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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 O_2 and CO_2 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 C_3 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% O_2 and 0.03% CO_2, no photosynthetic acclimation was observed in the woody species *Betula pubescens* and *Hedera helix* relative to those plants grown at 21% O_2. Leaf photosynthetic rates were 29% lower in the high O_2 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 O_2 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 wildfires, 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 CO_2 during the past 400 Ma of the Phanerozoic (figure 1). The reconstruction is characterized by high CO_2 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 CO_2 concentration is predicted to have increased again in the early Permian and then declined progressively over the past 200 Ma. This pattern of CO_2 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 1997*a*; 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 O_2 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% O_2 (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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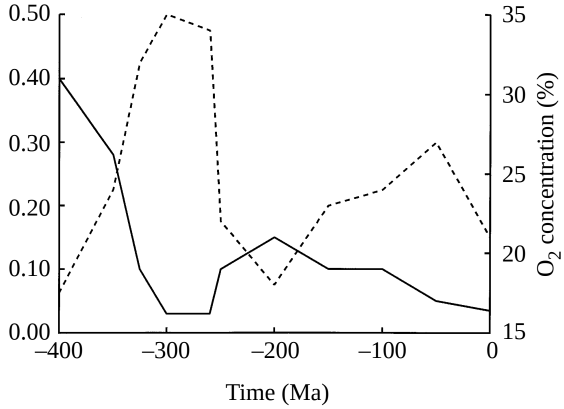


re 1. Variations in atmospheric CO_2 and O_2 over the past Ma predicted by the geochemical model of Berner (1994) Berner & Canfield (1989), respectively.

ooniferous would have had a strong impact on the tioning of terrestrial vegetation (Beerling & dward 1997*a*,*b*), particularly the functioning of ribu- 1,5-bisphosphate carboxylase/oxygenase (Rubisco), orimary C-fixing enzyme in C_3 land plants. Calcu- ns using the Farquhar *et al.* (1980) biochemical el of CO_2 assimilation, which accounts for the ive kinetic effects of CO_2 and O_2 on Rubisco ion, indicate that up to 40% of carbon fixed by osynthesis is lost via photorespiration at 35% O_2, % CO_2 and at a temperature of 25°C. Associated high photorespiration rates may also have been the tional energy costs of repairing damage caused by oxygen species (Raven 1991; Raven *et al.* 1994).

his paper investigates in more detail possible plant–osphere interactions in the Carboniferous using both rimental and modelling approaches. Plants were n experimentally at 35% O_2 and 21% O_2 in rolled environments to investigate short-term acclima- by the photosynthetic system to high O_2 levels. The riment was also designed to test for any O_2 effect on atal development. Carboniferous leaf fossils generally much higher values of stomatal density and index plant fossils from other geological eras (Beerling & dward 1997*a*). One possible explanation for this obser- on is that higher stomatal densities would have ased the diffusion rate of CO_2 into leaves under high onditions and the experiment was used to test whether it plants responded in this way. The experimental gn was also used to test the suggestion that plants of rent evolutionary origins may reflect some effects of CO_2/O_2 ratio under which they evolved (Beerling & dward 1996). This was addressed by making a set of gas exchange measurements on plants from a range of rent evolutionary groups (ginkgos, ferns, cycads and osperms), but grown at the current O_2 concentration.

ne experimental analyses provide a means of assessing physiological effects of high O_2 concentrations on ts under near constant growth conditions. Extending theme, a broader-scale assessment of the impact of O_2 and a cool Carboniferous climate in general on tation has been made through two modelling experi- s. In the first, the impact of geographical variations in onal climate on net primary productivity (NPP), leaf area index (LAI) and soil carbon (Soil C) concentration at 35% O_2 and 0.03% CO_2 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 O_2 content from 21% to 35% O_2, 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). CO_2 concentration and relative humidity were monitored from chamber outlets with an infrared gas analyser (CIRAS-1 PP systems, Hertfordshire, UK). Reduction in CO_2 concentration brought about by plant photosynthesis or gas dilution were compensated by supplementing the input gas with air containing 2% CO_2 (BOC) using mass flow controllers (Tylan GmbH, Munich, Germany); CO_2 was maintained between 300 and 350 ppm. Air flow into each chamber was controlled at $500\,\mathrm{cm^3\,min^{-1}}$ 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 $500\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ 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*

