Paleobiology, 31(1), 2005, pp. 141–150

Contrasting seasonal patterns of carbon gain in evergreen and deciduous trees of ancient polar forests

Dana L. Royer, Colin P. Osborne, and David J. Beerling

Abstract.—Polar deciduous forests were an important biome during much of the Mesozoic and Paleogene, occupying upwards of 40% of the total land surface. Little is known about their physiological ecology, however, because these types of forests do not exist for study today. Furthermore, the role of high atmospheric CO_2 levels in modulating the physiological response of ancient polar forests is poorly known. Here we report detailed measurements of whole-tree net carbon uptake over a full annual cycle for five tree species whose close ancestors were components of Cretaceous and Paleogene polar forests. Measurements were made on both evergreen and deciduous species after two years growth in a simulated Mesozoic polar (69°N) environment at either ambient (400 ppmv) or elevated (800 ppmv) levels of CO_2. The deciduous species exhibited a significant pulse in carbon uptake during the late summer and early autumn (August to mid-October) that enabled them to achieve annual carbon budgets similar to those of evergreen trees, despite incurring higher carbon losses through annual leaf shedding. Area-based photosynthetic rates dropped progressively in all species during the polar summer (June to mid-July), resulting in decreases in whole-tree carbon uptake late in the polar summer. The high-CO_2-grown trees were more strongly affected by this polar summer depression than the low-CO_2-grown trees. Our results indicate that, from a carbon balance perspective, deciduous taxa have no clear advantage over evergreens. Moreover, the seasonal patterns reported here suggest that at latitudes poleward of 69°, evergreens will be even more strongly favored. The consideration of factors not directly related to carbon budgeting is probably therefore required to fully understand the adaptive significance of the deciduous leaf habit in ancient polar forests.

Dana L. Royer, Colin P. Osborne, and David J. Beerling.*[†] *Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, United Kingdom. E-mail: c.p.osborne@sheffield.ac.uk, E-mail: d.j.beerling@sheffield.ac.uk*

*Present address: *Department of Geosciences, Pennsylvania State University, University Park, Pennsylvania 16802. E-mail: droyer@psu.edu*

[†]Corresponding author

Accepted: 28 June 2004

Introduction

Deciduous forests blanketed the polar regions up to 85° latitude for much of the Mesozoic and Paleogene (Jefferson 1982; Wolfe 1985; Spicer and Chapman 1990; Askin and Spicer 1995), an interval of Earth's history generally linked with high atmospheric CO_2 concentrations (Ekart et al. 1999; Berner and Kothavala 2001; Beerling and Royer 2002) and globally warm temperatures (Frakes et al. 1992; Zachos et al. 2001; Huber et al. 2002). The deciduous character of these forests has long remained enigmatic (e.g., Read and Francis 1992), principally because ancient polar forests have no modern analogue for study. Many deciduous plants today occupy environments that experience seasonal water deficits and/or subfreezing temperatures (Chabot and Hicks 1982; Woodward 1987; Givnish 2002); however, during much of the Mesozoic and Paleogene the polar regions were warm (coldest month mean temperature >0°C) (see Estes and Hutchison 1980; Tarduno et al. 1998; Tripati et al. 2001; Dutton et al. 2002) and wet (Herman and Spicer 1996; Francis and Poole 2002; Jahren and Sternberg 2003). The deciduous character of these ancient forests therefore may not obviously be related to water deficits.

Until recently, many paleobotanists have speculated that the warm, dark winters associated with ancient polar forests selected for the deciduous habit because evergreens would lose too much carbon via respiration to remain competitive (Chaney 1947; Hickey 1984; Wolfe 1985; Spicer and Chapman 1990; Falcon-Lang and Cantrill 2001; Wing et al. 2003). Royer et al. (2003b) tested this hypothesis by

© 2005 The Paleontological Society. All rights reserved. 0094-8373/05/3101-0009/$1.00

quantifying the carbon costs associated with the winter season (wintertime respiration + annual litter production) for five taxa, representing both leaf habits, whose closely related ancestors were important components of polar forests. Trees were grown and measured in a simulated polar environment at two different CO_2 levels. Over the course of a six-week-long polar winter, the amount of carbon lost by respiration was exceedingly small for both evergreen (3% of annual budgets) and deciduous taxa (2% of annual budgets), irrespective of CO_2 growth concentration. When the annual carbon costs of litter turnover were taken into account and scaled to mature stands, the deciduous leaf habit was twice as costly as a winter strategy (Royer et al. 2003a).

Although the deciduous taxa lost more carbon during the winter season than their evergreen counterparts, species from both leaf habits achieved comparable annual carbon budgets (evergreen = 23.7 ± 4.4 g C; deciduous = 21.9 ± 2.6 g C; $p = 0.67$), where annual carbon budget equals annual biomass increment (whole-tree net carbon uptake minus litter production). These patterns imply that deciduous species compensate for greater carbon losses incurred during the polar winters with greater net canopy carbon productivity relative to evergreen taxa (Osborne and Beerling 2003). Therefore, a central aim of the present work is to detect when in the seasonal cycle of canopy photosynthesis this unseen gain occurs, by tracking whole-tree carbon fluxes through an entire polar year.

Royer et al. (2003b) also showed that high CO_2 significantly stimulated annual whole-tree net carbon uptake by 41% ($p = 0.01$). This CO_2 effect provides one mechanism to explain the high productivities inferred for many ancient polar forests (Creber and Chaloner 1985; Beerling and Woodward 2001; Williams et al. 2003). Knowledge of the seasonal timing of this CO_2 stimulation (spring or autumn vs. polar summer) could, however, provide information on the competitive trade-offs of the two leaf habits, with particular relevance for the higher polar latitudes, where the periods of continuous daylight approach the total length of the growing season.

