Global Ecology and Biogeography (1999) **8**, 81–93

RESEARCH ARTICLE

Simulated effects of low atmospheric CO_2 on structure and composition of North American vegetation at the Last Glacial Maximum

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ABSTRACT

1. Physiological experiments have indicated that the lower CO_2 levels of the last glaciation (200 µmol mol^{-1}) probably reduced plant water-use efficiency (WUE) and that they combined with increased aridity and colder temperatures to alter vegetation structure and composition at the Last Glacial Maximum (LGM).
2. The effects of low CO_2 on vegetation structure were investigated using BIOME3 simulations of leaf area index (LAI), and a two-by-two factorial experimental design (modern/LGM CO_2, modern/LGM climate).
3. Using BIOME3, and a combination of lowered CO_2 and simulated LGM climate (from the NCAR-CCM1 model), results in the introduction of additional xeric vegetation types between open woodland and closed-canopy forest along a latitudinal gradient in eastern North America.
4. The simulated LAI of LGM vegetation was 25–60% lower in many regions of central and eastern United States relative to modern climate, indicating that glacial vegetation was much more open than today.
5. Comparison of factorial simulations show that low atmospheric CO_2 has the potential to alter vegetation structure (LAI) to a greater extent than LGM climate.
6. If the magnitude of LAI reductions simulated for glacial North America were global, then low atmospheric CO_2 may have promoted atmospheric warming and increased aridity, through alteration of rates of water and heat exchange with the atmosphere.

Key words. BIOME3, low atmospheric CO_2, Last Glacial Maximum (LGM), leaf area index (LAI), palaeoecology, vegetation modelling, water-use efficiency (WUE), North America.

INTRODUCTION

Atmospheric CO_2 has fluctuated significantly over the Earth's recent history (Raymo, 1992). Past concentrations of CO_2 can be measured directly from ancient gas trapped in polar ice cores or estimated indirectly through geochemical modelling and stable carbon isotope measurements (Berner, 1994; White *et al*., 1994; Bender *et al.* 1997; Druffel, 1997). Direct measurements of CO_2 in Antarctic and Greenland ice caps reveal that CO_2 levels during the coldest part of the last glaciation were on average 200 µmol mol^{-1}, over 35% lower than today (Barnola *et al*., 1987; Neftel *et al*., 1988; Leuenberger *et al.*, 1992; Jouzel *et al*., 1993; Smith *et al.*, 1997). CO_2 concentrations increased to $\approx$280 µmol mol^{-1} during the early part of the Holocene, at a rate of 11 µmol mol^{-1} per thousand years, and remained fairly steady until the late 19th century (Anklin *et al*., 1997).

Speculation concerning the effects of low CO_2 on vegetation at the Last Glacial Maximum (LGM, 21 kyr) has increased steadily over the last decade, with research coming from diverse disciplines, including plant physiology, palaeoecology and vegetation modelling (Solomon & Webb, 1985; Davis, 1989; Polley *et al*., 1993; Prentice *et al.*, 1995; Farquhar, 1997; Jolly & Haxeltine, 1997; Street-Perrott *et al*., 1997; Collatz *et al.*, 1998). As early as the mid-1980s, theories on the role of low CO_2 in altering the competitive balance between shade-tolerant and intolerant species, were being proposed to explain unique plant assemblages observed from North American pollen records

(Solomon & Shugart, 1984). Modelling of tropical glacial alpine vegetation indicates the potential role of low CO_2 in promoting the downward migration of montane vegetation in Africa during the last glaciation (Jolly & Haxeltine, 1997). LGM CO_2 may also have affected the balance between plants exhibiting the C_3 and C_4 photosynthetic pathways, resulting in an increase in the presence of C_4-plants, which are not as physiologically sensitive (responsive) to changes in CO_2 as are C_3-species (Collatz *et al*., 1998).

Growth chamber studies indicate that in a variety of C_3-annual plants, photosynthesis, seed yield and water-use efficiency (WUE; ratio of photosynthesis to transpiration) are reduced by up to 50% under LGM CO_2 levels, relative to modern CO_2 levels (Polley *et al*., 1993, 1995; Dippery *et al*., 1995; Sage, 1995; Tissue *et al*., 1995; Mayeux *et al*., 1997). Understanding the effects of low CO_2 on carbohydrate production and partitioning is critical because carbohydrates are the necessary building blocks for growth, and ultimately influence plant development, productivity and responses to environmental stress (Mooney, 1972; Pearcy *et al*., 1987; Chapin *et al*., 1990).

Changes in plant WUE, however, may also be important for phytogeography, through effects on vegetation form and function (Woodward, 1987; Stephenson, 1990). Decreases in atmospheric CO_2 are expected to lower C_3-WUE because of increased stomatal conductance (i.e. transpiration) and/or decreased rates of carbon assimilation (Sage & Reid, 1994). Research involving stable carbon isotopes of preserved leaves dating to periods throughout the Holocene (Araus & Buxo, 1993; Woodward, 1993) and leaf gas exchange measurements of plants grown in low-CO_2 growth chambers (Polley *et al*., 1993, 1995; Bert *et al*., 1997; Cowling & Sage, 1998) strongly support predictions of low plant WUE in carbon-deficient atmospheres.

