Physiological Ecology of Mesozoic Polar Forests in a High CO₂ Environment

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INTRODUCTION

Marine oxygen isotope data indicate that the Earth has been in a 'greenhouse' mode for approx. 80% of the past 500 million years (Spicer and Chapman, 1990; Frakes et al., 1992). Between the Mesozoic and early Tertiary (250 to 50 million years ago), the plant fossil record shows the presence of tall, dense coniferous forests on the high latitude landmasses (Spicer and Chapman, 1990). Such forests were important components of polar forests, and give results from the first year of treatment. Specifically, we tested the hypotheses that growth in elevated CO₂ (1) stimulates photosynthesis; (2) reduces photoinhibition during the polar summer; and (3) reduces respiration of above- and below-ground plant organs. Our results indicate that CO₂ fertilization generally does not affect photosynthesis under continuous daylight characteristic of the polar summer but does increase it when the period of illumination is shorter. Growth in elevated CO₂ did not alter the potential for photoinhibition. CO₂ enrichment significantly reduced leaf and root respiration rates by 50 and 25%, respectively, in a range of evergreen taxa. Incorporating these observed CO₂ effects into numerical simulations using a process-based model of coniferous forest growth indicates that a high palaeo-CO₂ concentration would have increased the productivity of Cretaceous conifer forests in northern Alaska. This results from decreased respiratory costs that more than compensate for the absence of high CO₂-high temperature interactions during the polar summer. The longer-term effects of CO₂ enrichment on seasonal changes in the above- and below-ground carbon balance of trees are discussed.

Key words: Atmospheric CO₂, carbohydrates, fossil plants, photosynthesis, photoinhibition.

Fossils show that coniferous forests extended into polar regions during the Mesozoic, a time when models and independent palaeo-CO₂ indicators suggest that the atmospheric CO₂ concentration was at least double that of the present day. Consequently, such polar forests would have experienced high CO₂ interacting with an extreme variation in light. Here we describe an experiment investigating this plant-environment interaction for extant tree species that were important components of polar forests, and give results from the first year of treatment. Specifically, we tested the hypotheses that growth in elevated CO₂ (1) stimulates photosynthesis; (2) reduces photoinhibition during the polar summer; and (3) reduces respiration of above- and below-ground plant organs. Our results indicate that CO₂ fertilization generally does not affect photosynthesis under continuous daylight characteristic of the polar summer but does increase it when the period of illumination is shorter. Growth in elevated CO₂ did not alter the potential for photoinhibition. CO₂ enrichment significantly reduced leaf and root respiration rates by 50 and 25%, respectively, in a range of evergreen taxa. Incorporating these observed CO₂ effects into numerical simulations using a process-based model of coniferous forest growth indicates that a high palaeo-CO₂ concentration would have increased the productivity of Cretaceous conifer forests in northern Alaska. This results from decreased respiratory costs that more than compensate for the absence of high CO₂-high temperature interactions during the polar summer. The longer-term effects of CO₂ enrichment on seasonal changes in the above- and below-ground carbon balance of trees are discussed.

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Leaf photosynthesis is typically stimulated by 40–80% during growth with double the present concentration of CO₂ (Drake et al., 1997; Curtis and Wang, 1998; DeLucia et al., 1999; Norby et al., 1999; LaDeau and Clark, 2001). Therefore, increased CO₂ concentration has the potential to counteract the limitation on the growth of polar forests imposed by the short, high-latitude growing season. Experimental evidence also suggests that the higher atmospheric CO₂ may decrease photoinhibition (Hymus et al., 1999; Roden et al., 1999; Terry et al., 2000), suggesting an important interaction for ancient polar forests experiencing continuous irradiance, with the potential to cause photoinhibition during the summer. In addition, the carbon balance of polar forests will be determined not only by photosynthesis but also by respiration, which itself can be influenced directly and indirectly by elevated CO₂ (Wullschleger et al., 1994; Bunce, 2001). For example, atmospheric CO₂ enrichment reduces the mitochondrial respiration rates of leaves, roots and stems, through direct inhibition of enzyme activity (Drake et al., 1999).

These potential interactions are important for understanding polar forest ecology. It has been suggested that the deciduous habit of polar forests reduced respiratory costs allowing plants to tolerate winter darkness and mild temperatures (Axelrod, 1984; Creber and Chaloner, 1985). But if respiration is decreased by elevated CO₂, the requirement for a deciduous habit is diminished. Alternatively, if elevated CO₂ affects respiration indirectly, for example by altering substrate availability and the demand for respiratory products, the respiration rates of leaves grown at elevated CO₂ may increase (Drake et al., 1999).