Here we report detailed measurements of whole-tree net carbon uptake, canopy growth, and CO_2 fertilization for five ancient taxa during their third year of growth in a simulated Mesozoic arctic climate. The primary objectives of this study were two-fold: (1) ascertain the growing season interval during which the deciduous taxa fix more carbon than the evergreens; (2) determine any relationships between the seasonal patterns of carbon exchange and a CO_2 enriched atmosphere.

Methods

Plant Growth.—The following five tree species were used in this study: *Taxodium distichum* (L.) Rich (deciduous taxodioid), *Metasequoia glyptostroboides* Hu & Cheng (deciduous taxodioid), *Sequoia sempervirens* (D. Don) Endl. (evergreen taxodioid), *Ginkgo biloba* L. (deciduous gymnosperm), and *Nothofagus cunninghamii* (Hook.) Oerst. (evergreen angiosperm). These taxa have long fossil records at the generic level (>65 Myr) (Chaney 1951; Tralau 1968; Hill 1991), and their ancestors were dominant elements in Cretaceous and Paleogene polar forests (Wolfe 1985; Spicer and Chapman 1990). They therefore represent the most appropriate modern physiological analogues to ancient high latitude forests (see also Royer et al. 2003b; Sun et al. 2003; Williams et al. 2003).

Multiple one-year-old saplings of each species were grown inside four fully replicated growth rooms located in Sheffield, United Kingdom, beginning in April 2000. Plants were grown in a silica sand-vermiculite-peat medium (13: 5: 2 ratio) in 2.2-liter pots, watered twice daily via an automated drip irrigator, and fertilized weekly with dilute (10%) Rorison's nutrient solution. Relative humidity within the growth rooms was maintained above 75% by using an automated misting system. The simulated photoperiod was equivalent to 69° latitude, which translates to six weeks of continuous daylight and darkness during the summers and winters, respectively. Growth room temperatures were maintained at 5°C above ambient Sheffield conditions but were never allowed to drop below 0°C. The mean annual temperature and coldest month mean temperature during the interval of study (2002) were 14.7°C and 8.5°C,

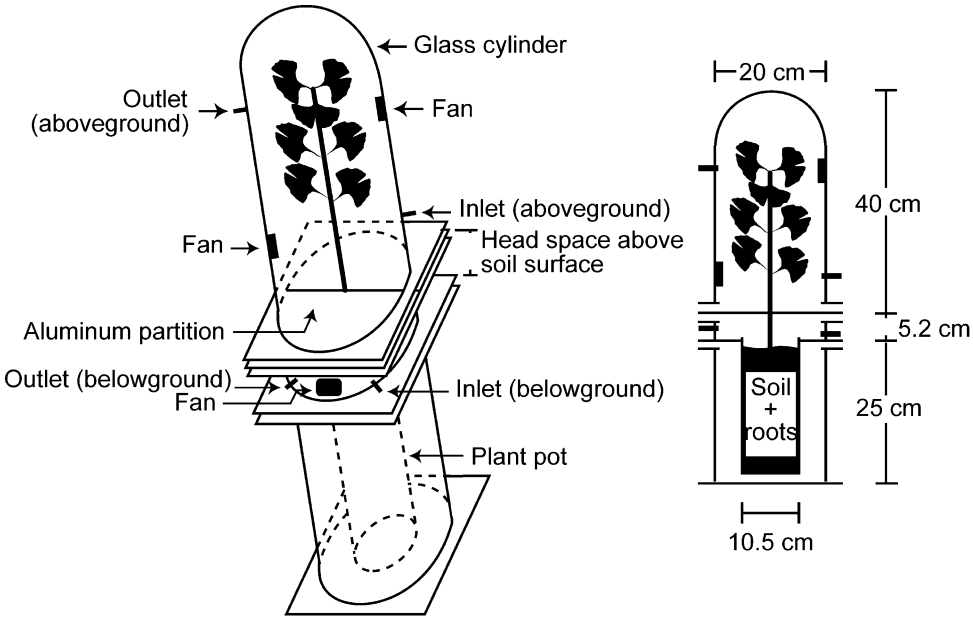


FIGURE 1. Schematic showing the design of the whole-tree gas exchange chambers. The right-hand diagram illustrates the chamber design in cross-section.

respectively. Each growth room was partitioned, with one half receiving elevated levels of CO_2 (800 ppmv) and the other half ambient levels (400 ppmv). These simulated environmental conditions are representative of the polar climates under which the plant lineages grew (Beerling and Osborne 2002; Royer et al. 2003b). (For further information on growth room design and performance, consult Beerling and Osborne 2002).

System Configuration and Operation.—Seasonal patterns of CO_2 exchange were quantified by using eight custom-built whole-tree chambers configured into an open gas exchange system. Chamber design was based on earlier systems (Eissenstat et al. 1993; Beerling et al. 1998) but modified to allow separation of above- and below-ground gas fluxes (Fig. 1).

A continuous flow of filtered air was maintained in the chambers. The air was first humidified by bubbling through water to approximate the vapor pressure of the growth rooms, and then divided into two streams. In one stream, the CO_2 concentration was elevated to 800 ppmv with the addition of pure CO_2 into a mixing volume; in the second stream, CO_2 remained at the ambient concentration (≈400 ppmv). The mean residence time of the air was approximately three minutes in the above-ground compartments (flow rate ≈four liters per minute) and two minutes in the below-ground compartments (flow rate ≈0.8 liters per minute).

