

The influence of Carboniferous palaeo-atmospheres on plant function: an experimental and modelling assessment

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Geochemical models of atmospheric evolution predict that during the late Carboniferous, *ca.* 300 Ma, atmospheric O₂ and CO₂ concentrations were 35% and 0.03%, respectively. Both gases compete with each other for ribulose-1,5-bisphosphate carboxylase/oxygenase—the primary C-fixing enzyme in C₃ land plants—and the absolute concentrations and the ratio of the two in the atmosphere have the potential to strongly influence land-plant function. The Carboniferous therefore represents an era of potentially strong feedback between atmospheric composition and plant function. We assessed some implications of this ratio of atmospheric gases on plant function using experimental and modelling approaches. After six weeks growth at 35% O₂ and 0.03% CO₂, no photosynthetic acclimation was observed in the woody species *Betula pubescens* and *Hedera helix* relative to those plants grown at 21% O₂. Leaf photosynthetic rates were 29% lower in the high O₂ environment compared to the controls. A global-scale analysis of the impact of the late Carboniferous climate and atmospheric composition on vegetation function was determined by driving a process-based vegetation-biogeochemistry model with a Carboniferous global palaeoclimate simulated by the Universities Global Atmospheric Modelling Programme General Circulation Model. Global patterns of net primary productivity, leaf area index and soil carbon concentration for the equilibrium model solutions showed generally low values everywhere, compared with the present day, except for a central band in the northern land mass extension of Gondwana, where high values were predicted. The areas of high soil carbon accumulation closely match the known distribution of late Carboniferous coals. Sensitivity analysis with the model indicated that the increase in O₂ concentration from 21% to 35% reduced global net primary productivity by 18.7% or by 6.3 Gt C yr⁻¹. Further work is required to collate and map at the global scale the distribution of vegetation types, and evidence for wild-fires, for the late Carboniferous to test our predictions.

Keywords: Late Carboniferous, general circulation models, photosynthesis, stomata, vegetation models

1. INTRODUCTION

Berner's (1994) geochemical model of the long-term carbon cycle, based on variations in solar radiation, silicate and carbonate rock weathering, plate uplift and subduction, and global run-off, predicts large variations in the concentration of atmospheric CO₂ during the past 400 Ma of the Phanerozoic (figure 1). The reconstruction is characterized by high CO₂ concentrations in the Devonian, followed by a reduction to lower-than-present concentrations in the Carboniferous, probably associated with the significant evolution and increased complexity of terrestrial vegetation. After the Carboniferous, the CO₂ concentration is predicted to have increased again in the early Permian and then declined progressively over the past 200 Ma. This pattern of CO₂ change has largely

been independently confirmed by isotopic analyses of marine and terrestrial organic carbon (see review by Berner (1997)) and changes in the stomatal characteristics of plant fossils (McElwain & Chaloner 1996; Beerling 1997a; Beerling & Woodward 1997). Mathematical modelling of the global oxygen cycle, based on rates of burial and weathering of organic carbon and pyrite sulphur, indicates that atmospheric O₂ also varied markedly during the Phanerozoic (figure 1) with values up to 35% in the late Carboniferous (300 Ma). This upper limit may be incompatible with the existence of terrestrial vegetation (Chaloner 1989; Robinson 1989) since experimental data suggest combustion of plant material is likely to occur at 35% O₂ (Watson *et al.* 1978). However, the experimental approach may not easily relate to the field and so further work is required to help resolve the uncertainties (Robinson 1989).

Taking the outputs of geochemical models at face value, the predicted atmospheric composition for the Late-

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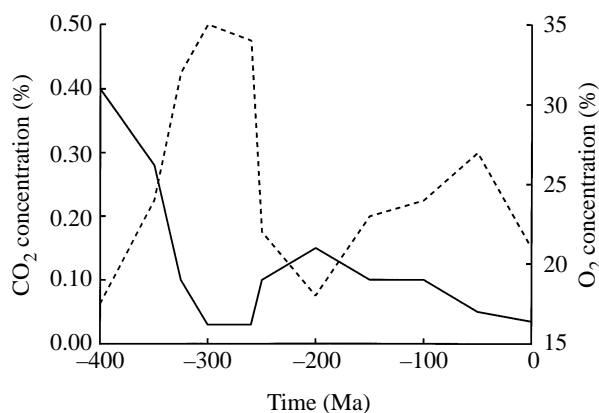


Figure 1. Variations in atmospheric CO₂ and O₂ over the past 400 Ma predicted by the geochemical model of Berner (1994) and Berner & Canfield (1989), respectively.

Carboniferous would have had a strong impact on the functioning of terrestrial vegetation (Beerling & Woodward 1997*a,b*), particularly the functioning of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), the primary C-fixing enzyme in C₃ land plants. Calculations using the Farquhar *et al.* (1980) biochemical model of CO₂ assimilation, which accounts for the relative kinetic effects of CO₂ and O₂ on Rubisco function, indicate that up to 40% of carbon fixed by photosynthesis is lost via photorespiration at 35% O₂, 0.03% CO₂ and at a temperature of 25°C. Associated with high photorespiration rates may also have been the additional energy costs of repairing damage caused by toxic oxygen species (Raven 1991; Raven *et al.* 1994).

This paper investigates in more detail possible plant-atmosphere interactions in the Carboniferous using both experimental and modelling approaches. Plants were grown experimentally at 35% O₂ and 21% O₂ in controlled environments to investigate short-term acclimation by the photosynthetic system to high O₂ levels. The experiment was also designed to test for any O₂ effect on stomatal development. Carboniferous leaf fossils generally have much higher values of stomatal density and index than plant fossils from other geological eras (Beerling & Woodward 1997*a*). One possible explanation for this observation is that higher stomatal densities would have increased the diffusion rate of CO₂ into leaves under high O₂ conditions and the experiment was used to test whether extant plants responded in this way. The experimental design was also used to test the suggestion that plants of different evolutionary origins may reflect some effects of the CO₂/O₂ ratio under which they evolved (Beerling & Woodward 1996). This was addressed by making a set of leaf gas exchange measurements on plants from a range of different evolutionary groups (ginkgos, ferns, cycads and angiosperms), but grown at the current O₂ concentration.