The effects of low CO_2 on plant-water relations may have resulted in the appearance of new xeric vegetation types in North America during the last glaciation (Davis, 1989). Eastern North American vegetation is generally distributed latitudinally on both temperature and moisture gradients, with the most drought- and cold-tolerant vegetation types, such as tundra, found in high latitudes, and the more drought- and cold-sensitive types, such as closed-canopy deciduous forests, in mid- to lower latitudes. Davis (1989) proposes that lower CO_2 levels at the LGM caused the more drought-sensitive forest to split into a northern portion dominated by xeric open woodland, and a southern portion dominated by closed-canopy forest. Changes in vegetation gradients such as this could have come about by the influence of low CO_2 in reducing plant WUE, and increasing sensitivity of vegetation to decreases in soil moisture. The *Picea* parkland (Wright, 1968), a xeric glacial vegetation assemblage with no modern analogue, may have formed across large areas south of the North American ice sheet (Webb, 1987) as a result not only of differences in climate (Jackson *et al*., 1997), but also because of the effect of low CO_2 on plant WUE (Davis, 1991).

In this paper, I present results of a modelling experiment aimed at investigating the influence of low atmospheric CO_2 on vegetation structure and composition during the LGM, specifically in altering vegetation types along a latitudinal gradient in eastern North America. A coupled biogeography-biogeochemistry model, BIOME3 (Haxeltine & Prentice, 1996) was used to simulate North American vegetation under LGM climate and CO_2. BIOME3 is a mechanistic (physiological) model, and as such can be used as a tool to determine ecosystem-wide changes in vegetation structure arising from physiological responses occurring at the plant-level. This study builds upon earlier simulations that used correlative or nonphysiologically based vegetation models to predict LGM vegetation (Prentice *et al*., 1992; Kutzbach *et al*., 1998). Factorial simulations were run to separate the independent effects of LGM climate and CO_2 on vegetation structure. Similar factorial designs have been employed to determine the sensitivity of late-Quaternary climate to changes in ice sheets, CO_2, and orbital insolation (Felzer *et al*., 1998). Leaf area index (LAI), the ratio of total leaf area to unit ground cover, was simulated because it can be used as a proxy for vegetation density and is sensitive to changes in plant-water relations (Chase *et al*., 1996; Fassnacht & Gower, 1997).

METHODS

Vegetation model

BIOME3 (Haxeltine & Prentice, 1996) is a coupled biogeography-biogeochemistry model that predicts structure and biogeochemical cycling of potential natural vegetation. BIOME3 excludes plant functional types (PFTs) from grid cells based on minimum temperature criteria. Competition between PFTs is modelled through differences in net primary production

Table 1. Kappa statistic assessment (evaluation of the similarity between observed and modelled vegetation distributions) of BIOME3 simulations of selected biomes in North America (from Haxeltine & Prentice, 1996), with corresponding Monserud (1990) classification. Kappa statistic values < 0.40 are assigned a rating of poor to very poor, 0.40–0.55 (fair), 0.55–0.70 (good), 0.70–0.85 (very good) and > 0.85 (excellent) (Monserud, 1990).

Vegetation type	Kappa statistic value	Monserud classification
Boreal deciduous	0.70	Very good
Boreal conifer	0.68	Good
Temperate/boreal mixed	0.43	Fair
Temperate conifer	0.15	Very poor
Temperate deciduous	0.40	Fair
Temperate broadleaf evergreen	0.43	Fair
Dry savanna	0.25	Poor
Tall grassland	0.25	Poor
Short grassland	0.39	Poor
Xeric woodland/scrub	0.26	Poor
Arid shrubland/steppe	0.56	Good
Arctic tundra	0.72	Very good

(NPP). On a grid cell basis, NPP is simulated for eighteen prescribed leaf area index values (LAI, ratio of leaf area per unit ground cover) (m^2m^{-2}), ranging from 0.05 m^2m^{-2}–5.75 m^2m^{-2}. The LAI that results in the highest NPP will be selected as the optimal LAI. The PFT that results in the highest NPP will be selected as the dominant PFT, with its corresponding optimal LAI also being assigned to the grid cell. High LAIs lead to higher rates of photosynthesis, but may also result in greater water loss through transpiration. BIOME3 simulates changes in LAI along moisture gradients as a consequence of the trade-off between light capture and water stress (Haxeltine & Prentice, 1996).

NPP is simulated using a coupled carbon and water flux model. C_3-photosynthesis calculations are based on Collatz *et al*.,'s (1991) simplification of Farquhar *et al*.,'s (1980) leaf photosynthesis model, and C_4-photosynthesis from Collatz *et al.* (1992). Actual and potential evapotranspiration (AET, PET) are calculated to determine the degree of plant-water stress, causing feedbacks on the carbon balance routine via changes in stomatal conductance. Stomatal conductance is not modelled explicitly *per se*, but responds to changes in atmospheric CO_2 through effects on photosynthesis. A more detailed description of the physiological equations and parametrizations incorporated in BIOME3 can be found in Haxeltine & Prentice (1996).