Air from each of the 16 chamber compartments was sampled in sequence; we used differential infrared gas analysis (CIRAS-1, PP Systems, Hitchin, Herts, U.K.) to measure corresponding CO_2 concentrations by comparison with the reference air supply. Samples were measured hourly for 25 hours, after first flushing air through the switching system and IRGA for 2 minutes. Sampling and recording were synchronized, and the IRGA zeroed hourly, by using a computerized automatic relay system (Mitsubishi FX-48MR, RS Components). A representative example of a 25-hour set of measurements is shown in Figure 2.

All plants were sealed inside the chambers for 24 hours before starting the gas exchange measurements. Of the eight chambers in our system, three were used for replicate plants from ambient CO_2 and three from elevated CO_2. The remaining two chambers were used for control pots, one from each CO_2 treatment. These contained the same mineral soil mix-

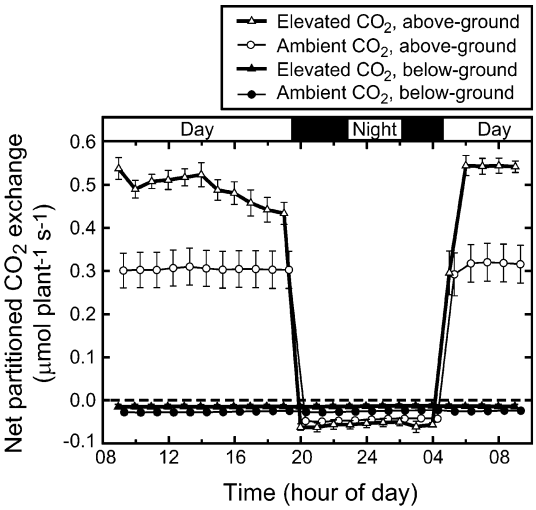


FIGURE 2. Daily pattern of CO_2 exchange for *Taxodium distichum* grown and measured at either ambient (400 ppmv) or elevated (800 ppmv) atmospheric CO_2 concentration. Measurements taken on 31 August 2002–01 September (15 hours day length). Fluxes are partitioned between the above- and below-ground components, and the values are mean ± SE (n=3).

ture as the other plants, watered with the same nutrient solutions, at the same frequency, but without the plants.

We repeated measurements of above- and below-ground gas exchange for each species ten times at regular intervals, from November 2001 to December 2002, resulting in a total of 20,000 discrete measurements (400 per 25-hour measurement period × 10 periods × 5 species). For each daily set of measurements (e.g., Fig. 2), the hourly data were added together and scaled to yield daily whole-tree net carbon uptake. A similar procedure was used to scale from daily to annual whole-tree net carbon uptake, except that adjacent sampling dates were linearly interpolated, and the resulting trapezoids were used as the integrating unit.

Canopy leaf areas were estimated non-destructively after each set of measurements by multiplying the total number of leaves (or branchlets, for the taxodiaceaous conifers) by the mean area of 40 representative leaves as calculated from digital photography (Coolpix 995, Nikon UK Ltd., Kingston upon Thames, Surrey, U.K.) and morphometric image analysis software (tpsDig 1.28; F. J. Rohlf, available at http://life.bio.sunysb.edu/morph). For *G. biloba*, canopy area was calculated directly because its canopy contained relatively few, large leaves. We estimated the annual carbon costs of litter production for each species were estimated by scaling subsamples collected in the autumn (see Royer et al. 2003a for more details).