H_2O and CO_2 were measured using an infrared gas analyser (LCA_3, Analytical Development Company Ltd,

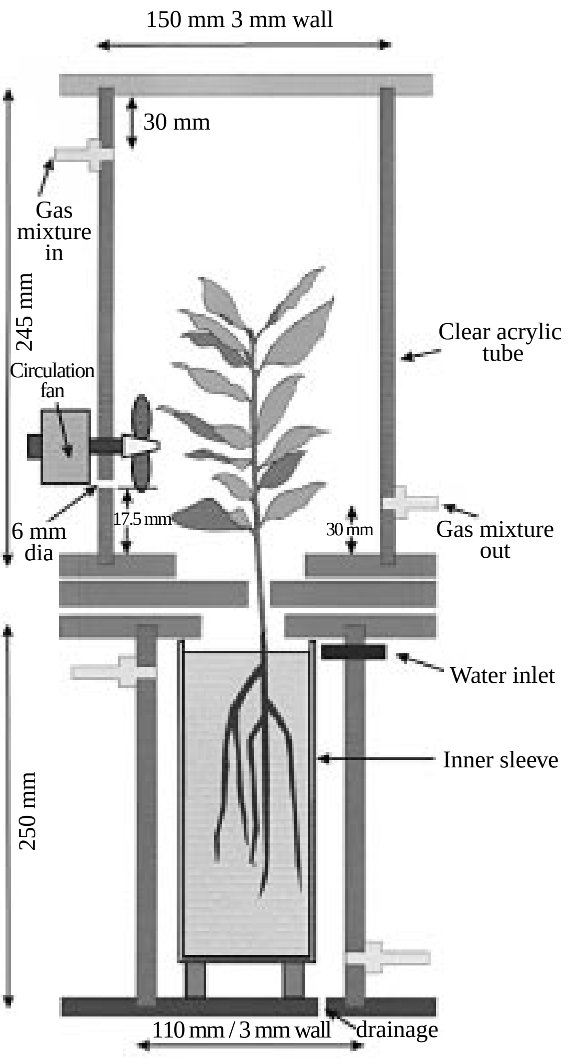


Figure 2. Schematic diagram of the controlled environment growth chamber.

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% CO_2 (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 $70 \pm 5\%$ relative air humidity within the leaf chamber. Fully expanded newly developed leaves were used for analysis. Irradiance was maintained at $1120\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ and leaf temperature was 25 ± 0.5 °C. For determination of A/c_i (assimilation/intercellular CO_2 concentration) response curves, CO_2 was decreased progressively from 1200 ppm and for A/O_2 response curves, CO_2 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 CO_2 concentration, c_i, (A/c_i) CO_2 responses curves were constructed across the CO_2 range 50–900 ppm using three leaves per individual and two individuals per treatment. Measurements were made under saturating irradiance ($1120\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$). A/c_i curves were fitted using the Farquhar *et al.* (1980) biochemical model of CO_2 assimilation, following the approach of Wullschleger (1993).