Depending on the simulated combination of dominant and secondary PFTs, biomes are assigned to each grid cell to permit direct comparison with vegetation maps. To evaluate the robustness of BIOME3 as a predictive model, Haxeltine & Prentice (1996) used a technique called kappa statistics (Prentice *et al.*, 1992), which allows a model's ability to predict present-day vegetation types to be assessed using a subjective scale. Table 1 summarises Haxeltine & Prentice's (1996) assessment of BIOME3s simulation of potential North American vegetation. Two major limitations are noted (Haxeltine & Prentice, 1996). First, BIOME3 predicts deciduous forest out-competing evergreen forest in the south-east of the United States, and second, the 'Prairie Peninsula' region of the mid-continental United States is poorly modelled, with the prairie–forest boundary being simulated west of its current location. Haxeltine & Prentice (1996) suggest that because BIOME3 does not simulate interannual variability of rainfall or fire disturbance, the outcome of tree-grass competition is less accurately predicted than are other features.

LGM climate

Baseline (modern) climate simulations were run with an updated (1994; W. Cramer, personal communication) version of Leemans & Cramer's (1991) climate database, interpolated to a 0.5° grid. LGM climate reconstructions were from simulations of the NCAR-CCM1 atmospheric general circulation model (AGCM), which are described in Kutzbach *et al.* (1998) and result from changes to boundary conditions in terms of ice sheets, sea level, CO_2 concentrations, and incoming radiation. Palaeoclimate anomalies of simulated mean monthly temperate and precipitation were interpolated from the coarser AGCM grid, to 0.5° resolution, and added to the baseline climatology. In both CCM1 and BIOME3, LGM atmospheric CO_2 was set at 200 µmol mol^{-1}, consistent with ice records (Raynaud *et al*., 1993), and was increased to 340 µmol mol^{-1} in BIOME3 as an example of recent CO_2 levels.

Experimental design

A two-by-two factorial design was employed, yielding four simulation combinations: (A) modern climate and modern CO_2; (B) modern climate and LGM CO_2; (C) LGM climate and LGM CO_2, and; (D) LGM climate and modern CO_2. Isolated effects of LGM climate and LGM CO_2 were determined by comparison of specific combinations of simulations. Differences between scenarios (A) and (B), for example, indicate the independent effect of LGM CO_2 on vegetation structure. Maps of simulated trends in LAI were constructed for each simulation scenario. A transect was run through 82°W longitude to illustrate changes in vegetation type along a north–south vegetation gradient. An eastern North American transect, running through Hudson Bay in northern Canada, was chosen because of the relatively high availability of sites in this region with 21 k year pollen records for data-model comparisons, and because there is a strong gradient from northern xeric vegetation types to southern closed-canopy forest. Average LAI of each of the transect vegetation types was identified in order to quantify changes in canopy density.

RESULTS

Strong correlations between moisture gradients and leaf area production are observed in modern simulations of LAI, where the highest LAIs are found along the moist North American east coast and the lowest LAIs are located in the arid American south-west (Fig. 1a). BIOME3 simulations of LAI are correlated to changes in moisture gradients through associated trade-offs between light capture and water stress (Haxeltine & Prentice, 1996). Surplus carbon can be invested into leaf surface area to increase photosynthetic carbon uptake, but can also lead to enhanced rates of transpiration. Where drought is common, compromising water conservation for greater carbon uptake may not increase plant growth, and lower LAIs, with reduced rates of water loss, may be a more successful plant strategy in such drought-prone environments.

Table 2. Leaf area index (LAI) ($m^2 m^{-2}$) observed for various vegetation types found in North America, presented as both ranges and most frequently cited value (modified from Larcher, 1995).

Vegetation type	LAI range	Most frequent LAI
Temperate deciduous	3–12	5
Boreal (evergreen)	7–15	12
Scrub	4–12	4
Savanna	1–5	4
Steppe	–	4
Tundra	0.5–2.5	2

Table 3. Ranges in BIOME3 simulation of leaf area index (LAI) ($m^2 m^{-2}$) (from Haxeltine & Prentice, 1996).

Vegetation type	LAI range
Boreal forest/woodland	0.05–5.75
Temperate/boreal mixed	1.5–5.75
Temperate deciduous	2.5–5.75
Tundra	0.05–5.75
Dry savanna	0.6–5.75
Tall grassland	3.0–5.75
Short grassland	0.4–5.75

Modern observed LAIs for vegetation types in North America are presented in Table 2. Tundra has very low LAIs, in the range of 2 $m^2 m^{-2}$, with grass and woodland ecosystems intermediate at 4 $m^2 m^{-2}$, and with closed-canopy boreal and deciduous forest having LAIs as high as 12 $m^2 m^{-2}$ (Larcher, 1995). BIOME3 simulates LAIs in the range of 0.05–5.75 $m^2 m^{-2}$, preserving LAI gradients from tundra (lowest LAIs) through to closed-canopy forest (highest LAIs) (Table 3). Haxeltine & Prentice (1996) classify boreal forest and boreal woodland together, thus LAI of boreal forest can be simulated close to zero, in contrast to the very high LAIs observed in modern boreal forests (Larcher, 1995). Generally, with BIOME3, LAIs that are less than 3 $m^2 m^{-2}$ indicate a transition from closed-canopy to open-canopy vegetation.

