Clim. Past Discuss., 5, 937–963, 2009
www.clim-past-discuss.net/5/937/2009/

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Ecosystem effects of CO_2 concentration: evidence from past climates

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Received: 17 February 2009 – Accepted: 18 February 2009 – Published: 12 March 2009

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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Abstract

Atmospheric CO_2 concentration has varied from minima of 170–200 ppm in glacials to maxima of 280–300 ppm in the recent interglacials. Photosynthesis by C_3 plants is highly sensitive to CO_2 concentration variations in this range. Physiological consequences of the CO_2 changes should therefore be discernible in palaeodata. Several lines of evidence support this expectation. Reduced terrestrial carbon storage during glacials, indicated by the shift in stable isotope composition of dissolved inorganic carbon in the ocean, cannot be explained by climate or sea-level changes. It is however consistent with predictions of current process-based models that propagate known physiological CO_2 effects into net primary production at the ecosystem scale. Restricted forest cover during glacial periods, indicated by pollen assemblages dominated by non-arboreal taxa, cannot be reproduced accurately by palaeoclimate models unless CO_2 effects on C_3-C_4 plant competition are also modelled. It follows that methods to reconstruct climate from palaeodata should account for CO_2 concentration changes. When they do so, they yield results more consistent with palaeoclimate models. In conclusion, the palaeorecord of the Late Quaternary, interpreted with the help of climate and ecosystem models, provides evidence that CO_2 effects at the ecosystem scale are neither trivial nor transient.

1 Introduction

Atmospheric CO_2 concentration has varied in a quasi-cyclical manner from minima of 170–200 ppm in glacials to maxima of 280–300 ppm in the recent “warm” interglacials, varying predictably with Antarctic temperature variations through the past 0.8 million years (Siegenthaler et al., 2005; Lüthi et al., 2008). Atmospheric CO_2 concentration (c_a) is a limiting factor for the photosynthesis of C_3 plants even at today’s elevated values (>380 ppm), and was much more strongly limiting at glacial values (Polley et al., 1993, 1995; Beerling and Woodward, 1993; Cowling and Sage, 1998; Guiot et al., 2001). Free Air Carbon dioxide Enrichment (FACE) experiments have shown that an increase of c_a by 200 ppm increases net primary production (NPP) in temperate forests by 23±2% (Norby et al., 2005). The response of photosynthesis to CO_2 in C_3 plants is a consequence of both substrate (CO_2) limitation and competition from O_2 at the reaction site on Rubisco, the enzyme reponsible for CO_2 fixation. Plants using the C_4 photosynthetic pathway are less strongly influenced by c_a because they are anatomically and physiologically adapted to low c_a, using mechanisms that concentrate CO_2 near the chloroplasts. Because CO_2 concentration affects C_3 photosynthesis, and must indirectly influence the competition between C_3 and C_4 plants (e.g. between C_3 trees and C_4 grasses in tropical savannas), it makes sense to look for CO_2 effects that might be superimposed on climate change effects in palaeoecological records. Moreover, if these variations in c_a have caused changes that are detectable in compositional data, such as pollen assemblages, then conventional approaches to reconstructing past climate using statistical or analogue methods – if applied to periods with c_a different from that of the late Holocene – are certain to yield incorrect results. Although this potential problem in palaeoclimate reconstruction has been known in principle for more than two decades (Solomon, 1984; Idso, 1989; Farquhar, 1997; Street-Perrott, 1994; Street-Perrott et al., 1997; Cowling and Sykes, 1999, 2000; Bennett and Willis, 2000; Williams et al., 2000; Loehle, 2007), until recently few systematic attempts have been made to rectify it.