The experimental analyses provide a means of assessing the physiological effects of high O₂ concentrations on plants under near constant growth conditions. Extending this theme, a broader-scale assessment of the impact of high O₂ and a cool Carboniferous climate in general on vegetation has been made through two modelling experiments. In the first, the impact of geographical variations in seasonal climate on net primary productivity (NPP), leaf

area index (LAI) and soil carbon (Soil C) concentration at 35% O₂ and 0.03% CO₂ was quantified at the global scale using the process-based University of Sheffield Dynamic Global Vegetation Model (SDGVM) (Woodward *et al.* 1995) coupled to a biogeochemistry model of carbon and nitrogen dynamics in vegetation and soils (Parton *et al.* 1993). The model was driven with a global palaeoclimatic simulation for the Carboniferous by the Universities Global Atmospheric Modelling Programme (UGAMP) General Circulation Model (GCM) (Valdes & Sellwood 1992; Valdes 1993). In the second modelling experiment, the limitation caused by an increase in atmospheric O₂ content from 21% to 35% O₂, on the same suite of vegetation characteristics (NPP, LAI and Soil C), is quantified at the global scale.

2. MATERIALS AND METHODS

(a) *Plant growth in simulated Carboniferous palaeoatmospheres*

(i) *Controlled environment chambers*

Plant growth chambers were constructed as shown in figure 2 and are based on the design described by Eissenstat *et al.* (1993). Four replicate chambers were used for each species and growth environment. Air containing 21% oxygen was supplied via a compressed air line. Air containing 35% oxygen was obtained by supplementing the air line with pure oxygen (BOC) using gas flow meters. The actual concentration of oxygen was calibrated by injecting samples of gas through a gas phase oxygen electrode (Hansatech, Kings Lynn, UK). CO₂ concentration and relative humidity were monitored from chamber outlets with an infrared gas analyser (CIRAS-1 PP systems, Hertfordshire, UK). Reduction in CO₂ concentration brought about by plant photosynthesis or gas dilution were compensated by supplementing the input gas with air containing 2% CO₂ (BOC) using mass flow controllers (Tylan GmbH, Munich, Germany); CO₂ was maintained between 300 and 350 ppm. Air flow into each chamber was controlled at 500 cm³ min⁻¹ using needle valves. The relative humidity within the chambers was not controlled and was largely determined by the rate of plant transpiration within the chamber; during the course of the experiment the relative humidity was 65 ± 5% for over 90% of the time. Sixteen chambers were placed in a controlled environment cabinet (Sanyo Gallenkamp Plc., Leicester, UK), set with a 12 h day/night photoperiod, an irradiance of 500 μmol m⁻² s⁻¹ and a 25/15 °C day/night temperature cycle. Plants were watered daily with 40% Long Ashton nutrient solution. *Hedera helix* were grown from 3 cm shoot cuttings and *Betula pubescens* from seed in sand in 2 l pots specifically designed to fit inside the environment chambers. When plants had either germinated or established they were transferred to individual environment chambers. Plants were allowed to grow for six weeks within the chambers prior to analysis. During this period several new leaves developed and these alone were used for subsequent analysis.

(ii) *Gas exchange measurements*

H₂O and CO₂ were measured using an infrared gas analyser (LCA₃, Analytical Development Company Ltd,

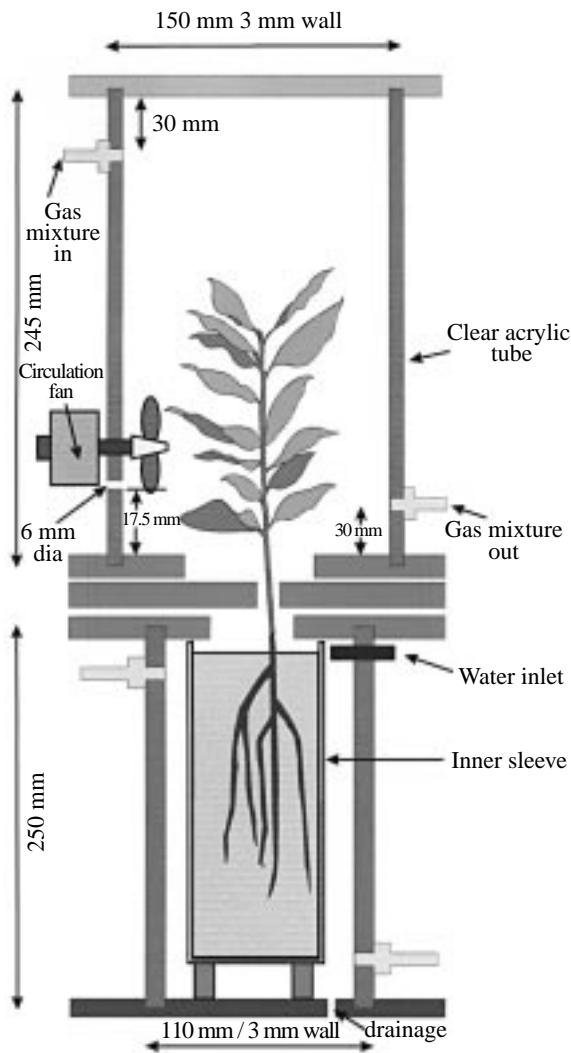


Figure 2. Schematic diagram of the controlled environment growth chamber.