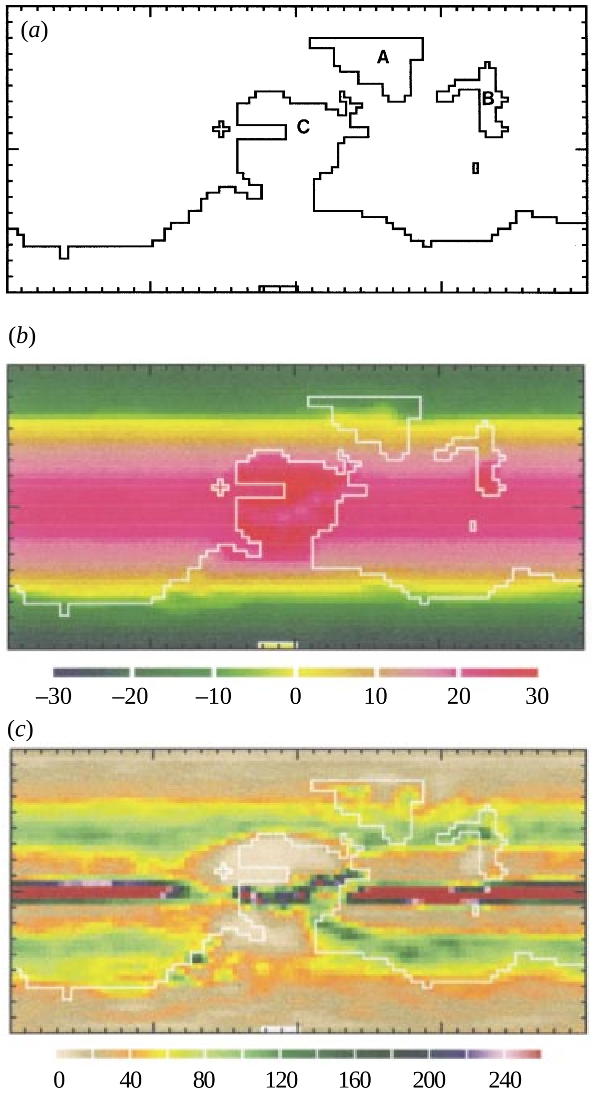


Figure 3. (*a*) Land–sea mask used in the UGAMP GCM (letters denote the major plates as follows: A = Eurasia, B = Kazakhstan and C = Gondwana); and global patterns of (*b*) mean annual temperature (°C), and (*c*) mean monthly precipitation (mm) for the Late Carboniferous.

(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*

993) so that the soils input data are now only soil re.

the model, LAI is the primary output. The model ılates the appropriate annual LAI, of any site or , which is that at which either vegetation evapotran- tion just exceeds annual precipitation, or the lowest layer in the canopy has an annual net primary uctivity of equal to or just less than zero. Plant litter the vegetation is decomposed in the various routines ıe Century model. Overall, decomposition is deter- d by temperature and litter water content and ity (lignin to nitrogen ratio). Modified versions of the ury model's sub-models of soil evaporation and snow mics are also included in the SDGVM.

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

General circulation model Carboniferous palaeoclimate simulation

ıe climate simulation used to drive the SDGVM is d on a version of the UGAMP GCM, and includes a cal range of processes. The basic starting point for all models is Newton's laws of motion. However, these tions can only be solved on a finite grid, and processes h are sub-grid scale have to be estimated (parameter- . The UGAMP GCM includes a full range of meterizations, including a full radiation scheme ı seasonal and diurnal variations), a relative humidity d cloud scheme, and a simple three-layer soil model. tation is not explicitly represented but its effects on albedo and surface roughness are included. A fuller ription of the model can be found in Valdes *et al.* 5).

ne aspect of the model which is important to note is it has an approximately 50% higher resolution than other GCMs used for palaeoclimate simulations. horizontal grid that the model uses is approximately orm and is 3.75° × 3.75°, and there are 19 levels in the cal. This extra resolution is important since it better esents the coastlines, and mid-latitude topographic not meteorological) depressions. This latter feature is ntral importance for a good simulation of climate in regions.

ne UGAMP climate model (Valdes & Sellwood 1992; es 1993) has been used to derive global predictions of Carboniferous palaeoclimate in the Westphalian 05 Ma) at a spatial resolution of 3.75° × 3.75°. This val was near the peak of the late Carboniferous ation, although there is sedimentary evidence for al–interglacial fluctuations at around this time zke 1990). Continental positions were those used by vley & Baum (1994); other significant boundary itions were a 3% lower solar luminosity than the nt day, an atmospheric CO_2 concentration of opm (Berner 1994) and orbital configurations of the tocene interglacials (Berger 1978). The UGAMP el does not explicitly model the oceans but instead prescribed sea surface temperatures based on simple gy balance model results. These sea surface tempera- are energetically consistent with the choice of CO_2 solar constant. The model was integrated for five years and the last two years averaged to produce the 'Carboniferous climate' consisting of monthly values of precipitation, temperature and humidity.

