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Vegetation–atmosphere interactions and their role in global warming during the latest Cretaceous

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Forest vegetation has the ability to warm Recent climate by its effects on albedo and atmospheric water vapour, but the role of vegetation in warming climates of the geologic past is poorly understood. This study evaluates the role of forest vegetation in maintaining warm climates of the Late Cretaceous by (1) reconstructing global palaeovegetation for the latest Cretaceous (Maastrichtian); (2) modelling latest Cretaceous climate under unvegetated conditions and different distributions of palaeovegetation; and (3) comparing model output with a global database of palaeoclimatic indicators. Simulation of Maastrichtian climate with the land surface coded as bare soil produces high-latitude temperatures that are too cold to explain the documented palaeogeographic distribution of forest and woodland vegetation. In contrast, simulations that include forest vegetation at high latitudes show significantly warmer temperatures that are sufficient to explain the widespread geographic distribution of high-latitude deciduous forests. These warmer temperatures result from decreased albedo and feedbacks between the land surface and adjacent oceans. Prescribing a realistic distribution of palaeovegetation in model simulations produces the best agreement between simulated climate and the geologic record of palaeoclimatic indicators. Positive feedbacks between high-latitude forests, the atmosphere, and ocean contributed significantly to high-latitude warming during the latest Cretaceous, and imply that high-latitude forest vegetation was an important source of polar warmth during other warm periods of geologic history.

Keywords: palaeoclimate, global warming, vegetation, cretaceous, modelling

1. INTRODUCTION

A major unsolved problem in palaeoclimatology is understanding how warm polar temperatures can be maintained during periods of global warmth such as the Late Cretaceous. Two commonly proposed mechanisms for warming polar temperatures are increased atmospheric pCO_2 (Barron & Washington 1985) and increased heat transport by the world's oceans (Rind & Chandler 1991). Increased atmospheric pCO_2 warms global climate by absorbing outgoing longwave radiation and re-radiating it back to the surface. This warms surface temperatures at both equatorial and high latitudes because of the rapid global mixing of CO_2 in the atmosphere (Crowley 1991). Increased ocean heat transport, in contrast, removes heat from equatorial latitudes and transports it to high latitudes, which simultaneously cools the tropics and warms the poles (Crowley 1991). The most commonly proposed mechanism for warming high-latitude oceans is the generation of warm saline bottom water at low latitudes and upwelling of bottom water at high latitudes (Brass *et al.* 1982). Warming polar oceans through either mechanism creates positive feedbacks that further impact climate. These feedbacks include inhibition of sea-ice development, which increases absorption of solar radiation through decreased ocean albedo, and increased concentrations of atmospheric water vapour at high latitudes, which enhance the greenhouse effect on a regional scale (but may also increase the cooling effect of clouds) (Rind & Chandler 1991). Both proposed mechanisms are supported by geochemical and oceanographic models (Berner 1991, 1994; Brass *et al.* 1982) and by proxy indicators of atmospheric pCO_2 and ocean surface temperature (Andrews *et al.* 1995; Cerling 1991; Freeman & Hayes 1992; Huber *et al.* 1995).

Despite evidence for the operation of both mechanisms during periods of warm climate, model simulations that incorporate increased pCO_2 and increased ocean heat transport cannot fully recreate the warmth documented by biotic indicators for periods such as the Eocene and the Cretaceous. For the Early Eocene, the warmest interval during the Tertiary (Wolfe 1994; Wolfe & Upchurch 1987), atmospheric general circulation models (GCMs) simulate continental-interior temperatures that are too cold to explain the geographic distribution of cold-sensitive plants such as palms and cycads (Sloan & Barron 1992; Wing & Greenwood 1993). For the Mid-Cretaceous, GCMs create winter surface temperatures that are too cold in continental interiors to explain the distribution of cold-sensitive fossil plants (Barron &

hington 1982). The problem with freezing continental iors can persist in model simulations that greatly ease ocean transport (e.g. Schneider *et al.* 1985; Sloan arron 1990), which indicates that a combination of hanisms may be needed to explain the warmth of ods such as the Eocene and the Cretaceous.

ne mechanism neglected in discussions of warm- ate dynamics is the role of the land surface in main- ng high-latitude warmth, and in particular the role vegetation plays in regulating fluxes of energy, water ur, and momentum between the land surface and the osphere (Dickinson *et al.* 1986; Sellers *et al.* 1986). tation absorbs a significant fraction of incoming radiation, which decreases surface albedo relative ure soil. Vegetation transpires significant quantities of r vapour from stomata during the uptake of carbon ide for photosynthesis, which increases the flux of t heat from the land surface. The extensive surface of vegetation created by leaves and stems increases erodynamic drag of the land surface (surface rough- , which increases the rate of transfer of mass and gy between the land surface and the atmosphere. A e example of vegetation's importance in regulating ate occurs in modern boreal regions, where the ence of forest vegetation controls the position of the r front, increases the length of the growing season, causes early snow melt relative to tundra (e.g. on 1966; Foley *et al.* 1994; Pielke & Vidale 1995). easing the areal extent of high-latitude forests has perature effects comparable to a doubling of green- e gases or orbital forcing (Bonan *et al.* 1992; Foley *et* 994). This implies that vegetation played an impor- role in maintaining warm polar climates during ods such as the Late Cretaceous, because high-lati- forests occupied extensive regions that today are pied by tundra or glacial ice (Creber & Chaloner ; Horrell 1991; Spicer & Parrish 1990; Wolfe & urch 1987).

ur study explores the importance of high-latitude ts in maintaining polar warmth during the Late aceous and feedbacks between the land, atmosphere, ocean. We do this through a combination of numer- climate modelling and comparison of model results a global data base of climatic indicators. We ine the importance of vegetation in the climate m by simulating latest Cretaceous (Maastrichtian) ate under different types of vegetation cover, then rmine the extent to which modelled climates resemble red climates. We focus on the Maastrichtian climate use of its importance for understanding extinctions e Cretaceous–Tertiary boundary. However, many of conclusions can be extrapolated to the Mid- and Cretaceous because these periods also were charac- ed by areally extensive polar forests (Spicer & ish 1990; Wolfe & Upchurch 1987). Here we focus on –atmosphere–ocean interactions to demonstrate the connectedness of the biosphere, atmosphere, and n.

ODEL DESCRIPTION

ne model used in this study is the National Center for ospheric Research (NCAR) GENESIS Global Climate Model, v. 1.02, which consists of submodels for the atmosphere, ocean, and land surface (Thompson & Pollard 1995*a*,*b*). The atmosphere submodel is derived from the NCAR Community Climate Model (CCM1), and is described by equations of fluid motion, thermodynamics, and mass continuity along with representations of radiative and convective processes, cloudiness, precipitation, and the orographic influence of terrain. The modified CCM1 code incorporates new physics for solar radiation, water vapour transport, convection, boundary layer mixing, and clouds. Horizontal resolution is R15 for the atmosphere (approximately 4.5° latitude by 7.5° longitude) and 2° by 2° for the land surface. The atmosphere is subdivided vertically into 12 levels.

The ocean submodel of GENESIS contains a 50 m deep mixed-layer ocean coupled to a thermodynamic sea-ice model, which crudely captures the seasonal heat capacity of the ocean mixed layer but ignores salinity, upwelling, and energy exchange with deeper layers. Poleward ocean heat transport is parameterized as diffusion using the '0.5 × OCNFLX' case of Covey & Thompson (1989). A six-layer sea-ice model, patterned after Semter (1976), predicts local changes in sea ice thickness through melting of the upper layer and freezing or melting of the bottom surface.

The land surface submodel of GENESIS (Pollard & Thompson 1995) incorporates a land surface transfer component (LSX) to account for the physical effects of vegetation, a six-layer soil component, and a three-layer thermodynamic snow component. Soils are categorized by colour and texture. Vegetation is represented by two layers: an upper layer of trees or shrubs, and a lower layer of grass or bare soil. Vegetation prescription includes type, leaf area index (LAI), fractional coverage of plants, canopy height, solar transmittance/reflectance, and stomatal resistance. The physical attributes of the vegetation are fixed: vegetation can respond to climate physiologically, but it cannot respond by changing LAI, fractional cover, or other structural attributes (Pollard & Thompson 1995).

The physical and biological realism in LSX and comparable models (e.g. the biosphere–atmosphere transfer scheme (BATS) of Dickinson *et al.* (1986)) represent a major improvement over the bucket hydrology and fixed surface albedoes of earlier GCMs. However, LSX makes certain simplifying assumptions about vegetation that are biologically unrealistic. For example, LAI, fractional coverage, and other attributes of a given vegetation type are fixed over its full geographic range and do not vary in response to regional differences in temperature, precipitation, or soil nutrient status. Minimum stomatal resistance is fixed at a predetermined value, rather than calculated as a function of atmospheric pCO_2. Many potentially interesting interactions between vegetation and climate cannot be investigated, including reciprocal and interactive changes over time between climate, LAI, and life-form abundance. However, LSX and similar models provide reasonable simulations of land surface albedo, surface roughness, and energy fluxes for the present day (e.g. Sellers & Dorman 1987), which enable us to the investigate first-order climatic effects of vegetation for periods of the geologic past.

