

JURASSIC PHYTOGEOGRAPHY AND CLIMATES: NEW DATA AND MODEL COMPARISONS

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ABSTRACT

Leaves are a plant's direct means of interacting with the atmosphere, and their morphology is often attuned to and reflects prevailing environmental conditions. Although better-understood and documented for angiosperms (or 'flowering plants'), non-angiosperms also exhibit a phytogeographic pattern linked most strongly to the evaporation/precipitation ratio, a relationship often reflected in their foliar morphologies. We have used this to interpret Jurassic terrestrial climate conditions along a spectrum defined by climate-sensitive lithological end-members such as evaporites and coals. Global climate zones, or biomes, were determined by exploring the foliar morphology/climate relationship using multivariate statistical analysis.

Jurassic plant productivity and maximum diversity was concentrated at mid latitudes, where forests were dominated by a mixture of ferns, cycadophytes, sphenophytes, pteridosperms and conifers. Low-latitude vegetation tended to be xeromorphic and only patchily forested, represented by small-leaved forms of conifers and cycadophytes. Polar vegetation was dominated by large-leaved conifers and ginkgophytes which were apparently deciduous. Tropical everwet vegetation was, if present at all, highly restricted. Five main biomes are recognised from the data: seasonally dry (summerwet or subtropical), desert, seasonally dry (winterwet), warm temperate and cool temperate. Their boundaries remained at near-constant palaeolatitudes while the continents moved through them (south, in the case of Asia, and north, in the case of North America). Net global climate change throughout the Jurassic appears to have been minimal.

The data-derived results are compared here with a new climate simulation for the Late Jurassic. The use of more detailed palaeogeography and palaeotopography has improved the overall data/model comparisons. Major discrepancies persist at high latitudes, however, where the model predicts cold temperate conditions far beyond the tolerance limits indicated by the plants. Nevertheless, our approach at

least enables direct comparison of global palaeoclimate interpretations from both a data and model perspective, and indicates future research directions.

INTRODUCTION

We can determine climate zones or biomes for intervals in the geological past by studying the morphology and distributional patterns of fossil leaves. These provide a 'palaeoclimate spectrum' between extreme end-member lithological indicators of climate such as coals and evaporites. There are three main reasons for believing this palaeobotanical approach to be valid: (1) global distributional patterns of modern vegetation show a strong relationship with climate, especially temperature and precipitation, and the way these parameters are distributed through the annual cycle (e.g. Walter, 1985; Prentice et al., 1992; Neilson, 1995); (2) leaves are a plant's direct means of interacting with the atmosphere, and their morphology is often attuned to and reflects prevailing environmental conditions; and (3) these relationships appear to have remained fairly constant since terrestrial vascular plants became established (e.g. Meyen, 1973). Fossil leaf genera and species are typically delimited taxonomically on the basis of relatively coarse characters such as size and shape, so are usually defined by morphological and not necessarily true biological criteria. Although such uncertainties may hinder evolutionary studies, these coarse subdivisions can be useful as palaeoclimatic tools if one accepts that leaf morphologies represent environmental adaptations.

The relationship between modern angiosperm leaf physiognomy and climate is particularly well-documented, from the early leaf margin analyses of Bailey and Sinnott (1915) to the advances made by J.A. Wolfe culminating in CLAMP (Climate Leaf Analysis Multivariate Program; see Wolfe (1993) for methodology). This technique has been applied to Tertiary and, more recently, Late Cretaceous floras (e.g. Herman and Spicer, 1996), resulting in quantitative estimates of climate parameters such as mean annual temperature and precipitation for these geological intervals. The results provide an important means of accurately determining palaeoclimate signals and testing general circulation models (GCMs), with their capacity to predict future climates. However, such studies have been limited to approximately the last 120 million years (from the time when angiosperms became significant components of vegetation). Derived interpretations have also been compromised by 'patchiness' of the observations.