The relative neglect of CO_2 effects in Quaternary palaeoecology may have been encouraged by an influential school of thought in contemporary biogeochemistry, which questions the relevance of plant-physiological effects of CO_2 over the long term and at the ecosystem scale (e.g. Körner, 2000). A much-debated hypothesis suggests, in particular, that limitations in the supply of nitrogen needed to support increased plant growth should over time reduce or eliminate any effect of c_a on NPP (Luo et al., 2004). However, clear evidence in support of this "Progressive Nitrogen Limitation" (PNL) hypothesis has not emerged to date (see e.g. Moore et al., 2006). Equivocal results from a single FACE experiment in a mature forest have been interpreted as indicating a limited or non-existent CO_2 fertilization effect in mature forests generally (Körner et al., 2005; see Norby et al., 2005 for a critique). Interpretations of experimental data have tended to emphasize the influence of N limitation on the CO_2 effect (e.g. Nowak et al., 2004). Nevertheless, it is well established that elevated CO_2 can increase NPP, even in ecosystems where N supply is demonstrably limiting to plant growth (e.g. Lloyd and Farquhar, 1996, 2000; Nowak et al., 2004). There is some evidence that plants can increase their N supply to support CO_2-enhanced growth, perhaps by increased root penetration or increased labile carbon subsidy to the rhizosphere (Finzi et al., 2007). The extent to which ecosystems can respond to CO_2 enhancement over timescales longer than a decade has not been unambigously demonstrated by experiments, and is subject to our still incomplete quantitative understanding of the mechanisms of N acquisition by plants.

Controversy thrives in this field in part because the evidence base from contemporary studies is, inevitably, limited. FACE has provided a great deal of extremely valuable information, and remains the key experimental technology needed to unravel CO_2 effects in intact ecosystems. However, FACE experiments are expensive and technically challenging, especially in forests. No feasible experiment can test the multidecadal responses of ecosystems and biomes on a large spatial scale. In this paper, we show that long-term, ecosystem- and biome-level effects of CO_2 effects on plant physiology can be inferred from the palaeorecord. We argue that CO_2 effects are fundamental in establishing consistency between palaeovegetation data and palaeoclimate models.

2 Background

The concentration of CO_2 in the substomatal cavity, or "internal" CO_2 concentration (c_i), is a key quantity for photosynthesis in C_3 plants. The internal concentration in illuminated leaves is less than the ambient concentration, because photosynthesis draws down CO_2 while the stomata present a resistance to the inward diffusion of CO_2. The relationship between photosynthesis and the CO_2 concentration gradient across the leaf epidermis is represented by the diffusion equation,

$$A = g(c_a - c_i) \tag{1}$$

where A is the net rate of carbon assimilation and g is the stomatal conductance (the reciprocal of resistance) to CO_2. Stomatal conductance is regulated in a way that maintains the c_i/c_a ratio typically around 0.7–0.8 in C_3 plants and 0.3–0.4 in C_4 plants under conditions of moderate vapour pressure deficit (vpd) and adequate soil moisture (Wong et al., 1979). Diffusion through the stomata also controls plant water loss:

$$E = 1.6gD \tag{2}$$

where E is the rate of transpiration per unit leaf area, and D is the vpd at the leaf surface. As D increases, g declines; in consequence, under conditions of increasing D, c_i/c_a is reduced while E increases towards a maximum (Monteith, 1995).

Equation (1) describes the control of c_i by A. At the same time, A is controlled by c_i, according to the following equation which summarizes the biochemical controls of photosynthesis (Farquhar et al., 1980, simplified here for expository purposes):

$$A = \min(A_c, A_j) - R_d \tag{3}$$

where:

$$A_c = V_{\mathrm{cmax}}(c_i - \Gamma)/(c_i + K),$$

$$A_j = \phi_o I(c_i - \Gamma)/(c_i + 2\Gamma),$$

$$R_d = bV_{\mathrm{cmax}}.$$

Here A_c is the Rubisco-limited photosynthetic rate, V_{cmax} is a maximum rate (dependent on the activity of Rubisco), Γ is the CO_2 compensation point (the concentration at which photosynthesis is zero), and K is an effective Michaelis-Menten coefficient (dependent on O_2 concentration, but this has not varied significantly over the time scales considered here). A_j is the light-limited photosynthetic rate, ϕ_o is the intrinsic quantum efficiency of photosynthesis, and I is the absorbed flux of photosynthetically active radiation (PAR). R_d is the respiration rate required to maintain the activity of Rubisco and other photosynthetic enzymes; b is a small constant, representing a respiratory loss of 1–2% of V_{cmax}.