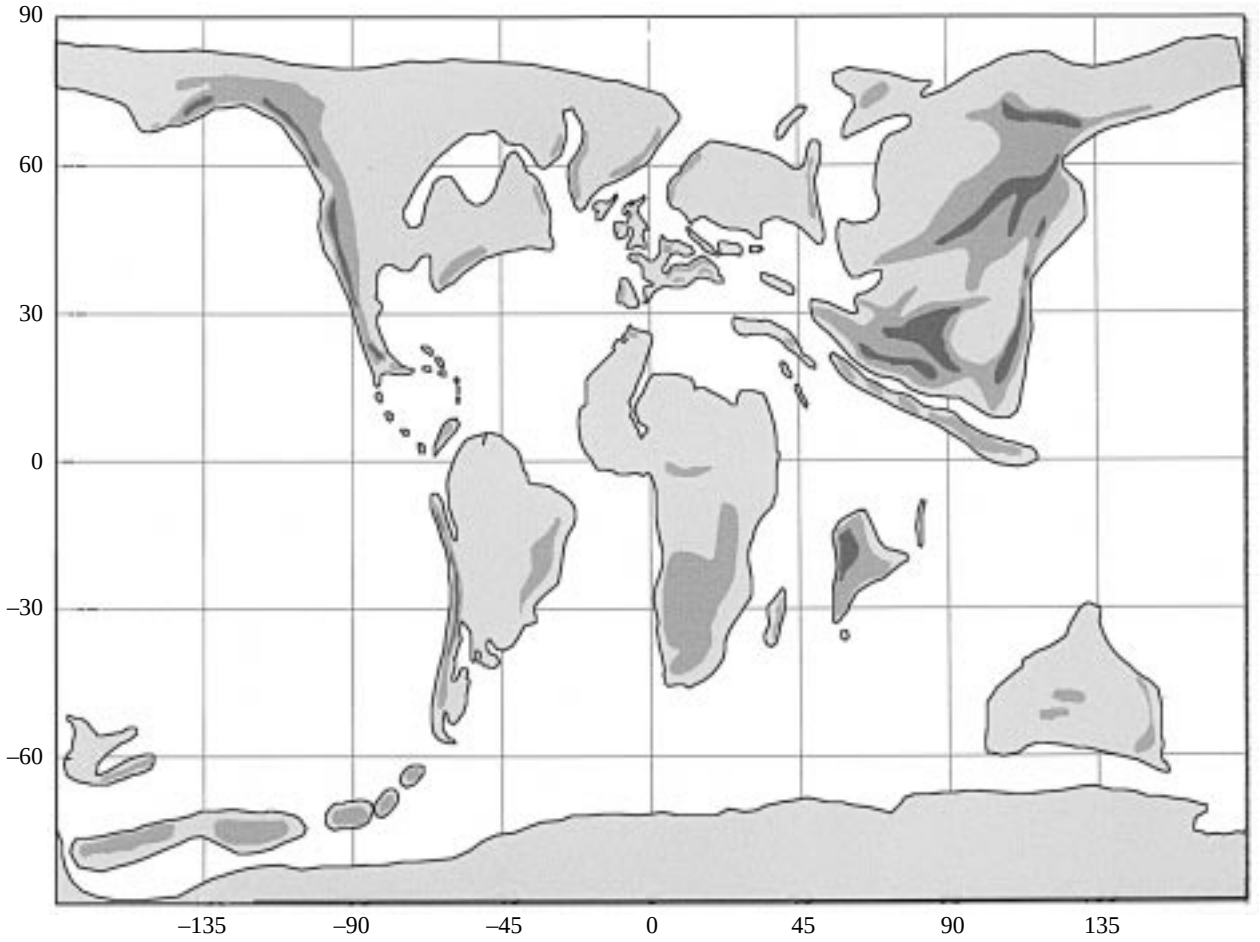


Figure 1. Palaeogeography for the latest Cretaceous (latest Maastrichtian). Lightly stippled areas designate lowlands, medium and dark stippled areas designate highlands.

3. SIMULATIONS

(a) *Boundary conditions*

Prescribed boundary conditions include pCO_2, land–sea distribution, elevation, and solar luminosity. Atmospheric pCO_2 is set at twice pre-industrial levels (580 ppm), a level slightly higher than the 'best estimate' of geochemical models (Berner 1994) and significantly lower than the best estimates of isotopic proxies (Andrews *et al*. 1995; Freeman & Hayes 1992). We set pCO_2 at this conservative figure to keep the high latitudes relatively cool. This allowed us to evaluate more clearly the temperature effects of high-latitude forests with our database of global palaeoclimatic indicators, which maps the position of a few important isotherms instead of providing estimates of mean annual temperature for numerous data sites. Palaeogeography (figure 1) is drawn for the latest Cretaceous (latest Maastrichtian), a time of regression for both the Western Interior seaway of North America and the Trans-Saharan seaway of Africa. Palaeoelevations are set to 250 m for lowlands and 1000 and 2000 m for uplands, a compromise between two palaeogeographic formulas (Hay 1984; Ziegler *et al*. 1985). Solar insolation conforms to present-day solar orbital configuration with the solar constant adjusted to 0.664% less than at present (Crowley & Baum 1992; Endal 1981).

(b) *Model experiments*

For our larger study, we conducted five simulations to explore the sensitivity of Late Cretaceous palaeoclimate to major changes in palaeovegetation. BARESOIL supplies benchmark statistics for a world with no vegetation, and is the boundary condition used in many earlier simulations of Cretaceous climate. Soil texture and colour are set to intermediate values in the range given by BATS, with an average snow-free land albedo of 15% (Dickinson *et al*. 1986). EVERGREEN TREE provides maximum LAI and fractional cover to explore the range of climatic effects exerted by areally widespread forests. Broad-leaved evergreen trees (tropical rainforest) are prescribed over all land surfaces at a fractional coverage of 98%; surface albedo over high-latitude land varies only slightly from 12% in summer to 18% in winter. An additional simulation, EVERGREEN TREE-OHT, adds tripled ocean heat transport to the effects of evergreen forest vegetation, to explore the sensitivity of a fully vegetated Earth to warm Cretaceous polar oceans.

The final two simulations are based on best estimates of vegetation (table 1, figure 1 and below). BESTGUESS uses the best estimate of vegetation based on a variety of lithologic and palaeontologic indicators (figure 2). An individual $2^\circ \times 2^\circ$ land surface grid was coded for a particular vegetation type based on a palaeontologic or

le 1. *Latest Cretaceous vegetation types and their defining features*[*]

biophysical parameters estimated for fossil vegetation represent unweighted averages of values listed for the closest SiB biomes man & Sellers 1989). The exception is our biome 3, which is weighted, as follows, to increase the importance of broadleaf greens: SiB biome (1+1+2)/3. Fractional cover for our biome 3 is based on the weighted average multiplied by 0.8. This ed the more open canopy conditions inferred from foliar physiognomy and *in situ* megafossil assemblages preserved in nic ash (Wing *et al*. 1993; Wolfe & Upchurch 1987).)

e ber	biome name	recognition criteria	closest SiB biomes	canopy height	areal cover	stomatal resistance (s m^{-1})
	tropical rainforest	equatorial latitude plus one or more of the following: coals, megafloras with large leaves and drip tips, tree ferns	1	35 m	0.98	154
	tropical semi-deciduous forest/woodland	tropical latitudes plus the absence of coals and evaporites; calcretes may be present	1, 6	26 m	0.64	160
	subtropical broad-leaved evergreen forest and woodland	middle latitudes; angiosperm dominance in megafloras and palynofloras plus megafloras with small evergreen leaves and few or no drip tips, presence of palms or gingers, fossil wood without growth rings, thick angiosperm leaf cuticles, cold-sensitive fungal taxa	1, 2	30 m	0.72	163
	desert and semi-desert	low and middle latitudes; evaporites, calcretes, or evidence for treeless conditions	9	0.5 m	0.10	855
	temperate evergreen coniferous and broad-leaved forest	high middle latitudes; high relative abundance and diversity of conifers in palynofloras and cuticle assemblages plus numerous probable evergreens in palynofloras and cuticle assemblages, cold-sensitive fungal taxa	4	17 m	0.75	233
	polar deciduous forest	high latitudes; megafloras without tundra leaf form and dominated by deciduous angiosperm and conifer leaves, fossil tree stumps with annual growth rings, at least 2–3 tree genera in pollen record	2, 5	17 m	0.62	206
	bare soil (used to code cold deserts)	calcretes present, associated with extremely low-diversity palynofloras	11	0.05 m	0.00	100

biome numbers correspond to those used in figure 1. Our biome 6, tropical savannah, is not mentioned in the table because grasses do ppear in the fossil record until the Tertiary. SiB refers to the Simple Biosphere Model (Dorman & Sellers 1989; Sellers *et al*. 1986). SiB es are as follows: 1, broadleaf evergreen trees; 2, broadleaf deciduous trees; 4, needleleaf evergreen trees; 5, needleleaf deciduous trees; oadleaf trees with ground cover (tropical savannah, only the upper story used); 9, broadleaf shrubs with bare soil; 11, no vegetation, soil.

logic indicator. For regions where geologic data were nt, output from EVERGREEN TREE-OHT was used escribe vegetation because the output of this simulabest-fit the record of palaeoclimatic indicators. While method of interpolation may seem somewhat circular, onsider it superior to intuition or guesswork. Physical physiological parameters were assigned to each fossil tation type by comparing each with the most similar nt vegetation type and using the parameters for extant tation listed by Dorman & Sellers (1989). When a biome had no extant counterpart, averages of the or three most similar extant biomes were used. No erstory layer was recognized for palaeovegetation use LSX only recognizes grass for the understory. ses do not appear in the fossil record until the Palaeo- (Crepet & Feldman 1991; Muller 1981), while grassland vegetation does not appear in the fossil record until the Miocene–Pliocene (Cerling *et al*. 1994).

BESTGUESS-RS2 is similar to BESTGUESS but it doubles the resistance of leaf stomata to diffusion of carbon dioxide and water vapour. We applied this doubling to all vegetation types to provide a parallel simulation to that of Pollard & Thompson (1995), who simulated modern climates under doubled stomatal resistance to approximate one aspect of future vegetational response to doubled pCO_2. In both studies, stomatal resistance was doubled in the absence of other vegetational changes to isolate the climatic effect of increased stomatal resistance from other changes, such as increased LAI resulting from increased productivity under elevated pCO_2.

