

Permian climates: Evaluating model predictions using global paleobotanical data

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ABSTRACT

The most recent global icehouse–hothouse climate transition in Earth history occurred in the Permian. Warmer polar conditions relative to today existed from the middle Permian through the Mesozoic and into the Cenozoic. We focus here on one particularly well-correlated middle Permian stage that postdated the deglaciation, the Wordian (267–264 Ma), integrating floral and lithological data to determine Wordian climates globally. Paleobotanical data provide the best means of interpreting terrestrial paleoclimates, often revealing important information in the continuum between “dry” and “wet” end-member lithological indicators such as evaporites and coals. New statistical analyses of Wordian floras worldwide have enabled a greater understanding of original vegetation patterns and prevailing climate conditions. The derived climate interpretations are compared with new Wordian atmospheric general circulation model simulations. The model matches the data well in the tropics and northern high latitudes, but predicts colder conditions in southern high latitudes. We discuss possible reasons for this discrepancy.

INTRODUCTION

The Permian was a time of one of the most dramatic global climate changes in the geologic record and permits us to study the most recent transition from a glaciated to a completely ice-free state. Also, Permian fossiliferous rocks are exceptionally widely distributed, allowing for a detailed understanding of the global paleogeography and vegetation, essential for paleoclimate interpretations. Our paleoclimate data and model comparisons use new paleogeographic maps (Ziegler et al., 1997) that include more detailed paleotopography than is available for any other pre-Quaternary interval. These are augmented by a greatly expanded database of Permian lithological climate indicators (Ziegler et al., 1998), as well as more detailed stratigraphical correlations (Jin et al., 1997), than used previously (Ziegler, 1990; Kutzbach and Ziegler, 1993). Finally, a new approach, involving statistical analyses of fossil leaf data from floral localities worldwide, ensures greater confidence in our data-derived climate interpretations.

Leaves are a plant's means of interacting directly with the atmosphere, and their morphology is often attuned to and reflects prevailing environmental conditions. Previous paleoclimate studies using fossil leaves have been based either on global distributions of selected taxa (e.g., Ziegler, 1990; Vakhrameev, 1991) or on quantitative estimates from selected regions such as northern high latitudes (e.g., Herman and Spicer, 1996). Quantitative studies (Wolfe, 1993; Herman and Spicer, 1996) use angiosperms, but these are limited to the last ~120 m.y. Non-angiosperms have a longer-ranging record (from ca. 400 Ma) and also exhibit environmental adaptations, enabling at least semiquantitative climate estimates (Rees et al., 1999). By adopting a global whole-flora approach and analyzing the data statistically, we introduce greater consistency to the interpretation of global vegetation

and climate patterns, even for pre-angiosperm times, enabling direct data and model comparisons.

WORDIAN VEGETATION AND CLIMATES

We focus here on one particularly well-correlated middle Permian stage, the Wordian (267–264 Ma; Jin et al., 1997; also known as the Kazanian). Wordian terrestrial environments were classified in terms of regional climate zones (biomes) by studying leaf morphologies, phytogeographical distributions, and climate relationships. Reproductive organs were excluded from our analyses, which were restricted to leaves as well as stems and roots (e.g., *Calamites*, *Lepidodendron*, *Stigmaria*, and *Vertebraria*) with more securely known affinities to foliage. To maximize taxonomic consistency, genera were synonymized where necessary by using the classification scheme of Meyen (1987), supplemented by Taylor and Taylor (1993). Based on these authorities, each genus was also assigned to 1 of 19 coarser morphological categories (or “morphocats”), enabling broader vegetational comparisons. This is illustrated in Figure 1A, which shows the locality abundances of genera belonging to selected gymnosperm morphocats (glossopterids, cordaites, and gigantopterids) that have better-defined geographical distributions and climate signals. Glossopterids and many cordaites have large, tongue- or strap-shaped leaves. They are often interpreted as deciduous, indicating cool temperate conditions (e.g., Ziegler, 1990), although the cordaite morphocat (and even the genus *Cordaite*) exhibits a wide range of morphological variability. Glossopterids occur predominantly in Gondwanan mid and high latitudes, and although cordaites are more widely distributed, they do become more dominant components of vegetation in northern high latitudes. Gigantopterids are restricted to low-latitude regions (e.g., China) with apparently higher temperatures and precipitation.