Leaves typically operate with values of V_{cmax} such that typical daytime values of A_c and A_j are similar, i.e. there is approximate co-limitation by Rubisco and PAR (Farquhar et al., 1980). Co-limitation yields the optimum assimilation rate, because a lower V_{cmax} would result in reduced utilization of available PAR while a higher V_{cmax} would increase the loss of carbon in maintenance respiration for no gain in photosynthesis (e.g. Haxeltine and Prentice, 1996a). In practice, with light and other environmental conditions varying over the diurnal cycle, photosynthesis can be limited by Rubisco at some times and by PAR at others. However, both rates are characterized by a response to c_i that increases most steeply just above $c_i=\Gamma$, and approaches an asymptote at high c_i. Thus, the response of A to c_a is steepest at low c_a and approaches saturation at high c_a. If V_{cmax} is optimal, increased c_a should lead to reduced V_{cmax} (this "down-regulation" of V_{cmax} has been observed widely in raised-CO_2 experiments: see e.g. Ainsworth and Long, 2005). Low c_a, similarly, should lead to increased V_{cmax}. Down-regulation of V_{cmax} at high c_a would tend to reduce the plant demand for N, while increasing A would tend to increase it. Allocation of carbon to fine roots is increased at high c_i, suggesting an adaptive response to an overall increased N demand (e.g. Palmroth et al., 2006). Provided that N demands are met, increased c_a should lead to increased NPP, and reduced c_a should lead to reduced NPP, although changing allocation patterns might limit the magnitude of this response.

The asymptotic nature of the relation between A and c_i, combined with the conservatism of c_i/c_a, implies that g should decline with increasing c_a. This stomatal response to CO_2 has been observed in many species. It could allow water conservation, further increasing photosynthesis in seasons and climates where soil moisture is limiting. Similarly, g should increase with declining c_a. Leaf area index (LAI) under changing CO_2 concentrations is therefore subject to several competing effects. With increasing c_a, increasing A should promote increased LAI, and increasing g might be compensated by increased LAI; but increasing below-ground allocation would reduce LAI. A survey of experimental results by Cowling and Field (2003) indicated that LAI generally declines as CO_2 decreases below present values, while at higher CO_2 levels there is no consistent response of LAI to CO_2.

C_4 plants, with their characteristic CO_2-concentrating leaf anatomy, are believed to have evolved and spread in response to low CO_2 levels (relative to earlier geological epochs) that developed during the Cenozoic (Cerling et al., 1993; Cowling, 2001; Sage, 2004). The rate of C_4 plant photosynthesis can be roughly approximated by disregarding CO_2 effects on A in Eq. (2) and using a reduced value for the quantum efficiency, representing the "cost" of the CO_2-concentrating mechanism. Using the known temperature dependencies of the various photosynthetic parameters, it can be shown that there is a crossover temperature above which C_4 plants can fix carbon at a faster rate than C_3 plants (Ehleringer et al., 1997). Below this temperature, C_4 plants fix carbon at a slower rate than C_3 plants. The crossover temperature increases with increasing CO_2 concentration. Thus, other things being equal, we would expect C_4 plants to be more competitive relative to C_3 plants at low CO_2 (Cole and Monger, 1994; Ehleringer et al., 1997; Collatz et al., 1998). In today's world, by contrast, C_3 plants should be gaining ground. A widespread trend towards an increase of (C_3) tree cover at the expense of (C_4) grasses has indeed been observed in tropical savannas, and may be an effect of increasing CO_2 concentration (Bond and Midgley, 2000; Eamus and Palmer, 2007). However, other factors including climate change and grazing intensity have been advanced as alternatives (e.g. Archer et al., 1995). This debate continues, while contemporary observations seem unable to resolve it.

