upper traces are averages of 40 responses. The stimulus artifact was reduced by subtracting from each record a standard baseline trace consisting of the average of ten responses of quantal failures (traces with no transmitter release). Action potentials were blocked with 200 ng/ml tetrodotoxin. CCCP was dissolved at 1 m*M* in dimethyl sulfoxide (DMSO), which was added to the bathing medium to give a final concentration of 10 μ*M* CCCP and 0.1 percent DMSO. Temperature was 13°C.

45. In Fig. 4, transmitter release is recorded as postsynaptic current from a large number of release sites in motor neuron terminals lying under a macro patch electrode. The latter is a fire-polished pipette, 50 μm (inner diameter) and 100 μm (outer diameter) connected in a voltage clamp configuration [see *16*, *29*, and J. Dudel, *Pflügers Arch. Gesamte Physiol. Menschen Tiere* **391**, 35 (1981)]. Stimulating pulses were applied to the presynaptic terminals through the patch pipette, using the circuits of Dudel (*14*, *29*) to reduce stimulus artifacts. Each trace is the average of 80 responses when pulses follow trains, and 500 responses when pulses are given alone. With this number of trials, standard errors were less than 20 percent for most points. Stimulus regimes were repeated at 0.1 Hz. Residual artifacts following the test pulse have been removed by subtracting from each record a baseline trace consisting of the average of ten responses of quantal failures to the test pulse alone. Spikes in Fig. 4B were elicited by stimulating the excitatory nerve with a suction electrode in the meropodite of the leg. Temperature was 13°C.

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Role of Seasonality in the Evolution of Climate During the Last 100 Million Years

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A simple climate model has been used to calculate the effect of past changes in the land-sea distribution on the seasonal cycle of temperatures during the last 100 million years. Modeled summer temperatures decreased over Greenland by more than 10°C and over Antarctica by 5° to 8°C. For the last 80 million years, this thermal response is comparable in magnitude to estimated atmospheric carbon dioxide effects. Analysis of paleontological data provides some support for the proposed hypothesis that large changes due to seasonality may have sometimes resulted in an ice-free state due to high summer temperatures rather than year-round warmth. Such "cool" nonglacials may have prevailed for as much as one-third of the last 100 million years.

DURING THE LAST 100 MILLION YEARS THE EARTH'S CLIMATE has changed from an ice-free state to one with polar ice caps (*1*). Previous modeling studies (*2*) have attempted to determine whether changing land-sea distribution may have contributed to temperature changes in high latitudes. However, simulated temperature changes do not seem to be large enough to trigger ice-cap formation. We now discuss a feature that might account for such a large climate change. We propose that changes in seasonality may have played a key role in the formation of polar ice caps. The present seasonal cycle is primarily controlled by the land-sea distribution (*3*). We suggest that past changes in the seasonal cycle were affected by changes in the land-sea distribution—the drift of continents into high latitudes, and the opening of polar seaways. Formulating a hypothesis in terms of seasonality allows us to focus on perhaps the single boundary condition most critical for maintenance of permanent ice cover—the summer temperature. Regardless of how cold it gets in the winter, it is not possible to initiate ice cap formation if it gets too hot in the summer. The hypothesis is based on the geological boundary condition known best about the past (the land-sea distribution) and it is supported by calculations involving a two-dimensional energy balance climate model.

Our modeling approach differs from previous model studies (*4*) that were mostly conducted with mean annual heating distributions (no seasons) and which stipulated high albedo (snow cover) for land areas in high latitudes. We include the seasons and do not allow snow-albedo changes. This approach isolates the role of seasonality without the complication of a strong and uncertain feedback mechanism. The reason that the analogous experimentation with three-dimensional general circulation models (GCM's) has not been conducted is the large expense incurred in obtaining the equilibrium seasonal cycle (at least 15 model years need to be simulated to approach equilibrium in a passive oceanic mixed layer). Furthermore, present GCM's are unable to reliably simulate precipitation in high latitudes. Restricting analyses to mean annual heating has resulted in the conclusion (*4*) that reasonable changes in albedo, cloudiness, and oceanic heat transport cannot explain the estimated large thermal changes and that changing atmospheric carbon dioxide levels (*5*) may have to be invoked in order to account for the differences. Inclusion of the seasonal cycle may significantly alter this conclusion.