These physiological considerations show that the effects of palaeo-CO₂ concentrations may be especially important in understanding polar forest physiology and should be assessed (Beerling, 1998, 2000). However, the responses of trees to CO₂ enrichment have not yet been assessed experimentally under a light regime relevant to polar forests. Here we describe an experimental approach investigating the effects of a high atmosphere CO₂ concentration on the physiology of some extant genera of plants that were important components of northern and southern hemisphere polar forests (Table 1). We recognize that, whilst the morphology of extant and fossil taxa are similar, the species may not be the same, but we assume that their physiological characteristics are similar. The responses of young trees to

**Table 1. Woody plant species grown under polar light conditions in a simulated Cretaceous environment with and without CO₂ enrichment**

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Life form</th>
<th>Native habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ginkgo biloba (maidenhair tree)</td>
<td>Ginkgoaceae</td>
<td>Deciduous tree</td>
<td>Uncertain, widely planted in urban environments, but probably sub-tropical forests of southern China*</td>
</tr>
<tr>
<td>Metasequoia glyptostroboides (dawn redwood)</td>
<td>Taxodiaceae</td>
<td>Deciduous conifer</td>
<td>Mesothermal forested regions of S.E. China²</td>
</tr>
<tr>
<td>Sequioa sempervirens (coastal redwood)</td>
<td>Taxodiaceae</td>
<td>Evergreen conifer</td>
<td>Low hills, near coastal regions of California³</td>
</tr>
<tr>
<td>Taxodium distichum (swamp cypress)</td>
<td>Taxodiaceae</td>
<td>Deciduous conifer</td>
<td>Tidal creeks, flood plains, southern USA</td>
</tr>
<tr>
<td>Araucaria araucana (monkey-puzzle)</td>
<td>Araucariaceae</td>
<td>Evergreen conifer</td>
<td>Forests in the southern Andes, Chile⁴</td>
</tr>
<tr>
<td>Nothofagus cunninghamii (southern beech)</td>
<td>Nothofagaceae</td>
<td>Evergreen tree</td>
<td>Cool/temperate forests, Australia/Tasmania⁵</td>
</tr>
</tbody>
</table>

* Tredici et al. (1992).
² Chaney (1948); Chu and Cooper (1950).
³ Waring and Franklin (1979).
⁵ Read (1999).
atmospheric CO₂ enrichment during their first year’s growth in a simulated polar light regime (equivalent to latitude = 69°) are reported. Utilizing this facility, we tested the hypotheses that elevated CO₂ (1) stimulates photosynthetic carbon gain and carbohydrate storage; (2) lowers the potential for photoinhibition during polar summers; and (3) suppresses rates of plant respiration. The experimental results have been incorporated into a process-based model of conifer forest growth (Osborne and Beerling, 2000) to provide a first assessment of the possible consequences of the interactions between CO₂ and light for the productivity of mid-Cretaceous north Alaskan coniferous forests.

MATERIALS AND METHODS
Experimental design and performance
The controlled environment facility (Tapton Experimental Gardens, University of Sheffield, UK) consists of four glasshouses, each divided into two isolated sections. This provides eight independent replicated environments: four maintained at ambient CO₂ (400 μmol mol⁻¹) and four at the target CO₂ concentration (800 μmol mol⁻¹). Control of temperature, humidity and CO₂ in each section was achieved using a programmable datalogger (CR10 Measurement and Control System; Campbell Scientific, Inc., Logan, Utah, USA). CO₂ was measured with an infrared gas analyser (IRGA) mounted in each glasshouse (CO₂ Gas Monitor, ADC 2000 Series; The Analytical Development Company Limited, Hoddesdon, Herts., UK). The calibration of each IRGA was checked monthly using a volumetrically mixed reference gas (Certified Standard ± 5 %; BOC Gases, Guildford, Surrey, UK). The CO₂ concentration was increased by frequent injection of pure CO₂ gas (BOC Gases, UK) into the circulating air of each section. During the first year of operation (treatments began in April 2000), daily mean CO₂ concentrations were maintained to within ± 5 % of the target values (Fig. 2A).