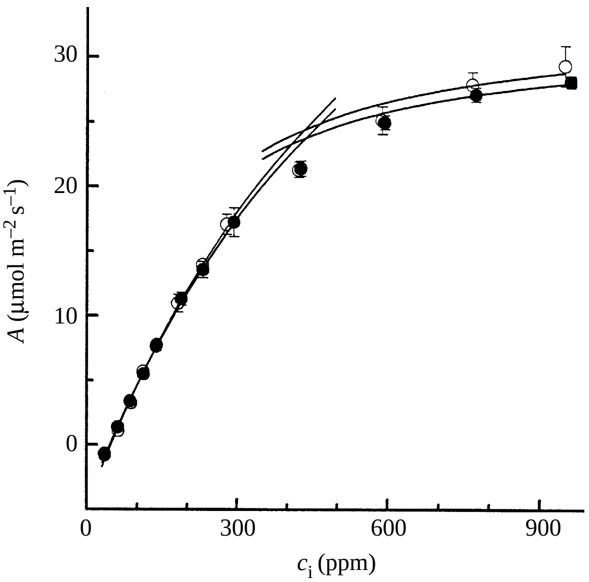


Figure 4. The response of photosynthesis (A) to changes in the intercellular CO_2 concentration (c_i) of leaves of *B. pubescens* grown for six weeks at 35% O_2 (●) and 21% O_2 (○). Measurements were made at 21% O_2. Curves were fitted as described in the text. For 35% O_2 grown plants, $V_{max} = 74.7$ μmol m^{-2} s^{-1}, $J_{max} = 176.2$ μmol m^{-2} s^{-1}; for 21% O_2 grown plants, $V_{max} = 71.8$ μmol m^{-2} s^{-1}, $J_{max} = 168.4$ μmol m^{-2} s^{-1}.

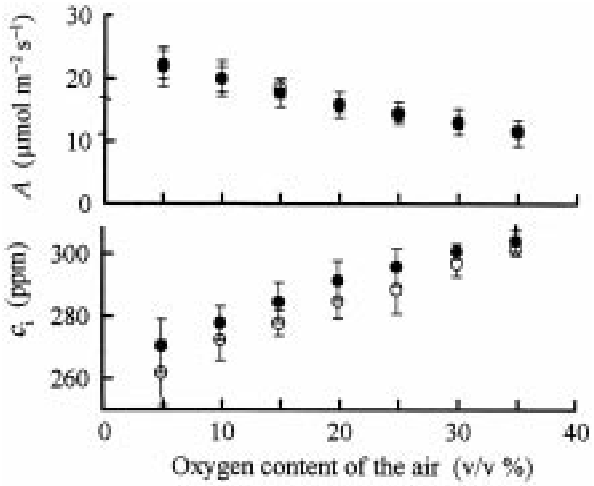


Figure 5. The response of leaf photosynthesis of *B. pubescens* (A) and intercellular CO_2 concentration (c_i) to a range of different O_2 concentrations for plants grown at 21% and 35% O_2. Symbols as in figure 4.

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

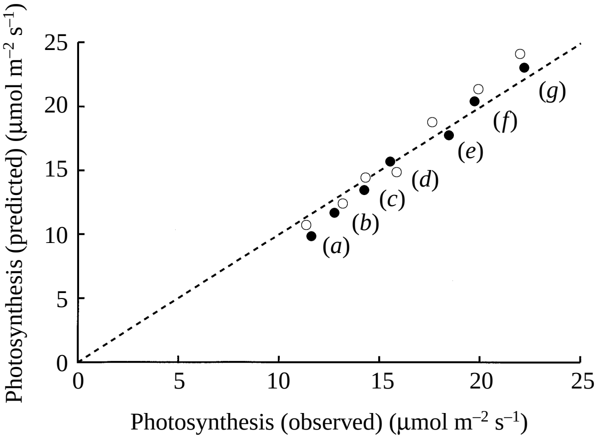


Figure 6. Comparison of observed rates of leaf photosynthesis (symbols as in figure 4), reported in figure 5, with values predicted by the Farquhar *et al.* (1980) biochemical model of leaf CO_2 assimilation. The dashed line indicates perfect fit between observations and models. (*a*) 35% O_2; (*b*) 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—a suggestion tested by the modelling described in the next section.