LGM climate causes LAI to decrease by over 25% (from ≈4–3 $m^2 m^{-2}$) in many locations in the eastern US, indicating a decrease in canopy cover (Fig. 1, scenario A relative to D). When low atmospheric CO_2

is combined with LGM climate, LAI in several eastern US regions decreases by an additional 50%, to 1.5 $m^2 m^{-2}$ and below, with the western coast also showing high reductions in LAI (Fig. 1c). LAI reductions of such a magnitude not only indicate a shift from closed- to open-canopy conditions, but also signal potential changes in vegetation type, from those dominated by woody species to those dominated by grasslands.

LGM climate and LGM CO_2 combine to influence the placement of vegetation types along the north–south gradient in eastern North America (Fig. 2). Modern simulations show northern boreal woodland south of Hudson Bay (Canada) giving way to closed-canopy conifer forest, mixed deciduous-conifer forest, and eventually to deciduous forest south of 40°N (Fig. 2a). Reduction of atmospheric CO_2 alters modern transects by increasing the latitudinal extent of conifer forest by over eight-fold, and reducing the extent of mixed-forest (Fig. 2b). Simulated LGM climate also reduces the latitudinal extent of conifer forest and results in the replacement of mixed forest with xeric vegetation types (short grassland, tall grassland and dry savanna) (Fig. 2d). Rather than identifying these vegetation types individually by name, they will be collectively referred to as *xeric vegetation types* throughout the remainder of the paper. Biome classifications are model-specific, thus for simplicity, a generalized description of the introduced vegetation types will be used. In BIOME3, dry savanna, tall grassland, and short grassland, are classified on the basis of having either dominant cool grass or warm grass PFTs, with LAI acting as the differential factor (Haxeltine & Prentice, 1996). BIOME3 defines short grassland as having LAIs as low as 0.4 m^2m^{-2}, dry savanna as low as 0.6 m^2m^{-2}, and the more productive tall grassland no lower than 3 m^2m^{-2}.

Although low atmospheric CO_2 does not independently result in the introduction of new xeric vegetation types within the north–south transect (Fig. 2b), it does play a significant role in their placement along the gradient (Fig. 2c). Under LGM climate and LGM CO_2, xeric vegetation (short grassland, dry savanna; also collectively termed xeric vegetation types) is simulated *north* of closed-canopy conifer forest, in contrast to the LGM climate simulation, wherein new xeric vegetation types are simulated *south* of the conifer forest. The latitudinal extent of conifer forest is also significantly reduced under LGM scenarios relative to modern controls.

Vegetation types identified along the longitudinal transects are similar between simulations, but optimal LAIs differ substantially (Table 4). Under modern climate and CO_2, vegetation types generally have higher LAIs than for other simulations. In order to assess the relative strength of low CO_2 and LGM climate in lowering LAIs, scenarios B and D were compared (Table 4). LAIs for woodland, conifer, and deciduous forest are consistently lower, by between 14 and 20%, under the low CO_2 scenario (simulation B) relative to the LGM climate scenario (simulation D). Under scenarios C and D, new xeric vegetation types collectively have an LAI 46% lower under conditions of low CO_2 relative to modern CO_2 (Table 4). Results indicate that low atmospheric CO_2 had the potential to play a stronger role than climate in modifying vegetation structure at the LGM.

DISCUSSION

LGM plant water relations

Introduction of additional xeric vegetation types in LGM simulations (Fig. 2) indicate altered plant-water relations arising from a combination of increased aridity, decreased temperatures and lowered plant WUE during the LGM. Palaeoclimate simulations and reconstructions of LGM temperature and precipitation indicate that North America as a whole was much colder and drier at the LGM relative to the present (Broccoli & Manabe, 1987; Prentice *et al*., 1991; Kutzbach & Guetter, 1996; Kutzbach *et al*., 1998). New xeric vegetation types are simulated only when associated with LGM climate, indicating that reduced precipitation and/or colder temperatures are the primary cause for their appearance in simulations. Low atmospheric CO_2, however, augments LGM aridity-effects by lowering WUE of glacial vegetation, and ultimately controls the placement of new xeric vegetation types north of closed-canopy forest. Low atmospheric CO_2 decreases plant WUE through increased stomatal conductance, and thus may have had a major effect in increasing drought susceptibility of closed-canopy forest during the last glaciation.

Several lines of evidence indicate that plant WUE was reduced under the low atmospheric CO_2 levels of the past, and subsequently had significant consequences for glacial vegetation structure. Because ^{13}C is discriminated against in C_3-plants by diffusion through the stomata, stable carbon isotopes can be used to estimate WUE averaged over the lifespan of the plant