Air temperature was measured in the immediate vicinity of plants using a shaded, ventilated copper–constantan thermocouple, and controlled in each section by air-conditioner units (Bradley Refrigeration, Sheffield, UK), which also served to mix and circulate air. Growth temperature within all sections was modified to track outside ambient values, but with a +5 °C warming to mimic the seasonal cycle simulated in high latitudes by general circulation modelling (GCM) studies for the mid-Cretaceous (Valdes et al., 1996; Price et al., 1997; Beerling, 2000). A minimum winter temperature of 5 °C prevents plants being damaged by frosts. The system provides an effective means of simulating an annual climate representative of the Cretaceous (Fig. 2B).

Atmospheric humidity near the plants was measured using a ventilated wet–dry bulb psychrometer with copper–constantan thermocouples, and the relative humidity within each glasshouse section was maintained to a minimum of 75 % using a horticultural misting system (LBS Horticulture, Colne, Lancs., UK).

Seasonal changes in daylength at 69°N were achieved by complete replacement of glass in the glasshouses with opaque, insulated panels and the installation of an automated lighting system to regulate the intensity and duration of lighting throughout the year. Two water-cooled light units (Sunbeam Hydrostar; Avon Gro-Lite Systems, Bristol, UK) were deployed in each of the eight sections, each unit providing 300–400 μmol m⁻² s⁻¹ of photosynthetically active radiation (PAR) over approx. 2 m² ground area. Thus lighting was supplied and controlled artificially all year round. Daylength was adjusted weekly to simulate the seasonal changes calculated from standard equations (Monteith and Unsworth, 1990) for 69°N (Fig. 2C).

Plant materials
The tree species (Table 1) were grown from seed at Llangwm Arboretum (Usk, UK), and 1-year-old saplings were acclimated to the Sheffield climate in a polythene tunnel for 2 months before transfer to the glasshouses in April 2000. Each tree species was represented by two individuals per glasshouse, a total of eight per CO₂ treatment. Plants were grown in 2 l pots in a medium designed to have good water holding and pH-buffering capacity, and a high mineral content, and consisting of lime-free silica sand (Pioneer Supamix Ltd, Nuneaton, UK), fine vermiculite (LBS Horticulture) and peat (Midland Irish Peat Moss Ltd, Rathlowen, Co. Westmeath, Ireland) in the ratio 13 : 5 : 2. As gymnosperms are naturally associated with vesicular–arbuscular (VA) mycorrhizas (Khan and Valder, 1972), even in Antarctic Triassic fossils (Stubblefield et al., 1987); and contemporary Nothofagus is commonly ectomycorrhizal (Warcup, 1980), mycorrhizal symbioses were established in the experiment by inoculating roots with spores of generalist fungal species during potting (MycorTree Root Dip; Plant Health Care, Berkhamsted, Herts., UK).

Plants were drip irrigated regularly using an automated system (Nutriculture Ltd, Mawdsley, Lancs., UK), and supplied weekly during the growing season with a nutrient solution appropriate for VA mycorrhizal systems (10 % Rorison’s Nutrient Solution).

Leaf gas exchange and carbohydrate status
Leaf photosynthetic responses and carbohydrate contents of five tree species grown with either 400 or 800 μmol mol⁻¹ CO₂ were determined during their first year under a polar light regime. All measurements on leaves were made using a portable open gas exchange system (CIRAS-1; PP-Systems, Hitchin, Herts., UK) on foliage that developed under the experimental conditions. Gas exchange was measured at a PAR flux of 600 μmol m⁻² s⁻¹, previously shown to saturate photosynthesis (data not shown), a leaf temperature of 25 °C and a leaf-air vapour pressure deficit of 1.0 kPa. Measurements were made during the summer (plants under continuous light) and the autumn (plants under a daylength of 10 h), at CO₂ concentrations of 400 and 800 μmol mol⁻¹, i.e. at the growth CO₂ concentrations.

Following the method of Scholes et al. (1994), leaf carbohydrate content was determined three times during the year: in summer and autumn, in parallel with leaf
photosynthesis measurements and in midwinter, during continuous darkness. For photosynthesis and carbohydrate measurements, the mean of two leaves, i.e. one leaf sampled from each of two plants, was used as the replicate, giving $n = 4$ measurements at each CO$_2$ concentration for each species.