Hoddesden, UK), equipped with a modified plant leaf cuvette chamber to allow temperature control and illumination and detection of chlorophyll fluorescence (PAM fluorimeter, Heinz Walz GmbH, Effeltrich, Germany) via a fibre optic. Gas composition was controlled by mixing oxygen, nitrogen and air containing 5% CO₂ (British Oxygen Company), using mass flow controllers (Brooks Instruments B.V., Veenendaal, Holland). Air humidity was controlled using a temperature trap and was maintained at 70 ± 5% relative air humidity within the leaf chamber. Fully expanded newly developed leaves were used for analysis. Irradiance was maintained at 1120 μmol m⁻² s⁻¹ and leaf temperature was 25 ± 0.5 °C. For determination of *A/c_i* (assimilation/intercellular CO₂ concentration) response curves, CO₂ was decreased progressively from 1200 ppm and for *A/O₂* response curves, CO₂ was maintained at 350 ppm and oxygen was progressively increased from 5% v/v. Gas exchange parameters were recorded after 20 min acclimation in each gaseous environment and when chlorophyll fluorescence (monitored continuously) indicated that steady-state photosynthesis had been achieved.

Assimilation, *A*, versus intercellular CO₂ concentration, *c_i*, (*A/c_i*) CO₂ responses curves were constructed across the

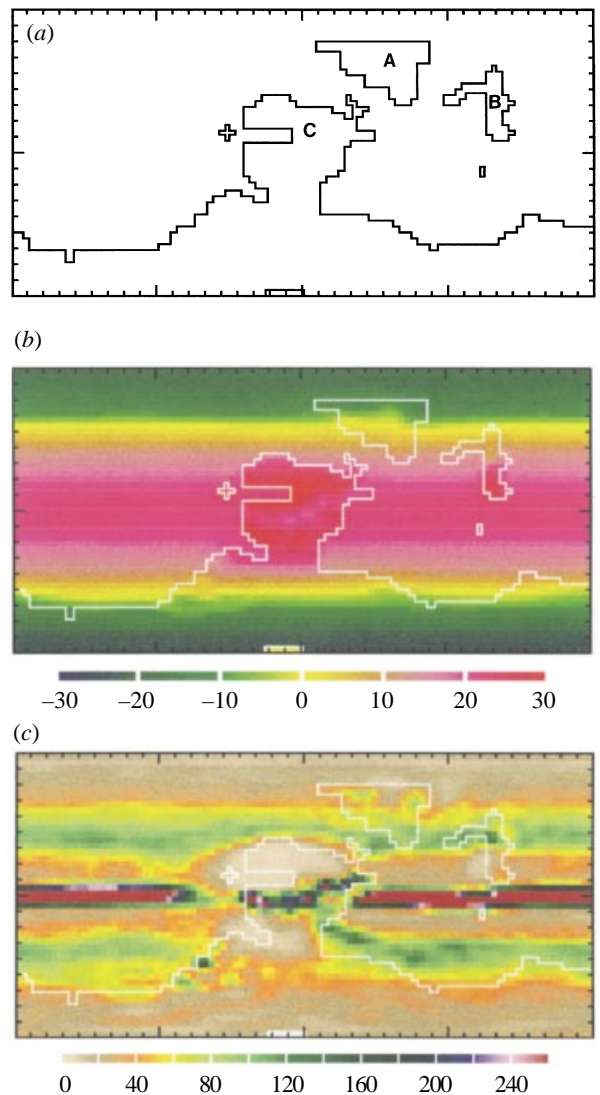


Figure 3. (a) Land–sea mask used in the UGAMP GCM (letters denote the major plates as follows: A = Eurasia, B = Kazakhstan and C = Gondwana); and global patterns of (b) mean annual temperature (°C), and (c) mean monthly precipitation (mm) for the Late Carboniferous.

CO₂ range 50–900 ppm using three leaves per individual and two individuals per treatment. Measurements were made under saturating irradiance (1120 μmol photons m⁻² s⁻¹). *A/c_i* curves were fitted using the Farquhar *et al.* (1980) biochemical model of CO₂ assimilation, following the approach of Wullschlegel (1993).

(b) *Global modelling of plant function during the Carboniferous*

This section provides a basic description of the SDGVM and the UGAMP GCM used in the global Carboniferous simulations.

(i) *University of Sheffield Dynamic Global Vegetation Model (SDGVM)*

The SDGVM builds on a previously published land primary productivity and phytogeography model (Woodward *et al.* 1995). The model only requires climatic and soils input data. The SDGVM now incorporates the Century model of carbon and nitrogen cycling (Parton *et*

al. 1993) so that the soils input data are now only soil texture.

In the model, LAI is the primary output. The model calculates the appropriate annual LAI, of any site or pixel, which is that at which either vegetation evapotranspiration just exceeds annual precipitation, or the lowest leaf layer in the canopy has an annual net primary productivity of equal to or just less than zero. Plant litter from the vegetation is decomposed in the various routines of the Century model. Overall, decomposition is determined by temperature and litter water content and quality (lignin to nitrogen ratio). Modified versions of the Century model's sub-models of soil evaporation and snow dynamics are also included in the SDGVM.

The SDGVM calculates annual NPP and LAI of terrestrial vegetation and the underlying soil nutrient status from a prescribed climate. Details of the model testing and its application to palaeoclimate data sets are in press (Beerling & Woodward 1997*b*; Beerling *et al.* 1997, 1998).

(ii) *General circulation model Carboniferous palaeoclimate simulation*

The climate simulation used to drive the SDGVM is based on a version of the UGAMP GCM, and includes a typical range of processes. The basic starting point for all such models is Newton's laws of motion. However, these equations can only be solved on a finite grid, and processes which are sub-grid scale have to be estimated (parameterized). The UGAMP GCM includes a full range of parameterizations, including a full radiation scheme (with seasonal and diurnal variations), a relative humidity based cloud scheme, and a simple three-layer soil model. Vegetation is not explicitly represented but its effects on the albedo and surface roughness are included. A fuller description of the model can be found in Valdes *et al.* (1996).

One aspect of the model which is important to note is that it has an approximately 50% higher resolution than most other GCMs used for palaeoclimate simulations. The horizontal grid that the model uses is approximately uniform and is $3.75^\circ \times 3.75^\circ$, and there are 19 levels in the vertical. This extra resolution is important since it better represents the coastlines, and mid-latitude topographic (i.e. not meteorological) depressions. This latter feature is of central importance for a good simulation of climate in these regions.