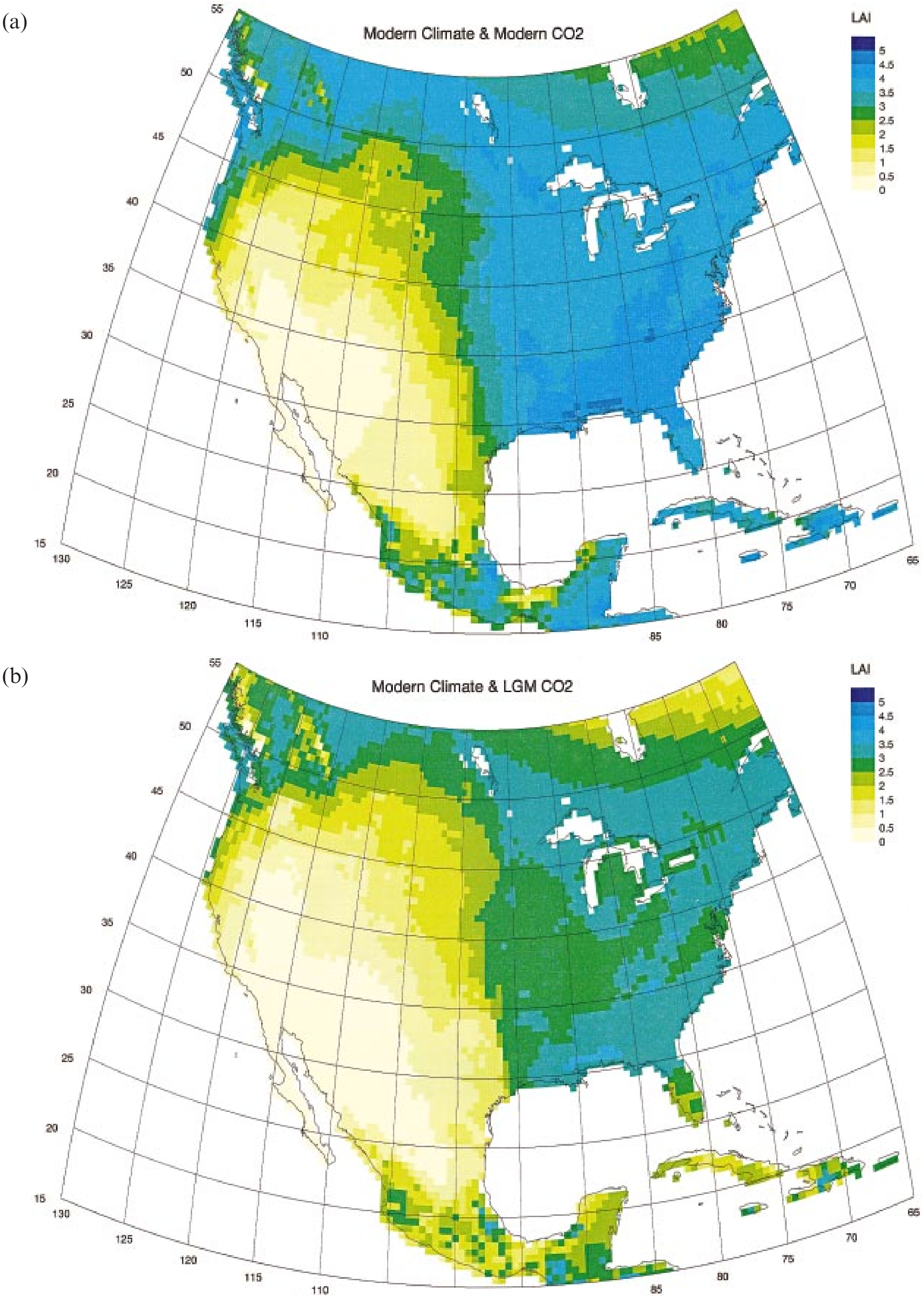

Fig. 1. Simulated trends in leaf area index (LAI) (m^2m^{-2}) under: (a) modern climate and modern CO_2; (b) modern climate and LGM CO_2; (c) LGM climate and LGM CO_2, and; (d) LGM climate and modern CO_2.