Palaeoclimate interpretations using non-angiosperm leaf taxa (e.g. for the Jurassic: Barnard, 1973; Vakhrameev, 1991 and references therein) have been limited

to the demarcation of floristic provinces based upon the distributions of only a few genera (e.g. *Dictyophyllum*, *Otozamites*, *Frenelopsis*) or orders (e.g. the Czekanowskiales). This was partly due to uncertainty regarding the climate tolerances of non-angiosperm fossils, given that most are now either extinct or at best 'relictual' in their distributions, having been marginalised by flowering plants. Another limitation was the absence of a method to arrange and analyse all of the available fossil plant data.

One means of compensating for the inferior non-angiosperm climate signal is to use a global 'whole-flora' approach to data collection, combined with statistical ordinations of the data. This is the approach we have used to interpret the Jurassic 'greenhouse' world. One purpose of this contribution is to show that we can use broad non-angiosperm leaf morphological characters combined with our 'whole-flora' approach to determine palaeoclimates for pre-angiosperm times, and that it is possible to unravel the multiple effects (or constraints) of floral provinciality and evolution, taxonomic and taphonomic bias, continental motion and true global climate change. This is illustrated here with examples of results from multivariate statistical analyses of Jurassic floras, as well as climate modelling for the Late Jurassic. Our statistical approach enables us to interpret palaeobotanical evidence of past climates in a more rigorous and repeatable manner. It also provides geologists and palaeoclimate modellers with a means of utilising directly and easily the detailed work of the palaeobotanical community.

BACKGROUND

Broad-scale patterns of Jurassic climates have already been described, based upon various lines of sedimentological and palaeobotanical evidence (e.g. Krassilov, 1972; Barnard, 1973; Hallam, 1984, 1994; Vakhrameev, 1991; Frakes et al., 1992; Ziegler et al., 1994, 1996; Price et al., 1995, including previous authors referred to in each of these publications). Before describing our new approach we highlight some of the limitations, both of data and technique, of previous studies.

Jurassic vegetation is commonly represented by leaf remains preserved as impressions or coalified compressions which, when no features (e.g. cuticle or fertile structures) are preserved to demonstrate that they are different, often leads to the creation of poorly-defined and probably artificial groupings of leaf species and genera (e.g. *Cladophlebis*, *Sphenopteris*, *Taeniopteris*). This in turn has often given the impression of an apparent global homogeneity of Jurassic floras (see comments by Wesley, 1973). Other problems occur, such as taphonomic and collection bias,

taxonomic inconsistency, poor stratigraphic control, uncertainty concerning the relation of foliar organs to each other and to other plant organs, poor preservation of most material, and morphological variability of different species of the same genus. In spite of these problems, strong patterns have emerged indicating that certain morphologies/taxa consistently co-occur, and that there is a correlation between the kind of foliage preserved and its palaeogeographic distribution. However, previous studies using Jurassic plants to interpret global climates relied upon the distributional patterns of only a few individual genera or groups. Such an approach enables major differences to be highlighted, but does not show gradations in vegetation and climate. Since these are so obvious today, it seems reasonable to assume that they also existed in the geological past. Another disadvantage of the 'single genus' approach (e.g. Krassilov, 1972) is that the framework collapses when individual genera become extinct. Hence, this method does not provide a consistent and repeatable means of interpreting climates through time.

The Russian palaeobotanist V.A. Vakhrameev recognised the limitations of this approach, in a series of papers culminating in his posthumously-published synthesis (Vakhrameev, 1991). He commented (1991:4) that "names for phytochoria [territorial floristic units] should be geographical rather than based on the terms of predominant plants since the areas of the latter undergo substantial changes with geological time". His interpretations of Jurassic climates are based, nonetheless, upon the distributions of only a few plant genera or groups to delineate 'phytochoria' (i.e. proxies for phytogeographic and climate zones). The use of such terminology (phytochoria, as well as province, region and area) results in uncertainty when a given region has moved tectonically with respect to latitude, particularly when the geographical term is retained for floras that have changed in response to climate by migration rather than evolution (see Ziegler, 1990). Hence, terms such as 'Euro-Sinian' and 'Siberian-Canadian' are not used here. We prefer to use descriptors derived from observations of modern vegetation and climate, independent of continent positions through time.