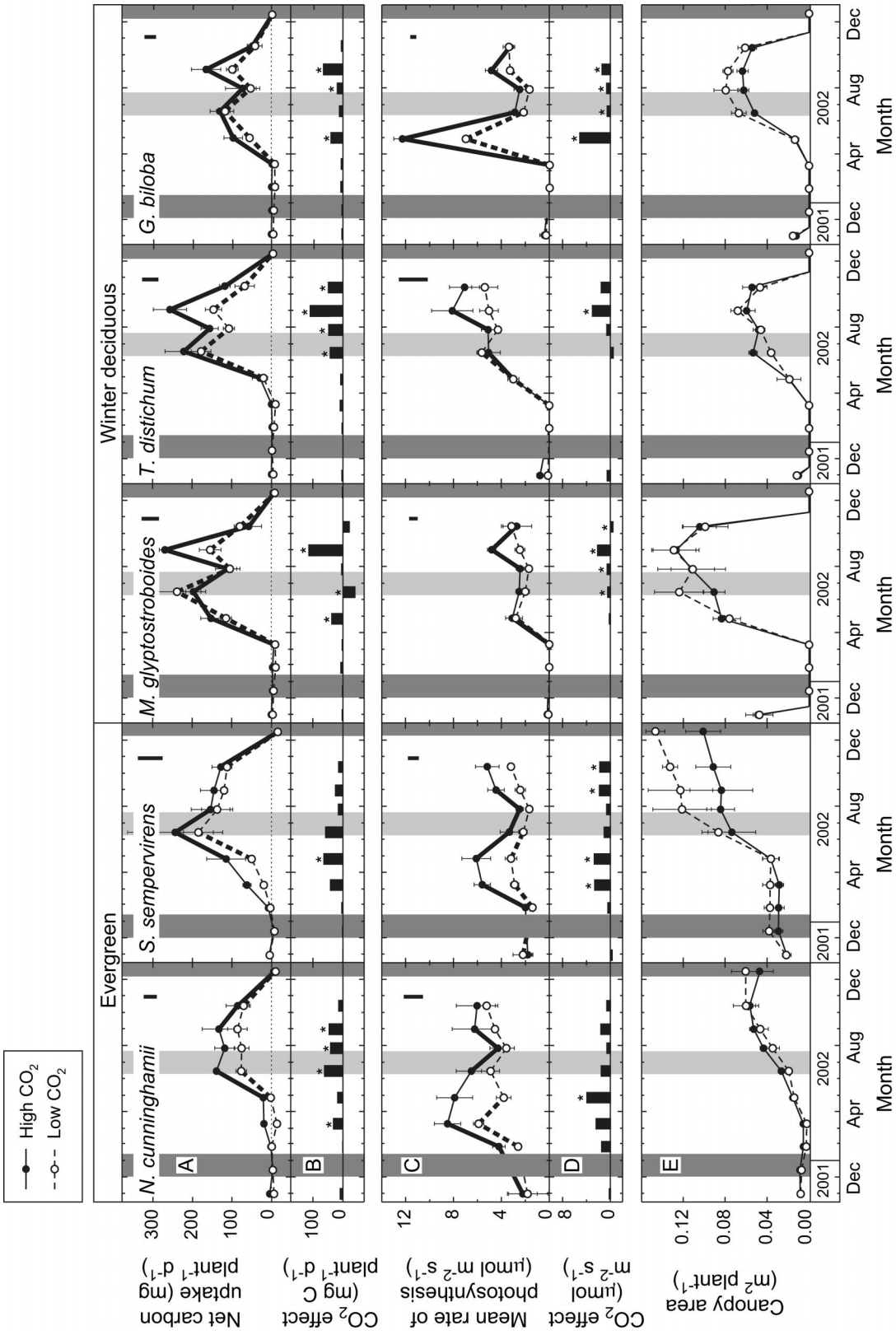
CO_2 and leaf habit effects within the carbon budgets were evaluated by using a two-way ANOVA (CO_2 × leaf habit) with unequal but proportional subclass sizes (Sokal and Rohlf 1995). Time effects within each species were analyzed by using a repeated measures ANOVA (CO_2 × time). The least significant difference (LSD) was then computed, LSD = $t_{\alpha[v]}\sqrt{[2 \times MS/n]}$, where $t_{\alpha[v]}$ is the critical value for Student's distribution for v within-group degrees of freedom at α level of significance (0.05 is adopted here), MS is the within-group mean squares, and n is the sample size (number of sampling dates × replicates) (Milliken and Johnson 1992). An observed pattern, such as a peak in carbon production, was considered significant if the data of interest were different from the pre- and postevent data by values exceeding the LSD.

Results

The evergreens showed either a broad plateau (*N. cunninghamii*) or a single early sum-

→

FIGURE 3. Seasonal patterns of whole-tree gas exchange for five ancient taxa. Light gray vertical bands correspond to intervals of continuous daylight (polar summer), and dark gray bands correspond to intervals of continuous darkness (polar winter). Standard errors are plotted (n=3 per CO_2 treatment). A, Whole-tree net carbon uptake. Each data point integrates a full set of daily measurements (e.g., Fig. 2). Black vertical bars represent least significant differences (LSDs) for α=0.05 (Milliken and Johnson 1992; see methods). Thickened lines indicate significant differences between the two flanking measurements. B, Difference in the CO_2 treatments for net carbon uptake. Significant differences based on LSDs (α=0.05) are marked by asterisks. C, Mean rate of area-based photosynthesis. Each data point represents the mean photosynthetic rate during the daylight hours. Black vertical bars and thickened lines as in panel A. D, Difference in the CO_2 treatments for mean photosynthetic rates. Asterisks as in panel B. E, Canopy area.


High CO_2
Low CO_2
Evergreen
Winter deciduous
N. cunninghamii
S. sempervirens
M. glyptostroboides
T. distichum
G. biloba
A
B
C
D
E
Net carbon uptake (mg plant^{-1} d^{-1})
CO_2 effect (mg C plant^{-1} d^{-1})
Mean rate of photosynthesis (µmol m^{-2} s^{-1})
CO_2 effect (µmol m^{-2} s^{-1})
Canopy area (m^2 plant^{-1})
Month
Dec
Apr
Aug
Dec
2001
2002

mer peak (*S. sempervirens*) in whole-tree net carbon uptake during the summer (Fig. 3A). In contrast, the deciduous taxa exhibited not only an early summer peak, but also an additional second peak of similar magnitude later in the summer, after the return of day-night irradiance cycles. This ''double peak'' was significant in all three deciduous taxa (thickened lines in Fig. 3A), except for the low CO_2-grown *T. distichum*, which only showed the early summer peak. CO_2 stimulation of net carbon uptake in deciduous trees was diminished under the continuous light of the polar summer (except *T. distichum*, which had no early season CO_2 stimulation), whereas the evergreens exhibited either an early summer CO_2 stimulation (*S. sempervirens*) or a consistent CO_2 stimulation throughout the growing season (*N. cunninghamii*; Fig. 3B).

To determine the seasonal patterns in leaf photosynthetic rate, we recalculated the rates of canopy net carbon uptake on a per-unit leaf area basis. Most species showed reduced photosynthetic rates during the polar summer, irrespective of leaf habit (Fig. 3C). In the case of *G. biloba* and the high-CO_2-grown evergreens *N. cunninghamii* and *S. sempervirens*, this polar summer depression was statistically significant, and all species grown at high CO_2 showed significant increases in photosynthetic rate late in the summer, after the close of the polar summer. Parallel to the patterns of whole-tree net carbon uptake, all species showed stimulations in area-based photosynthetic rate attributable to CO_2 enrichment (Fig. 3D). Few seasonal patterns were evident, although in the evergreen *S. sempervirens* the CO_2 effect was significantly diminished during the polar summer (Fig. 3D). For all species, no strong CO_2 stimulation was observed during the polar summer.