Past environments offer a variety of scenarios involving large and long-lasting CO_2 changes. Although CO_2 changes are inevitably accompanied by climate changes due to the greenhouse effect of CO_2, the involvement of other climate drivers (orbital variations and ice-sheet growth and decay) implies a degree of decoupling between CO_2

and climate which is potentially useful for attempts to attribute causes. Here however we concentrate exclusively on the major shifts in CO_2, climate and vegetation between the last glacial maximum (LGM) and the Holocene, and we use climate and ecosystem modelling results to separate effects of CO_2 from effects of climate on vegetation. In doing so, we briefly survey the history of attempts to depict and model glacial-interglacial variations in the terrestrial biosphere. This endeavour has included some false starts but has now led to a broad consensus, with wide-ranging implications for palaeoclimatology and for carbon cycle science.

3 Glacial-interglacial variations in carbon storage

Shackleton (1977) noted that the calcium carbonate shells of subfossil benthic forminifera from the last glacial period are light in ^{13}C, presumably indicating a change in the stable isotope composition of dissolved inorganic carbon (DIC) in the ocean. His estimate of the δ^{13}C offset was −0.7‰ for the LGM, relative to the Holocene. His hypothesis to explain this offset relies on a transfer of carbon between the land and ocean reservoirs. Terrestrial organic carbon is depleted in ^{13}C, so a simple mass balance can be used to infer that terrestrial organic carbon storage was substantially reduced in glacial times.

A glacial-interglacial shift in the δ^{13}C of DIC has been confirmed, although its global mean value appears to be smaller, in the range of −0.3 to −0.4‰ (Curry et al., 1988; Duplessy et al., 1988; Sarnthein et al., 1988; Ku and Luo, 1992). Using a canonical value of −0.32‰, Bird et al. (1994, 1996) estimated a terrestrial carbon storage reduction of 310–550 Pg C at the LGM relative to pre-industrial time. This calculation took account of changes in atmospheric CO_2 content and its δ^{13}C, as measured in ice cores, and a possible shift in land carbon towards values up to 2‰ heavier in glacial time (Crowley, 1991). Allowing for further uncertainty in the isotopic shift, Bird et al. (1996) obtained a range of 300–700 Pg C. Later estimates have continued to lie within this interval, for example 430–665 Pg C (Street-Perrott et al., 1998) and 550–680 Pg C (Beerling, 1999), respectively constrained by observations and modelling of the ^{13}C content of land carbon at the LGM. Ikeda and Tajika (2003) estimated 630 Pg C, by assimilating atmospheric CO_2 concentration and surface- and deep-water ^{13}C records into a box model of the ocean carbon cycle. Köhler and Fischer (2004) estimated 600 Pg C, using ice-core measurements of the concentration and $\delta^{13}C$ of atmospheric CO_2 to constrain a box model of the land carbon cycle.

Various sources of bias in this ocean carbon isotope constraint on terrestrial carbon storage have been suggested, including a dependence of isotopic fractionation during shell formation on carbonate ion concentration (Spero et al., 1997; Pedersen et al., 2003) and degassing of CH_4 clathrates with strongly negative isotopic signatures followed by conversion of the degassed CH_4 to CO_2 (Maslin and Thomas, 2003). We do not attempt a critical analysis of these mechanisms; however, none of them is likely to have a large enough effect to overturn Shackleton's hypothesis, or to require substantial revision of the broad range of estimates of LGM terrestrial carbon storage indicated by Bird et al. (1996). In particular, we note that hypotheses seeking to explain glacial-interglacial CO_2 changes by increased carbon storage during glacial times, e.g. buried under ice (Zeng, 2003) or in permafrost soils (Zimov et al., 2006), are manifestly incompatible with the ocean carbon isotope constraint.