Vakhrameev's floristic and climatic interpretations for the Jurassic are further compromised since, of the plant taxa shown, only one fern genus (Dictyophyllum), two cycadophyte genera (Otozamites, Ptilophyllum) and one order (the Czekanowskiales) appear on each of his Jurassic maps. Studies of Present vegetation and climates do not use such limited data. Clearly, such a palaeobotanical approach does not provide a reliable means of comparing global climates through Jurassic intervals which span some 60 million years. In spite of this, the Jurassic climate zones recognised by Vakhrameev and other palaeobotanists agree, at least in the very broadest sense, with previous climate model results (e.g. Moore et al., 1992a,b; Valdes and Sellwood, 1992; Valdes, 1994). However, any attempt to advance the role of fossil

plants as palaeoclimate indicators should be based upon as much as we know of the original plant assemblage and the global occurrences of such assemblages. Although imperfect, due to factors such as taphonomic, taxonomic and collection bias, this approach provides our best proxy for original vegetation and therefore climate regimes in the geological past. We may not understand past vegetation and climates as completely as today's, but we can improve the palaeoclimate data and model techniques to derive a closer approximation to real conditions.

NEW DATA AND METHODS

Fossil leaf genera, multivariate analysis and 'floral gradients'

Our study uses multivariate analysis, specifically correspondence analysis (CA), to assess co-occurrences and distributional patterns of fossil leaves at the genus level. This has ensured a more standardised approach to identifications and comparisons; fossil plant specimens are far more likely to have been assigned to the 'correct' genus or form genus than species.

For the Jurassic, we assembled a literature-derived floral database comprising 782 plant localities and 8175 genus occurrences worldwide. Lists of taxa from 644 Northern Hemisphere localities were submitted to correspondence analysis, those with only 1 or 2 leaf genera or spanning more than one Jurassic interval being omitted. Our analyses of these data represent an attempt to quantify gradations between floral provinces that have been identified previously by Russian authors (e.g. Vakhrameev et al., 1978; Krassilov, 1981; Dobruskina, 1982; Vakhrameev, 1991). All have delineated climate zones using the floras; our aim is to explore the character of what is, in reality, a smooth gradient, but in a more rigorous and repeatable manner. For many years, Chinese and 'former Soviet' (FSU) geologists and palaeobotanists have collated palaeofloristic data in the form of comprehensive taxonomic lists from specified sites covering a wide geographical area. The Chinese reports contain detailed information about sedimentary sequences from all regions of China, with lists of plant fossil species given for each fossiliferous stratigraphic unit, and the FSU taxon lists are of comparable quality (see Ziegler et al. (1994, 1996) for references). Central co-ordination ensured a taxonomic uniformity and 'whole-flora' approach seldom matched in the West; Asian data therefore provide, at present, the most obvious starting point for determining Jurassic phytogeography and climates. All lists and references are contained in databases of the Paleogeographic Atlas Project, University of Chicago. Using correspondence analysis these floral lists can be used to derive phytogeographic patterns and, because at the generic level the taxonomy of fossil

vegetative organs reflects physiognomy, these patterns may be expected to have some correlation with climate.

We should point out that the use of palaeobotanical genera for determining Mesozoic vegetational units or biomes is not a nearest living relative (NLR) approach because these taxa are not being compared directly with living forms. As with all fossils the name primarily denotes a morphotype that in many instances conveys the physiognomy of a particular organ. Indeed, it is sometimes necessary to 'side-step' traditional palaeobotanical taxonomy, which is often hindered by political and regional biases (ensuring a highly-specialised local but limited global view), as well as stratigraphic biases (with what is effectively the 'same' fossil plant type being assigned to a different genus or species depending upon its age). The morphotype approach can work in the palaeoclimatologist's favour, once the taxonomic nomenclature is understood in terms of basic morphological characters, phytogeographic distributions and likely palaeoclimatic regimes.