![Diagram](image)

**Fig. 2.** A, Measurements of atmospheric CO$_2$ concentrations in the ambient and elevated CO$_2$ glasshouses during the first year (2000) of treatment. Values are means of four replicates at each concentration. The vertical box denotes the range of uncertainty in CO$_2$ predictions of a geochemical model for the mid-Cretaceous. B, Seasonal temperature (solid line) within both the ambient and elevated CO$_2$ glasshouses during 2000. For comparison, the outside air temperature in Sheffield (UK) is shown (broken line). Temperatures at 69$^\circ$N from a climate modelling study for the mid-Cretaceous (Valdes et al., 1996) are shown for comparison. C, Calculated and experimentally imposed changes in day length at 69$^\circ$N. Also shown, for comparison, is the seasonal change in daylength experienced at Sheffield (53$^\circ$N).
**Photoinhibition**

The maximum quantum efficiency of photosystem II photochemistry (Genty et al., 1989) was assessed in situ using periodic measurements of the dark-adapted variable to maximum fluorescence ratio ($F_v/F_m$) using a portable modulated system (FMS-2 Field Fluorescence Monitoring System; Hansatech Instruments Ltd, King’s Lynn, UK), with replication as for photosynthesis. To determine the effects of growth CO₂ concentration on $F_v/F_m$, plants were exposed for 2 h to warm temperatures (32 °C) and a PAR of 1000 µmol m⁻² s⁻¹, under the CO₂ concentration in which they grew (i.e. either 400 or 800 µmol mol⁻¹). A baseline set of measurements was established before and after this treatment from plants placed in cool (22 °C), low light (PAR = 150 µmol m⁻² s⁻¹) conditions under growth CO₂ concentrations.

**Plant respiration**

Measurements were made on *Sequoia sempervirens* and *Nothofagus cunninghamii*, as evergreen taxa representing elements of the northern and southern hemisphere polar forests, respectively, using a portable open gas exchange system (CIRAS-1; PP-Systems, Hitchin, Herts., UK). A mean value for each leaf was obtained from 30 measurements made at 1-min intervals under the mean ambient temperature for January (7 °C), with replication as for photosynthesis. Direct or indirect effects of CO₂ were measured by reciprocal transfer of plants grown in ambient temperature for January (7 °C) with replication as for photosynthesis. To determine the effects of growth CO₂ concentration on respiration, plants were exposed for 2 h to warm temperatures (32 °C), with replication as for photosynthesis. To determine the effects of growth CO₂ concentration on respiration, plants were exposed for 2 h to warm temperatures (32 °C), with replication as for photosynthesis.

Rates of root respiration were measured for *Araucaria araucana* and *S. sempervirens* during early and late autumn, when daylengths were 12 and 3 h, respectively. These two species were selected because of their differential accumulation of carbohydrates in leaves, which could influence root carbohydrate content (Ekblad and Högbom, 2001). Respiration rates of excised roots were measured as the quantity of O₂ consumed using a liquid phase oxygen electrode (Model LD 2/2 oxygen electrode; Hansatech Instruments, King’s Lynn, UK) maintained at a constant temperature of 20 °C. Roots were then dried at 40 °C for 48 h to obtain dry mass, and respiration rates were expressed as µmol O₂ consumed g⁻¹ dry matter h⁻¹.

**RESULTS**

**Leaf gas exchange and carbohydrate status**

After 4 weeks of continuous light during the polar summer, CO₂ enrichment stimulated photosynthesis by 47 % in *Ginkgo biloba* and 42 % in *Metasequoia glyptostroboides* ($P = 0.05$). However, this did not occur in *S. sempervirens*, *N. cunninghamii* and *Taxodium distichum* (Fig. 3A), indicating marked photosynthetic acclimation in these species. In contrast, photosynthetic rates in the autumn were significantly higher in elevated than in ambient CO₂ for all species except *M. glyptostroboides* (which was showing visible signs of leaf senescence by this time) (Fig. 3B). The response to CO₂ in species previously showing acclimation shows that acclimation is reversible, and suggests that the earlier acclimation was not caused by limited rooting volume. In addition, photosynthetic rates in *N. cunninghamii* and *T. distichum* were higher in autumn than in summer (Fig. 3A, B), suggesting that photosynthetic activity was limited during the summer in these species irrespective of CO₂ treatment. Responses to CO₂ were not related to leaf habit, either in the summer or autumn.