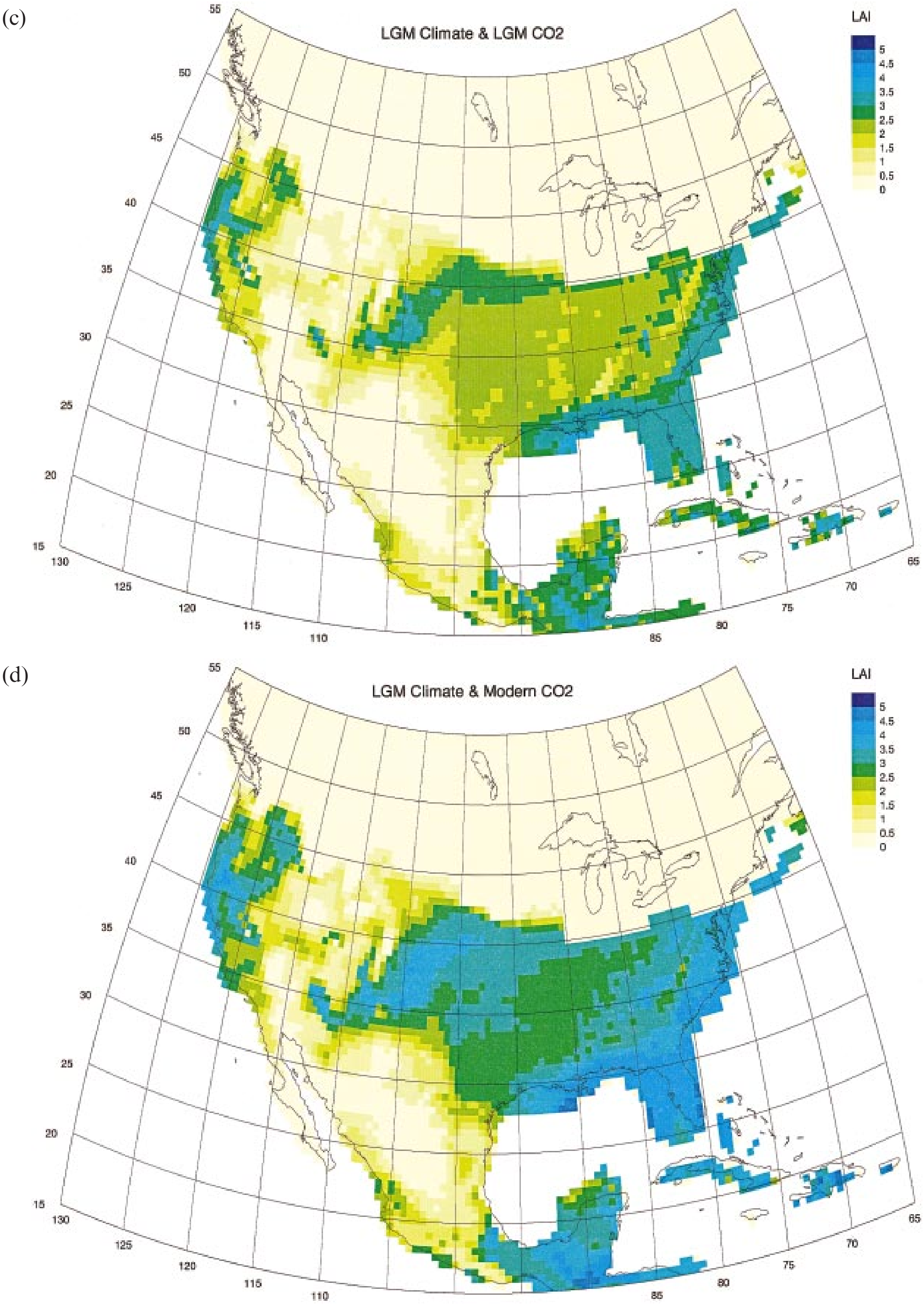
(c)
LGM Climate & LGM CO2
(d)
LGM Climate & Modern CO2
LAI
5
4.5
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Fig. 1. contd

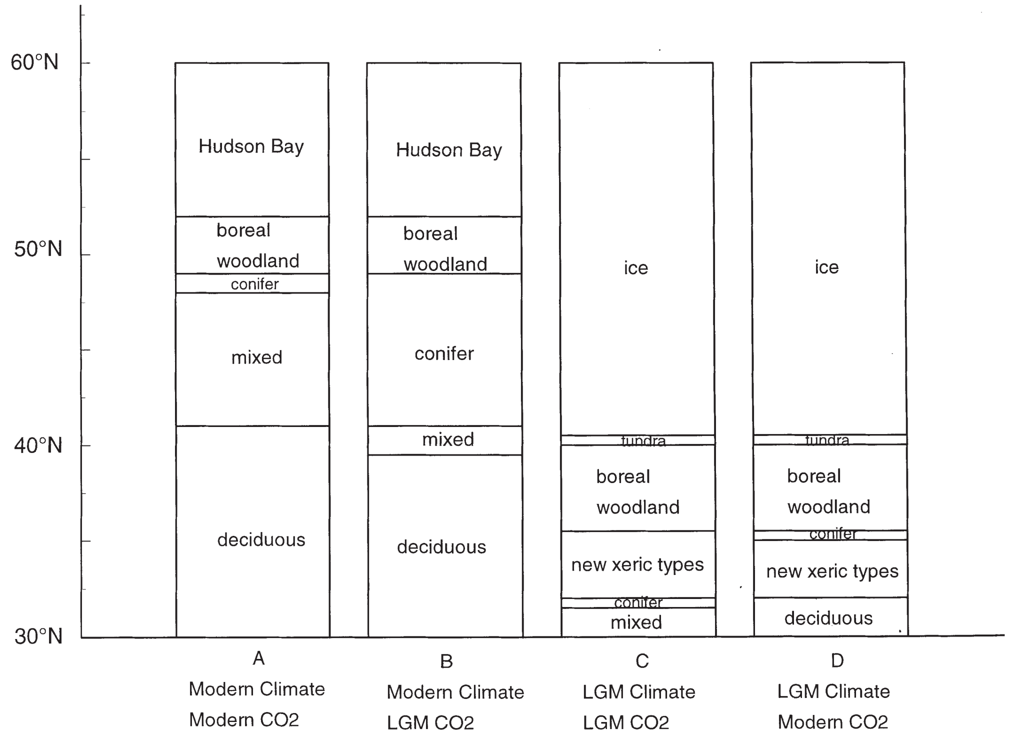

Fig. 2. Simulated effects of Last Glacial Maximum (LGM) CO_2 and climate on vegetation types along an 82°W longitudinal transect under: (a) modern climate and modern CO_2; (b) modern climate and LGM CO_2; (c) LGM climate and LGM CO_2, and; (d) LGM climate and modern CO_2. 'New xeric types' collectively refers to dry savanna, short grassland and tall grassland under LGM climate and modern CO_2 (simulation D), while under LGM climate and LGM CO_2 (simulation C), 'new xeric types' refers to dry savanna and tall grassland.