We use correspondence analysis to arrange the fossil leaf genera from our 644 Jurassic Northern Hemisphere localities according to their degree of association with one another. Three separate analyses were carried out on data summed over relatively long time intervals (i.e. Early, Middle and Late Jurassic), due to limitations in stratigraphic correlation and dating. A presence/absence matrix was constructed for each interval from locality taxonomic lists assembled throughout the Northern Hemisphere. These were then submitted to correspondence analysis (CA), which is a method used commonly in studies of modern ecology and vegetational succession. The advantages of CA are that it provides the same scaling of sample (locality) and character (taxa) plots, enabling direct comparison, and can accommodate 'incomplete' data matrices where some information is missing (Hill 1979; Gauch 1982). The version used is one of the programs in the CANONICAL Community Ordination (CANOCO) package compiled by Ter Braak (1992), an extension of the Cornell Ecology Program DECORANA of Hill (1979). The general procedure has been described by Shi (1993): "Geometrically, ordination involves rotation and transformation of the original multidimensional co-ordinate system and reduction of high dimensionality so that major directions of variation within the data set can be found and more readily comprehended than by looking at the original data alone". Thus, we use CA as a means of arranging all of the elements (whether genera or localities) relative to axes in multidimensional space according to their similarity to each other. Most of the variation occurs on the first axis, with other axes accounting for progressively less, so two-dimensional plots (one for genera and the other for localities) were produced showing the variance within data sets on the two principal axes. Genera that frequently co-occur plot closest together on axis 1, whilst those that

rarely co-occur are furthest apart. The same applies to the localities plot; those which share many floral elements plot closest to one another, whilst those with little in common plot furthest apart.

Ordination results for 57 Early Jurassic leaf genera from 196 Northern Hemisphere localities are shown in Figure 1. Microphyllous (i.e. small-leaved) cycadophytes and microphyllous conifers plot to the left of axis 1, with macrophyllous (large-leaved) conifers and ginkgophytes towards the right. Thus, the plants of these two groups rarely co-occur, which makes sense if we consider their leaf morphologies in terms of climate (small-leaved forms of cycadophytes and conifers, often with thick cuticles, adapted to hot dry environments versus large and presumably deciduous leaves of conifers and ginkgophytes adapted to seasonally cool and/or dark conditions). Other plant groups such as sphenophytes, ferns and macrophyllous cycadophytes occupy the central and right hand portions of axis 1, presumably since few of them were tolerant of water stress. It should be emphasised however that the symbols on the generic plot indicate only the centroids of the various floral elements and individual ones may have wide ranges. The corresponding Early Jurassic locality plot (Fig. 2) shows a broad correlation between axis 1 score and palaeolatitude. This becomes better-defined when the localities are plotted on palaeogeographic maps, where it is clear that factors such as longitudinal east vs. west, continental interior vs. maritime, and even topographic variations also contribute, just as in the modern world.

We can therefore interpret Early Jurassic phytogeographic patterns based on the axis 1 scores of individual leaf genera and corresponding plant localities, due to their relative degrees of association. We can then understand these climatically in terms of the basic morphological characteristics of individual leaf genera and the palaeogeographic distribution of plant localities. However, this is an improvement on previous work only in that we have adopted a 'whole-flora' approach and applied statistical rules to arrange the data. How can we compare vegetation and climate signals from successive time intervals in a more rigorous and repeatable manner? By repeating the exercise for Middle and Late Jurassic floras, we arrive at three separate ordinations (for J1, J2 and J3 intervals, comprising 196, 288 and 160 Northern Hemisphere plant localities respectively). The ordering of leaf genera along axis 1 remains fairly constant in each interval, since overall floristic change was minimal throughout the Jurassic. By averaging the scaled (0 to 100) axis 1 scores of the 32 genera common to all three intervals, we derive a Jurassic 'floral gradient' (Fig. 3). This shows the gradient score for each genus, which is based upon its averaged axis 1 position relative to all other genera throughout the Jurassic. Microphyllous conifers and microphyllous cycadophytes have low scores, whereas macrophyllous conifers

and ginkgophytes have high ones. Ferns (e.g. *Todites*, *Cladophlebis*, *Coniopteris*) and macrophyllous cycadophytes occupy the central portion of the gradient, along with sphenophyte genera such as *Equisetites* (fossil 'horsetails' or 'scouring rushes'). Using the floral gradient, we can assign a value to any Jurassic plant locality (whether J1, J2 or J3) simply by averaging the scores of its constituent leaf genera. Indeed, anyone can place a new locality list on the gradient by averaging the score for each of the 32 genera represented. It should be stressed that the score of each genus on the gradient represents its 'centroid' in the Northern Hemisphere latitudinal spectrum; most genera appear in at least some lists throughout this range. This is due in part to the general uniformity of Mesozoic floras and in part to time-averaging of the taxonomic lists. The gradients are subtle and may only be determined by reference to the entire assemblage. Such a method at least provides the best available proxy for original vegetation and prevailing climate conditions at a given locality.