The effect of CO₂ on total non-structural carbohydrate (TNC) content of leaves in the polar summer was an increase in *G. biloba* and *M. glyptostroboides* by 73 % and 59 %, respectively, compared with their counterparts in ambient CO₂ (Fig. 4A), but there were no significant effects in the other species. This pattern mirrors the photosynthetic responses (Fig. 3A). By contrast, TNC content in autumn was similar in all species (Fig. 4B) with no effects of growth in elevated CO₂, a pattern seemingly unrelated to the autumnal photosynthetic responses (Fig. 3B). In winter, the TNC contents of the evergreen species were depleted relative to the summer and autumn (Fig. 4C) due to respiration under continuous darkness without photosynthetic replenishment. Growth CO₂ concentration had no effect on the TNC content of leaves of *S. sempervirens* and *N. cunninghamii*, but increased it in the leaves of *A. araucana* (Fig. 4C).

**Effects of CO₂ on photoinhibition**

All species, from both ambient and elevated CO₂, showed a progressive time-dependent reduction in $F_v/F_m$ on exposure to saturating irradiance, reflecting a decrease in the efficiency of photochemical energy dissipation. The decrease in $F_v/F_m$ was largely reversed after a return to cool, low light conditions (Fig. 5). Four of the six tree species
grown in elevated CO₂ showed no significant (P < 0.05) differences in the response of $F_v/F_m$ to high irradiance when compared with their ambient CO₂-grown equivalents (Fig. 5). The two species showing differences in $F_v/F_m$ due to CO₂ treatment responded in different ways: in *S. sempervirens*, $F_v/F_m$ was greater in elevated CO₂ conditions on
exposure to high irradiance compared with ambient CO₂ controls, whereas in *T. distichum*, \( F_v/F_m \) was lower in plants grown in elevated CO₂ (Fig. 5).

**Plant respiration**

After 2 months of permanent darkness in elevated CO₂, dark respiration rates of *S. sempervirens* leaves were reduced by 61 % (\( P < 0.05 \)) compared with plants grown under ambient CO₂ (Table 2). *N. cunninghamii* responded similarly, with respiration rates being reduced by 38 %, although this was not statistically significant because of large variability between individuals (Table 2). Transfer of plants grown in ambient CO₂ to elevated CO₂ markedly suppressed rates of leaf respiration in both *S. sempervirens* and *N. cunninghamii*, whilst the transfer from elevated- to ambient-CO₂ increased them (Table 2).

Respiration rates of roots of *S. sempervirens* and *A. araucana* grown in elevated CO₂ were lower in both the early and late autumn than those of plants grown in ambient CO₂ (Table 3). Overall, root respiration was suppressed by 10 and 40 % in early and late autumn, respectively, in both species, but as with leaf respiration, the large variation between individuals resulted in a significant effect of CO₂ treatment on *A. araucana* during the autumn (Table 3).

**DISCUSSION**

Understanding polar forest ecology of the Mesozoic requires that key aspects of tree physiology, and particularly the effects of light, atmospheric CO₂ and their interactions with physiology be considered (Beerling, 1998, 2000). To do so requires information on plant taxa of this extinct biome. As this is impossible, we have used closely related extant species. Our experiment is designed to provide data allowing us to address this fundamental requirement by assessing three determinants of the plant carbon balance (photosynthesis, photoinhibition and respiration). Contrary to expectations, we found that stimulation of leaf photosynthesis by elevated CO₂ was not generally evident during the polar summer, i.e. under conditions of continuous sunlight (24 h), but did occur under shorter days (10 h). Measured TNC contents of leaves were not directly

**Table 2.** Responses of leaf respiration (\( R, \mu \text{mol m}^{-2} \text{s}^{-1} \)) of *Sequoia sempervirens* and *Nothofagus cunninghamii* to CO₂ enrichment in a polar light regime during midwinter

<table>
<thead>
<tr>
<th>CO₂ concentration during measurement</th>
<th><em>S. sempervirens</em> (400 µmol mol⁻¹)</th>
<th><em>N. cunninghamii</em> (400 µmol mol⁻¹)</th>
<th><em>S. sempervirens</em> (800 µmol mol⁻¹)</th>
<th><em>N. cunninghamii</em> (800 µmol mol⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ambient CO₂</td>
<td>0.13 ± 0.02</td>
<td>0.32 ± 0.01</td>
<td>0.11 ± 0.03</td>
<td>0.26 ± 0.10</td>
</tr>
<tr>
<td>Elevated CO₂</td>
<td>0.05 ± 0.01</td>
<td>0.19 ± 0.06</td>
<td>0.05 ± 0.01</td>
<td>0.20 ± 0.06</td>
</tr>
</tbody>
</table>