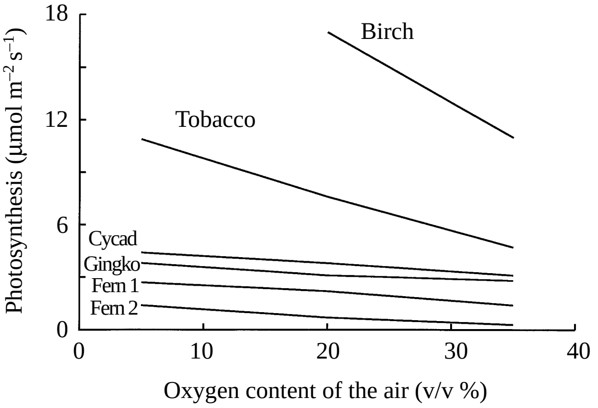
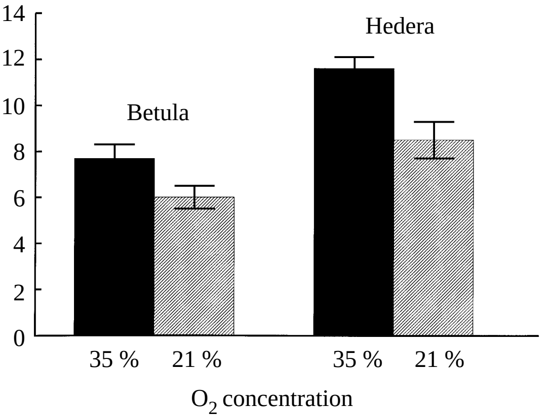


Figure 7. Photosynthetic responses of a range of different plant groups to changes in O_2 concentration. Species were as follows: birch, *Betula pubescens*; tobacco, *Nicotiana tabacum*; cycad, *Cycas revoluta*; gingko, *Ginkgo biloba*; fern 1, *Cyrtomium falcatum*; fern 2, *Polypodium vulgare*.

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



re 8. Stomatal index changes in leaves of *B. pubescens* and ɛlix which developed at 35% and 21% O_2, respectively.

ıbescens and *H. helix* grown at 35% O_2 show slightly er values than those of leaves grown at 21%, esting a possible influence of O_2 on stomatal initiation re 8). It is interesting to note that the fossil record of atal density indicates that plants tended to have the est densities of the past 400 Ma during the Carboniıs. One interpretation of these high values is that they ved greater photosynthetic capacity, and high rates of diffusion into the leaf to replenish CO_2 depletion e the leaf due to photosynthesis (Beerling & Woodl 1997*a*,*b*). This would have the effect of reducing orespiratory losses at high O_2 concentrations by ving the intercellular CO_2 concentration to increase. $_2$ could influence stomatal development, then an ospheric O_2 content of 35% may have driven the tion towards plants with a higher stomatal density. lst these new data are intriguing, further work is ired to determine the impact of O_2 on stomatal develent and operation across a wider range of species.