The UGAMP climate model (Valdes & Sellwood 1992; Valdes 1993) has been used to derive global predictions of the Carboniferous palaeoclimate in the Westphalian (*ca.* 305 Ma) at a spatial resolution of $3.75^\circ \times 3.75^\circ$. This interval was near the peak of the late Carboniferous glaciation, although there is sedimentary evidence for glacial–interglacial fluctuations at around this time (Witzke 1990). Continental positions were those used by Crowley & Baum (1994); other significant boundary conditions were a 3% lower solar luminosity than the present day, an atmospheric CO₂ concentration of 300 ppm (Berner 1994) and orbital configurations of the Pleistocene interglacials (Berger 1978). The UGAMP model does not explicitly model the oceans but instead uses prescribed sea surface temperatures based on simple energy balance model results. These sea surface temperatures are energetically consistent with the choice of CO₂ and solar constant. The model was integrated for five

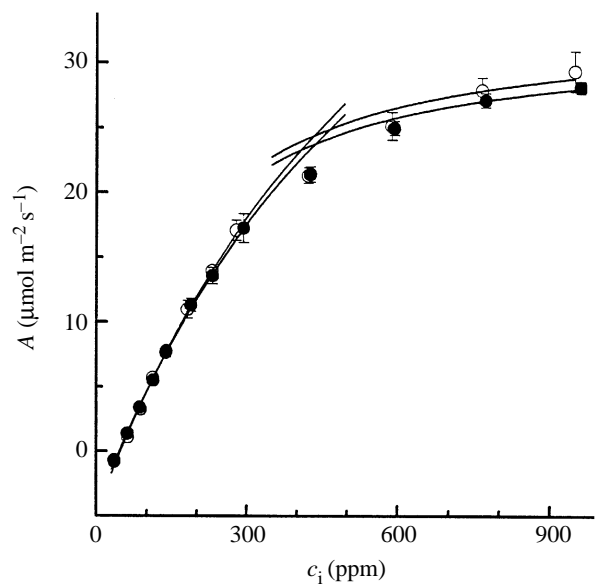


Figure 4. The response of photosynthesis (A) to changes in the intercellular CO₂ concentration (c_i) of leaves of *B. pubescens* grown for six weeks at 35% O₂ (●) and 21% O₂ (○). Measurements were made at 21% O₂. Curves were fitted as described in the text. For 35% O₂ grown plants, $V_{\max} = 74.7 \mu\text{mol m}^{-2} \text{s}^{-1}$, $J_{\max} = 176.2 \mu\text{mol m}^{-2} \text{s}^{-1}$; for 21% O₂ grown plants, $V_{\max} = 71.8 \mu\text{mol m}^{-2} \text{s}^{-1}$, $J_{\max} = 168.4 \mu\text{mol m}^{-2} \text{s}^{-1}$.

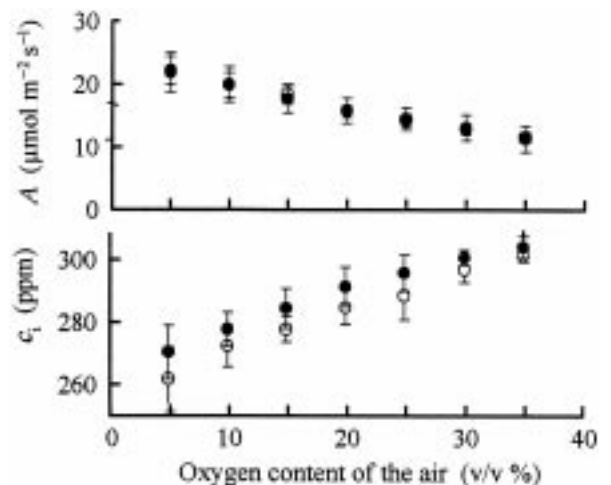


Figure 5. The response of leaf photosynthesis of *B. pubescens* (A) and intercellular CO₂ concentration (c_i) to a range of different O₂ concentrations for plants grown at 21% and 35% O₂. Symbols as in figure 4.

years and the last two years averaged to produce the 'Carboniferous climate' consisting of monthly values of precipitation, temperature and humidity.

The land–sea mask used for the late Carboniferous is given in figure 3*a*, with the major plates as labelled. The GCM-derived global temperature and precipitation driving data for the SDGVM, summarized as average monthly values (figure 3*b,c*), show a warm equatorial temperature band, particularly over the land masses of Gondwana and southern Kazakhstan and a general cooling towards higher latitudes with sub-zero temperatures near the poles and on the edges of the land masses

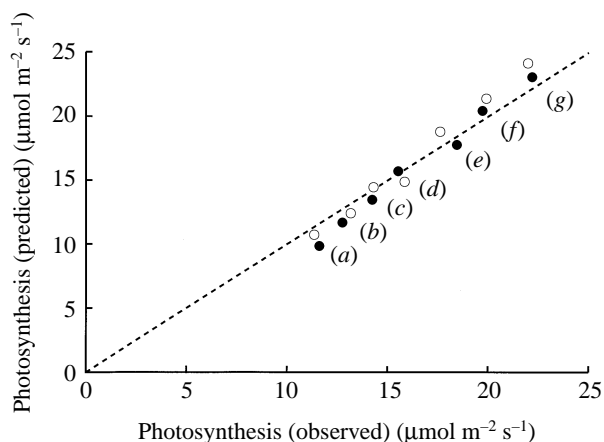


Figure 6. Comparison of observed rates of leaf photosynthesis (symbols as in figure 4), reported in figure 5, with values predicted by the Farquhar *et al.* (1980) biochemical model of leaf CO_2 assimilation. The dashed line indicates perfect fit between observations and models. (a) 35% O_2 ; (b) 30% O_2 ; (c) 25% O_2 ; (d) 20% O_2 ; (e) 15% O_2 ; (f) 10% O_2 ; (g) 5% O_2 .

of Eurasia in the northern hemisphere and Gondwana in the southern hemisphere (figure 3*b*). These features are consistent with the geological evidence for southern hemisphere high latitude glacial episodes during the Westphalian (see data summarized by Crowley & Baum (1994)). The global precipitation pattern is generally quite heterogeneous but with the largest gradients occurring in the central equatorial regions (figure 3*c*). Overall, the climatic picture in the Carboniferous is one of much cooler temperatures than the present day, with bands of higher than current average precipitation.

