O data from calcitic marine shells provide temperature information for the oceans. Oceans are the largest reservoirs of

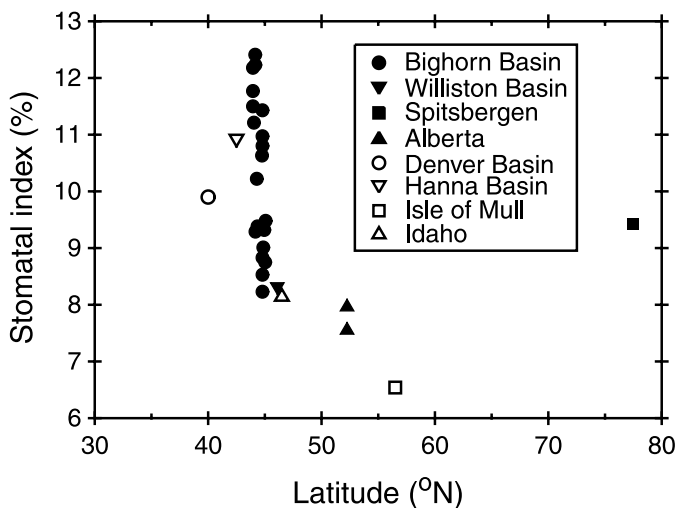


Figure 4. Correlation between latitude and stomatal index for fossil sites. Present-day latitudes are plotted, but should reflect their corresponding paleolatitudes to within 5° (Schettino and Scotese, 2001).

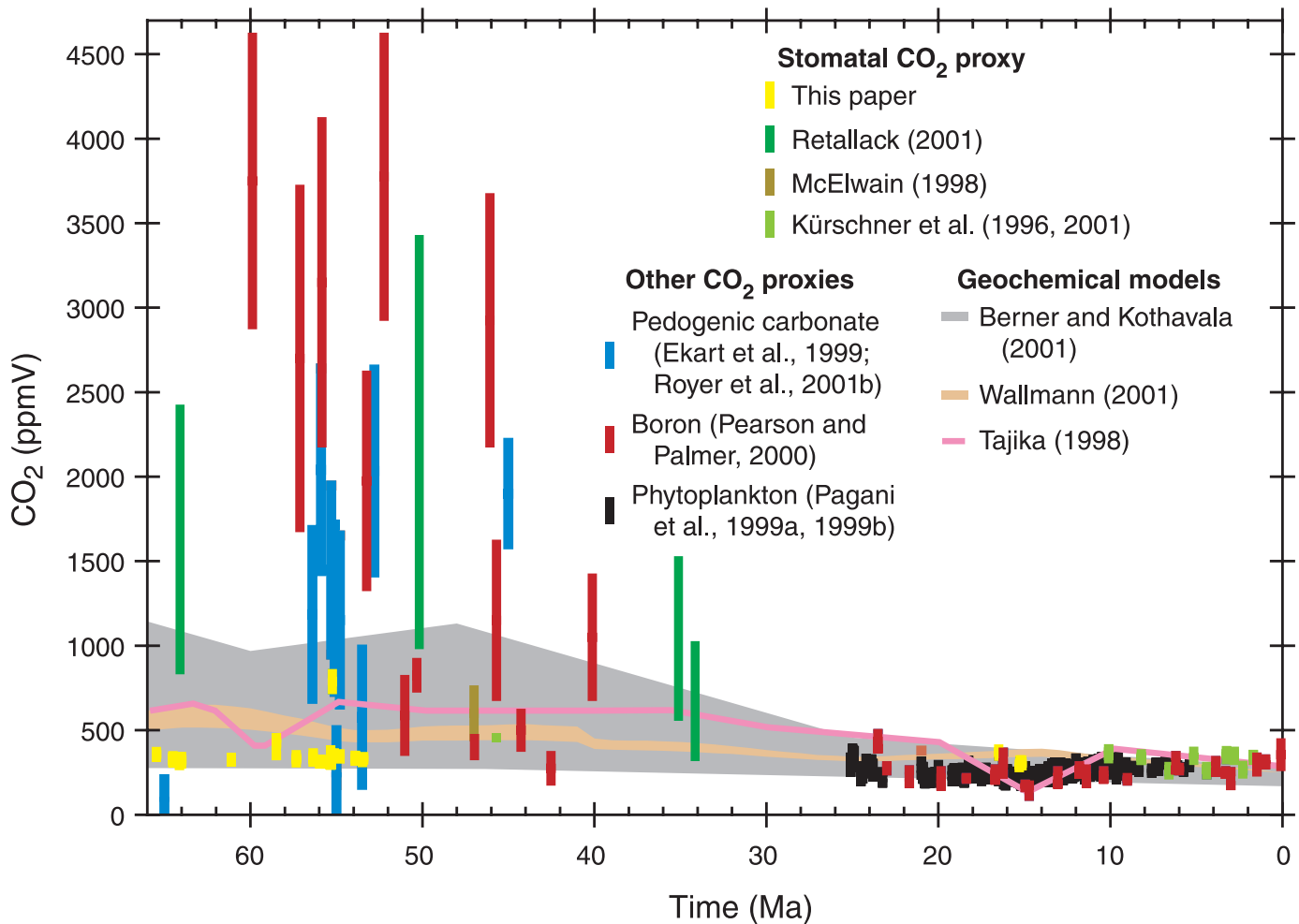


Figure 5. A compilation of CO<sub>2</sub> reconstructions for the Tertiary. In the case of Retallack (2001), only those sites for which  $n=5$  cuticle fragments were counted are plotted. No pedogenic carbonate-derived estimates are plotted for the Neogene because their margins of error are much larger relative to the other methods (cf. Ekart et al., 1999; Royer et al., 2001a).