lobal pattern of terrestrial vegetation productivity nd function in the Carboniferous

edicting vegetation function under a Carboniferous ate and atmosphere, using the SDGVM driven by GCM-derived palaeoclimate data set (figure 3*b*,*c*), les derivation of the equilibrium model solutions of , LAI and soil C (figure 9). The general pattern of LAI, NPP and soil C all tend to mirror each other a band of high values for each variable through ıern Gondwana. Patterns of NPP and LAI tend to the driving climate data set, particularly precipita- (figure 3). In almost all other areas of the exposed surface terrestrial productivity and LAI values are low. LAI was *ca.* 4–5 and maximum NPP values -6 t C ha^{-1} yr^{-1}. Global NPP at 35% O_2 was Gt C yr^{-1}. Soil C concentrations show very high es throughout Eurasia, the northern part of Kazakhand through the northern extension of Gondwana re 9). This build-up in soil C is due to a combination igh precipitation and cool temperatures reducing mposition rates in these regions. The global pattern is xcellent agreement with the distribution of Carboniıs coals (Crowley & Baum 1994). Model predictions gh soil C concentration in large areas of the southern 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 tilites (Crowley & Baum 1994).

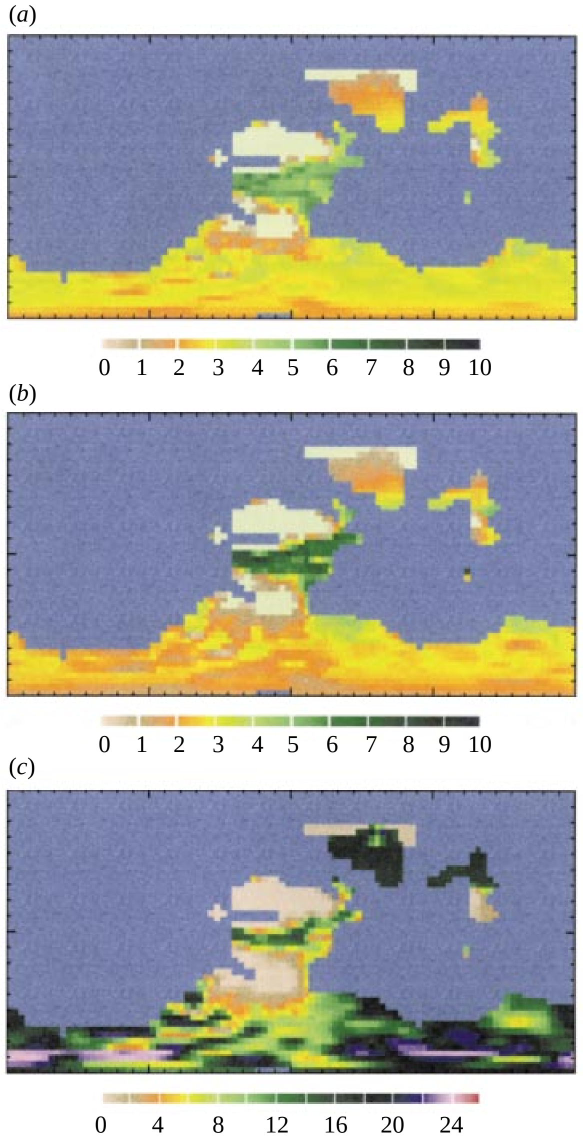


Figure 9. Global equilibrium patterns of (*a*) LAI, (*b*) NPP (t C ha^{-1} yr^{-1}), and (*c*) soil C (kg C m^{-2}), predicted by the SDGVM when driven by the UGAMP Late Carboniferous palaeoclimate data set.

A second model run was conducted using the same palaeoclimate data set but with a present-day O_2 concentration of 21%, in order to assess the extent to which 35% O_2 was limiting vegetation function. The difference between the 21% and 35% O_2 runs represents the effects of O_2 on the structural and/or functional attribute under investigation. A positive difference indicates a limitation at 35% O_2. In general, the globally mapped differences are positive indicating that the high O_2 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 O_2 on Rubisco function in the leaf gas exchange sub-model. Any change in LAI results from changes in the rates of CO_2 fixation and loss of water via transpiration.