3. RESULTS AND DISCUSSION

(a) *Effects of 35% O_2 on leaf gas exchange and morphology*

Measurements of photosynthetic rates (A), made at 21% O_2 , on newly expanded leaves of *B. pubescens* after six weeks growth in both 35% and 21% O_2 , showed no differences in responses to a range of intercellular CO_2 concentrations (c_i) (figure 4). A similar lack of O_2 effect was also apparent from the light response curves (data not shown). The similarity of the A/c_i curves from the two sets of plants, obtained under a common O_2 concentration, indicates a lack of acclimation in the photosynthetic systems of these plants. Leaf photosynthesis and intercellular CO_2 concentrations also showed no differences between ambient and elevated O_2 plants in their responses to a wide range of O_2 concentrations (figure 5), although leaf photosynthetic rates at 35% O_2 were 29% lower than those at 21% O_2 —a result in agreement with expectations based on Rubisco CO_2 – O_2 competition. The similarity of both groups of plants provides further confirmation of a lack of acclimation in the short-term and is in agreement with previous growth experiments at high O_2 concentrations (Quebedaux & Hardy 1975; Quebedaux & Chollet 1977). Summarizing the available data on plant- O_2 responses, Raven *et al.* (1994) noted that generally photosynthetic reductions are translated into plant dry mass reductions—

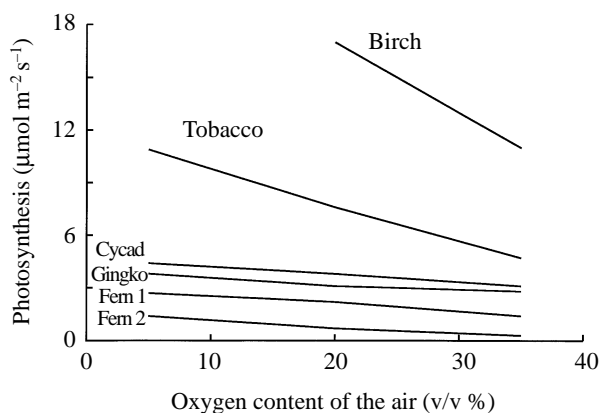


Figure 7. Photosynthetic responses of a range of different plant groups to changes in O_2 concentration. Species were as follows: birch, *Betula pubescens*; tobacco, *Nicotiana tabacum*; cycad, *Cycas revoluta*; ginkgo, *Ginkgo biloba*; fern 1, *Cyrtomium falcatum*; fern 2, *Polypodium vulgare*.

a suggestion tested by the modelling described in the next section.

The lack of acclimation in plants grown at 35% O_2 allows us to test the capability of the Farquhar *et al.* (1980) biochemical model of CO_2 assimilation at predicting leaf gas exchange responses to variations in O_2 concentration. Using the rates of maximum electron transport (J_{max}) and carboxylation (V_{max}) derived from the A/c_i response curve analysis (figure 4), leaf photosynthetic rates reported in figure 5 were predicted for both ambient and elevated O_2 grown plants. The results (figure 6) indicate the excellent capability of the model to predict quantitatively leaf photosynthetic responses to O_2 variations. This CO_2 fixation model is embedded within the SDGVM and so the favourable comparison improves our confidence in this aspect of the global scale predictions of vegetation function, discussed in the next section.

We investigated further the responses of CO_2 assimilation to variations in the atmospheric O_2 concentration in a wide range of species from several evolutionary taxonomic groups (ferns, cycads, ginkgos, and angiosperms) grown at an ambient O_2 concentration of 21%. These measurements test the suggestion that those groups evolving under periods of high O_2 and low CO_2 concentrations may have photosynthetic systems with differential sensitivities to O_2 (Beerling 1994; Beerling & Woodward 1996), possibly due to differences in their Rubisco specificity factors (Tolbert *et al.* 1995). A similar carry-over of these palaeoatmospheric signatures has also been suggested with respect to absolute values of stomatal density (Beerling & Woodward 1996), chemical composition (Robinson 1991) and light-saturated rates of photosynthesis (Long *et al.* 1993; Beerling 1994). Our new measurements indicate that the more ancient taxa were less sensitive to changes in the atmospheric O_2 concentration than the two more recently evolved species we investigated (figure 7). In addition, chlorophyll fluorescence measurements made at the same time and on the same species suggested that the ferns, cycads and ginkgo were more able to use O_2 as an electron acceptor than the modern *B. pubescens* and *T. nicotiana*.

Stomatal index counts (the ratio of stomata to epidermal cells) made on fresh fully expanded leaves of

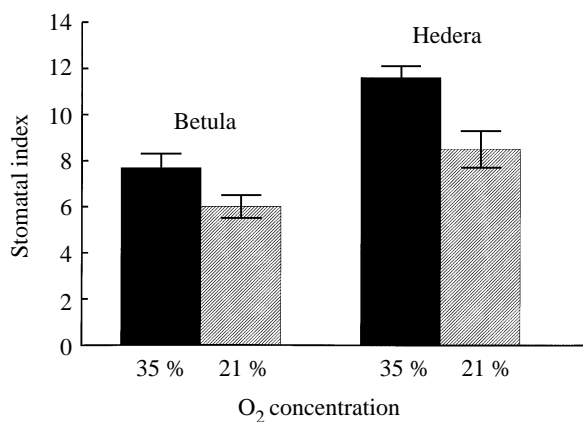


Figure 8. Stomatal index changes in leaves of *B. pubescens* and *H. helix* which developed at 35% and 21% O₂, respectively.