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To enable a more rigorous and comprehensive assessment of Wordian phytogeographic patterns and climates, we then analyzed 69 genera from 121 known Wordian plant localities worldwide (a total of 908 occurrences) using correspondence analysis (CA), a multivariate statistical method used commonly in studies of modern ecology and vegetational succession (Gauch, 1982; Ter Braak, 1992). With this method, multi-dimensional relationships are reduced to show variance within data sets on a series of two-dimensional axis plots. The advantages of CA are that it provides the same scaling of sample (locality) and character (genus) plots, enabling direct comparison, and can accommodate incomplete data matrices where some information is missing, as normally occurs with the fossil record (Rees and Ziegler, 1999; Rees et al., 1999).

Figure 1B shows CA axis 1 vs. axis 2 results for the 121 Wordian localities, colored according to geographical region. The relative position of each locality is defined by its constituent leaf genera; localities sharing many genera plot closest together, those with little in common plot farthest apart. Gondwanan (Southern Hemisphere) sites have high axis 1 scores, Angaran (Northern Hemisphere mid to high latitude) sites have high axis 2 scores, and Chinese (low latitude) sites have low scores on both axes. The corresponding genus plot (Fig. 1C) shows distributions of the 69 Wordian genera. The relative position of each genus is defined by its degree of association with other genera. To assist interpretation, genera belonging to the glossopterid, cordaite, and gigantopterid morphocats are highlighted. Glossopterids and cordaites plot high on axis 1 and axis 2, respectively, whereas the gigantopterids have low scores on both axes (cf., Fig. 1A). Axis 1 accounts for the highest degree of variance in the data, so Gondwanan localities and glossopterid genera plot high on this axis (Fig. 1, B and C), being distinct both in a geographical and taxonomic sense. Differences between Northern Hemisphere localities and genera are therefore expressed on axis 2, which accounts for less variance in the data but which nevertheless shows vegetational and inferred climatic patterns. Figure 1D shows the averaged axis 1 and axis 2 scores for each floral locality, as well as the geographical distributions of coals and evaporites, climate-sensitive lithological indicators. Given the general symmetrical distribution about the equator of coals and evaporites, as well as leaf morphocats (e.g., Fig. 1A), it seems reasonable to average the floral locality axis 1 ("southern") and axis 2 ("northern") CA scores in order to enable the broad global patterns to be shown.

The combined floral and lithological data were used to determine Wordian biomes (Fig. 2A). We use a classification in which the "macroclimate" of the present-day land surface is expressed in terms of ten major biomes (Walter, 1985). The classification is simple and therefore more readily applicable in the geologic past, for which detailed knowledge of biomes is limited (Ziegler, 1990; Rees and Ziegler, 1999; Rees et al., 1999). However, the classification retains important information on temperature, precipitation, and seasonality—factors that are critical in controlling vegetation patterns. In the Wordian, dry biomes are characterized by evaporites, whereas the tropical everwet biome is typified by coals, high floral diversities, and low CA axis scores. Poleward changes through the temperate biomes (warm, cool, and cold) are reflected in transitional changes in dominance of different plant types (e.g., from ferns and pteridosperms to glossopterids or cordaites), as well as in decreasing floral diversities and increasing CA scores. By combining and appraising all of these different aspects, we then determined the global biome patterns (Fig. 2A).

DATA AND MODEL COMPARISONS

The Wordian map of Ziegler et al. (1997) was used as a boundary condition for experiments using the GENESIS (version 2) general circulation model (GCM; Thompson and Pollard, 1997). These experiments were run for 20 model years, with appropriately reduced solar luminosity (by 2.1% relative to the present) and varied levels of atmospheric CO₂ (4× and 8× present value). We find features that are typical of many previous Pangean climate model simulations, such as high aridity in central Pangea, large monsoons along the Tethyan margins, and precipitation focused around

tropical mountains (Otto-Bliesner, 1993; Kutzbach and Ziegler, 1993; Barron and Fawcett, 1995; Crowley et al., 1996). By using a previous scheme (Kutzbach and Ziegler, 1993), we expressed the simulated Wordian climate (temperature, precipitation) in terms of biomes (Fig. 2B), to compare with the observed biome distributions (Fig. 2A). Although our simulation used the same paleogeographic reconstruction as the data, slight differences in map projection mean that the simulated low latitude areas appear slightly larger and high latitude areas smaller, which should be borne in mind when comparing the two figures. The model performs reasonably well in the tropics and northern high latitudes, approaching the data-derived patterns. An obvious discrepancy exists between the data and model results for Mongolia (Fig. 2, A and B). Mongolian floras are more similar to those from Angara than to those from China (Fig. 1, A, B, and D) and indicate a cool temperate biome (Fig. 2A), whereas the model (Fig. 2B) predicts a warm temperate one. We believe that the problem is with the paleogeographic reconstruction, which should be modified to position Mongolia closer to Angara, as implied by the floral data (cf., Ziegler et al., 1996). This explains why the model predicts a warm rather than cool temperate biome here, being reasonable for the prescribed (but incorrect) paleolatitude in this simulation.