Here we expand on the results presented in Otto-Bliesner & Upchurch (1997). We focus on the BARESOIL

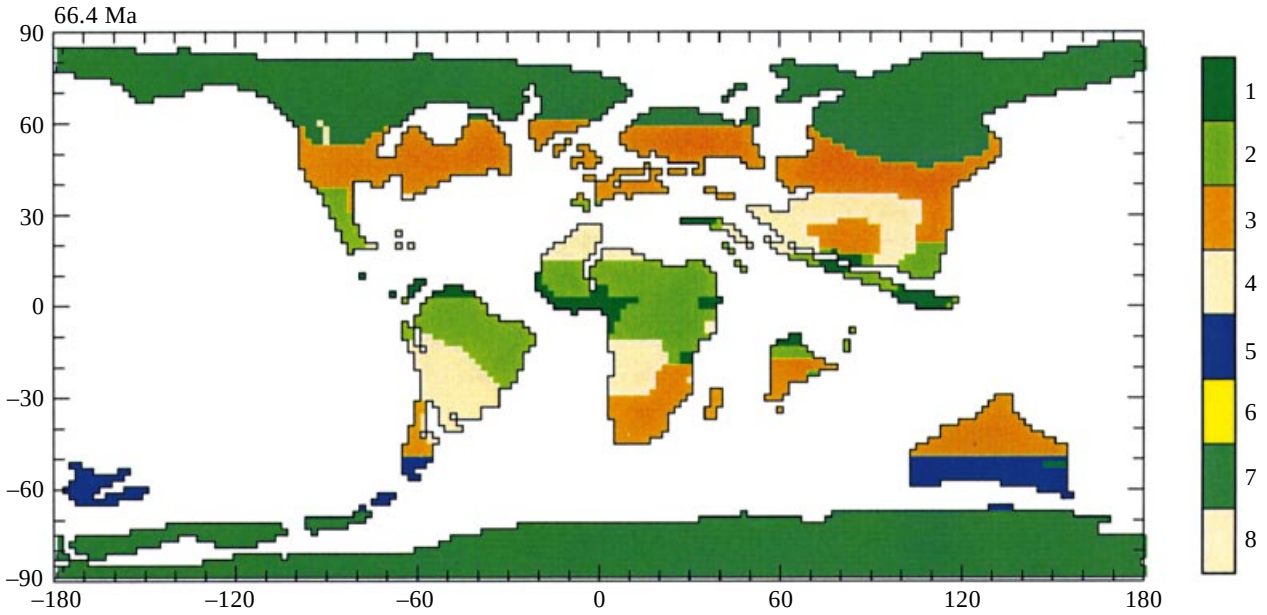


Figure 2. BESTGUESS estimate of Maastrichtian vegetation. Lithologic and palaeontologic indicators were used as primary data, and output from the EVERGREEN TREE-OHT simulation (not reported in this paper) was used to code regions between data points. Vegetation categories and criteria for recognition are explained in table 1. Polar deciduous forest is inferred for Antarctica based on the prevalence of such vegetation at high latitudes in the Northern Hemisphere. Bare soil is used to code for cold deserts with extremely low floristic diversity that are located near the Laramide Front in the Western Interior of North America. Subtropical woodlands have indicators of above-freezing winters such as palms. No Maastrichtian equivalent of Mediterranean woodlands and chaparral is used in BESTGUESS simulations, although some model simulations predict the occurrence of such vegetation in restricted regions. Legend: 1, tropical rainforest; 2, tropical semi-deciduous forest; 3, subtropical broad-leaved evergreen forest and woodland; 4, desert and semi-desert; 5, temperate evergreen broad-leaved and coniferous forest; 6, tropical savannah (not used here); 7, polar deciduous forest; 8, bare soil.

and BESTGUESS simulations to illustrate the important effects of palaeovegetation on global and regional palaeoclimate. A fuller description of other simulations, including the statistical significance of differences between simulations, is provided elsewhere (Upchurch *et al*. 1998).

(c) *Palaeovegetation and palaeoclimatic data*

All simulations were compared with a global data base of palaeovegetation indicators to evaluate the success of each simulation in reproducing the Maastrichtian climate. Palaeobotanical indicators of vegetation and climate include the physiognomy of leaf megafossils (Wolfe & Upchurch 1987), life form as inferred from leaf megafossils and fossil woods (Upchurch & Wolfe 1993), the physiognomy of dispersed leaf cuticles (Upchurch 1995), and the anatomy of fossil woods (e.g. the presence or absence of growth rings) (Creber & Chaloner 1985). Palynologic data were used selectively because of problems associating many palynomorphs with individual life forms. Palynologic indicators employed in this study included (1) the spores of *Sphagnum* moss, which were used an indicator of wet soils; (2) the spores of aquatic ferns, which were used as indicators of ponded water; (3) structurally complex spores and pollen of tree ferns and palms, which were used as indicators of above-freezing conditions; and (4) the presence of at least two or three genera of pollen whose extant relatives comprise trees, which were used as evidence for forest vegetation.

Global palaeobotanical data were particularly useful in reconstructing two isotherms that delimit vegetation boundaries: (1) a warm-month mean of 10 °C, which delimits the boundary between forest and tundra vegetation (Köppen 1936; Wolfe 1979), and (2) a cold-month mean of 1 °C, which is the lowest monthly mean temperature that delimits the boundary between vegetation with freeze-sensitive life forms and vegetation dominated by freeze-tolerant life forms (Wolfe 1979). Warm-month means higher than 10 °C were documented by indicators of the tree growth habit, including fossil woods greater than 10 cm in diameter, leaf megafossil assemblages with physiognomy indicative of forest (rather than tundra) vegetation (Bailey & Sinnott 1916), and the presence of at least 2–3 genera of fossil pollen whose living relatives comprise trees. Cold-month means of greater than 1 °C were documented by fossil organisms whose life form and physiology make them susceptible to hard freezes. These organisms include (i) fossil palms, tree ferns, and evergreen cycads, which have the freeze-sensitive rosette tree or rosette shrub growth habit (Box 1981); (ii) epiphyllous fungi (Loculoascomycetes belonging to the genus *Trichopeltinites*), which are sensitive to below-freezing temperatures (Dilcher 1965); and (iii) woods that have no growth rings, which indicate poorly developed dormancy mechanisms (Creber & Chaloner 1985).

The location of the forest–tundra boundary and the line of hard freezing were emphasized in model evaluation because these vegetation boundaries are best predicted by temperature, rather than moisture availability (Köppen 1936; Wolfe 1979). This is because vegetation boundaries during the Late Cretaceous probably were delimited by different precipitation values than those of the Recent due

hanced water-use efficiency of Late Cretaceous plants r elevated pCO_2. We make this uniformitarian mption with the caveats that (1) the effect of elevated $_2$ on physiological processes at low temperatures is well understood; and (2) the temperature parameters delimited vegetation during the Late Cretaceous may been somewhat different from those of today ause of elevated pCO_2 and the evolutionary status of aceous floras.

diment types supplemented palaeobotanical data and particularly important in the tropics and in regions y climates. Coals served as indicators of wet soils and -round rainfall (Ziegler *et al.* 1987), and in equatorial ns served as an indicator of tropical rainforest rrell 1991). Evaporites and calcretes served as indica- of seasonal or annual moisture deficit (Ziegler *et al.*), with evaporites tentatively associated with arid itions and calcretes associated with seasonally dry itions. Approximately 500 individual citations of plants and sediment types were used in recon- ting late Maastrichtian global vegetation and ate. The most important of these citations are plotted aps in this paper and are provided as supplementary mation in Otto-Bliesner & Upchurch (1997) and as ppendix in Upchurch *et al.* (1998).

ESULTS OF SIMULATIONS

BARESOIL and BESTGUESS surface temperatures (figures 3–7; table 2)

the BARESOIL simulation, January surface air eratures (temperatures simulated at 2 m above the ce) are warmer than for the present day, but still are emely cold at high latitudes in the Northern Hemi- re. The freezing isotherm extends equatorially to 45° er North America and 38° N over eastern Asia. The ern Interior Seaway of North America is almost letely frozen, and temperatures as low as −34 °C modelled over the Asian interior. Mean cold-month ce temperatures for most of Europe are below ing. Surface temperatures in Antarctica and Australia bove freezing during the austral summer. Antarctica no permanent ice cover because all snow cover melts ng the summer months. Mean surface temperatures uly are well below zero over Antarctica, and sea-ice es the continent. Subfreezing temperatures also r over the southern portions of Australia.

both hemispheres, cold winter temperatures at high ades result from extensive snow cover and its high ctivity. Mean land surface albedo ranges from 0.39– with values as high as 0.84 during the winter. Mean cal temperatures range from 25–35 °C. Global mean ce temperature in the BARESOIL simulation is °C, one degree warmer than what the model predicts he present day (14.8 °C).

he late Maastrichtian land surface in BESTGUESS is red with vegetation types that vary from tropical forest to cold desert (figure 2). Tropical rainforests are icted in areal distribution relative to the Recent and r in Colombia, central Africa, Somalia, and south- Asia. Deserts and semi-deserts occur over large areas entral Asia, South China, northern Africa, south- rn Africa, and central South America. Tropical deciduous forests are inferred to have occupied most regions between tropical rainforest and desert vegetation.

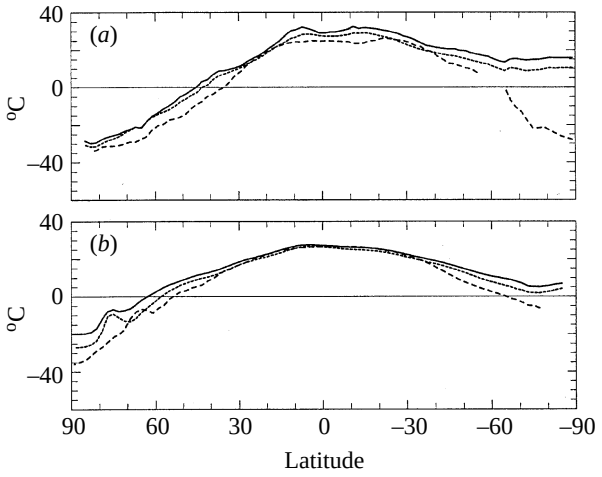


Figure 3. Zonally averaged surface temperature (at a height of 2 m) simulated by the GENESIS climate model in January for (*a*) land and (*b*) ocean. The solid line (top line) is the BESTGUESS simulation and the dotted line (middle line) is the BARESOIL simulation. The dashed line is the present-day control simulation.