B. pubescens and *H. helix* grown at 35% O₂ show slightly higher values than those of leaves grown at 21%, suggesting a possible influence of O₂ on stomatal initiation (figure 8). It is interesting to note that the fossil record of stomatal density indicates that plants tended to have the highest densities of the past 400 Ma during the Carboniferous. One interpretation of these high values is that they allowed greater photosynthetic capacity, and high rates of CO₂ diffusion into the leaf to replenish CO₂ depletion inside the leaf due to photosynthesis (Beerling & Woodward 1997*a,b*). This would have the effect of reducing photorespiratory losses at high O₂ concentrations by allowing the intercellular CO₂ concentration to increase. If O₂ could influence stomatal development, then an atmospheric O₂ content of 35% may have driven the selection towards plants with a higher stomatal density. Whilst these new data are intriguing, further work is required to determine the impact of O₂ on stomatal development and operation across a wider range of species.

(b) *Global pattern of terrestrial vegetation productivity and function in the Carboniferous*

Predicting vegetation function under a Carboniferous climate and atmosphere, using the SDGVM driven by the GCM-derived palaeoclimate data set (figure 3*b,c*), enables derivation of the equilibrium model solutions of NPP, LAI and soil C (figure 9). The general pattern of high LAI, NPP and soil C all tend to mirror each other with a band of high values for each variable through northern Gondwana. Patterns of NPP and LAI tend to track the driving climate data set, particularly precipitation (figure 3). In almost all other areas of the exposed land surface terrestrial productivity and LAI values are very low. LAI was *ca.* 4–5 and maximum NPP values *ca.* 5–6 t C ha⁻¹ yr⁻¹. Global NPP at 35% O₂ was 33.7 Gt C yr⁻¹. Soil C concentrations show very high values throughout Eurasia, the northern part of Kazakhstan and through the northern extension of Gondwana (figure 9). This build-up in soil C is due to a combination of high precipitation and cool temperatures reducing decomposition rates in these regions. The global pattern is in excellent agreement with the distribution of Carboniferous coals (Crowley & Baum 1994). Model predictions of high soil C concentration in large areas of the southern

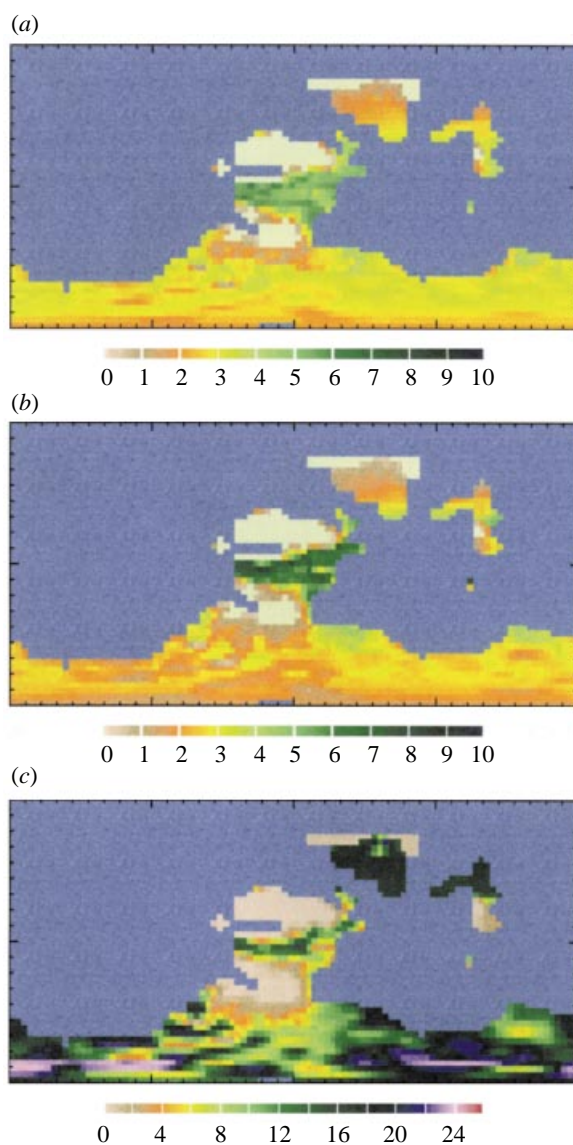


Figure 9. Global equilibrium patterns of (a) LAI, (b) NPP (t C ha⁻¹ yr⁻¹), and (c) soil C (kg C m⁻²), predicted by the SDGVM when driven by the UGAMP Late Carboniferous palaeoclimate data set.

margins of Gondwana are unlikely to have been realized by vegetation in the Carboniferous because of the presence of ice sheets in these regions—as indicated by the presence of abundant tillites (Crowley & Baum 1994).

A second model run was conducted using the same palaeoclimate data set but with a present-day O₂ concentration of 21%, in order to assess the extent to which 35% O₂ was limiting vegetation function. The difference between the 21% and 35% O₂ runs represents the effects of O₂ on the structural and/or functional attribute under investigation. A positive difference indicates a limitation at 35% O₂. In general, the globally mapped differences are positive indicating that the high O₂ content was limiting LAI, NPP and soil C (figure 10). The limitation on NPP and LAI occurs mainly through the representation of the effects of O₂ on Rubisco function in the leaf gas exchange sub-model. Any change in LAI results from changes in the rates of CO₂ fixation and loss of water via transpiration.