Our study is focused on the interval (80 million to 20 million years ago) between the maximum ice-free state of the mid-Cretaceous (*6*) and the time that is generally accepted as the minimum age for the formation of the Antarctic ice cap (*1*). The general trend of climate change is summarized in Fig. 1. Although detailed interpretation of this record has been questioned (*7*), comparison of the data with other paleoclimatic indices (*8–10*) suggests that, on balance, the Late Cretaceous–early Cenozoic had less ice than the present.

Geologic setting. Plate reconstructions for the last 100 million years indicate the continued breakup of Pangaea, with the net result

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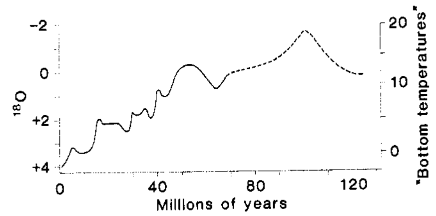
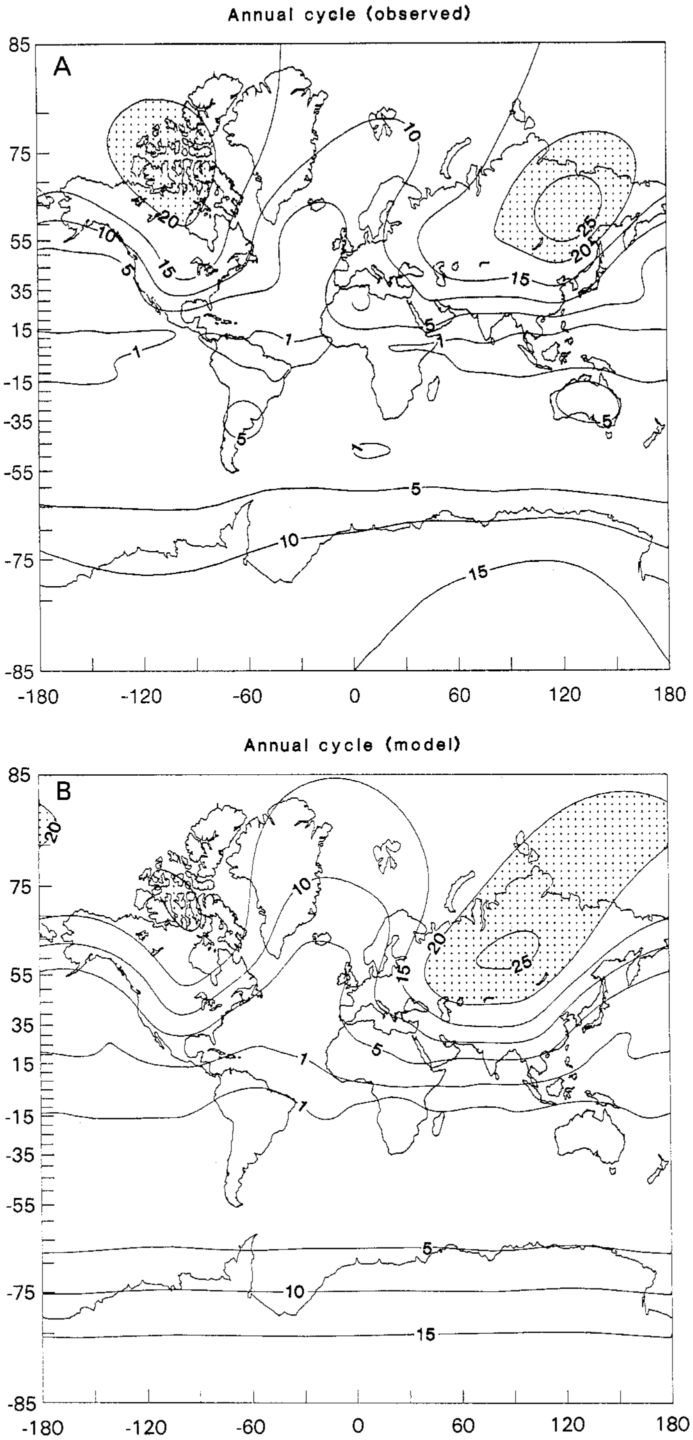