Mid- and high-latitude vegetation types show strong poleward displacement relative to their Recent counterparts. Warm-temperate to subtropical evergreen forests and woodlands with cold-sensitive plants such as palms occur over most mid-latitude regions as far poleward as 50° latitude. Poleward of 50° N in the Northern Hemisphere, these evergreen forests/woodlands are replaced by polar deciduous forest, which occupies extensive regions of Canada, Alaska, and Siberia. Poleward of 50° S in the Southern Hemisphere, these evergreen forests are replaced by temperate evergreen coniferous and broad-leaved forests. These forests, which occur in northern Australia, New Zealand, and the Antarctic Peninsula, are similar in their inferred physiognomy and floristic composition to Recent forests of New Zealand. Deciduous forests are inferred to have been present on mainland Antarctica, but direct evidence for their existence is lacking because relevant geologic strata are covered with glacial ice.

In the BESTGUESS simulation, surface temperatures at high latitudes are warmer, most notably during the summer. January land surface temperatures are up to 2–4 °C warmer over high northern latitudes (e.g. Siberia, Alaska), and the average position of the 1 °C isotherm shifts somewhat poleward (figure 11). Subfreezing temperatures still exist over the northern interior regions of North America and Asia. January temperatures over Siberia are as much as 8 °C cooler in BESTGUESS relative to BARESOIL; the reason for this cooling requires further study. July surface temperatures are up to 8 °C warmer over high northern latitudes. The Antarctic interior is 4–8 °C cooler in the BESTGUESS simulation, although this cooling of the Antarctic interior is generally not statistically significant. Mean tropical surface temperature warms by 1.5 °C, with regions of semi-deciduous forest in Africa and South America warming by as much as 4 °C. This warming results from a decrease in albedo and a corresponding increase in absorbed solar radiation. Global mean surface temperature warms by

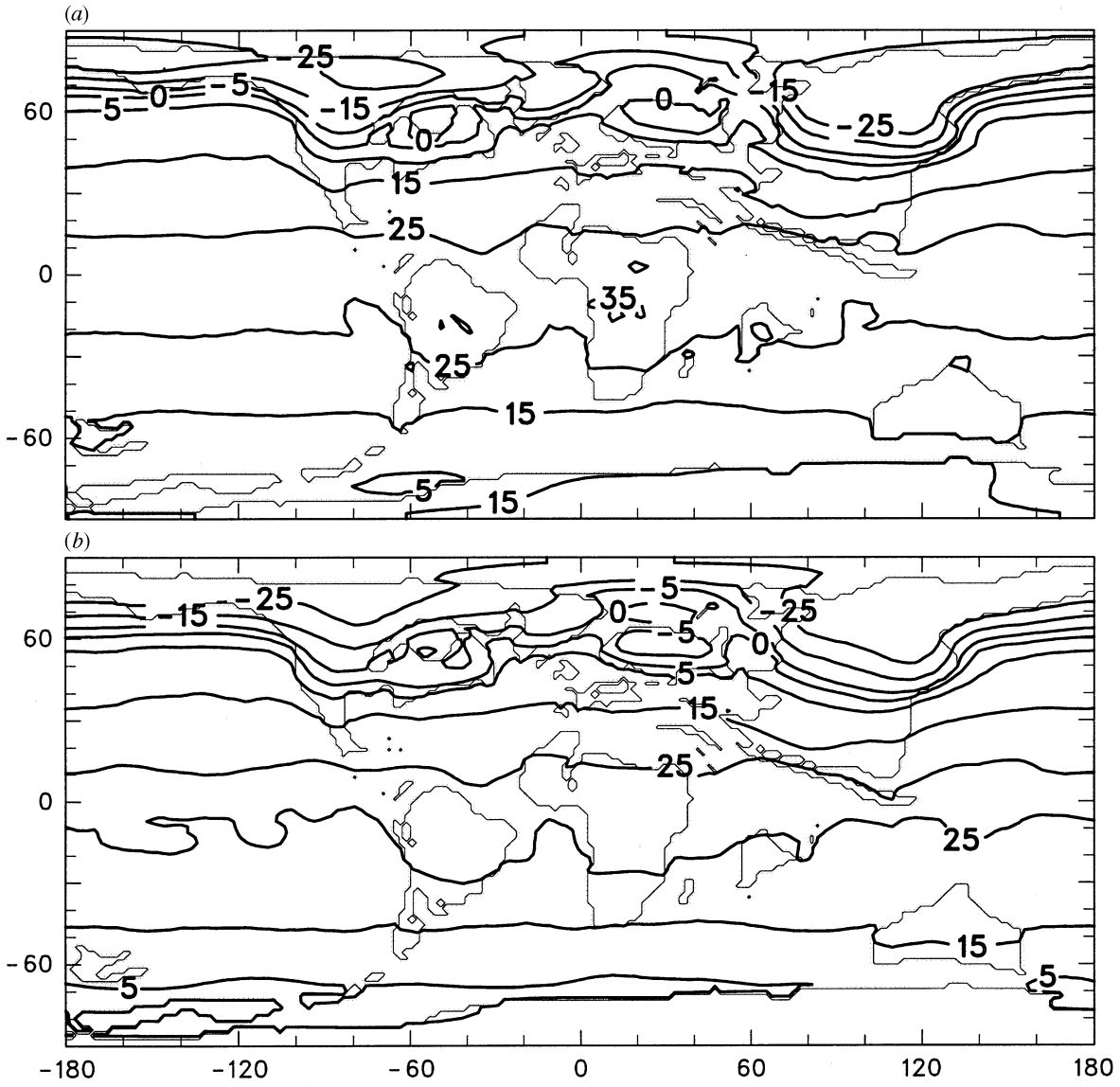


Figure 4. January mean surface air temperature (°C) for (*a*) BESTGUESS and (*b*) BARESOIL simulations.

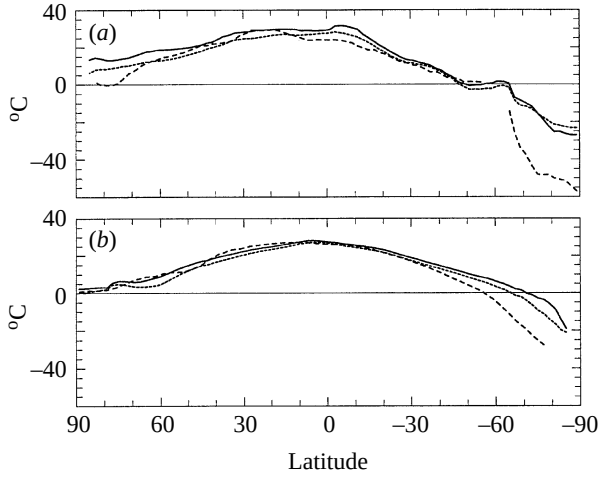


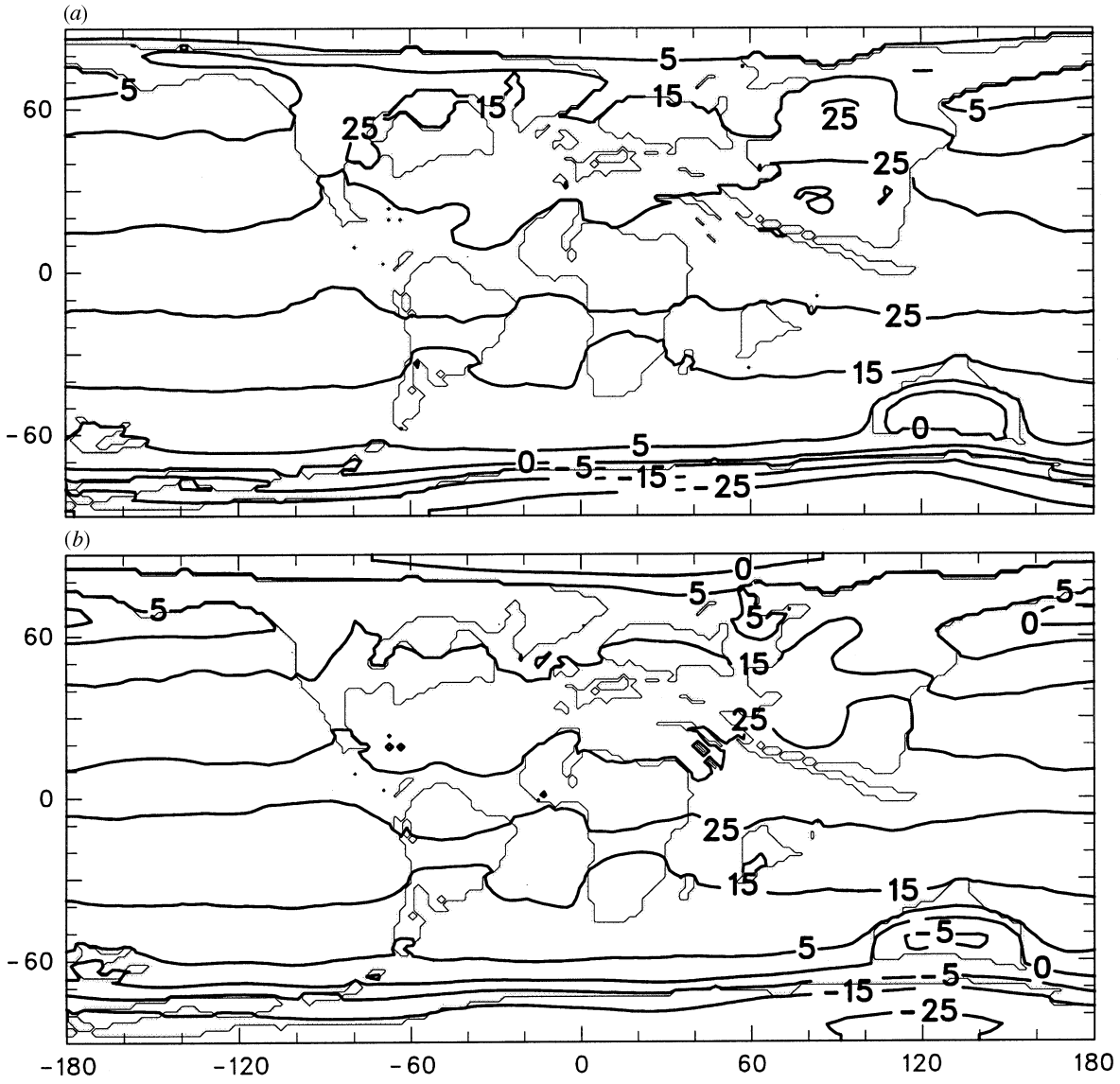
Figure 5. Zonally averaged surface temperatures (°C) in July for (*a*) land and (*b*) ocean. The solid line is the BESTGUESS simulation and the dotted line is the BARESOIL simulation. The dashed line is the present-day control simulation.