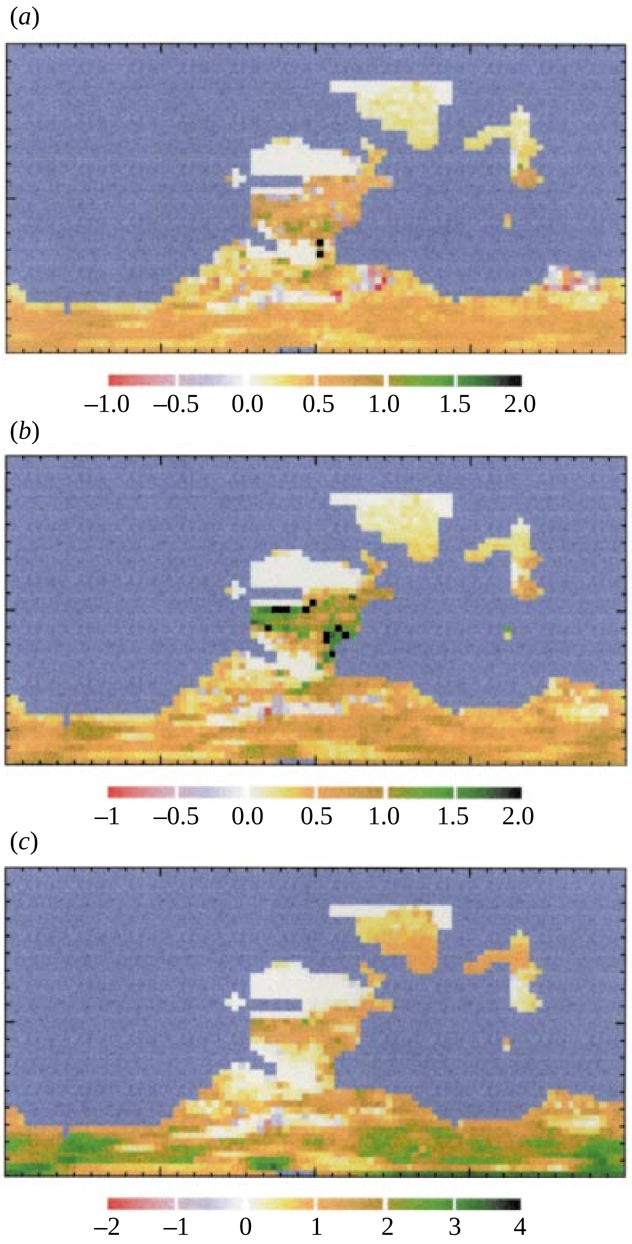


Figure 10. The impact of a Late Carboniferous rise from 21% to 35% O_2 on the global patterns of (*a*) LAI, (*b*) NPP (t C ha^{-1} yr^{-1}) and (*c*) soil C (kg C m^{-2}) concentration. Maps show the difference between vegetation model runs at 21% O_2 and 35% O_2.

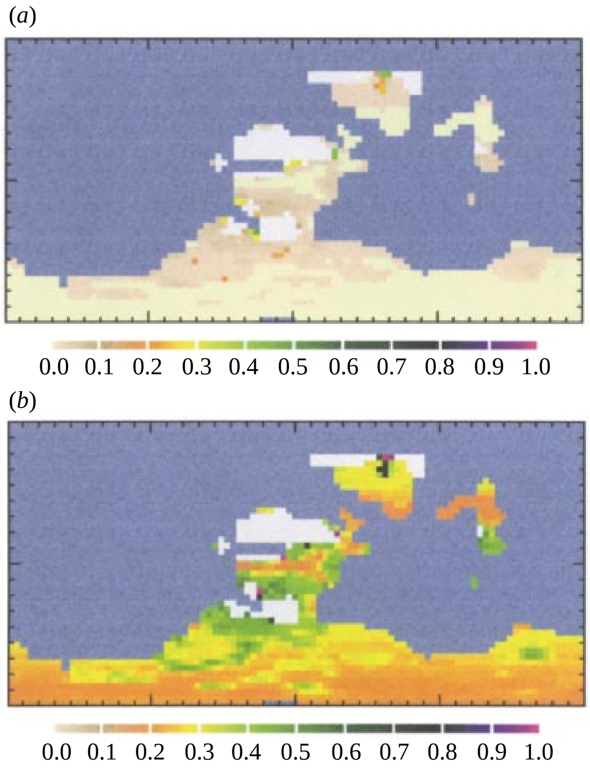


Figure 11. Global pattern of annual fire probability in the Late Carboniferous, calculated from the relative water content of the litter layer, from the equilibrium solution of the SDGVM in (*a*) using equation (1), and (*b*) with O_2 effects using equation (2).