Reduced carbon storage on land cannot be accounted for simply by the presence of continental ice sheets, because the area of exposed continental shelf – mainly in the Tropics – roughly balanced the land area occupied by ice (Prentice et al., 1993; Montenegro et al., 2006). The explanation requires a change in the distribution of terrestrial biomes, and/or their carbon content. During the early 1990s, many independent estimates of terrestrial carbon storage change between glacial and interglacial regimes were made using "book-keeping" methods that assign fixed vegetation and soil carbon storage per unit area to each biome. Such estimates were based either on cartographic reconstructions of past vegetation (e.g. Adams et al., 1990; van Campo et al., 1993; Crowley, 1995; Maslin et al., 1995; Adams and Faure, 1998; and numerous regional studies not cited here), or on palaeoclimate and biogeography modelling using the simple models available at that time (Prentice and Fung, 1990; Friedlinsgtein, 1992; Prentice, 1993; Prentice et al., 1993; Prentice and Sykes, 1995). All of these estimates should now be rejected, because (a) they overlook variations in carbon storage within biomes, which are large today, and might well vary systematically between climate states; (b) they exclude a priori any effect of CO_2 concentration on carbon storage; and (c) the data-based estimates, in particular, offer no consistent way to deal with pollen assemblages that lack modern analogues.

The first modelling studies on this topic produced no reduction in carbon storage at the last glacial maximum (LGM) (Prentice and Fung, 2000), or too small a reduction (e.g. Friedlingstein et al., 1992; Prentice et al., 1993). This last study invoked peatland development as an additional cause of net postglacial carbon accumulation, but this now seems implausible: there is abundant evidence for glacial-age peats in tropical lowlands, including the exposed continental shelf, which may have stored on the order of 200 Pg C that has largely been removed subsequently (Faure et al., 1996). Esser and Lautenschlager (1994), Peng et al. (1995, 1998) and Friedlingstein et al. (1995) applied early process-based land carbon cycle models to simulate changes in carbon storage since the LGM. These studies noted the potential of physiological CO_2 effects to further reduce carbon storage, and used empirical formulations to demonstrate that the impact could be substantial. Friedlingstein et al. (1995), for example, obtained a total reduction in carbon storage of 470 Pg C when the CO_2 effect was included. They also showed that the near-zero carbon change previously simulated by Prentice and Fung (1990) was an artefact, caused by an uncorrected bias in the model used to simulate the LGM climate. Thus, although much was made in older literature of a supposed discrepancy between a small or zero shift in carbon storage (based on models) and a very large shift (based on observations), neither the model-based or the observationally-based estimates can now be considered well-founded.

More recent studies have exploited the advances in palaeoclimate and biosphere modelling made since the 1990s. The current standard approach starts with a palaeoclimate simulation made with a general circulation model (GCM), and applies anomalies (differences in mean monthly climate variables between the simulation and the GCM's control run) to correct a baseline climatology; the altered climate then drives a terrestrial biosphere model (e.g. François et al., 1998). Current models calculate the CO_2 effect based on the Farquhar equations to give changes in photosynthesis, which are propagated through carbon allocation and plant competition algorithms to generate effects at the ecosystem level. Snapshot analyses (e.g. comparisons between the LGM and pre-industrial time slices) can be made using equilibrium models such as CARAIB (Warnant et al., 1994); transient analyses apply dynamic global vegetation models such as LPJ (Sitch et al., 2003). A consensus finding has emerged from these analyses, namely that a carbon shift of approximately the right magnitude can be reproduced – but only if physiologically mediated effects of CO_2 are included (François et al., 1998, 1999; Otto et al., 2002; Kaplan et al., 2002). These recent analyses have shown consistently that the carbon storage reduction (LGM minus pre-industrial Holocene) with the CO_2 effect "turned off" either is too small, or in some cases even has the wrong sign, i.e. the terrestrial biosphere is modelled to have slightly (<100 Pg C) greater carbon storage at the LGM than during the Holocene. The result of François et al. (1998) is typical: producing a carbon storage reduction of 610 Pg C when the physiological effect of CO_2 is included, but only 160 Pg C when it is not.