2.2 °C to a value of 18.0 °C in a late Maastrichtian world covered with realistic vegetation.

Terrestrial vegetation causes significant changes in ocean temperature. Surface temperatures over tropical and mid-latitude oceans warm by up to 4 °C in the BESTGUESS simulation because energy is transferred from land to the adjacent ocean. High-latitude oceans warm by as much as 12 °C, resulting in substantially lower fractional coverage of sea-ice in BESTGUESS relative to BARESOIL (0.06 verus 0.17 in the Southern Hemisphere and 0.23 versus 0.38 in the Northern Hemisphere). The average winter sea-ice position moves poleward from 60° N to 65° N in January and from 65° S to 73° S in July.

(b) *The surface energy budget at high latitudes (figures 8–9)*

The presence of forest vegetation at high latitudes initiates feedbacks between albedo, surface temperature, and snow and ice cover that result in a much warmer climatic regime. This is dramatically illustrated by a comparison of the BARESOIL and BESTGUESS simulations for regions



re 6. July mean surface air temperature (°C) for (*a*) BESTGUESS and (*b*) BARESOIL simulations.

)0° N. Vegetation reduces land surface albedo year-
d, especially from January through June when inci-
solar radiation is increasing at high northern
ıdes. From late winter to early spring, the trees
ally mask the snow on the ground and absorb more
ning radiation because of their lower albedoes. In
spring to early summer, surface albedoes are lower,
forest vegetation occurring due to earlier spring
ing of snow cover and the presence of leaves on the
. Fractional snow cover for May is only 50% in the
TGUESS simulation, but remains greater than 80%
ıe BARESOIL simulation, even for June. The net
t of the lower surface albedoes is to allow more solar
ıtion to be absorbed at the land surface in the BEST-
SS simulation (78% more than in the BARESOIL
lation for April to June).

r high northern latitudes, changes in the other
ponents of the surface energy budget moderate the
ınse of the vegetated land surface to changes in
rbed solar radiation. In late winter to early spring,
ncreases in absorbed solar radiation in BESTGUESS are largely offset by (1) increased surface cooling due to enhanced longwave radiation, and (2) decreased transfer of sensible heat from the atmosphere to the land surface. From April to June, however, vegetation increases absorbed solar radiation by an average of 65 W m^{-2}, an increase that is only partially offset by increased energy fluxes from the land surface. The result is an average net energy gain of 6 W m^{-2}, which produces warmer surface temperatures and faster snow melt. Average land surface temperature from 60–90° N in BESTGUESS rises above freezing by mid-April and above 10 °C by late May, and remains above freezing until late October. In contrast, average land surface temperature from 60–90° N in BARESOIL rises above freezing in early May, reaches a maximum of 10 °C in early July, and falls below freezing by late September.

A portion of the extra energy absorbed by vegetated land areas is advected to nearby high-latitude oceans, which initiates feedbacks between surface temperature, ice cover, surface albedo, and the surface energy budget. In BESTGUESS, the average ocean temperature from

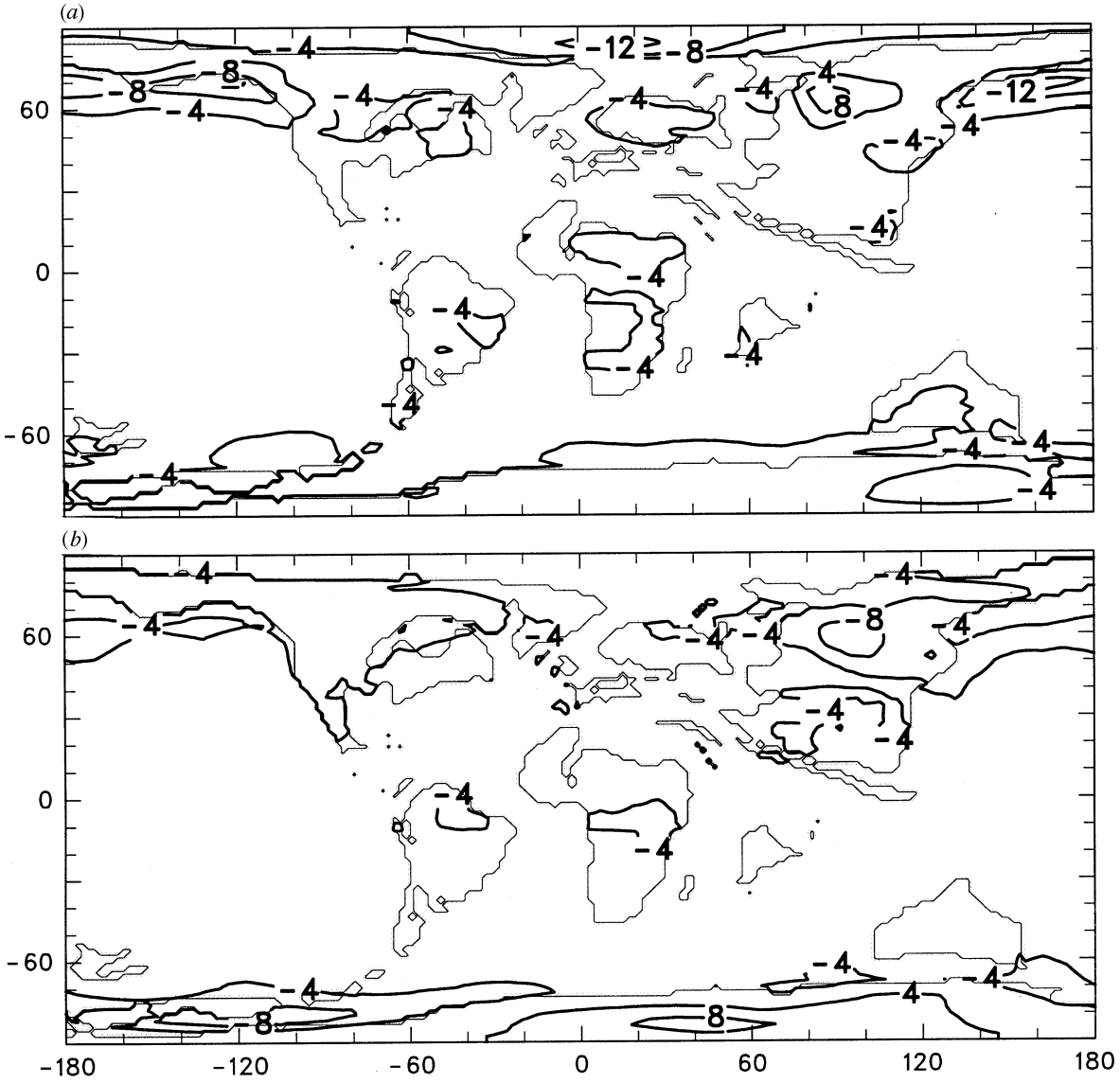


Figure 7. Changes in surface air temperature (°C) for (*a*) January BARESOIL minus BESTGUESS, and (*b*) July BARESOIL minus BESTGUESS. Negative values mean that the BESTGUESS simulation was warmer than the BARESOIL simulation, while positive values indicate that the BESTGUESS simulation was colder.

60–90° N falls below freezing (−2 °C) for only four months, rather than six months as in BARESOIL. Average fractional coverage of sea-ice in BESTGUESS exceeds 50% only from mid-February to early May. This causes large decreases in ocean surface albedo relative to BARESOIL from April to June and large increases in absorbed radiation. The result of these changes is a net warming of oceans, which inhibits the development of sea-ice during the subsequent autumn and winter. Ocean warming, in turn, ameliorates winter temperatures on land, especially for regions immediately adjacent to the coast (figure 7*a*,*b*).

(c) *Regional variation in climate (figure 10)*

The Köppen system correlates Recent vegetation with climate using monthly mean temperature and precipitation. For the Late Cretaceous, when elevated pCO_2 may have altered the climatic tolerances of individual life forms and vegetation types, the Köppen system provides a simple and convenient means of visualizing regional climatic variation. The GENESIS climate model accurately reproduces the modern-day distribution of Köppen climate types, especially the boundary between warm-temperate (C), cool-temperate (D), and tundra (E) climates. Regional features, such as rain-shadow deserts and the Indian monsoon, are inadequately simulated because of model-smoothing of mountain topography. This deficiency is not critical for evaluating latitudinal variation in climate. Our comparison here is based on a modified Köppen system where the boundary between warm-temperate (C) and cool-temperate (D) corresponds to a cold-month mean of 1 °C (Wolfe 1979), rather than −8 °C (Köppen 1936), and the boundary between subtropical (Cfa) climates with angiosperm-dominated vegetation and marine (Cfb, Cfc) climates with conifer-dominated vegetation is set at a warm-month mean of 20 °C, based on the temperature parameters of Recent forests in east Asia (Wolfe 1979).