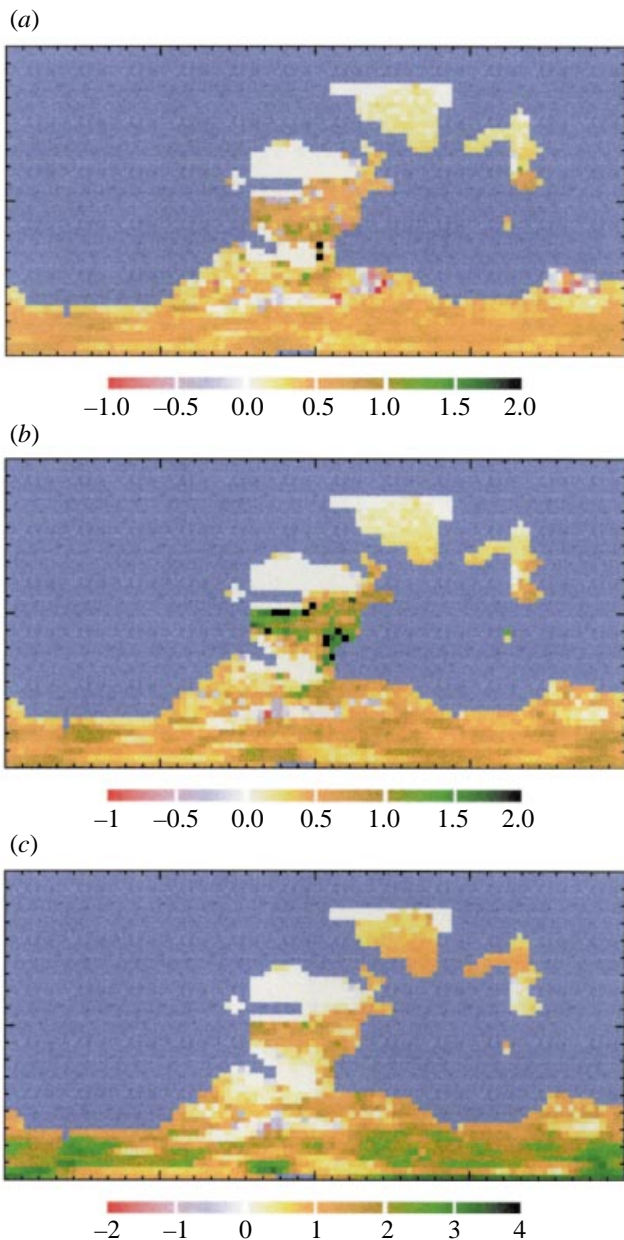


Figure 10. The impact of a Late Carboniferous rise from 21% to 35% O₂ on the global patterns of (a) LAI, (b) NPP (t C ha⁻¹ yr⁻¹) and (c) soil C (kg C m⁻²) concentration. Maps show the difference between vegetation model runs at 21% O₂ and 35% O₂.

At 21% O₂, canopy conductance (stomatal conductance of each layer in the canopy summed) is typically higher than at 35% O₂, because of higher photosynthetic rates and lower intercellular CO₂ concentrations. Higher canopy conductances lead to higher rates of canopy transpiration, under the same climate, but as long as this is less than or balances the available precipitation, the LAI increases in concert with CO₂ assimilation. This response is most typical of the model results (figure 10). In some areas LAI and NPP show small decreases at 21% O₂ relative to 35% O₂ (figure 10), due to increases in evapotranspiration.

Global NPP at 21% O₂ was 40 Gt C yr⁻¹, 18.7% greater than under the Carboniferous high O₂ atmosphere.

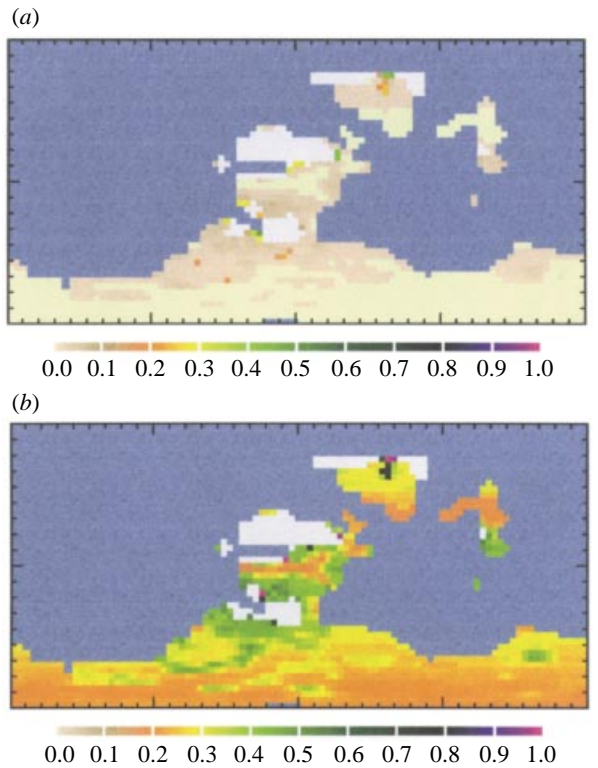


Figure 11. Global pattern of annual fire probability in the Late Carboniferous, calculated from the relative water content of the litter layer, from the equilibrium solution of the SDGVM in (a) using equation (1), and (b) with O₂ effects using equation (2).

Generally, higher soil C concentrations at 21% O₂ concentration occur because of the greater accumulation of litter from the more productive vegetation. Analysis on a pixel by pixel basis shows that the magnitude of the NPP changes at 21% O₂ were climatically dependent (i.e. sites with a favourable climate show the greatest response to a decrease in O₂ content).

In the final global scale analysis, the relative water content of the litter layer in the model was used to predict the annual probability of fires. Two key features are critical in determining the occurrence of fires, litter dryness and litter quantity (Johnson & Gutsell 1994). A very simple approach has been taken to modelling fires in the SDGVM based on litter water content. The water content of the leaf litter, on the soil surface, is first predicted. The relationship between litter water content (*lwc*, %) and the probability of fire (p_{fi}) has been determined empirically, for the present day climate and atmospheric composition, by correlating model predictions of litter water content and fire intervals at particular sites and regions for which there are published data (Archibold 1995), and is described by:

$$p_{fi} = 1 - e \left[\frac{-1}{0.4 \times e^{(lwc \times 0.071)}} \right] \quad (1)$$

Global scale predictions of fire intervals have then been made over the 1970 to 1980 period and successfully tested against observations from a separate source (Olson 1981).