heat in the biosphere, and therefore provide the best proxy for globally averaged temperatures. Based upon the  $\delta^{18}\text{O}$  compilations of Zachos et al. (1994) and Zachos et al. (2001), benthic temperatures were 8–12 °C warmer than the present day during the early Paleogene, and high-latitude near-surface temperatures were >15 °C warmer. Using late Paleocene near surface paleotemperature data and present-day levels of atmospheric CO<sub>2</sub> as input into a GCM, O’Connell et al. (1996) calculated a GMST 3 °C warmer than the present day.

During the mid-Miocene thermal maximum (~17–14.5 Ma), benthic waters warmed 1–2 °C to temperatures 6 °C warmer than the present day (Lear et al., 2000; Zachos et al., 2001). Plant distributions (White et al., 1997; Utescher et al., 2000) and leaf physiognomic characters (Wolfe, 1994) also indicate substantial warming at midlatitudes.

If my stomatal-based CO<sub>2</sub> reconstruction is correct, then, factors in addition to carbon dioxide are required to explain

these two intervals of global warmth, and these intervals may not serve as good analogs for understanding future climate change. It is crucial to emphasize that low concentrations of atmospheric CO<sub>2</sub> during intervals of global warmth do not counter the theory of the greenhouse effect (for this, high CO<sub>2</sub> levels are required during globally cool intervals); instead, they indicate that other thermal forcings were more important at those times than they are today.

Traditionally, modelers interested in warm climates have struggled to match their output with the geologic data (Barron, 1987; Sloan and Barron, 1990, 1992), particularly when using low CO<sub>2</sub> levels (Sloan and Rea, 1995). Recent work, however, has begun to resolve these discrepancies (Otto-Bliesner and Upchurch, 1997; Sloan and Morrill, 1998; Sloan and Pollard, 1998; DeConto et al., 1999; Upchurch et al., 1999; Sewall et al., 2000; Sewall and Sloan, 2001; Sloan et al., 2001). It will be crucial to understand the various roles CO<sub>2</sub> plays during globally warm pe-

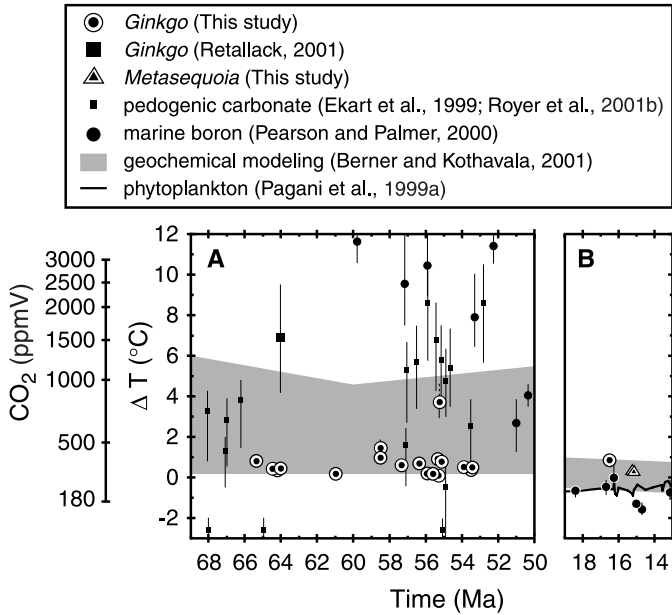


Figure 6. Estimates of  $\text{CO}_2$  from Figure 5 and their corresponding model-determined temperature departures ( $\Delta T$ ) of global mean surface temperature (GMST) from present day for the (A) very latest Cretaceous to early Eocene and (B) middle Miocene. Paleo-GMST calculated using the  $\text{CO}_2$ -temperature sensitivity study of Kothavala et al. (1999). Present-day reference GMST calculated using the preindustrial  $\text{CO}_2$  value of 280 ppmV (14.7 °C). The error range of GMST predicted from the geochemical modeling-based  $\text{CO}_2$  predictions of Berner and Kothavala (2001) corresponds to the model's sensitivity analysis. Most error ranges derived from my stomatal data set are smaller than the plotted symbols. Error ranges derived from the phytoplankton methods are not shown.

riods, particularly as atmospheric  $\text{CO}_2$  rises to levels in the very near future that are perhaps unprecedented for the past 65 m.y.

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