Using the floral gradient, we can compare Early, Middle and Late Jurassic plant localities objectively, observe any spatial and temporal changes, and interpret these in terms of floral provinciality, continental motion and global climate change. Figure 4 shows the correlation between floral gradient score and palaeolatitude for Early Jurassic localities worldwide. Although based upon Northern Hemisphere ordinations (given the relative paucity and poor stratigraphic control of Southern Hemisphere/Gondwanan Jurassic floras), the derived floral gradient can also be used to assign scores to these Gondwanan localities. As with the Early Jurassic axis 1 ordination for the Northern Hemisphere (Fig. 2), a broad correlation of gradient score with palaeolatitude is still evident, indicating a symmetry of Jurassic climate zones about the equator, consistent with coal, evaporite and aeolian sand distributions.

Lithological indicators of climates

The study of fossil leaf morphologies, associations and distributional patterns provides a spectrum of climate information between end-member climatically-sensitive lithologies such as coals (precipitation > evaporation) and evaporites (evaporation > precipitation). The global distributions of these lithologies provide another important data source. Occurrences of coal, lacustrine, evaporite and aeolian sand deposits were compiled from the literature and are recorded in Paleogeographic Atlas Project databases. There is an apparently symmetrical arrangement of Jurassic evaporites and coals about the equator, shown in Figure 5. These lithological patterns provide information about climate extremes in terms of net evaporation and precipitation, and support the new palaeobotanical interpretations. They also indicate that global application of the Northern Hemisphere floral gradient (e.g. Fig. 4)

and direct Northern and Southern Hemisphere floristic comparisons are valid. Although there are as yet no data from East Antarctica (i.e. the continental interior of southern Gondwana), we believe it reasonable to infer that fossil leaf genera such as *Phoenicopsis*, *Czekanowskia* and *Podozamites* (or at least large-leafed and deciduous morphological equivalents) would have been present there during the Jurassic, similar to contemporaneous forms growing at high northern latitudes.

Our global climate interpretations are based upon the occurrences and ordinations of leaf genera, as well as selected lithological indicators. More localised distributional patterns of fossil palynomorph taxa such as *Classopollis*, indicative of dry conditions (e.g. Volkheimer, 1970; Vakhrameev, 1991 and references therein), as well as information from palaeosols (e.g. Sellwood and Price, 1994; Singer et al., 1994), support our new results for the low latitude regions.

Leaf morphological categories

We assigned all Jurassic leaf genera, whether or not they were included in the correspondence analysis, to ten coarser morphological categories: sphenophytes, ferns, pteridosperms, microphyllous cycadophytes, unassigned (intermediate or morphologically variable) cycadophytes, macrophyllous cycadophytes, ginkgophytes, microphyllous conifers, unassigned (intermediate or morphologically variable) conifers, and macrophyllous conifers ('sphenoph, fern, fern2, microcyc, cyc, macrocyc, ginkgoph, microcon, con, and macrocon'). The palaeolatitudinal distribution of these morphological categories ('morphocats') is shown in Figure 6. Individual points represent the total numbers of morphocats within each 10⁰ interval, whereas the curve represents an average of Northern and Southern Hemisphere data. Shaded areas represent the approximate latitudinal extent of East Antarctica. As with the lithological distributions shown in Figure 5, the curve was calculated because the paucity of Southern Hemisphere data, particularly the 'datahole' caused by present-day Antarctic ice cover, otherwise renders such broad inter-hemisphere comparisons problematical. Highest numbers occur at mid-latitudes, decreasing pole- and equatorwards in each hemisphere, although with a small peak about the equator. The patterns are of interest if we accept them as a crude proxy for vegetational diversity; highest at mid-latitudes, decreasing pole- and equatorwards, but with some possible tropical diversity.