There is no net annual snow accumulation at low elevations in the model, consistent with the observed record of ice-free conditions in the Wordian (Ziegler et al., 1998). However, even with the highest reasonable CO₂ level (8× the present value) given the uncertainties in geochemical modeling estimates (Berner, 1994), model summer temperatures only just rise above freezing in the highest southern latitudes. This region contains the largest data vs. model discrepancy; cold temperate conditions (biome 8) are indicated by the paleobotanical data, whereas tundra (biome 9) is predicted by the model (Fig. 2).

DISCUSSION AND CONCLUSIONS

The only other Permian global data vs. model comparison so far conducted (Kutzbach and Ziegler, 1993) also showed a discrepancy in the southern high latitudes. Their results (using the NCAR Community Climate Model, version 1; CCM1) predicted cold temperate conditions (biome 8) whereas their data indicated a cool temperate biome 6. However, Kutzbach and Ziegler (1993) noted (citing Truswell, 1991) that a cold temperate biome 8 could be assigned on the basis of relatively low floristic diversity in this region compared with elsewhere in Gondwana, which is supported by our new results (Fig. 1D, 2A). Intriguingly then, the new data interpretations presented here match the older CCM1 simulation better than the new GENESIS simulation for this region, even though the CCM1 model resolution is coarser (4.5° latitude × 7.5° longitude) than that of GENESIS 2. It should be noted, however, that CCM1 predicts too warm conditions in the northern high latitudes compared to the data. Although Kutzbach and Ziegler (1993) used different values of atmospheric CO₂ level (5× the present value) and solar luminosity reduction (reduced by 1% relative to the present), the net radiative forcing is essentially the same in both models. We attribute this model-model difference primarily to different representations of latitudinal averages of poleward ocean heat transport within the simple mixed-layer ocean scheme used by both models. Kutzbach and Ziegler (1993) prescribed values of ocean heat transport based on estimates from an ocean GCM experiment with an idealized Pangean paleogeography (Kutzbach et al., 1990). In contrast, the GENESIS 2 scheme (Thompson and Pollard, 1997) predicts substantially lower ocean heat transport values, on the basis of the latitudinal sea surface temperature gradient.

Our new results indicate that an elevated CO₂ level alone is insufficient to maintain warm high-latitude temperatures in the Permian. One solution may be a "warm polar current" (Ziegler, 1998), which the GENESIS 2 model would be unable to resolve. GCMs cannot realistically fully reproduce past climates unless the atmosphere can interact with the ocean and vice versa. Preliminary experiments with equilibrium asynchronous coupling (Kutzbach and Liu, 1997) between an atmosphere and an ocean GCM show that simple modifications of today's geography and sill depths