Fig. 1. Schematic representation of the evolution of high-latitude ice volume as inferred by oxygen isotope estimates of bottom water temperatures. Cenozoic data from Savin (*8*); Cretaceous data after Frakes [figures 6 and 7 in (*9*)].



being the drift of Northern Hemisphere continents into high latitudes and the isolation of key high-latitude land masses (Greenland and Antarctica) by water. The climate was cooler than the Cretaceous but apparently still ice-free until at least 37 million years ago (*1, 11*).

In the Northern Hemisphere, the opening of the Labrador Sea 60 to 70 million years ago separated Greenland from North America (*12*). An intermittent shallow water connection with the Arctic may have developed by about 60 million years ago (*13*). Shortly thereafter the axis of spreading jumped to the Norwegian Sea, which opened like a seam from south to north for the next 10 million years (*14*). A land connection between Greenland and northwestern Europe existed about 50 million years ago (*15*). An Arctic connection through the Norwegian Sea was established by about 36 million years ago (*14*).

In the Southern Hemisphere, South America was isolated from North America but connected to Antarctica until the opening of the Drake Passage sometime in the Oligocene [30 to 37 million years ago (*16*)]. Australia was still connected to Antarctica, although recent evidence indicates that some initial rifting between the two may have begun as early as 80 million years ago (*17*). A final separation did not occur until about 37 million years ago at the Eocene-Oligocene boundary (*18*).

Climate reconstructions provide a somewhat hazy picture of the climate of the Late Cretaceous—early Cenozoic. In addition to the general trend (Fig. 1), there were some significant fluctuations. The beginning of the interval was apparently marked by considerable warmth (*19*), but a pronounced cooling then developed by about 60 million years ago (*20*). A climate warming was initiated in the Late Paleocene and culminated in the Lower Eocene (50 million to 54 million years ago) with the warmest interval of the entire Cenozoic (*10*). The climate of the following Oligocene epoch is more open to conjecture. Oxygen-18 values changed dramatically after the Middle Eocene (Fig. 1) and suggest cooler conditions. The magnitude of the cooling is still uncertain, but oxygen-18 records are consistent with perhaps 30 to 50 meters of sea-level ice volume equivalent in the Oligocene (25 to 35 million years ago) (*11*). Both marine and land records indicate cooler conditions (*10*).

Seasonal energy balance model. Since our model has already been discussed (*21*), its description here is brief. The model may be summarized by its single governing equation:

$$C(r)\frac{\delta T\ (r,\ t)}{\delta t} - \nabla[D(r) \cdot \nabla T(r,\ t)] + A + BT(r,\ t) = QS(r,\ t)a(r)$$

where $T(r, t)$ is the surface temperature field; r is a point on earth surface; t is the time of the year; $C(r)$ is the effective heat capacity of the earth-atmosphere column [large over ocean, small over land, intermediate over (prescribed) perennial sea ice (60:1:9 ratio)]; $D(r)$ is the isotropic heat diffusion coefficient, with smooth latitude dependence; A and B are empirical infrared coefficients; Q is the solar constant divided by 4; $S(r, t)$ is the seasonal distribution of solar radiation; and $a(r)$ is the coalbedo of earth-atmosphere, dependent only on latitude.