Determination of biomes

Our approach enables direct comparison of vegetation patterns throughout the Jurassic and means that we can determine biomes or climate zones in a more rigorous fashion. Although multivariate analysis serves to identify the degree of variance in the data it cannot, of course, specify the sources of variance. It is the physiognomy implicit in the names of individual fossil leaf genera that ultimately enables the determination of global palaeoclimates. Ordinations of fossil leaf genera and localities are derived from the primary literature and these, combined with lithological data, enable climate zones (biomes) to be drawn on palaeogeographic maps. An individual leaf genus is defined by basic morphological characters such as size and shape that can be interpreted in terms of prevailing environmental conditions. The relative position of each genus on a generic ordination plot is defined by its degree of association with other leaf genera. The relative position of each floral locality on a corresponding locality plot is defined by its constituent leaf genera. Correspondence analysis simply provides an objective assessment of variance in the original data matrix. The generic and locality plots both show that the data arrays are gradational rather than disjunct, indicating that climate influenced the patterns and not geographic barriers. This poses a problem in classification because there are no natural breaks in the distributions, but this is also true of the Present.

We use the biome scheme developed by Walter (1985), in which he reduced the macroclimate of the present-day land surface to nine major biomes. He compiled 'ecological climate diagrams' showing monthly temperature, precipitation and other statistics for some 8000 meteorological ground stations worldwide and combined these with details of the corresponding vegetation. In effect, his choices of climatic boundary conditions were influenced by natural transitions in the vegetation. One attractive aspect of Walter's scheme is that it is simple and therefore applicable to the geological past, thus overcoming deficiencies inherent in the fossil record. The scheme (as modified by Ziegler (1990); see comments therein for further details) also retains information on seasonality of temperature and precipitation, factors that are of fundamental importance to controlling vegetation patterns and our derived interpretations of Jurassic climates. It is significant that fossil leaf morphologies are similar at a given palaeolatitude (whether Northern or Southern Hemisphere), often regardless of conventional taxonomic status. This would appear to indicate that plants developed similar strategies to maximise their efficiency in a given environment, regardless of their botanical affinities. Indeed, it should be emphasised that few fossil plant taxa are, in fact, true biological ones, being instead an

approximation based upon morphological similarity rather than biological compatibility.

There are two extremes of vegetation type in our Jurassic example: localities comprising wholly microphyllous forms (of conifers and cycadophytes) and localities comprising wholly macrophyllous conifers and ginkgophytes. Based on leaf morphologies, these can be interpreted as plants adapted to hot dry, and seasonally cool and/or dark conditions respectively. These plant types do occasionally co-occur but it is relatively easy to define end-member biomes based on the locality scores defined by these leaf genera. Microphyllous plant localities occur at low palaeolatitudes and can be assigned to a seasonally dry biome, this being consistent with evaporite and aeolian sand distributions. The macrophyllous conifer/ginkgophyte localities occur at high palaeolatitudes and can be assigned to a cool temperate biome, based upon the deciduous nature of the foliage. It is harder to define the latitudinal boundaries between these and the intermediate warm temperate biome. However, the occurrence of macrophyllous cycadophytes and ferns, changes in their relative abundance with respect to microphyllous and macrophyllous/ginkgophyte forms, and coal distributions, all enable subdivisions of the floral and climate spectrum. The patterns become even clearer when individual localities are plotted on the new palaeogeographic maps shown in Figure 7.

JURASSIC CLIMATE INTERPRETATIONS

Our palaeogeographic maps (Fig. 7) illustrate the latitudinal consistency of biomes (or climate zones) throughout the Jurassic. Care must be taken to differentiate between real global climate change and observed effects due to continents passing beneath climate zones (see Ziegler et al., 1996). For example, clockwise motion about an axis in Europe resulted in a polewards motion of North America and the reverse in eastern Asia. The latitudinal transitions between floras remained fairly constant, so we maintain that no net global change occurred in the area occupied by the individual biomes. Thus, while the climate of Asia became warmer and drier through the Middle and Late Jurassic, the reverse was true of North America. Climate changes that have been described for Eurasia (e.g. Vakhrameev, 1991; Hallam, 1994) are in our view the effect of the continent moving with respect to the climate zones, rather than the reverse (see Ziegler et al., 1994, 1996). While Asia moved southwards, North American Lower and Middle Jurassic deserts represented by the Navajo and Entrada Formations (Parrish and Peterson, 1988) gave way to seasonally dry Upper Jurassic climates of the Morrison Formation (Dodson et al., 1980), followed by temperate coal

swamps in the Cretaceous (Horrell, 1991) as that continent continued moving polewards.