The experiments of Watson *et al.* (1978) however indicate that the probability of ignition for a natural fuel source is also dependent upon the atmospheric O₂ concentration. Therefore equation (1) has been empirically modified to include the effects of 35% O₂ ($p_f(35\% \text{ O}_2)$) using the data of Watson *et al.* (1978) giving:

$$p_f(35\% \text{ O}_2) = 1.261 \times p_f^{0.314} \quad (2)$$

Global maps of the annual probability of fire in the soil-litter layer for the Carboniferous using the SDGVM litter water content output and either equation (1) or (2) are given in figure 11. Where O₂ effects are excluded (equation (1)), fire probabilities are uniformly rather low (0.1–0.2) and translate into the prediction of a fire once every *ca.* 5–10 years. This fire regime is predicted in regions of low rainfall (figure 3) but with adequate amounts of litter. When the direct effects of O₂ are included the geographical extent and the probability of fire increases (figure 11). However, it should be noted that the model only predicts fires in the soil litter layer, lightning ignition of foliage, rather than leaf litter, is not considered. The presence of swamp vegetation in regions with poor drainage would obviously preclude the possibility of extensive fires. In addition, we make no predictions of the proportion of a given pixel which would burn or the length of time a fire may continue. Nevertheless, the result from this simple fire modelling exercise is that the majority of the land surface with vegetation would have been likely to experience fires on a fairly frequent basis (every 3–6 years), allowing the development of vegetation with a short lifespan in these regions, although in some swamp regions the frequency is much less than this and we would expect the establishment of more mature vegetation in these areas. Other areas with reasonable NPP values (figure 9), but low rainfall, are predicted to experience an almost annual regime. The results appear therefore to go some way towards resolving the incompatibility of the 35% O₂ prediction of Berner & Canfield's (1989) geochemical model and the experimental results of Watson *et al.* (1978).

Compilation, by global mapping, of different vegetation types at 300 Ma, as deduced from fossils (cf. DiMichele & Phillips 1994), and the occurrence of fossil evidence for wildfire, in the form of fusain (Robinson 1991; Scott & Jones 1994) would provide a valuable basis for assessing the utility of the fire probability map, NPP and LAI maps.

4. CONCLUSION

The probably high atmospheric O₂ and low CO₂ concentrations of the Carboniferous created a unique condition for the terrestrial biosphere. These unusual atmospheric conditions, in addition to a return to cool climates exerted severe limitations on the vegetation. The low CO₂ concentration will have severely limited photosynthetic rates and any increases in atmospheric O₂ concentration above the current ambient will have directly reduced photosynthetic rates (figure 5) through increases in the rates of photorespiration. The likely plant responses to these limiting conditions appear to be the development of very high stomatal densities (Beerling & Woodward 1996), which will have maximized CO₂

concentrations within the intercellular spaces of leaves. It is interesting to note that both low CO₂ concentrations (Woodward 1987) and high O₂ concentrations (figure 8) have the capacity to increase stomatal density, and therefore diffusive capacity into the leaf. Photosynthetic rate is reduced directly with increases in O₂ concentration (figures 5 and 7) and although acclimation of Rubisco would diminish this effect, it is again interesting to note that evolutionary ancient species are more able to use O₂ as an electron acceptor than modern species. At the global scale, terrestrial productivity in the Carboniferous is generally limited by the 35% O₂ concentration, even with a cool climate. Vegetation function, in terms of transpiration, would also have been affected with a feedback on climate. Such feedbacks on climate have not yet been included within GCMs (Beerling 1997*b*) and represent a necessary next stage for improved palaeoclimate modelling.

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Discussion

M. TESTER (*Plant Sciences, Cambridge, UK*). Could increased O₂ cause increased sensitivity of plants to low water supply, via increased free radical production, and thus increase the effects you have already described of O₂ on vegetation?

D. J. BEERLING. As far as I am aware, there have been no studies dealing with the possible effects of above ambient atmospheric O₂ concentrations conferring drought tolerance in plants. However, the lower assimilation rates of plants at high O₂ would increase intercellular CO₂ concentrations and lower leaf stomatal conductance. If this effect was sustained for a suitable period during plant growth under limited water supply then lower transpiration rates, for a given temperature, humidity and irradiance, would ensue with the possible consequence of increased 'drought tolerance'. The role of free radicals in contributing or mediating such a response remains uncertain.

A. C. SCOTT (*Geology Department, Royal Holloway University of London, UK*). Your models referred to Carboniferous vegetation. It is important to note the striking difference in Lower and Upper Carboniferous vegetation (Scott & Galtier 1996; Scott 1979) and most of your models refer to later Carboniferous systems. Your fire frequency models are interesting but are not constrained by field data. We have noted changes in the nature and effects through the Carboniferous (Scott & Jones 1994). Lower Carboniferous fires in the tropics appear to be few, but widespread and intense when they occur. In contrast, fires within the Upper Carboniferous mire systems occur very frequently and appear to be an integral part of the ecosystem development. We need, however, more observations on late Carboniferous (as opposed to Permian) mire systems outside the equatorial belt before your proposed model can be tested. It may be dangerous to predict fire frequencies based upon models developed for recent systems in that not only, as you have pointed out, the oxygen content of the atmosphere was likely to be much higher but also the plant growth strategies (fast growing cheaply constructed trees lacking significant secondary xylem) of the main peat-forming plants, the arborescent lycophytes, were quite different from modern plants (DiMichele & Phillips 1994, 1995).

D. J. BEERLING. The rather simple fire frequency model we have described is entirely derived and tested against field observations and has been specifically adapted to include the influence of 35% O₂ on the probability of litter ignition, the latter based on experimental data. Furthermore, the models represent the first step towards assessing the probability of fire in the Carboniferous at the global scale and the results link many ecosystem processes driven by the Carboniferous palaeoclimate simulations. Our fire probability maps specifically deal only with litter ignition since this a standard model output; extrapolation to calculate the probability of ignition for living foliage of more ancient plant groups is not possible without more experimental data. The challenge now is for palaeobotanists to map, at the global scale, the geographical incidence of major fossil fire, within the narrow stratigraphic range of the late Carboniferous, for comparison with the model predictions.

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