There is a simple reason why climate change alone is not sufficient to account for the glacial-interglacial change in terrestrial carbon storage. Other things being equal, the (dominant) soil component of terrestrial carbon storage increases as global temperatures decline, due to slow decomposition of soil organic matter. This explains, for example, why the highest soil carbon storage today occurs in the boreal zone and not in the Tropics. This response is steeper than the positive response of NPP to warming, over a wide range of temperatures. It is a key component of the feedback mechanism believed to be responsible for the small reduction in atmospheric CO_2 content during the Little Ice Age (Joos and Prentice, 2004; Cox and Jones, 2008). Gerber et al.'s (2004) equilibrium sensitivity analysis with the LPJ model suggested that global cooling to LGM levels would have had a minor impact on total terrestrial carbon storage, whereas the CO_2 change would have reduced terrestrial carbon storage substantially. Kaplan et al. (2002) used LPJ to perform transient simulations of land carbon storage changes since the LGM. They obtained an increase of 820 Pg C after the LGM, mainly due to the CO_2 effect. Without the CO_2 effect, the simulated increase was only 210 Pg C (Joos et al., 2004). The increase implies a net extraction of carbon from the ocean to build biospheric carbon on land. This in turn triggered the carbonate compensation mechanism in the ocean, and if the larger figure for post-LGM carbon storage increase is accepted, this mechanism accounts for the greater part of the observed rise in atmospheric CO_2 concentration during the pre-industrial Holocene (Joos et al., 2004).

The carbon isotope palaeorecord of deep ocean water as preserved in benthic foraminiferal shells, combined with process-based modelling studies to separate the climate and CO_2 effects, thus contains two important messages for contemporary biogeochemistry. (1) The 100 ppm increase in CO_2 concentration from the last glacial period to the Holocene had a major, long-lasting effect on NPP and carbon storage. (2) The approximate magnitude of this effect can be predicted (within the uncertainties of the models and the ocean carbon isotope constraint), but only by models that propagate the physiological effect of CO_2 on photosynthesis into NPP. The earlier proposal by Prentice and Sarnthein (1993) – that climate-induced biome shifts alone might be sufficient to explain glacial-interglacial changes in carbon storage – can no longer be supported. The available evidence on glacial-interglacial changes in terrestrial carbon cycling indicates an important role for physiological effects of CO_2.

4 Biome shifts

The reconstruction of glacial-interglacial changes in terrestrial carbon storage is indirect and therefore subject to rather large uncertainties, as discussed above. The reconstruction of biome shifts is more directly linked to the extremely rich set of observations in the form of pollen and plant macrofossil records from terrestrial sediments. Here, too, current evidence supports a major role for changes in CO_2. Although climate change can certainly influence biome distribution, physiological CO_2 effects modify the growth and competition of different plant functional types (PFTs) and thereby are expected to influence vegetation composition, LAI, structure and biome boundaries (Cowling, 1999a, b, 2004; Bond et al., 2003; Cowling and Shin, 2006).

Jolly and Haxeltine (1997) used BIOME3, a process-based coupled biogeochemistry-biogeography model (Haxeltine and Prentice, 1996b), to show that CO_2 changes could profoundly affect montane vegetation zonation in the African Tropics. BIOME3 is a forerunner of LPJ that lacks only the transient vegetation dynamics which LPJ simulates; it mimics the response of LAI and NPP of different PFTs to climate and CO_2, and competition among PFTs. Jolly and Haxeltine (1997) were the first to use a process-based model to analyse the effects of changing CO_2 concentration on ecosystem composition and structure in a palaeoecological context. Their analysis indicated that the large elevational extension of the heath belt on East African mountains was a predictable consequence of the low CO_2 concentration in glacial time. Indirect support for this finding came from ^{13}C measurements on leaf waxes preserved in the sediments of a high-elevation lake in the region, which indicated a marked shift towards C_4 plant dominance during the last glacial period (Street-Perrott et al., 1997; Huang et al., 1999). Boom et al. (2002) produced similar results for South America, and used BIOME3 to derive a function relating C_4 plant abundance (as indicated by leaf-wax ^{13}C measurements) to temperature and CO_2 concentration which they then inverted to yield a proxy CO_2 record that is broadly consistent with ice-core measurements – a further, indirect confirmation of the role of CO_2 in controlling C_3/C_4 plant competition over glacial-interglacial cycles.