Values are means ± s.e. of eight plants. Two-way analysis of variance indicated a significant (\( P < 0.01 \)) effect of CO₂ concentration during measurement on leaf respiration of *S. sempervirens*, but no effect of the CO₂ concentration during growth. CO₂ concentrations during growth and measurement had no significant effects on the respiration rates of *N. cunninghamii* leaves. There were no significant interactions between measurement and growth CO₂.
correlated with absence of CO₂ stimulation of photosynthesis (Figs 3 and 4), in contrast with previous studies (Drake et al., 1997; Curtis and Wang, 1998). The reasons for the unresponsiveness of TNC to CO₂ are uncertain, but possibly the storage capacity of leaves was similar in both ambient and elevated CO₂ treatments, and saturated during the continuous light of the polar summer. If this is the case, the TNC content of trunk wood might have increased in elevated CO₂, since the trunk is a major site for storage in trees (Larcher, 1995).

Growth in elevated CO₂ can increase photochemical energy use when there is a large demand for assimilates but not when demand is low (Hymus et al., 1999). This indicates the potential for increased photoinhibition during periods of carbohydrate accumulation. Measured TNC contents of leaves were highest in the polar summer (Fig. 4) under conditions of continuous irradiance. Our measurements of F₆/F₇₄ were therefore made at a time when the risk of CO₂-induced photoinhibition was high. Despite this, there was scant evidence to suggest that growth in an elevated CO₂ atmosphere, representative of the Mesozoic, affected photoinhibition during the polar summer in either evergreen or deciduous taxa (Fig. 5).

The observed reductions in rates of leaf (Table 2) and root (Table 3) respiration for plants grown with CO₂ enrichment are consistent with results from numerous studies of plants exposed to elevated CO₂. Lambers et al., 1996; Norby et al., 1999). Reductions in the respiration rates of roots of plants grown in elevated CO₂ are likely to be caused by acclimation of the respiratory system, by decreased supply of respiratory substrate or by decreased demand for the products of respiration (Ryan, 1991; Amthor, 2000). Interestingly, however, the effect of elevated CO₂ on leaf respiration (50 % decrease) in our polar experiment was greater than that shown by a number of tree species (mean 19 %) in experiments with regular 12–16 h daylengths (Drake et al., 1999). This difference is consistent with the idea (Bunce, 2001) that the CO₂-sensitivity of mitochondrial respiration is greatest after a period of prolonged darkness, when respiration becomes substrate-limited (Fig. 4). Data from the reciprocal transfer experiment (Table 2) indicate that dark respiration rates of leaves of S. sempervirens and N. cunninghamii were directly suppressed by CO₂ inhibiting the biochemistry of respiratory pathways, possibly by reducing activity of cytochrome-c-oxidase and succinate dehydrogenase (Drake et al., 1999). Analyses of carbohydrates in leaves suggest that reserves accumulated during the polar summer were largely depleted during the winter in these two species (Fig. 4C). Thus, limited stores of TNC, and of respiratory substrate in leaves during winter, may explain why no indirect effects of CO₂ on leaf respiration rates were observed then.

Suppression of respiration of above- and below-ground plant organs by elevated CO₂, if a consistent feature of the experimental treatment, implies that the high concentration of atmospheric CO₂ in the Mesozoic played an important role in decreasing respiratory demand of an evergreen canopy during the mild winters. Furthermore, it is possible that plants acclimated with decreased respiration to a warm winter climate, as seen in the field (e.g. Mooney and Brayton, 1966) and in controlled environment studies (Tranquillini et al., 1986). Suppression of plant respiration by the joint action of a high CO₂ atmosphere (Tables 2 and 3), and physiological acclimation to warmer climates, suggests that the deciduous habit in northern hemisphere polar forests may not have been such a crucial adaptation for reducing canopy respiratory CO₂ losses as previously suggested (Axelrod, 1984). Critical to this conclusion is further investigation of CO₂-related effects on leaf and root respiration, especially in the longer term (Bunce, 2001).