The BARESOIL and BESTGUESS simulations contrast markedly with each other and with the present day. In BARESOIL, tropical rainforest (Af) is restricted to small regions in Colombia, west Africa, India, and south-east Asia. Marine climates (Cfb, Cfc) with cool

le 2. *Simulated mean annual climate statistics*

rages for years 14–20 of the BARESOIL and TGUESS simulations. All Cretaceous simulations use $_2$ of 580 ppm, or twice the pre-industrial value. perature values are for 2 m above the land or ocean ce. The Bowen ratio is the ratio of sensible to latent heat

iment	BARESOIL	BESTGUESS
ce temperature (°C)		
bal	15.8	18.0
–90° N	−5.5	−1.4
° N–15° S	26.1	27.6
–90° S	−0.8	2.6
60–90° N		
al cloudiness	0.65	0.63
face albedo	0.40	0.19
face absorbed ar radiation (W m^{-2})	72.1	93.1
surface infrared diation (W m^{-2})	33.1	41.1
face sensible at flux (W m^{-2})	5.8	12.8
face latent at flux (W m^{-2})	32.6	39.2
wen ratio	0.16	0.36
face temperature (°C)	−7.5	−3.3
ctional snowcover	0.62	0.52
60–90° S		
al cloudiness	0.70	0.69
face albedo	0.39	0.18
face absorbed ar radiation (W m^{-2})	64.8	84.0
surface infrared diation (W m^2)	30.5	37.7
face sensible at flux (W m^{-2})	4.7	9.4
face latent at flux (W m^{-2})	29.7	37.2
wen ratio	0.14	0.26
face temperature (°C)	−5.8	−2.5
ctional snow cover	0.63	0.52
60–90° N		
face temperature (°C)	−3.3	0.7
fraction	0.38	0.23
60–90° S		
face temperature (°C)	1.8	5.3
fraction	0.17	0.06
15° S15° N		
face temperature (°C)	25.8	26.9

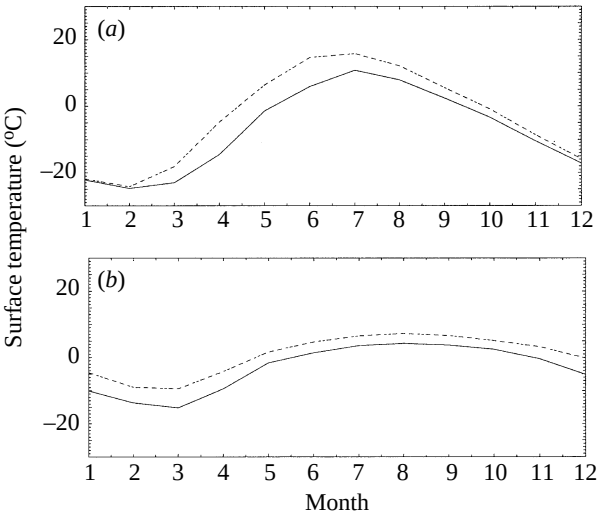


Figure 8. Annual cycle of surface temperature for BESTGUESS (dashed lines) and BARESOIL (solid line) simulations. Month 1 is January. (*a*) Land areas from 60–90° N. (*b*) Ocean areas from 60–90° N.

mers, mild winters, and evergreen forests cover hern Africa, southern South America, and the hern margins of Europe and North America. Cool-perate (D) climates with below-freezing winters and d-leaved deciduous or boreal forests cover much of h America, Asia, and Antarctica. Tundra (ET) is icted for much of Asia and coastal regions of North rica and Antarctica.

BESTGUESS, tropical rainforest climate increases eal extent in South America, south-east Asia, India, east Africa, and replaces 'savannah-type' (Aw) climate in southern Mexico and west Africa (Somalia). Subtropical (Cfa) climates replace marine climates (Cfb, Cfc) in North America and Europe because of warmer summer temperatures. Marine climates migrate poleward and replace cool-temperate (D) climates in Europe, North America, and New Zealand, while cool-temperate climates migrate poleward and replace tundra (ET) climates in the Arctic and Antarctic. Lowland tundra is greatly restricted in areal extent and occupies just a few grid cells along the fringes of the Arctic Ocean.

5. COMPARISON OF SIMULATIONS AND PALAEOCLIMATIC INDICATORS

Comparison of the BARESOIL and BESTGUESS simulations with the global distribution of palaeoclimatic indicators demonstrates that inclusion of forest vegetation improves correspondence between simulated and actual palaeoclimate. The BARESOIL simulation (figure 10*a*) incorrectly predicts tundra (ET) climates for large regions of Alaska, Siberia, and coastal Antarctica, regions where fossil assemblages indicate forests (and hence warm-month means higher than 10 °C). The areal distribution of tropical rainforest is also underestimated relative to proxy data, especially for Africa. In contrast, the BESTGUESS simulation (figure 10*b*) shows a much better fit, with indicators of forest vegetation. Forest vegetation is correctly predicted for Siberia, Alaska, and the southern Antarctic Peninsula, in contrast to BARESOIL. This improved correspondence between model output and indicators of forest vegetation indicates that the presence of trees causes warm-month means to exceed 10 °C and creates the conditions needed for the persistence of forest vegetation. Tropical rainforest sites are better predicted by the BESTGUESS simulation than by the BARESOIL simulation, a result that parallels model simulations for the Recent tropics (Dickinson & Henderson-Sellers 1988; Shukla *et al*. 1990). For the Recent tropics, replacement of tropical rainforest by grasslands creates hotter and drier

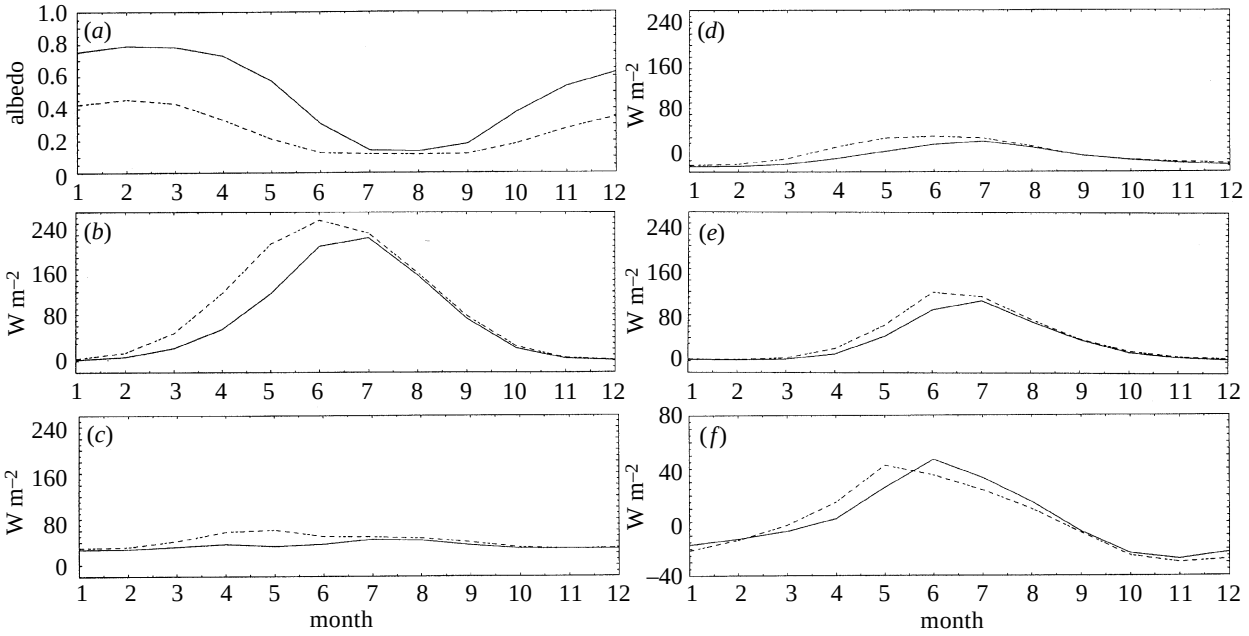


Figure 9. Annual cycle of the surface energy budget for land areas 60–90° N, BESTGUESS (dashed lines) and BARESOIL (solid lines) simulations. (*a*) Surface albedo, (*b*) surface absorbed solar radiation (W m^{-2}), (*c*) net surface infrared radiation (W m^{-2}), (*d*) surface sensible heat flux (W m^{-2}), (*e*) surface latent heat flux (W m^{-2}), (*f*) net surface heat flux (W m^{-2}).

conditions. These results mean that the presence of trees in equatorial regions can help to create the climatic conditions that favour the persistence of tropical rainforests.