Some early discussions had assumed that effects of glacial CO_2 concentration would be greater at higher elevations, because of low atmospheric pressure (implying a low partial pressure of CO_2 for the same concentration). However the elevation effect also lowers the partial pressure of O_2, which competes with CO_2 at the Rubisco reaction sites; this effect counters the hypothesized effect of a low partial pressure of CO_2 at high elevations (Terashima et al., 1995). In fact, the effects are expected a priori to be greater in warmer climates because the O_2 competition effect is stronger at high temperatures, as reflected in the temperature dependence of the photosynthetic parameters (Cowling, 1999a). Indeed there is abundant evidence in pollen and carbon isotope records from tropical lowland regions for shifts away from forest, toward C_4 dominated vegetation, during glacial times. This evidence comes principally from records of the $\delta^{13}C$ changes in lake sediments (e.g. Talbot and Johanessen, 1992; Giresse et al., 1994), which can be related to changes in the relative abundance of C_3 and C_4 plants. Modelling with BIOME3 has also indicated consequences for the structure of tropical forests ecosystems which would be largely "silent" in terms of the palaeorecord, yet could be profoundly significant for biogeography (Cowling et al., 2001).

Harrison and Prentice (2003) quantified CO_2 effects at a global scale, based on the BIOME 6000 synthesis, which compiled mid-Holocene and LGM pollen records worldwide and assigned a biome to each record using a standardized method (Prentice et al., 2000). The effect of LGM climate was accounted for by using all of the available GCM experiments from the Palaeoclimate Modelling Intercomparison Project (PMIP) to drive BIOME3. The results were unambiguous. Whichever GCM was used to simulate the LGM climate, the extent of simulated global forest reduction fell short of that observed when CO_2 effects were neglected; but became closer to observations when these effects were included. The influence of CO_2 was largest and most consistent in the Tropics, but not confined there: the same effect was seen in the Northern and Southern Extratropics as well. Thus finding is consistent with that of Cowling (1999b), who had also used BIOME3 to show that the pattern of LGM vegetation in Eastern North America can be explained satisfactorily only through consideration of reduced water use efficiency (A/g) by C_3 plants in low CO_2, favouring more drought-tolerant plant types, as well as climate change; a point also taken up by Loehle (2007).

The conclusion from these studies is that physiological CO_2 effects, as simulated by models based on the fundamentals of photosynthesis and propagated into the simulation of LAI and NPP of different PFTs, are essential in order to fully account for global shifts in forest cover, and probably also to explain a wider range of changes in the relative abundances of PFTs, between glacial and interglacial regimes.

5 Climate reconstruction

Until recently, methods to reconstruct past climates from palaeovegetation data were all statistical, based on the assumption that the climate controls on plant distribution are invariant. These methods broadly fall into two families: those based on some form of regression, and those based on modern analogues – either using a direct search among a set of analogues, or using response surfaces to fit the empirical relationship between the abundances of pollen taxa and climate variables (see e.g. Brewer et al., 2008). It has occasionally been noted that physiologically mediated CO_2 effects could compromise climate reconstructions made by such methods (e.g. Idso, 1989; Cowling and Sykes, 1999), but this observation had no impact on research practice until Guiot et al. (2000) developed a novel approach to palaeoclimate reconstruction, based on the numerical inversion of BIOME3.