The terms in the energy balance equation can be described as follows. The first term represents the instantaneous rate of storage of energy per unit area in the earth-atmosphere column; the storage

Fig. 2. Comparison of the modeled present seasonal cycle with data. (A) The amplitude of the annual harmonic (°C) in the observed annual cycle of surface temperature. Climatological data were smoothed by a spatial filter which preserves features having a length scale larger than about 1600 km. For further comparisons including phase lags, higher harmonics, and polar projections see (*21, 28*). (B) As in (A), but for the model. [Courtesy of American Geophysical Union]

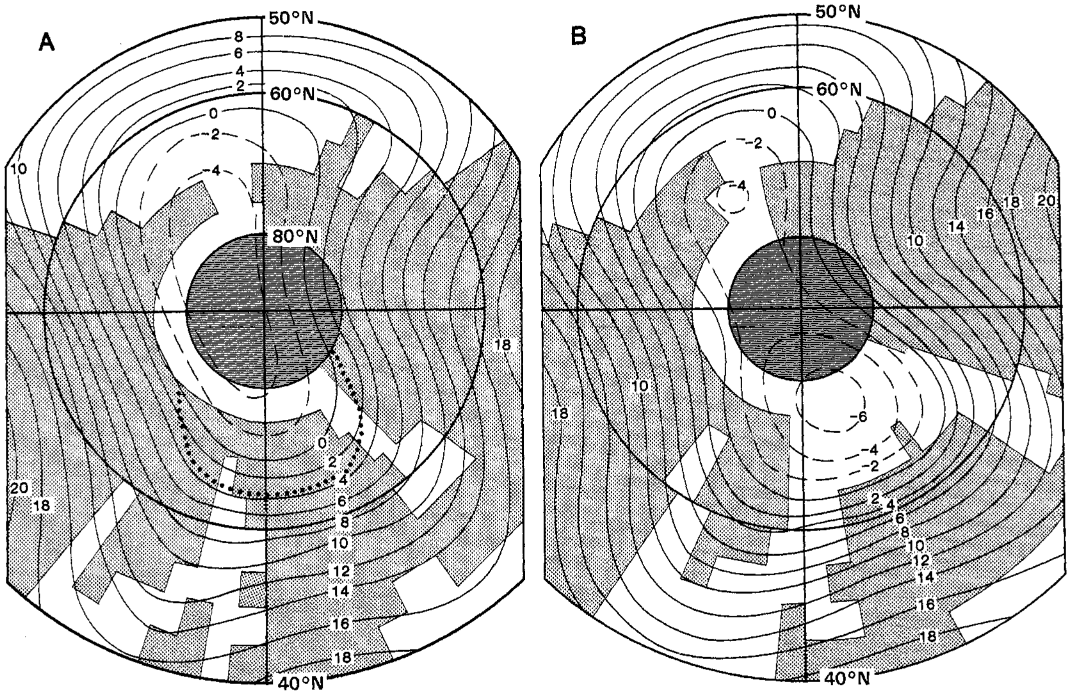


Fig. 3. (A) Mid-July surface temperature simulated for the Northern Hemisphere continental configuration 60 million years ago. Removal of the land bridge connecting Greenland with Europe results in a southward displacement of the 0°C isotherm, as shown by the heavy dotted contour (see text). Geographic detail (after *45*) is fed into the model on a 5° by 5° latitude/longitude grid as indicated by the coarse continental outlines. In all simulations the intermediate (sea ice) heat capacity (*21*) is assumed poleward of 80°N (*46, 47*). (B) As in (A), except for 40 million years ago.

rate is much larger over ocean since the heat is shared throughout the turbulent mixed layer, whose depth is about 75 meters. The second term is the divergence of horizontal heat flux, equivalent to heat transport into a column. The last two terms on the left-hand side represent the terrestrial radiation to space as described by the parameters used by Budyko (*22*) and recently compared to satellite data (*23*). The term on the right-hand side is the seasonal forcing term, the solar radiation absorbed per unit area.

In this version, the model is linear and can be solved by the usual methods of linear analysis (*21, 24*). From a spherical harmonic basis set truncated at degree 11, all solution fields are effectively smoothed to include no features of scale smaller than about 1600 km.

Among the many features not included in the model are topography, albedo contrast between land and sea, and differences in transport strength over land and over ocean. The reason for these seemingly unnecessary simplifications is to keep the number of tunable parameters small. We wish to avoid as much as possible the charge of "fitting" the model results to the present climate without any physical basis in the model. In such an approach some sacrifice of physical detail is made to avoid needless obfuscation of the main mechanisms and linkages operating. We have the simplest form of a realistic model under these constraints.