Table 4. The effects of LGM climate and LGM CO_2 on leaf area index (LAI) of vegetation types along an 82°W longitudinal transect. LAI values (m^2m^{-2}) are presented as averages.

	Simulation scenarios			
Vegetation type	Modern[1] climate Modern CO_2	Modern climate LGM[2] CO_2	LGM climate LGMCO_2	LGM climate Modern CO_2
Tundra	–	–	2.75	3.25
Woodland	3.25	2.75	2.41	2.89
Conifer	3.75	3.0	3.25	3.75
Mixed	3.75	2.75	2.75	–
Deciduous	4.0	3.0	3.25	3.75
Xeric types	–	–	1.71	3.17

[1] Modern or present-day.

[2] Last Glacial Maximum.

(Farquhar *et al*., 1989). Carbon isotopes of ancient leaves and tree cellulose indicate a strong positive correlation between atmospheric CO_2 and intrinsic WUE (Araus & Buxo, 1993; Woodward, 1993; Bert *et al*., 1997). Additionally, empirical growth chamber studies with low CO_2 support claims of reduced WUE in carbon-deficient atmospheres (Polley *et al*., 1993, 1995; Cowling & Sage, 1998). Previous modelling research with BIOME3 shows that reductions in plant WUE associated with low atmospheric CO_2 may have been in part responsible for the observed downward migration of alpine species in tropical Africa during the last glaciation (Jolly & Haxeltine, 1997).

Evidence that plant WUE was lower during periods of low atmospheric CO_2 holds critical consequences for palaeoclimate reconstructions, which are based on the assumption that plant–climate interactions remain the same through time. Decreases in glacial precipitation derived from pollen response-surface estimates (e.g. Prentice *et al*., 1991; R. Webb *et al*., 1993; T. Webb *et al*., 1998) may be overestimated because low CO_2 may decrease WUE and increase plant susceptibility to drought stress. Thus, glacial environments may have appeared more arid than they actually were as a result of the physiological responses of plants to low atmospheric CO_2 (Idso, 1989; Polley *et al*., 1993; Woodward, 1993).

Density of glacial vegetation

LAI is often used as a proxy for canopy density (Chase *et al*., 1996). A decline in LAI from 4 to 2 m^2m^{-2} indicates that the canopy has altered in structure from an approximately four-layer to two-layer cover. In BIOME3, where a maximum LAI of less than 6 m^2m^{-2} is simulated, such a decrease in LAI would signal a transition from closed-canopy to more open-canopy conditions. LGM simulations, which show a decrease of between 25 and 60% in vegetation LAI in several regions of central and eastern US, support claims that vegetation during the last glaciation was significantly more open than today (Wright, 1968; Watts, 1983; Gaudreau & Webb, 1985; Webb, 1987; Fredlund, 1995; Maenza-Gmelch, 1997). Simulations also indicate that open glacial landscapes may have been caused more by low atmospheric CO_2 than by LGM climate. LAIs of most vegetation types along the 82°W transect were significantly reduced in the low CO_2 (simulation B) relative to LGM climate scenarios (simulation D) (Table 4).

Palaeovegetation simulations such as this one can be used in conjunction with pollen records to determine amongst other things, changes in canopy closure at the stand-scale (i.e. Solomon & Shugart, 1984; Solomon & Webb, 1985; Solomon & Bartlein, 1992). LGM simulations of LAI across North America indicate *general* continental decreases in canopy closure, although conclusions at much finer scales cannot be made due to the inability of AGCMs to simulate climate on the resolution needed for regional or stand-scale assessments. With the recent development of regional climate models (RCMs) like the Canadian-RCM (Caya *et al*., 1995), UKMO-RCM (Gregory & Mitchell, 1995) and NCAR-RCCM2 (Hahmann & Dickinson, 1997), the consequences of LGM climate and CO_2 for vegetation structure at the regional scale can soon be evaluated.

Data-model comparisons

BIOME3 simulations generally support the hypothesis that low atmospheric CO_2 can alter vegetation types along a latitudinal gradient in North America. LGM climate and CO_2 simulations (scenario C) result in the creation of new xeric vegetation types between the transition from open to closed vegetation types. LGM climate appears to be the primary causal factor, however, low atmospheric CO_2 contributes significantly to the placement of these vegetation types between open woodland and closed-canopy conifer forest.

The simulation that introduces drought-tolerant biomes south of boreal woodland and north of closed-canopy forest (Fig. 2; LGM climate and LGM CO_2) is most consistent with maps of late-Quaternary pollen data for eastern North America (Overpeck *et al*., 1992; Williams *et al*., 1999). At 21 k year, *Picea*-dominated biomes (termed *tundra* and *forest tundra*) were shown to dominate much of the northern United States above 35°N latitude, with higher sedge values in fossil samples to suggest that landscapes were more open than their modern counterparts (Webb, 1987; Overpeck *et al*., 1992). Simulations of LGM LAIs indicate that forest density increased south of about 32°N, with xeric open vegetation extending north to 40°N.