Importantly, these calculated seasonal trends in photosynthesis match leaf-level measurements made on the same plants at the same times (Osborne and Beerling 2003). Similar leaf-level patterns were also observed during the first year of treatments in 2000, when the plants were smaller and younger (Beerling and Osborne 2002), strongly suggesting that the imposed polar environment is responsible for the midsummer reduction in plant productivity, rather than being an effect of pot size or plant age. Furthermore, both the lack of carbohydrate accumulation in the leaf tissues during the polar summer (Osborne and Beerling 2003) and the recovery of CO_2-stimulated photosynthetic rates after the polar summer in four out of five species (Fig. 3C), also argue against a strong influence of pot size or plant age on our results.

The seasonal patterns of instantaneous photosynthetic rates did not directly mirror those of whole-tree net carbon exchange. Specifically, photosynthetic rates in most species declined at the onset of continuous daylight (Fig. 3C), whereas rates of whole-tree net carbon gain were maintained until late in the polar summer in all species (Fig. 3A). This lag was driven by continued increases in both canopy area (Fig. 3E) and day length. The deciduous plants showed the patterns of canopy area development expected of mature trees, whereas canopies in the evergreens increased in size throughout the duration of the experiment owing to their young age (Fig. 3E). In both *S. sempervirens* and *G. biloba*, the canopies of ambient CO_2-grown plants were larger than their high CO_2 counterparts, which reduced the CO_2 stimulation of net carbon uptake (Fig. 3A) relative to that of photosynthetic rate (Fig. 3C).

Discussion

A central aim of this study was to identify the interval during which deciduous plants fixed more carbon than their evergreen counterparts. We found that all deciduous taxa exhibited a significant pulse in net carbon gain during the late summer and early autumn, after the termination of the polar summer (Fig. 3A). In contrast, evergreens showed little to no late summer increase. Specifically, the deciduous plants grown at high CO_2 fixed on average 4.5 g more carbon during this interval (27 July–13 October; 15% of annual whole-tree net carbon uptake) than their evergreen counterparts, and 2.7 g more at ambient CO_2 (12% of annual whole-tree net carbon uptake). This leaf habit effect is highly significant ($F_{1,6}$ = 35.2; p = 0.001). Given that the deciduous species lost on average 4.0 g more carbon during the polar winter than the evergreens (respi-

TABLE 1. Evaluation of late summer (27 July–31 August) patterns of carbon uptake. The changes in whole-tree net carbon gain from the July to August sampling dates are given in row A. In rows B through F, the carbon contribution of each component to A is given, such that B + C + D + E + F = A. Rows B through D were calculated by multiplying the observed change in each factor by the corresponding July net carbon uptake value; rows E and F were measured empirically. Numbers in parentheses refer to percent change in raw values from July to August sampling dates (note that the large percent changes in nighttime respiration were due to the longer [329&percent;] August nights relative to July).

		Evergreen		Deciduous	
		High CO_2 (mg C d^{-1})	Low CO_2 (mg C d^{-1})	High CO_2 (mg C d^{-1})	Low CO_2 (mg C d^{-1})
A	Net carbon uptake (Fig. 3A)	18 (14)	−21 (−17)	121 (89)	50 (55)
B	Day length	−34 (−27)	−33 (−27)	−38 (−27)	−26 (−27)
C	Photosynthesis rate (Fig. 3C)	83 (75)	27 (26)	112 (79)	46 (52)
D	Canopy area (Fig. 3E)	10 (10)	15 (18)	47 (26)	32 (27)
E	Nighttime respiration	−16 (390)	−15 (362)	−15 (302)	−8 (148)
F	Below-ground respiration	−25 (81)	−15 (70)	15 (−37)	6 (−15)

ration + litter production), irrespective of CO_2 treatment, this pulse in carbon acquisition largely resolves the observed disparity of deciduous taxa losing more carbon than evergreens during the winter but having similar annual carbon budgets. These data also suggest that deciduous leaf forms may have been more competitive than evergreens at high CO_2 because the magnitude of their excess carbon production during the late summer was significantly greater relative to the evergreens in the high CO_2 treatment (4.5 vs. 2.7 g C; $F_{1,6} = 14.8$; $p = 0.008$).

The reasons underpinning the contrasting patterns of seasonal carbon uptake by evergreen and deciduous trees are complex, because they are determined by a combination of changes in day length, canopy area, leaf area-based photosynthetic rates, and nighttime and below-ground respiration rates. However, breaking down the carbon budgets of the trees into each component allows us to identify the dominant process responsible for the differences. During the late summer pulse in carbon gain of the deciduous taxa (Fig. 3A; 27 July–31 August), daily net whole-tree carbon uptake increased approximately 70% in the deciduous taxa, but changed only marginally in the evergreens (see Table 1). Across this same interval, day length shortened from 20.5 to 15 h, but markedly increased photosynthetic rates in deciduous (≈65%) and evergreen species (≈50%; see Table 1) compensated for this. Canopy area and nighttime respiration also increased in all species (Table 1). If changes in net carbon uptake from the July to August sampling dates are calculated by using only these changes in day length, photosynthetic rate, canopy area, and nighttime respiration, the resulting predictions are too high for the evergreens but too low for the deciduous taxa relative to the actual measured values (Table 1). The final component to consider, then, is below-ground respiration rates, which in the deciduous taxa decreased approximately 25% from the July to August sampling dates, but increased about 75% in the evergreens. Below-ground respiration rates thus close the carbon budgets (see Table 1) and are a moderately important component in the late summer/early autumn patterns of whole-tree net carbon uptake.