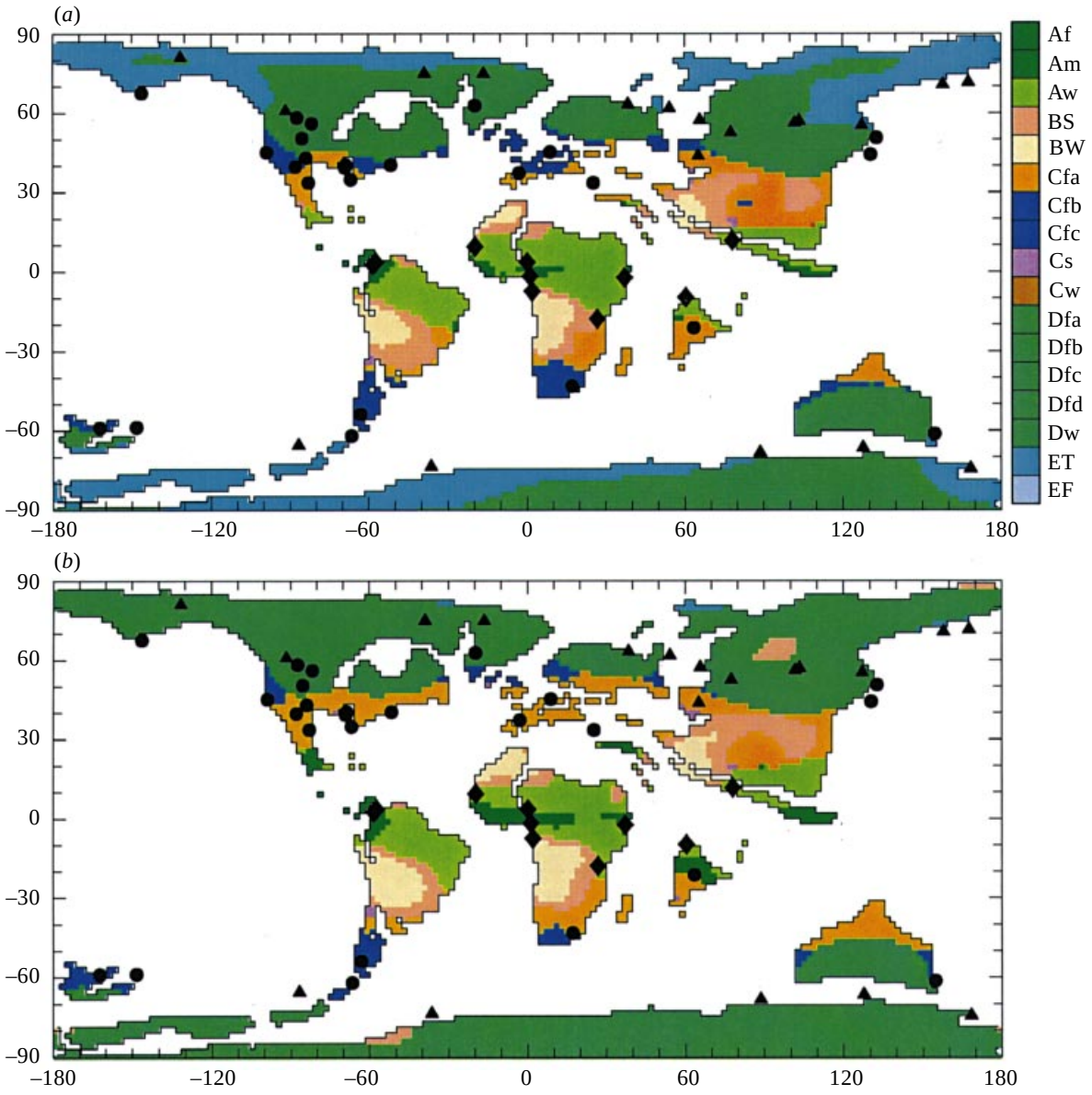
Greater discrepancies exist between model simulations and proxy data for middle latitudes. Simulated climates for latitudes between 35° and 55° are too cool to support the warm-temperate to subtropical broad-leaved vegetation prescribed in the BESTGUESS run. Palaeobotanical indicators of above-freezing winter temperatures conflict with predicted cold-month means in continental interiors at high middle latitudes (figure 11). Cold-month means of 5 °C and 1 °C, which predict the occurrence of biologically significant freezing on a global scale (Prentice *et al.* 1992) and in East Asia (Wolfe 1979), respectively, occur as much as 15° south of above-freezing indicators in all simulations in the Northern Hemisphere. Indicators of above-freezing winters are diverse, and include palms and gingers which cannot tolerate below-freezing cold-month means and prolonged exposure to hard freezes (Box 1981; Wing & Greenwood 1993). Also indicative of above-freezing conditions are Greenland leaf assemblages with inferred mean annual temperatures greater than 20 °C (lower Atanikerdluk leaf assemblages) (Wolfe & Upchurch 1987). Modern climates with mean annual temperatures greater than 20 °C always have cold-month means that are well-above freezing (Wolfe 1979, plate 2).

6. DISCUSSION

Our simulations indicate that forest vegetation played an important role in maintaining high-latitude warmth during the Late Cretaceous, and underscore the importance of vegetation as an active agent of global climate change. The presence of high-latitude deciduous forests significantly decreases albedo and significantly increases fluxes between the land surface and the atmosphere. Changes in albedo are greater than changes in surface fluxes, and result in a net warming of the land surface. Warming occurs year-round but is most pronounced in late spring and summer during maximal solar insolation. This causes an increase in summer temperatures and a lengthening of the growing season to a point at which the local climate is favourable to forest vegetation.

Previous authors have suggested that vegetation has properties that alter climate and ensure its persistence on the landscape. In a study of the grassland–forest boundary, Woodcock (1992) suggested that grassland vegetation helps to maintain dry conditions and a propensity to burning through its relatively high albedo, low LAI, and high production of leaf litter. This reduces rainfall through reduced evapotranspiration and reduced absorption of solar radiation and creates conditions favourable to the ignition of fires. Forest vegetation, in contrast, helps to maintain wetter conditions and a lower propensity to burning through its low albedo, high LAI, and low production of leaf litter relative to stem material. This increases rainfall through increased evapotranspiration and increased absorption of solar radiation, and creates conditions less favourable to the ignition of fires. Bonan *et al.* (1995) compared the climatic effects of evergreen boreal coniferous forest and tundra vegetation. Their results indicate that evergreen boreal conifer forests create feedbacks with the climate that regulate surface temperature and help create the climatic conditions necessary for their existence.

Our simulations provide additional evidence that albedo, LAI, and other attributes of forest vegetation help to create the climatic conditions that favour the persistence of forests on the landscape. At high latitudes, this property of forest vegetation is markedly illustrated by a comparison of the BARESOIL and BESTGUESS simulations. Here, the presence of temperate deciduous forests



re 10. Predicted climates and the distribution of forest/woodland vegetation under (*a*) BARESOIL and (*b*) BESTGUESS lations. Climates correspond to the modified Köppen scheme described in the text (Köppen 1936). The humid–subhumid dary has been altered to account for overestimation of precipitation in GENESIS v. 1.02. Tundra (ET) and boreal (D) forests eparated by a warm-month mean temperature of 10 °C; subtropical (Cfa) and marine (Cfb, Cfc) climates are separated by a n-month mean temperature of 20 °C; warm-temperate (C) and cool-temperate (D) climates are separated by a cold-month of 1 °C. The basis for inferring forest and woodland vegetation is explained in the text. Diamonds, tropical forest; circles, opical forest; triangles, cool-temperate (deciduous) forest.

es an increase in summer temperatures, and a length- g of the growing season beyond the threshold needed ree growth. Late Cretaceous deciduous forests of high udes, like Recent evergreen boreal forests, helped re their own persistence on the landscape because of low albedoes resulting from high LAI, high frac- l cover, and masking of snow cover.

ata on vegetation cover for the latest Cretaceous cs are sparse, but our simulations indicate that indivi- tropical forest types also may have altered regional ate in a manner favourable to their own persistence. ical rainforest vegetation shows a greater areal extent e BESTGUESS simulation than in the BARESOIL lation. Regions of tropical deciduous vegetation show change in areal distribution between simulations, but have surface temperatures that are as much as 4 °C higher in the BESTGUESS simulation relative to the BARESOIL simulation. This increase in surface temperature results from a decrease in albedo, which causes a corresponding increase in absorbed solar radiation. Increased heating of the land surface in the absence of compensatory changes increases drought stress on vegetation, which decreases the adaptive advantage of tropical rainforest life forms relative to those of drier and hotter climates (Box 1981).

Our model simulations demonstrate important climatic linkages between the land surface, atmosphere, and oceans at high latitudes. These indicate that forest vegetation may be an important factor in maintaining ice-free conditions at high latitudes, a critical factor in maintaining warm polar temperatures during geologic intervals such as the

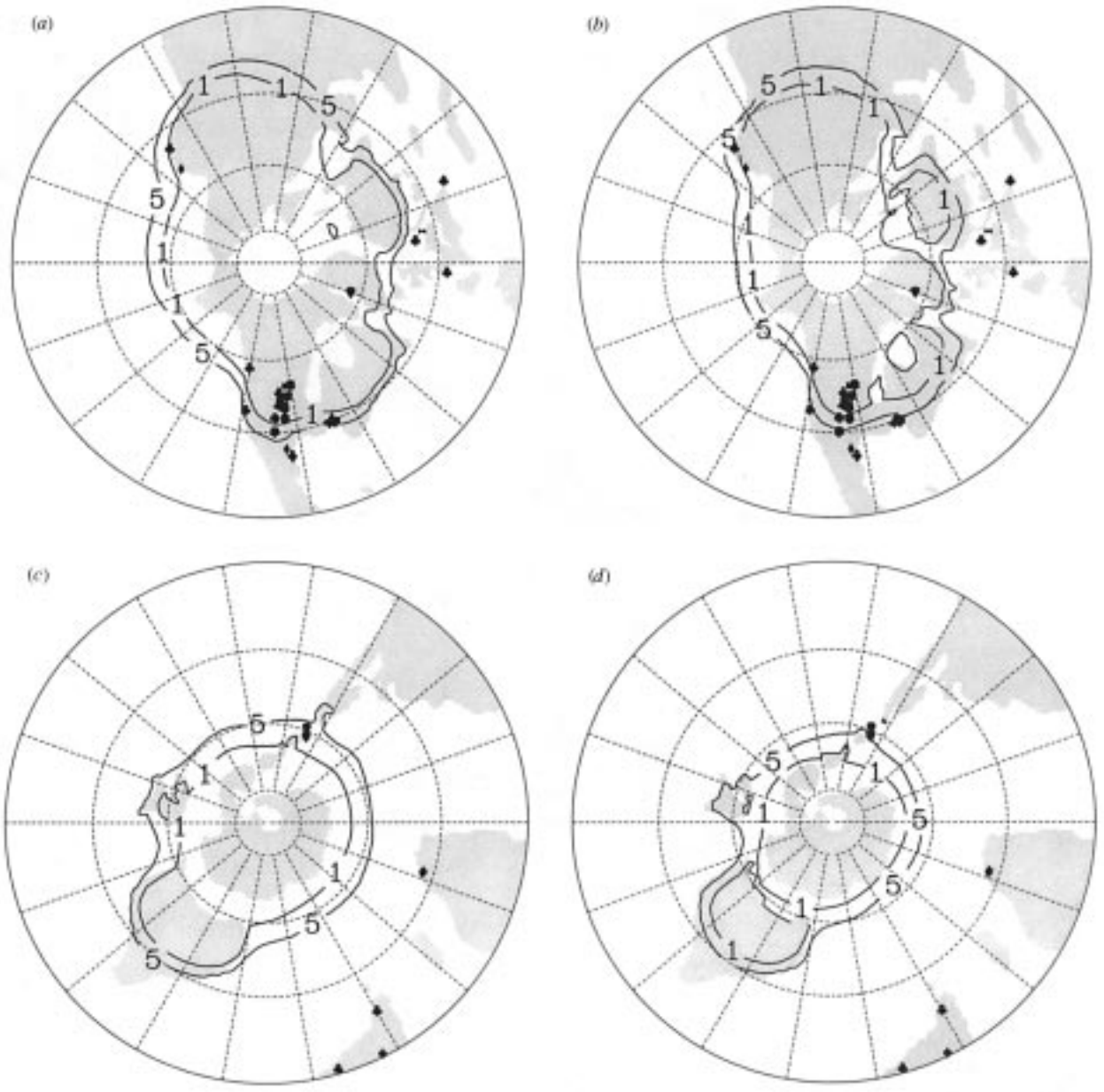


Figure 11. Predicted distribution of 1 °C and 5 °C cold-month means and the distribution of above-freezing palaeobotanical indicators, Northern and Southern Hemispheres. (*a*) BARESOIL, Northern Hemisphere (January), (*b*) BESTGUESS, Northern Hemisphere (January), (*c*) BARESOIL, Southern Hemisphere (July), (*d*) BESTGUESS, Northern Hemisphere (July). Note how the above-freezing indicators extend poleward of the simulated isotherms in the Western Interior of North America and in Greenland.