Williams *et al*.,'s (1999) biome classification of eastern North American LGM pollen data indicate latitudinal vegetation types ranging from steppe and taiga, to cool mixed forest with open conifer woodland. In creating a classification scheme to describe Quaternary pollen data, a new biome termed *open conifer woodland* (i.e. *Picea* parkland) had to be created to account for the existence of this unique vegetation type during the last glaciation. A more rigorous data-model comparison is made difficult because of a lack of abundant sites with well-dated 21 k year pollen records, and also due to differences in the classification of biomes from model to model and from fossil pollen data. Prentice & Webb (1998) propose strategies to overcome these difficulties by standardizing biome classification of modelled and pollen data for the specific purpose of comparing the two data sets.

Vegetation-climate feedbacks

The magnitude of simulated decreases in LAI at the LGM indicates possible consequences for vegetation-climate feedbacks, particularly those mediated by changes in stomatal conductance. Only recently has the role of vegetation as an important interactive process in global climatology been recognized by climate modellers (Henderson-Sellers, 1993; Claussen, 1994). Changes in vegetation structure are speculated to have provided important feedbacks on global climate during the late Cretaceous (Otto-Bliesner & Upchurch, 1997), the start of the last glaciation (de Noblet *et al.*, 1996; Gallimore & Kutzbach, 1996), and the mid-Holocene warming (Foley *et al.*, 1994; Kutzbach *et al.*, 1996; TEMPO, 1996; Ganopolski *et al.*, 1998), and potentially to be important in relation to future increases in CO_2 (Friend & Cox, 1995).

Recent studies illustrate the importance of ice-age vegetation for glacial climates (Claussen *et al.*, 1998; Crowley & Baum, 1998). Crowley & Baum (1997), using a climate model (GENESIS) incorporating simulated LGM changes in vegetation distributions, indicate that expansion of xeric vegetation results in a 15–30% enhancement of LGM cooling for tropical regions in Australia and Africa, while conversion of conifer forest to tundra in high latitudes decreases temperatures by 2–4 °C. A simulated 50% increase in stomatal conductance associated with lower glacial CO_2 levels, however, did not result in any significant alterations to ice-age climate (Crowley & Baum, 1997).

Most of these studies, however, stress the importance of changes in surface albedo and roughness for climate, but changes in LAI may also play a significant part in vegetation-climate feedbacks (Chase *et al.*, 1996; Betts *et al.*, 1997). Two estimates of global LAI, one determined from satellite data (normalized difference vegetation index, NDVI) and the other predicted by vegetation modelling, were used in an AGCM by Chase *et al.* (1996) to evaluate the sensitivity of LAI changes for global climatology. Although differences in LAI distributions did not result in alterations to global average surface climate, regional climate patterns were significantly altered. Increasing leaf surface area resulted in greater rates of transpiration, thereby changing the partitioning of surface heat fluxes. Variations to circulation patterns and to the strength and location of jet streams and monsoons, may all be potentially influenced by changes in global leaf area (Chase *et al.*, 1996).

CONCLUSIONS

The simulation results indicate that LGM climate and LGM CO_2 probably had significant consequences for vegetation structure during the last glaciation. New xeric vegetation types appear in LGM simulations as a direct consequence of low soil moisture and/or reduced temperatures, although low atmospheric CO_2 augments the effects of LGM aridity by lowering WUE of glacial vegetation. Changes in plant-water relations caused by low CO_2 indicate potential biases for reconstructions of past moisture values. Reconstructions in which lowered CO_2 is accounted for will be needed in the future.

Simulated LGM LAIs for many central and eastern regions of the US were between 25 and 60% lower relative to modern simulations, supporting claims that vegetation during the last glaciation was significantly more open than today. If the underlying theories and parameterizations in BIOME3 are correct, then open glacial landscapes were likely caused more by LGM CO_2 level than by LGM climate. Simulations using vegetation models with different theoretical parametrizations, however, might not show the effects of low CO_2 on vegetation structure over-riding those from LGM climate. Modelled glacial vegetation could be used in conjunction with pollen reconstructions to determine the degree of stand-scale forest canopy closure, and could be used in conjunction with AGCMs to determine potential vegetation-climate feedbacks arising from altered vegetation LAI. The integration of physiological, modelling and palaeoecological research should help yield a better understanding of the importance of palaeo-atmospheric CO_2 for ancient ecosystems.

ACKNOWLEDGMENTS

The author wishes to thank Colin Prentice, Shinya Sugita, Al Solomon, Martin Sykes and two anonymous reviewers for comments and suggestions made to previous drafts of this manuscript, Sandy Harrison for providing NCAR-CCM1 LGM reconstructions, which were generated as part of the TEMPO project, and Jack Williams for sight of work, in press. While completing this research, SAC was funded by a Natural Sciences and Engineering Research Council of Canada Postgraduate Fellowship, and by the Foundation for Strategic Environmental Research's Sustainable Forestry in Southern Sweden (SUFOR) Project.

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