Clearly, the effects of continental motion can be pronounced and must be considered when interpreting palaeoclimates. Differences observed vertically within a sequence preserved at a particular locality may be due to local variations influenced by sedimentological and taphonomic biases, the effects of latitudinal motion through climate zones, genuine global climate change, or combinations of these factors. Further detailed studies and correlations between sequences are required in order to understand whether such locally-observed variations are caused principally by regional or global climate changes. For the Jurassic, we subscribe to the former view, given the evidence for marked latitudinal migrations of the North American and Asian continents. We also maintain that interpretations of global palaeoclimate conditions based upon global data collection are more robust than those derived from selective observations (e.g. Hallam, 1984, 1994; Vakhrameev, 1991; Frakes et al., 1992).

We have no geological evidence in the Jurassic for tropical everwet and, at the other extreme, tundra or glacial biomes. The equatorial regions were markedly dryer than today, with large continental interiors. Admittedly, since large areas of the equatorial zone are devoid of Jurassic deposits, the lack of rainforests could be a preservational effect. Nonetheless, a large continent on the equator in the form of the combined Africa and South America must have experienced effects detrimental to everwet conditions. Much of this landmass would be remote from moisture sources and the latitudinal excursion of the Intertropical Convergence Zone (ITCZ) would be more extreme (see Ziegler et al., 1987). Large excursions away from the equator, allowed by weak polar highs in a warm world, would have led to little or no constantly wet zones, merely seasonally wet areas. So, the limited moisture available to the system is theorised to have been spread over a wider area. The zone of peak productivity therefore shifts from low to higher latitudes at times of global warmth.

The fact that we do not recognise tundra vegetation at high latitudes in the Jurassic does not mean that the biome approach is invalid. Even if it were argued that modern vegetation and climate regimes cannot be used as a basis for assigning strictly similar biomes in the geological past, the lack of evidence for persistent polar ice (either from data or models) during this period of globally warm conditions means that a similar absence of tundra and permafrost is unsurprising. Of course, such vegetation may have existed during other geological intervals but may be hard to recognise as such, given that small-stature plants belonging to low diversity floras would have had a correspondingly reduced preservation potential.

Based on the global distributions of lithological climate indicators such as coals (precipitation > evaporation), as well as evaporites and aeolian sands (evaporation >

precipitation), a general symmetry of climate zones about the (palaeo)equator is seen throughout the Jurassic (Fig. 7). Such indicators provide useful information about extreme climate conditions (e.g. Lottes and Ziegler, 1994; Price et al., 1995), but it is fossil plant data which enable the entire terrestrial climate spectrum to be determined, particularly when analysed using our more rigorous 'whole-flora' approach. A problem arises with Jurassic floral sites from Gondwana; data are relatively sparse and stratigraphic control is often less certain, which means there are only 50 usable localities (cf. 644 in the Northern Hemisphere). In addition, key high-latitude information is typically missing, potential localities being covered today by the Antarctic icesheet. All of this prevents an intra-Gondwanan floral gradient from being compiled and so the Northern Hemisphere one is used. Nevertheless, relative spatial and temporal variations of floral gradient score and inferred climate signal calculated for these Gondwanan localities are consistent with lithological indicators, palaeoclimate models and the palaeogeography of the continent (Fig. 7). Most plant localities in southern Gondwana have similar gradient scores to those in the Northern Hemisphere interpreted as belonging to the warm temperate biome. One exception is the Argentine floras, most of which have low gradient scores indicative of seasonally dry conditions. Palynological data from Argentina (e.g. Volkheimer, 1970) agree with our biome designation for this region. These differences in floral gradient score across southern Gondwana are also consistent with the distributional patterns of lithological indicators such as coals (which are common in Australia) and aeolian sandstones (preserved in southern Africa and South America). There is no direct geological evidence for a cool temperate biome in Gondwana similar to that interpreted from high latitude sites in Eurasia. However, given the otherwise-symmetrical arrangement of biomes about the equator, it is reasonable to infer such a biome for areas distant from maritime influence in the interior of southern Gondwana.