A comparison of modeled and observed seasonal cycle indicates good agreement (Fig. 2). Less favorable correspondence (*21*) applies to the mean annual simulation because this field is more influenced by features such as ocean circulation, topography, and albedo. But these features have less influence on the amplitude of the annual cycle, which is primarily controlled by land-sea distribution and which is the main focus of our study.

Model simulations of past climates involved no additional adjustments of parameters. This approach attempts to avoid arriving at conclusions as a result of preconceived ideas about mechanisms. Because of the limitations of this approach, our experiments can only be considered as pilot studies for future experiments with more realistic models. Rather than simulations of past climates, results should be considered as sensitivity tests to changes in an important boundary condition.

Results of model simulations. The evolution of simulated July temperatures for two key time intervals illustrates the importance of seasonality variations (Fig. 3). The mid-Paleocene (60 million years ago) time interval was chosen because the continentality effect was maximized due to relatively low sea level (*25*) and close proximity of North America and Europe. The 0°C isotherm is almost restricted to the Arctic Ocean, implying snow-free conditions for most of the Northern Hemisphere. This result is probably fortuitous, and the choice of 0°C for the snow–no snow boundary is arbitrary, although intuitively appealing. There is sufficient uncertainty in the model to raise doubts about the absolute values of simulated temperatures. However, we believe these shortcomings do not seriously jeopardize the main conclusions, because we focus on the differences between model results for different time periods. Such an approach presumably holds model bias constant and minimizes uncertainties as to the choice of the critical temperature for snow–no snow conditions.

Simulated summer temperatures are considerably cooler for the Late Eocene (40 million years ago) (Fig. 3B). Compared with the 60-million-year simulation (Fig. 4), summer temperatures over central Greenland decreased by 6° to 8°C—a response attributed in part to the more northerly position of Greenland and in part to the moderating effect of the Norwegian Sea. This last feature may seem at first counterintuitive, because the maritime effect is often associated with mild climates. However, the maritime effect also acts to suppress the magnitude of summer warming. A large reduction may have been sufficient to depress maximum summer temperatures below the critical snow–no snow limit. Permanent snowcover is therefore implied. Permanent snowcover may lead rather quickly (10,000 to 100,000 years) to permanent ice cover. Thus, our results imply that the Greenland ice sheet could have formed as early as 40 million years ago. Actual evidence bearing on this suggestion is scanty, but there is some indication of active North Atlantic deepwater production (*26*) and cooler Northern Hemisphere land temperatures during the Oligocene (*10, 11*).

A similar set of experiments was conducted for the South Polar region during the last 100 million years. We have focused on the effect of the separation of Australia from Antarctica on the magnitude of summer warming. A "before-and-after" simulation (Fig. 5) indicates surprisingly high summer temperatures on Antarctica 80

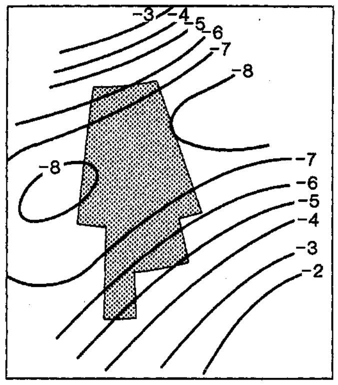


Fig. 4. The change in simulated mid-summer temperatures over Greenland as it drifted northward between 60 and 40 million years ago.

million years ago (maximum temperatures 13° to 14°C), with a subsequent reduction of temperatures by 5° to 8°C (*27*). Previous sensitivity tests (*28*) with the nonlinear ice-albedo feedback version of the model suggest that once temperatures are this low, Antarctica would ice over. Thus, our model predicts that continental-scale glaciation on Antarctica could have occurred as early as 40 million years ago. Oxygen-18 analyses (*11*) and some geological data from the Antarctica region (*29*) provide support for this prediction.

The time evolution of summer temperatures over Greenland and Antarctica illustrates that the large changes discussed above are part of an even larger trend over the last 100 million years (Fig. 6). Even with all the uncertainties inherent in a highly simplified model, the simulated changes are so large as to imply that seasonality has played a major role in the evolution of climate over this time span.