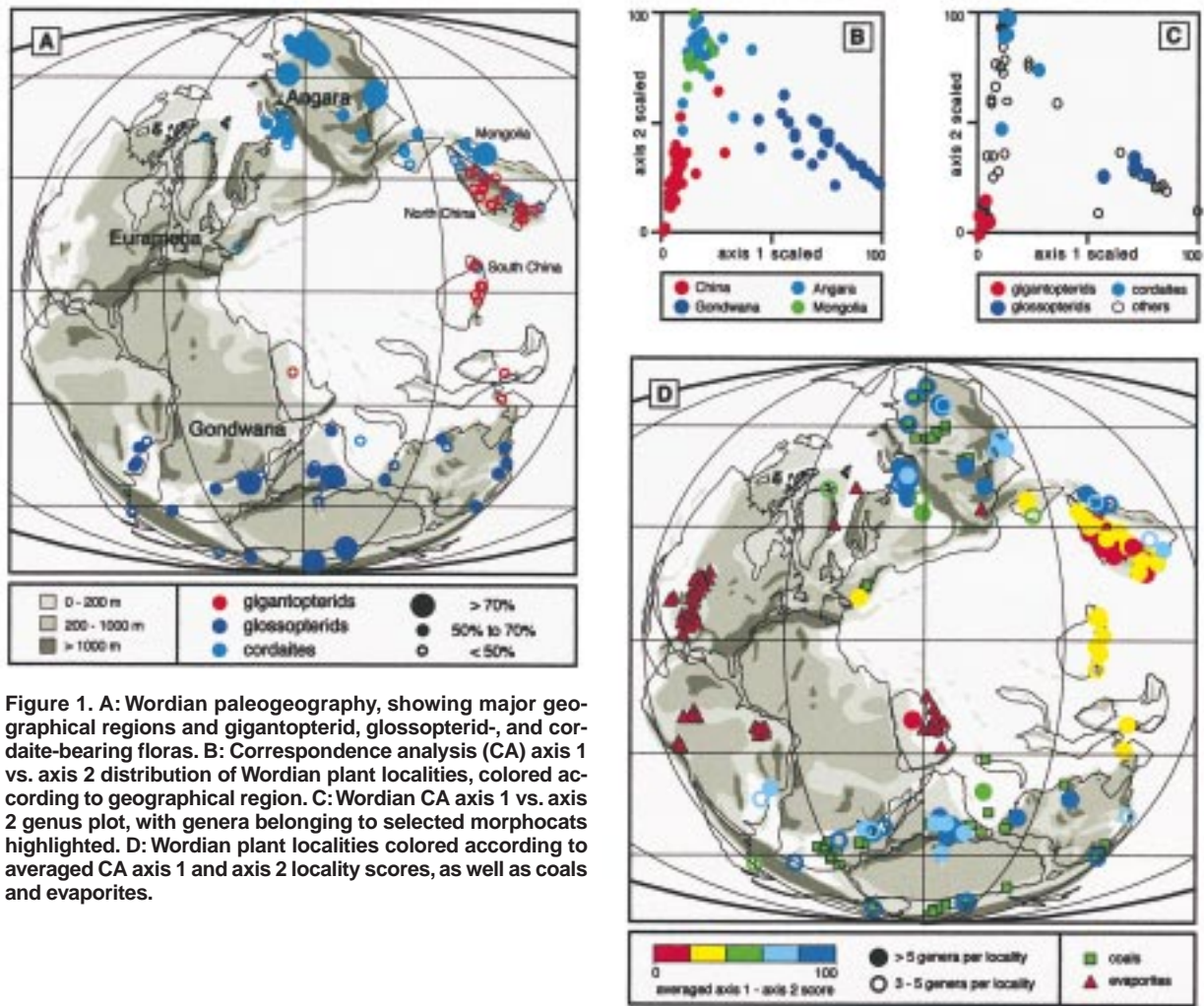


Figure 1. A: Wordian paleogeography, showing major geographical regions and giantopterid, glossopterid-, and cordaites-bearing floras. B: Correspondence analysis (CA) axis 1 vs. axis 2 distribution of Wordian plant localities, colored according to geographical region. C: Wordian CA axis 1 vs. axis 2 genus plot, with genera belonging to selected morphocats highlighted. D: Wordian plant localities colored according to averaged CA axis 1 and axis 2 locality scores, as well as coals and evaporites.