In inversion-based palaeoclimate reconstruction, a climate change (between the past time under consideration and recent times) is selected using a search algorithm that seeks to maximize goodness of fit between the palaeodata and simulated ecosystem composition (in terms of simulated abundances or productivity of PFTs). A major advantage of using inversion is that it allows the CO_2 level to be accounted for, as it can be prescribed to the model independently of the palaeovegetation data. Guiot et al. (2000) found that prescribing the correct (low) CO_2 made a substantial difference to LGM climate reconstructions. A key finding was that when low CO_2 was prescribed for the LGM, reconstructed winter conditions in the Mediterranean region became (a) warmer than in earlier, analogue-based reconstructions, and (b) systematically closer to the predictions made by climate models for the LGM (Ramstein et al., 2007). This result is all the more remarkable because BIOME3 does not model any direct effect of CO_2 on plants' low-temperature tolerance. However, low atmospheric CO_2 implies both reduced NPP (so that the distribution of trees towards climates offering low potential production becomes more restricted) and increased water use per unit of NPP, reinforcing this restriction. As a consequence, steppe vegetation can expand under low CO_2 at the expense of forest. The earlier, analogue-based methods has selected modern analogues for the glacial steppe in Central Asia in climates with very cold winters and short growing seasons. Low CO_2, however, permitted the occurrence of steppe vegetation under milder conditions. An expanded set of analogues produced milder reconstructed winters than the original set, but could not produce consistency with palaeoclimate model results. This case study illustrates a relatively little-discussed problem with analogue methods. Although the "no-analogue" problem (fossil pollen assemblages for which similar modern pollen assemblages cannot be found) is well known, there is also potentially a "wrong-analogue" problem whereby the method of modern analogues selects similar pollen assemblages that actually originated in very different physical environments. The Mediterranean case study shows how this problem can be alleviated through the inversion of process-based models. The inversion method has been applied in three continents (Wu et al., 2007a, b; Guiot et al., 2008).

The use of inverse modelling to reconstruct past climates has further advantages that are beginning to explored, using BIOME3 and most recently its successor, BIOME4 (Kapan et al., 2003). Inverse modelling provides a natural way to incorporate additional observational constraints, such as palaeo ^{13}C information (e.g. Hatté and Guiot, 2005; Rousseau et al., 2006; Hatté et al., 2009; Guiot et al., 2009). It makes it straightforward to incorporate additional external forcing of vegetation changes, such as insolation changes caused by orbital variations, and by the differences in latitude between locations at which particular vegetation types occured during glacial versus interglacial climates; these differences may have implications for plant productivity and water use (Kaplan et al., 2003). The involvement of a process-based model should also allow the use of a data-assimilation approach to the reconstruction of ecosystem properties that palaeodata do not directly record, such as NPP and carbon storage (Wu et al., 2009). Finally, a recent development of the inversion approach builds on a version of the LPJ model to allow time-dependent climate reconstruction taking account temporal lags in the response of vegetation to climate (Guiot et al., 2009). What began as a solution to a specific problem in palaeoclimate reconstruction may turn out to be a tool with a wide field of application in palaeoclimatic analysis.

6 Conclusions

Despite persistent controversies about the contemporary and future effects of rising CO_2, surprisingly few attempts have been made to use palaeorecords to help resolve them. We have summarized evidence based on a model-assisted interpretation of the palaeorecord, which supports the idea that physiological effects scale up to ecosystem effects through changes in primary production and through competition between plants with different photosynthetic pathways, with implications for global carbon storage and regional vegetation patterns. This evidence also implies that for palaeoclimate reconstruction involving periods with substantially different CO_2 levels, inversion of process-based models is likely to yield more realistic results than statistical modelling that excludes physiological effects of CO_2. Recent advances in inverse vegetation modelling offer a promising way forward for the integration of biophysical process understanding into palaeoclimate analysis.

Acknowledgements. Dominique Jolly made pioneering contributions to Quaternary palaeoecology, especially of Africa. He was closely involved in the development of the data analysis technique called “biomization” which made the global BIOME 6000 project possible, and he developed a vision of how modelling and data analysis could work together to achieve new insights about the past. He also produced the first global-scale simulations of the LGM world that took low CO_2 into account, using an early version of BIOME3. These results were showcased in Berrien Moore III’s plenary presentation at the first International Geosphere-Biosphere Programme Congress in 1996, and presented as an example of how different disciplines of global change science could productively collaborate, and of the power of the new process-based approaches to terrestrial biosphere modelling. We have dealt here with a few of the themes

to which Dominique contributed important results and insights. We dedicate this article to the memory of an inspiring colleague and friend.

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