The evolution of the annual cycle over Greenland during the last 100 million years (Fig. 7) provides some additional insight into the processes responsible for the simulated temperature changes. The gradual decrease of maximum summer temperatures from 100 to 60 million years ago is due to the northward motion of Greenland. Continued drift and the widening of the Norwegian Sea reduced the maximum temperatures significantly between 60 to 40 million years ago. The phase of the annual cycle shifted to be more in line with a region under marine influence. Between 40 million years and the present, the northward drift of Greenland was mainly responsible for the continued decrease in maximum summer temperatures (once the Norwegian Sea widened sufficiently, it no longer exerted any additional moderating influence). Thus, Fig. 7 shows that the relative importance of drift and the maritime effect differed for different time intervals.

Implications for interpretations of past climates. Before discussing the implications of the model simulations, it is first necessary to examine the limit of credibility of simple climate model results. How sensitive are the conclusions to uncertainties in land-sea distribution? Sensitivity tests indicate some small differences in results but nothing large enough to discredit the main conclusion. For example, arbitrary removal of the Spitsbergen land bridge and flooding of the Barents Sea at 60 million years ago (Fig. 3A) results in only a relatively small reduction in maximum summer temperatures over central Greenland (indicated by the small displacement of dotted zero degree isotherm). The lack of a hydrologic cycle is another obvious shortcoming of the model. Since it is generally inappropriate to simulate a hydrologic cycle in such a simple model, the role of this and other important climate feedbacks must await examination with more complicated models including an annual cycle. However, the physical basis of our postulate is so clearly grounded on an important, unambiguous, and neglected concept that further model simulations should support our results. To some extent they already have. For example, we have compared our model with the responses of two general circulation models with significantly different levels of complexity (*30*). In that comparison we examined the seasonal temperature response to variations in the seasonal cycle of insolation during the early part of the present Holocene interglacial. Calculations show that greater summer insolation caused large changes over land and small changes over sea. The larger the landmass, the larger the temperature change. The magnitude and location of the maximum responses are similar (Fig. 8). This result is consistent with our contention that inclusion of feedbacks will not alter the conclusion that the primary control on past changes in the annual cycle is the land-sea distribution.

The calculated large temperature changes encourage us to speculate that seasonal cycle variations may sometimes maintain an ice-free state. Since warm summers are counterbalanced by cold winters in our model, this hypothesis implies that an ice-free earth may not necessarily be a particularly warm earth. It is important to consider such a possibility, especially since recent calculations (*31*) suggest that for the last 75 to 80 million years carbon dioxide levels may have been at most twice the present.