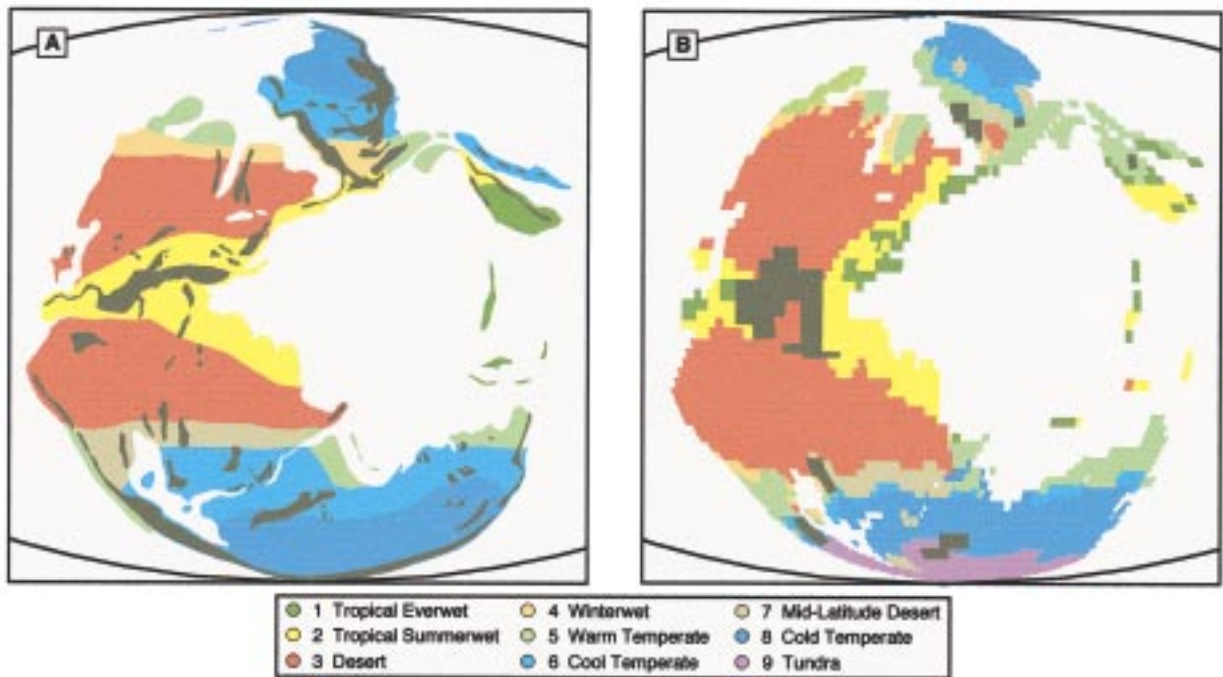


Figure 2. A: Wordian data-derived biomes. B: Wordian model-derived biomes (from 8x Present CO₂ experiment). Glacial biome (10) is not recognized, either from data or model. Elevations above 1000 m are shown in black; model elevations are averages at a 3.75° latitude x 3.75° longitude scale.

(e.g., a wider and deeper Bering Strait) allow warm currents to extend poleward of present limits (Ziegler, 1998). A warm polar current could have arisen under the paleogeographic regime of the middle Permian, where one large supercontinent lay just off the South Pole. The northward shift of Gondwana through the Permian (Ziegler et al., 1997), coupled with a rise in atmospheric CO₂ (Berner, 1994), may have initiated deglaciation and polar warming by allowing warm ocean currents to reach the south polar region.

A warm polar current, however, could only explain warm conditions at high-latitude coastal sites. Heat from such a source would not be advected far enough inland to compensate for radiation cooling in the interior of a large landmass in winter (Crowley, 1994). High-latitude data vs. model discrepancies in continental interiors are common to other warm geologic intervals (e.g., Herman and Spicer, 1996; Huber et al., 1999; Rees et al., 1999), and fully resolving them remains a fundamental problem in paleoclimatology (Crowley and North, 1996; Huber et al., 1999). A potentially important point is that local riparian vegetation (i.e., adapted to life on river or lake margins) is probably over-represented in many fossil plant assemblages, which may produce a significant bias affecting data and model biome comparisons. For instance, in areas today where the regional vegetation is tundra, evergreen or even some deciduous trees often grow along river margins. Riparian plants are also more likely to have been preserved in fossil depositional environments and tundra vegetation, comprising small-stature plants, will be less recognizable as such even if preserved occasionally in these fossil assemblages (often being described as "unidentifiable leaf fragments" or else ignored). It is therefore possible that a cold (or even in some cases cool) temperate biome could be assigned to what was regionally tundra. The consequences of taphonomic biases inherent in the fossil record should be borne in mind when comparing the data directly with coarse-resolution model results. For example, the spatial resolution of the GENESIS 2 model used here is 3.75° latitude × 3.75° longitude (typical of most current GCMs), and so more local effects (at a 1–10 km scale) will not be captured.

Multivariate statistical analyses provide a consistent and objective means of determining patterns that exist in the floral data. The interpretation of these patterns requires a knowledge of fossil plant taxonomy as well as paleogeography since, although such analyses serve to identify degrees of variance in the data, they cannot specify the causes of such variance. By analyzing the data using a global and "whole-flora" approach, we derive the closest possible approximation to original vegetation and prevailing climate conditions. This ensures greater accuracy of data-derived climate interpretations and enables more rigorous evaluation of the corresponding climate model simulations.

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