Cretaceous (Rind & Chandler 1991). High-latitude forests, with their low surface albedo relative to bare soil, warm adjacent oceans by as much as 12 °C. The first steps in this process are (1) increasing land surface temperatures; (2) transferring heat from the land surface to the atmosphere; and then (3) transferring heat from the atmosphere to the oceans. The extra heat transferred from the atmosphere to the oceans initiates a series of positive feedbacks that result in additional warming. Ocean warming causes a delay in the formation of sea-ice in winter and a reduction in its thickness and fractional cover. This causes sea-ice to melt faster and earlier in the spring because of its reduced thickness and fractional cover. Earlier melting of sea-ice allows greater ocean warming during the spring and summer, which further inhibits sea-ice development during the autumn and winter. Inhibition of sea-ice development lowers the average albedo of the ocean and causes the ocean to absorb more solar radiation.

7. CONCLUSIONS

High-latitude deciduous forests played an important role in maintaining polar warmth during the latest Cretaceous. The presence of high-latitude deciduous forests in model simulations warms temperatures relative to bare soil conditions and creates the necessary warmth for the persistence of trees rather than tundra herbs. This warming occurs by a decrease in albedo of forest vegetation relative to bare soil, and a corresponding increase in absorbed solar radiation. Much of the extra energy

rbed by the land surface is transferred to adjacent ns, which initiates a series of positive feedbacks that n the oceans and land climate.

ne combined success and failure of our climate simula- in recreating latest Cretaceous terrestrial climate ies that several mechanisms probably acted in ert to create the warm conditions of the Late Cretac- and other periods of high global temperature. eased atmospheric pCO_2 increased absorption of red radiation, both directly and through its effect on spheric water vapour, a potent greenhouse gas. lly extensive polar forests increased absorption of radiation at high latitudes and warmed temperatures -round. Increased ocean (and atmospheric?) heat sport may have increased high-latitude winter peratures while simultaneously preventing the tropics overheating under strong greenhouse forcing. Posi- feedbacks between the land, ocean, and atmosphere ier increased high-latitude temperatures. A multi- anism model with positive feedbacks is intuitively aling and explains many seemingly unrelated ndary conditions for the Late Cretaceous. However, ltimate validity of this hypothesis will be determined ture modelling studies performed in conjunction with stringent comparisons of model output and the eoclimatic record.

hank S. Thompson and D. Pollard for providing us with the ESIS climate model, and E. Becker and T. Morgan for assis- with graphics. Research was supported by the Texas Higher ation Coordinating Board Advanced Research Program, t 3615-029, and by a Southwest Texas State University rch Enhancement Grant. Computer simulations were per- ed at the University of Texas Center for High-Performance puting and the National Center for Atmospheric Research, is supported by the US National Science Foundation.

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Discussion

T. LENTON (*School of Environmental Sciences, University of East Anglia, Norwich, UK*). Could part of the reason that your model gives high-latitude winter temperatures that are too cold be that you cannot iterate the warming effect of forest, which might cause it to spread further?

G. UPCHURCH. Our simulation of winter temperatures is too cold for at least three reasons. First, our BESTGUESS simulation prescribes winter-deciduous trees for the Arctic and much of the Antarctic. This prescription is based on extensive palaeobotanical evidence for widespread polar deciduous forest during the Late Cretaceous. Prescribing a vegetation of dense evergreen trees, as we did in our EVERGREEN TREE simulation, increases winter warming because the snow blows off green leaves in the canopy. The exposed green leaves effectively mask the snow, which decreases albedo and increases absorbed solar radiation. Polar deciduous forests have no leaves during the winter, so winter albedo in BESTGUESS is higher than that in EVERGREEN TREE because bare stems provide less masking of snow cover.

Second, even with a prescribed vegetation of evergreen trees our model cannot transport sufficient heat to the poles to explain the record of winter-temperature proxies, especially cold-sensitive plants at high middle latitudes. This could result from inadequacies in the GENESIS atmospheric model. Alternatively, it could result in our underestimating ocean heat transport, which is prescribed at modern-day values in four of our five simulations. Increasing ocean heat transport increases high-latitude warming beyond the effects of vegetation. The importance of increased ocean-heat transport is currently unclear because ocean modellers do not yet agree on whether Cretaceous oceans actually transported greater amounts of heat than Recent oceans and, if so, exactly how.

Finally, we could have prescribed levels of atmospheric pCO_2 in our simulations that were much lower than the actual values for the latest Cretaceous. Our prescribed levels (580 ppm) are higher than Bob Berner's best estimate from geochemical modelling but are significantly lower than estimates from isotopic proxies, which place the value as high as 1400–1500 ppm.

P. VALDES (*Department of Meteorology, University of Reading, UK*). Much of the data on warm winters is for coastal sites, especially for those regions where the 'all soil' model differs from the 'realistic vegetation' model. What is the importance of ocean heat transport?

G. UPCHURCH. Enhanced ocean heat transport, if it existed during the Late Cretaceous, would help solve the problem of winter warmth at high latitudes, especially for coastal regions where most of the temperature proxies are located.

ur opinion, however, proponents of enhanced ocean heat sport have yet to prove their case. Stronger surface ls on the ocean, one possible mechanism of enhancing transport, are not likely based on the wind fields in our lations. Generation of warm saline bottom water, the commonly proposed mechanism for enhancing ocean transport and creating warm polar oceans, is plausible has yet to be demonstrated conclusively through either geologic record of isotopic proxies or ocean general ulation models (OGCM's). Physically, making warm r sink is much more difficult than making cold water even if the warm water is saline.

. Beerling (*Department of Animal and Plant Sciences, ersity of Sheffield, UK*). If I understand your modelling ectly, you have assigned fixed values of leaf area x (LAI) and stomatal conductance (g_s) to each type of tation based on those of the closest modern analogues. ractice, however, the LAI and stomatal resistance es even within a given vegetation type, will be strongly ndent on climate (leaf-to-air vapour pressure deficit, erature, precipitation regime), and particularly on the entration of atmospheric CO_2. Have you investigated ensitivity of the magnitude of vegetation feedbacks on ate to variations in LAI and g_s?

Upchurch. I will first explain the two terms for the ral reader, then answer the question. LAI measures umber of leaf layers in the canopy. Rain forest vegeta- has high LAI (typically 5–6) while desert vegetation ow LAI (typically 1 or less). Stomatal conductance (g_s) e rate at which CO_2 diffuses into the leaf and water ur diffuses out. Stomatal conductance is determined he size and number of stomata (gas-exchange pores), extent to which the stomata open, available soil ture and the vapour-pressure deficit between the leaf atmosphere.

AI in the GENESIS model is prescribed; in our eoclimate simulations we make it vary with the n if such variation occurs in the modern analogue tation. We investigated LAI and its effects on climate hree simulations: (1) BARESOIL (LAI = 0, or no s whatsoever for the entire land surface), (2) EVER- EN TREE (LAI = 6, or the dense leaves of rain forest tation for the entire land surface), and (3) BEST- SS (LAI varies with vegetation types, which ranges desert to tropical rain forest). Finer-scale studies, in which LAI varies over the geographic range of a single vegetation type, were not conducted.

Increasing LAI decreases surface albedo while simultaneously increasing surface roughness and the flux of water vapour to the atmosphere. These effects are of opposite sign and feed back into such atmospheric processes as cloud formation to determine the radiation budget of the land surface.

Two comparisons illustrate the effects of LAI on surface warming. First, comparison of our EVERGREEN TREE simulation (maximum leaf area over the land surface) with our BARESOIL simulation (no leaves), indicates that an increased LAI can cause surface warming. Global temperatures are 2.5 °C higher in EVERGREEN TREE because the decrease in surface albedo causes an increase in absorbed solar radiation. This warming affects most regions of the world.

Comparison of our EVERGREEN TREE simulation with our BESTGUESS simulation indicates that high LAI can have a cooling effect relative to moderate LAI (LAI = 2–4, or the leaf area typical of a deciduous forest in the spring and summer). High LAI increases evaporative cooling and the flux of water vapour to the atmosphere relative to moderate LAI. This, in turn, can cause an increase in clouds, which reflect more of the incoming solar radiation and cause the land surface to absorb less energy. In our simulations this cooling under high LAI is especially pronounced in two regions: (1) tropical regions that support dry-season deciduous vegetation, and (2) high-latitude regions that support forest vegetation.

Stomatal conductance (g_s) in GENESIS is based on a prescribed maximum conductance and physiological response functions for light and temperature taken from the closest modern analogue vegetation. Transpiration is determined by these functions in combination with the values for light, temperature, and soil moisture at the land surface. To approximate the effects of elevated atmospheric pCO_2 on stomatal conductance we halved the maximum conductance for all vegetation types. The major effect we observed in our simulations was a slight increase in sensible heating of the land surface, which was statistically significant only over limited regions.

These results are described and illustrated more fully in Upchurch *et al.* (1998).