A more complete assessment of the effects of CO₂ on whole plant carbon balance, particularly the distribution of dry matter between above- and below-ground parts, is clearly required. The complexity of whole tree responses to elevated CO₂ is exemplified by controlled environment microcosm experiments with Pseudotsuga menziesii (Lin et al., 2001). They showed that increased root growth under elevated CO₂ more than compensated for reduced respiration rates per unit weight of root, so that the total respiration of the rhizosphere increased under high CO₂. In the context of polar forests, measurements throughout the year of carbon fluxes associated with shoots and roots of trees and with the soil are an important requirement of future studies, and will be made as the experiment progresses.

Simulation modelling

Collectively, the effects of CO₂ on carbon gain by photosynthesis and carbon loss by respiration in extant species show the potential of CO₂ to modify the primary production of ancient polar forests. We assessed
this potential using a process-based generic model of
coniferous forest productivity (Osborne and Beerling,
2000), and a simulated Mid-Cretaceous climate for
northern Alaska (72° N), as in the study conditions
(Beerling, 2000). Northern Alaska was selected because
analyses of the fossil record indicate that Cretaceous
forests in this region included a mixture of deciduous
and evergreen taxa (Falcon-Lang, 2000; Falcon-Lang
and Cantrill, 2000, 2001). The model of Osborne and
Beerling mathematically describes forest carbon, nitro-
gen and water fluxes by scaling up widely applicable
relationships between leaf lifespan and function (Reich
et al., 1997). It is therefore uniquely sensitive to
prescribed leaf lifespan, and includes representation of
the environmental influences on photosynthesis, respira-
tion and stomatal activity, and is sensitive to soil
nutrient and water status. From climatic and soil
information it predicts the structural (leaf area index)
and functional [net primary productivity (NPP), canopy
transpiration, etc.] characteristics of coniferous forests.

Five simulations were performed to account for the
separate and combined effects of elevated CO₂. In each
case, leaf lifespans of either 8 (deciduous) or 60 months
(evergreen) were used in the model.

Simulation 1. Control, no changes to the conifer growth
model, CO₂ concentration of 800 μmol mol⁻¹.

Simulation 2. As for the control, but with a 50 %
reduction in leaf respiration rates (Table 2).

Simulation 3. As for the control, but with a 25 %
reduction in root respiration rates (Table 3).

Simulation 4. As for the control, but without photosyn-
thetic CO₂ stimulation during the polar summer, when
daylength was greater than 20 h (Fig. 3).

Simulation 5. As for the control, but with effects 2–4
applied together.

Each effect of elevated CO₂ has a different impact on the
simulated productivity of north Alaskan coniferous forests
(Fig. 6). Reductions in leaf and root respiration by elevated
CO₂ increased forest NPP, whilst the absence of stimulation
of photosynthesis by CO₂ during the summer reduced NPP
(Fig. 6). These effects of CO₂ are largest for trees with long-
lived foliage (evergreen) (Fig. 6). Decreased leaf respiration
increases forest NPP, relative to the control simulation,
because it reduces the light compensation point of photo-
synthesis. This allows a positive net carbon gain for a longer
period of each day (Long and Drake, 1991; Osborne
et al., 1997) and in a greater fraction of the canopy (Osborne
et al., 1998). Reduced root respiration rates decrease the demand
for carbohydrates, allowing root growth to increase, with a
resulting improvement in nutrient and water uptake ef-
ciency. If photosynthesis is not increased by elevated CO₂
during the warm polar summer, NPP is reduced (Fig. 6),
because stimulation of photosynthesis by elevated CO₂ is
strongly dependent upon temperature (Long, 1991), and is
therefore greatest in summer. When all three physiological
effects of CO₂—leaf and root respiration and photosyn-
thesis—operate together, their non-linear interactions result
in a net increase in forest productivity with the decreased
respiratory costs more than compensating for loss of high
CO₂–high temperature interactions during the polar summer
(Fig. 6).

We conclude that the effects of elevated CO₂ observed in
six species of deciduous and evergreen trees, representing
some ancient taxa of polar forests, are likely to be important
modifiers of whole tree carbon balance. According to the
results of our simulations, trees with long-lived foliage will
show the greatest benefit from growth in a high CO₂
environment (Fig. 6). This is because the growing season of
above- and below-ground plant organs is longer in ever-
green than in deciduous trees. They are therefore better
placed to exploit the interaction between high CO₂ and warm spring and autumnal temperatures to increase photosynthetic carbon gain, whilst at the same time incurring reduced respiratory costs of fine root production. These considerations provide some physiological clues that might explain the geographical separation between the northern and southern hemispheres of polar forests with a predominantly evergreen or deciduous leaf habit.

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