At 21% O_2, canopy conductance (stomatal conductance of each layer in the canopy summed) is typically higher than at 35% O_2, because of higher photosynthetic rates and lower intercellular CO_2 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 CO_2 assimilation. This response is most typical of the model results (figure 10). In some areas LAI and NPP show small decreases at 21% O_2 relative to 35% O_2 (figure 10), due to increases in evapotranspiration.

Global NPP at 21% O_2 was 40 Gt C yr^{-1}, 18.7% greater than under the Carboniferous high O_2 atmosphere. Generally, higher soil C concentrations at 21% O_2 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% O_2 were climatically dependent (i.e. sites with a favourable climate show the greatest response to a decrease in O_2 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_{f1}) 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:

$$p_{f1} = 1 - e\left[\frac{-1}{0.4 \times e(lwc \times 0.071)}\right] \qquad (1)$$

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).

e experiments of Watson *et al.* (1978) however ate that the probability of ignition for a natural fuel e is also dependent upon the atmospheric O_2 concen- on. Therefore equation (1) has been empirically ified to include the effects of 35% O_2 (p_f(35% O_2)) the data of Watson *et al.* (1978) giving:

$$p_f(35\%O_2) = 1.261 \times p_{f1}^{0.314} \qquad (2)$$

al maps of the annual probability of fire in the soil- layer for the Carboniferous using the SDGVM litter r content output and either equation (1) or (2) are in figure 11. Where O_2 effects are excluded (equation fire probabilities are uniformly rather low (0.1–0.2) translate into the prediction of a fire once every *ca.* 5– ears. This fire regime is predicted in regions of low all (figure 3) but with adequate amounts of litter. n the direct effects of O_2 are included the geogra- al extent and the probability of fire increases (figure However, it should be noted that the model only icts fires in the soil litter layer, lightening ignition of ge, rather than leaf litter, is not considered. The ence of swamp vegetation in regions with poor drai- would obviously preclude the possibility of extensive In addition, we make no predictions of the propor- of a given pixel which would burn or the length of a fire may continue. Nevertheless, the result from simple fire modelling exercise is that the majority of and surface with vegetation would have been likely xperience fires on a fairly frequent basis (every 3–6 s), allowing the development of vegetation with a lifespan in these regions, although in some swamp ons the frequency is much less than this and we would ct the establishment of more mature vegetation in areas. Other areas with reasonable NPP values re 9), but low rainfall, are predicted to experience an st annual regime. The results appear therefore to go way towards resolving the incompatibility of the O_2 prediction of Berner & Canfield's (1989) hemical model and the experimental results of on *et al.* (1978).

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

ONCLUSION

e probably high atmospheric O_2 and low CO_2 entrations of the Carboniferous created a unique ition for the terrestrial biosphere. These unusual spheric conditions, in addition to a return to cool ates exerted severe limitations on the vegetation. The CO_2 concentration will have severely limited photo- etic rates and any increases in atmospheric O_2 entration above the current ambient will have tly reduced photosynthetic rates (figure 5) through ases in the rates of photorespiration. The likely plant nses to these limiting conditions appear to be the lopment of very high stomatal densities (Beerling & dward 1996), which will have maximized CO_2 concentrations within the intercellular spaces of leaves. It is interesting to note that both low CO_2 concentrations (Woodward 1987) and high O_2 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 O_2 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 O_2 as an electron acceptor than modern species. At the global scale, terrestrial productivity in the Carboniferous is generally limited by the 35% O_2 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 O_2 cause increased sensitivity of plants to low water supply, via increased free radical production, and thus increase the effects you have already described of O_2 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 O_2 concentrations conferring drought tolerance in plants. However, the lower assimilation rates of plants at high O_2 would increase intercellular CO_2 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% O_2 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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