Another major feature of the seasonal gas exchange data is that all species exhibited reduced area-based photosynthetic rates during the period of continuous daylight of the polar summer, irrespective of leaf habit (Fig. 3C), although in *M. glyptostroboides* and *T. distichum* the drop was not significant ($p > 0.05$). These reductions depressed rates of whole-tree carbon gain late in the polar summer (mid-July; see Fig. 3A). Such patterns differ from plants grown in lower latitude photoperiods with no intervals of continuous daylight, where well-watered trees typically show broad peaks in area-based photosynthetic rates across the summer (e.g., Ellsworth 2000; Lloyd et al. 2002; Stylinski et al. 2002; Damesin 2003). Plants native to the Arctic today also appear to lack any significant mid-summer dip in

TABLE 2. Comparison of carbon fluxes early and late in the growing season. E = evergreen; D = deciduous.

		Percentage of carbon fixed relative to annual budget			
		Early season (27 Jan–10 Mar)		Late season (01 Nov–30 Nov)	
Species	Leaf habit	High CO_2	Low CO_2	High CO_2	Low CO_2
N. cunninghamii	E	1.6	−3.0	3.5	5.2
S. sempervirens	E	4.3	1.3	2.7	2.6
M. glyptostroboides	D	−1.0	−2.8	−0.7	−1.2
T. distichum	D	−0.5	−2.7	−0.7	−0.9
G. biloba	D	−0.3	−4.5	−0.7	−0.7
		ANOVA results			
		$F_{(1,6)}$	p	$F_{(1,6)}$	p
CO_2		10.0	0.02	0.1	0.76
Leaf habit		8.7	0.03	68.5	<0.001

photosynthetic rates (e.g., Tieszen 1975; Starr et al. 2000; Hari and Mäkelä 2003), however it should be noted that in many areas of the Arctic the beginning of the growing season is nearly coincident with the onset of the polar summer. Detailed analyses of leaf carbohydrates, nitrogen content, and photosynthesis in our plants indicate that the patterns of carbon uptake during the polar summer are probably a result of an imbalance between carbon and nitrogen availability, not photoinhibition or the accumulation of leaf starches and soluble sugars (Osborne and Beerling 2003). The polar summer reductions in carbon uptake are also not caused by increases in canopy respiration rate (e.g., Griffis et al. 2003), because it peaks during the warmest intervals of late July and August, after the termination of continuous daylight (data not shown).

One potential advantage of the evergreen leaf habit is the ability to fix carbon at the beginning and end of the growing season when deciduous plants are leafless (e.g., Givnish 2002). During a six-week period early in the season before the deciduous plants produced leaves (27 January–10 March), however, evergreens fixed only 1% of their annual carbon; the deciduous taxa lost 2% of their annual carbon during the same period (Table 2). Later in the season, during the interval between leaf fall in the deciduous taxa (ca. 01 November) and the onset of the polar winter (01 December), the gap between the net carbon fixation in evergreen and deciduous taxa was slightly larger (+3.5% vs. −0.8% relative to annual budgets; see Table 2). A mild CO_2 stimulation was evident during the early season interval; no CO_2 effect was present during the late-season interval (Table 2). Evergreens, therefore, did not strongly capitalize on these intervals representing 23% of the total length of their growing season.

Our results are directly relevant to ancient forests growing at 69° latitude. Given that intervals of continuous daylight likely reduced the rates of carbon uptake in these forests, we expect that the patterns observed here would be amplified for forests at higher latitudes where the polar summers and winters are longer. For example, annual whole-tree net carbon uptake could be lower because the depressed photosynthetic rates in the summer would be lengthened and the early and late-season intervals of vigorous photosynthesis shortened (Fig. 3A). This response would operate independently of the temperature dependency of productivity (Rustad et al. 2001), which would also act to reduce carbon productivity at higher, colder latitudes. It is possible that the deciduous taxa would suffer greater losses in annual whole-tree net carbon uptake than the evergreens because of a shorter late-summer window of high productivity specific to the deciduous habit (Fig. 3A). In addition, for forests growing when atmospheric CO_2 was higher, the CO_2 fertilization effect during the polar summer would be diminished in the deciduous species relative to the evergreen species (Fig. 3B).

Conclusion

Seasonal patterns of whole-tree carbon uptake were determined under a simulated polar climate with and without CO_2 enrichment for deciduous and evergreen tree species whose close ancestors grew at polar latitudes during the Cretaceous and Paleogene. Deciduous taxa exhibited enhanced rates of carbon uptake relative to evergreen taxa during late summer and autumn, largely canceling the carbon deficit that they had accrued during the winter. These results therefore help explain how deciduous species achieve annual carbon budgets similar to those of evergreens, despite incurring greater losses of carbon through annual leaf shedding (Royer et al. 2003a). All species displayed some level of depressed photosynthesis on an area basis during the polar summer, possibly highlighting an unusual feature in ancient polar forests that would have strongly reduced carbon uptake. We found no evidence to explain the dominance of deciduous leaf forms in ancient polar forests. Furthermore, for latitudes poleward of 69° we predict that conditions would also favor the evergreen leaf habit. It may be therefore that other factors not directly related to carbon budgets, for example ecologic or phylogenetic factors, were important in maintaining the deciduous character of these ancient polar forests (e.g., Axelrod 1966; Wolfe 1987; Sweet and Braman 2001; Jagels et al. 2003).