If our hypothesis is valid, there may actually be two types of

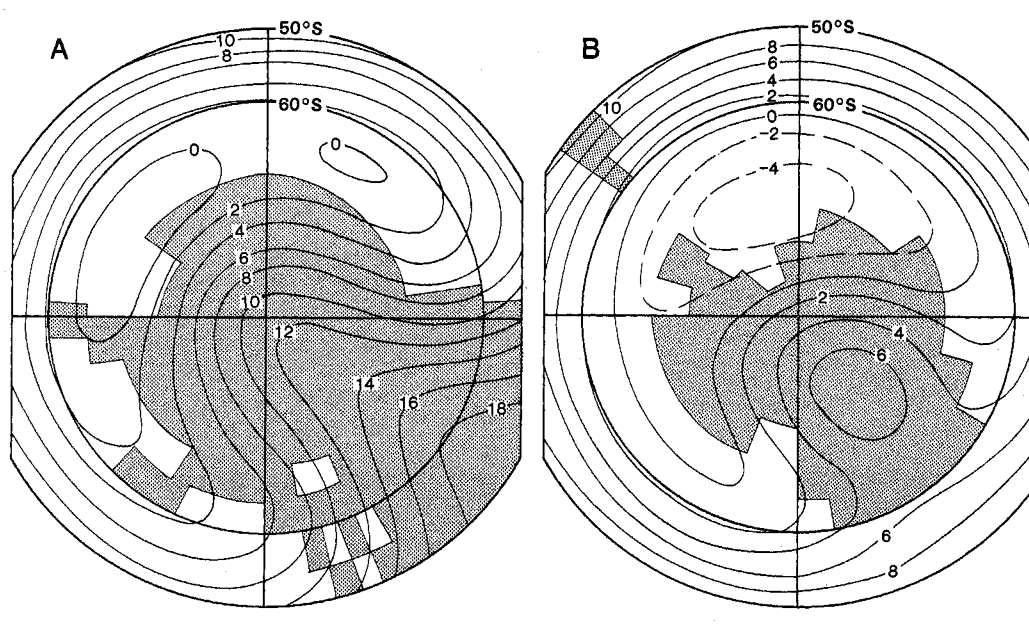


Fig. 5. (A) Mid-January surface temperature simulated for the Southern Hemisphere continental configuration 80 million years ago. These simulations are for no ice-albedo feedback and zero elevation of the continent. (B) As in (A) but for 20 million years ago.

Fig. 6. Mid-summer temperatures over central Greenland and the South Polar region for the continental configurations of 100, 80, 60, 40, 20, and 0 million years ago.

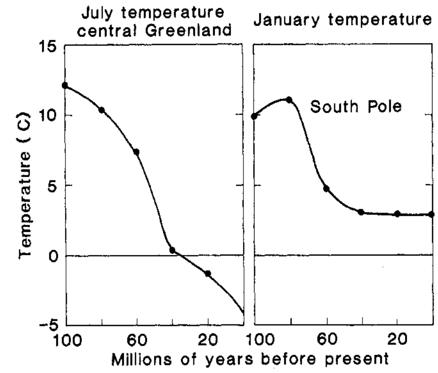
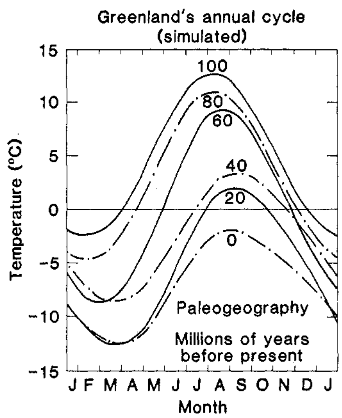


Fig. 7. The seasonal cycle of surface temperature over central Greenland for 100, 80, 60, 40, 20, and 0 million years ago.



nonglacials—"cool" nonglacials, in which permanent ice cover is prevented by warm summers, and "warm" nonglacials, in which globally averaged temperatures are higher. The latter requires an additional mechanism in order to explain the phenomenon. An examination of evidence for year-around warmth in high latitudes indicates that most citations are based on only two time intervals—the mid-Cretaceous (about 80 to 115 million years ago) and the Lower Eocene (about 50 to 54 million years ago). Since the earliest estimates of significant ice cover are 37 million years ago (*11*), our hypothesis implies that as much as one third of the last 100 million years may fall into the category of cool nonglacials (that is, Campanian-Eocene, 80 to 40 million years ago). The postulated climate state may therefore be an important feature of the earth's past climate.

The hypothesis of cool nonglacials is testable. Indirect testing can be accomplished through experimentation with more elaborate seasonal climate models (such as GCM's). Some geological data already support our model. For much of the time interval between 80 to 40 million years ago, a mixed conifer-hardwood forest blanketed regions north of the Arctic Circle (*32, 33*). Such a distribution is consistent with a seasonality interpretation in which there is sufficient summer warmth to support forests, but cold winters which cause deciduous plants to lose their leaves. Low winter temperatures are also indicated by scattered evidence for ice in Arctic rivers and coastal areas (*34*) during parts of the Late Cretaceous and early Cenozoic. Recent analyses of eolian input in marine sediments (*35*) indicate unexpectedly high input in the Paleocene (65 to 55 million years ago). This result may reflect cold winters and stronger winds during a cool nonglacial period. Additional tests may come from studies of seasonal growth bands in shallow-water mollusks (*36*) and isotopic analyses of single-specimen foraminifera (*37*).