Acknowledgments

We are grateful for the invaluable assistance in system construction and development provided by S. Pearce, T. Haycock, and K. Parkinson. We thank W. P. Quick for useful comments and discussion, and C. Williams and T. Kolb for helpful reviews. D.L.R. was supported by a US National Science Foundation Graduate Research Fellowship and U.S. Department of Energy grant (DE-FG02-01ER15173), awarded to R. A. Berner. D.J.B. gratefully acknowledges funding through a Royal Society University Research Fellowship and the Leverhulme Trust. Experimental work was funded through the award of a U.K. Natural Environment Research Council research grant (GR3/11900) to D.J.B.

Literature Cited

Askin, R. A., and R. A. Spicer. 1995. The Late Cretaceous and Cenozoic history of vegetation and climate at northern and southern high latitudes: a comparison. Pp. 156–173 *in* Effects of past global change on life. Studies in Geophysics Series, National Research Council. National Academy Press, Washington, D.C.

Axelrod, D. I. 1966. Origin of deciduous and evergreen habits in temperate forests. Evolution 20:1–15.

Beerling, D. J., and C. P. Osborne. 2002. Physiological ecology of Mesozoic polar forests in a high CO_2 environment. Annals of Botany 89:329–339.

Beerling, D. J., and D. L. Royer. 2002. Fossil plants as indicators of the Phanerozoic global carbon cycle. Annual Review of Earth and Planetary Sciences 30:527–556.

Beerling, D. J., and F. I. Woodward. 2001. Vegetation and the terrestrial carbon cycle: modelling the first 400 million years. Cambridge University Press, Cambridge.

Beerling, D. J., F. I. Woodward, M. R. Lomas, M. A. Wills, W. P. Quick, and P. J. Valdes. 1998. The influence of Carboniferous palaeoatmospheres on plant function: an experimental and modelling assessment. Philosophical Transactions of the Royal Society of London B 353:131–140.

Berner, R. A., and Z. Kothavala. 2001. GEOCARB III: a revised model of atmospheric CO_2 over Phanerozoic time. American Journal of Science 301:182–204.

Chabot, B. F., and D. F. Hicks. 1982. The ecology of leaf life spans. Annual Review of Ecology and Systematics 13:229–259.

Chaney, R. W. 1947. Tertiary centers and migration routes. Ecological Monographs 17:139–148.

———. 1951. A revision of the fossil *Sequoia* and *Taxodium* in western North America based on the recent discovery of *Metasequoia*. American Philosophical Society Transactions 40: 171–263.

Creber, G. T., and W. G. Chaloner. 1985. Tree growth in the Mesozoic and Early Tertiary and the reconstruction of palaeoclimates. Palaeogeography, Palaeoclimatology, Palaeoecology 52:35–60.

Damesin, C. 2003. Respiration and photosynthesis characteristics of current-year stems of *Fagus sylvatica*: from the seasonal pattern to an annual balance. New Phytologist 158:465–475.

Dutton, A. L., K. C. Lohmann, and W. J. Zinsmeister. 2002. Stable isotope and minor element proxies for Eocene climate of Seymour Island, Antarctica. Paleoceanography 17(2), 1016, doi: 10.1029/2000PA000593.

Eissenstat, D. M., J. H. Graham, J. P. Syvertsen, and D. L. Drouillard. 1993. Carbon economy of sour orange in relation to mycorhiza colonization and phosphorus status. Annals of Botany 71:1–10.

Ekart, D. D., T. E. Cerling, I. P. Montañez, and N. J. Tabor. 1999. A 400 million year carbon isotope record of pedogenic carbonate: implications for paleoatmospheric carbon dioxide. American Journal of Science 299:805–827.

Ellsworth, D. S. 2000. Seasonal CO_2 assimilation and stomatal limitations in a *Pinus taeda* canopy. Tree Physiology 20:435–445.

Estes, R., and J. Hutchison. 1980. Eocene lower vertebrates from Ellesmere Island, Canadian Arctic Archipelago. Palaeogeography, Palaeoclimatology, Palaeoecology 30:325–347.

Falcon-Lang, H. J., and D. J. Cantrill. 2001. Leaf phenology of some mid-Cretaceous polar forests, Alexander Island, Antarctica. Geological Magazine 138:39–52.

Frakes, L. A., J. E. Francis, and J. I. Syktus. 1992. Climate modes of the Phanerozoic: the history of the earth's climate over the past 600 million years. Cambridge University Press, Cambridge.

Francis, J. E., and I. Poole. 2002. Cretaceous and Tertiary climates of Antarctica: evidence from fossil wood. Palaeogeography, Palaeoclimatology, Palaeoecology 182:47–64.

Givnish, T. J. 2002. Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. Silva Fennica 36: 703–743.

Griffis, T. J., T. A. Black, K. Morgenstern, A. G. Barr, Z. Nesic, G. B. Drewitt, D. Gaumont-Guay, and J. H. McCaughey. 2003. Ecophysiological controls on the carbon balances of three southern boreal forests. Agricultural and Forest Meteorology 117:53–71.

Hari, P., and A. Mäkelä. 2003. Annual pattern of photosynthesis in Scots pine in the boreal zone. Tree Physiology 23:145–155.

Herman, A. B., and R. A. Spicer. 1996. Palaeobotanical evidence for a warm Cretaceous Arctic Ocean. Nature 380:330–333.

Hickey, L. J. 1984. Eternal summer at 80 degrees north. Discovery 17(1):17–23.