The concept of cool nonglacials is not necessarily in conflict with some geological data that have been used to infer year-around warmth in high latitudes. For example, mid to late Cenozoic fauna from marine deposits east of Nova Scotia and from Western Europe indicate very warm, tropical temperatures (*15*). However, low winter temperatures could still have occurred on adjacent land masses. For comparison, the present-day Gulf Stream flows within 100 km of the eastern North America shoreline as far north as Cape Hatteras. Yet winter temperatures inland can still be quite cold. A similar strong gradient can also be found in some high-latitude fossil sites. In Late Cretaceous (Maastrichtian, 70 million years ago) deposits from the Labrador Sea, temperate latitude species in a nearshore site occur at about the same latitude as an offshore site dominated by tropical species (*13*).

Other evidence traditionally cited to support year-around warmth in high latitudes may also be open to reinterpretation. For example, Axelrod (*33*) has suggested that dinosaur remains in high latitudes might reflect seasonal poleward migrations in search of food. Large tropical vertebrates may also be able to adapt to large seasonal changes in temperature. For example, hippopotamus, rhinoceros, and elephant remains have been reported from the last interglacial of England (*38*). Any warmth greater than the present may have primarily been seasonal in origin (*30*). Finally, ecological calculations (*39*) suggest that sometimes leaf adaptations of broadleaf evergreens may be a response to low light intensity. The interpretation of high-latitude "tropical" fossil flora solely in terms of temperature may be affected by this calculation.

The seasonality model does not account for some important features of the geological record. Axelrod (*40*) has pointed out that although summer temperatures are often above freezing in our model, they are still not sufficiently high to be compatible with fossil plant data (*32, 33*). Nor can the model explain mild climates in the high latitudes of the Northern Hemisphere as late as 2.4 million years ago (*41*) or significant reversals in the long-term cooling patterns (*8, 10, 42*) such as occurred in the Lower Eocene (50 to 54 million years ago), Middle Miocene (15 to 18 million years ago), and Lower Pliocene (4 to 5 million years ago). Since estimated carbon dioxide levels were relatively low between 80 million years ago and the present (*31*), these discrepancies point to other factors

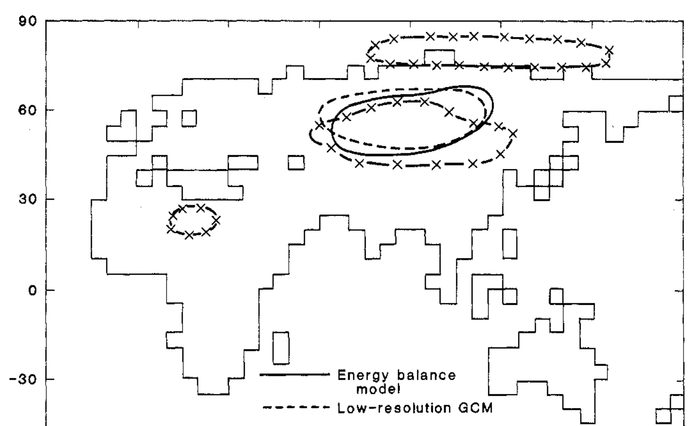


Fig. 8. A comparison of energy balance and general circulation model (GCM) responses to increased summer insolation. Time interval is about 10,000 years ago. The 4°C contours indicate the difference between the model response for 10,000 years ago and the present (earlier time period warmer). The energy balance model is from North *et al.* (*21*); the low-resolution model and the NCAR models are from Kutzbach and Otto-Bliesner and Kutzbach and Guetter (*30*), respectively.

that may contribute to changes in high-latitude temperatures, such as changes in oceanic heat transport (*43*).

It was enlightening to compare the summer temperature perturbations due to seasonality with the postulated effect due to increases in atmospheric carbon dioxide. The comparison was focused on the time period since the mid-Cretaceous thermal maximum. We utilized the maximum response from our study and GCM estimates (*44*) for the high-latitude response resulting from a doubling of CO_2—the maximum estimated increase for the last 80 million years (*31*). Past high-latitude summer temperature changes due to seasonality are comparable in magnitude to GCM estimates of changes due to a doubling of CO_2 (5° to 8°C). This comparison supports our proposition that seasonality has played an important role in the evolution of climate over a significant span of earth history.

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