Hill, R. S. 1991. Tertiary *Nothofagus* (Fagaceae) macrofossils from Tasmania and Antarctica and their bearing on the evolution of the genus. Linnean Society Botanical Journal 105:73–112.

Huber, B. T., R. D. Norris, and K. G. MacLeod. 2002. Deep-sea paleotemperature record of extreme warmth during the Cretaceous. Geology 30:123–126.

Jagels, R., G. E. Visscher, J. Lucas, and B. Goodell. 2003. Palaeoadaptive properties of the xylem of Metasequoia: mechanical/hydraulic compromises. Annals of Botany 92:79–88.

Jahren, A. H., and L. S. L. Sternberg. 2003. Humidity estimate for the middle Eocene Arctic rain forest. Geology 31:463–466.

Jefferson, T. H. 1982. Fossil forests from the Lower Cretaceous of Alexander Island, Antarctica. Palaeontology 25:681–708.

Lloyd, J., O. Shibistova, D. Zolotoukhine, O. Kolle, A. Arneth, C. Wirth, J. M. Styles, N. M. Tchebakova, and E. D. Schulze. 2002. Seasonal and annual variations in the photosynthetic productivity and carbon balance of a central Siberian pine forest. Tellus B 54:590–610.

Milliken, G. A., and D. E. Johnson. 1992. Analysis of messy data, Vol. I. Designed experiments. Van Nostrand Reinhold, New York.

Osborne, C. P., and D. J. Beerling. 2003. The penalty of a long, hot summer. Photosynthetic acclimation to high CO_2 and continuous light in ''living fossil'' conifers. Plant Physiology 133: 803–812.

Read, J., and J. Francis. 1992. Responses of some Southern Hemisphere tree species to a prolonged dark period and their implications for high-latitude Cretaceous and Tertiary floras. Palaeogeography, Palaeoclimatology, Palaeoecology 99:271–290.

Royer, D. L., L. J. Hickey, and S. L. Wing. 2003a. Ecological conservatism in the ''living fossil'' *Ginkgo*. Paleobiology 29:84–104.

Royer, D. L., C. P. Osborne, and D. J. Beerling. 2003b. Carbon loss by deciduous trees in a CO_2-rich ancient polar environment. Nature 424:60–62.

Rustad, L. E., J. L. Campbell, G. M. Marion, R. J. Norby, M. J. Mitchell, A. E. Hartley, J. H. C. Cornelissen, and J. Gurevitch. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126:543–562.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry, 3d ed. W. H. Freeman, New York.

Spicer, R. A., and J. L. Chapman. 1990. Climate change and the evolution of high-latitude terrestrial vegetation and flora. Trends in Ecology and Evolution 5:279–284.

Starr, G., S. F. Oberbauer, and E. W. Pop. 2000. Effects of lengthened growing season and soil warming on the phenology and physiology of *Polygonum bistorta*. Global Change Biology 6: 357–369.

Stylinski, C. D., J. A. Gamon, and W. C. Oechel. 2002. Seasonal patterns of reflectance indices, carotenoid pigments and photosynthesis of evergreen chaparral species. Oecologia 131: 366–374.

Sun, B., D. L. Dilcher, D. J. Beerling, C. Zhang, D. Yan, and E. Kowalski. 2003. Variation in *Ginkgo biloba* L. leaf characters across a climatic gradient in China. Proceedings of the National Academy of Sciences USA 100:7141–7146.

Sweet, A. R., and D. R. Braman. 2001. Cretaceous-Tertiary palynofloral perturbations and extinctions within the *Aquilapollenites* phytogeographic province. Canadian Journal of Earth Science 38:249–269.

Tarduno, J. A., D. B. Brinkman, P. R. Renne, R. D. Cottrell, H. Scher, and P. Castillo. 1998. Evidence for extreme climatic warmth from Late Cretaceous arctic vertebrates. Science 282: 2241–2244.

Tieszen, L. L. 1975. CO_2 exchange in the Alaskan arctic tundra: seasonal changes in the rate of photosynthesis of four species. Photosynthetica 9:376–390.

Tralau, H. 1968. Evolutionary trends in the genus *Ginkgo*. Lethaia 1:63–101.

Tripati, A., J. Zachos, L. Marincovich, and K. Bice. 2001. Late Paleocene Arctic coastal climate inferred from molluscan stable and radiogenic isotope ratios. Palaeogeography, Palaeoclimatology, Palaeoecology 170:101–113.

Williams, C. J., A. H. Johnson, B. A. LePage, D. R. Vann, and T. Sweda. 2003. Reconstruction of Tertiary *Metasequoia* forests. II. Structure, biomass, and productivity of Eocene floodplain forests in the Canadian Arctic. Paleobiology 29:271–292.

Wing, S. L., G. J. Harrington, G. J. Bowen, and P. L. Koch. 2003. Floral change during the Initial Eocene Thermal Maximum in the Powder River Basin, Wyoming. *In* S. L. Wing, P. D. Gingerich, and E. Thomas, eds. Causes and consequences of globally warm climates in the early Paleogene. Geological Society of America Special Paper 369:425–440.

Wolfe, J. A. 1985. Distribution of major vegetational types during the Tertiary. Pp. 357–375 *in* E. T. Sundquist and W. S. Broecker, eds. The carbon cycle and atmospheric CO_2: natural variations, Archean to present. Geophysical Monograph Series No. 32. American Geophysical Union, Washington, D.C.

———. 1987. Late Cretaceous-Cenozoic history of deciduousness and the terminal Cretaceous event. Paleobiology 13:215–226.

Woodward, F. I. 1987. Climate and plant distribution. Cambridge University Press, Cambridge.

Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292:686–693.