From the combined floral and lithological data, the Jurassic world is interpreted as essentially one in which low latitudes were seasonally dry (summerwet or subtropical), succeeded polewards in both hemispheres by desert, seasonally dry (winterwet), warm temperate and cool temperate biomes (Fig. 7). Despite the caveats outlined above (primarily due to patchiness of the geological record) the biome concept provides, at present, the most rigorous method for interpreting climate signals from pre-angiosperm floras. Furthermore, the standard scale presented here (Fig. 3; modified from Ziegler et al., 1996) at least enables direct comparison of such fossil plant assemblages worldwide. Comparisons of our new approach with results of palaeoclimate modelling are of particular interest, enabling us to understand Jurassic climates from both a biological and physical perspective.

COMPARISON OF LATE JURASSIC DATA AND MODEL RESULTS

New model results for the Late Jurassic can be compared with climate predictions based on the GCM simulations of Moore et al. (1992a,b), Valdes and Sellwood (1992) and Valdes (1994). These model simulations showed broad agreement but there were differences at high latitudes, where Moore et al. (1992a) produced results significantly colder than those of Valdes and Sellwood (1992). However, these simulations used different palaeogeographic reconstructions and hence it is difficult to accurately compare these model simulations to the data. For this reason, we have performed a new simulation so that the GCM uses exactly the same palaeogeography as the data. The previous model was based on Kimmeridgian palaeogeography, whereas the new one uses our more-refined Volgian reconstruction. In all other aspects the GCM is identical, including prescribed CO₂ concentrations of 4x present day, to that used by Valdes (1994; see that paper for a detailed description of physical parameterisations). The model is typical of most current GCMs; it includes a detailed radiation scheme with both seasonal and diurnal variations, an interactive, relative humidity based cloud scheme, the Betts-Miller convection scheme, and a simple 3-layer surface parameterisation.

The model has 19 levels in the vertical and the simulation described here uses a spectral representation with a triangular truncation at total wavenumber 31. All physical processes are considered on a grid approximately 4 x 4 degrees, although the true resolution of the model is somewhat poorer. The effect of this relatively-coarse resolution can be seen in Figure 8, which compares the detailed (data-derived) palaeogeography with that used in the model. The GCM provides a good approximation, despite its relative coarseness; all of the major mountain ranges are represented, although there is a tendency to broaden the relatively narrow features on the western side of the Americas. The model has been run for a total of 7 years and the last 5 years have been averaged to give the predicted climatology. It should be noted that this simulation used the same prescribed sea surface temperature as in Valdes (1994). This means that the model reaches a dynamic equilibrium relatively rapidly and an extended length of run is not essential.

The major changes between this reconstruction and that used by Valdes and Sellwood (1992) are seen in the Southern Hemisphere. The new reconstruction indicates a major seaway extending across Gondwana, so that South America and Africa are now separated from Antarctica, India, and Australia. Due to the ameliorating effects of this large water mass, the regions adjacent to it are likely to have had a smaller seasonal range of temperatures, but would have been generally moister. One other important modification is that there is considerably larger

orography on the Antarctic peninsula and much-reduced orography in the centre of the African/South American continent. This is likely to have had important effects on precipitation and temperature patterns. Figure 9 shows the predicted seasonal patterns of surface air temperature. The model is predicting cold temperatures during the winters in northern America, northern Eurasia, and Antarctica. In this last region, the temperatures decrease to -24°C or less over a substantial part of the continent. This is somewhat colder than shown in the model produced by Valdes (1994), which used the previous (restricted-seaway) palaeogeographic reconstruction. It appears to be due to two different factors. Firstly, the general elevation of the region is greater and hence there is a simple effect of lapse rate. This can contribute quite significantly, since a typical change of temperature with altitude is approximately 6.5°C per 1000m. In addition, it appears that the enhanced orography on the western side of Antarctica effectively blocked the flow of relatively warm oceanic air in winter, resulting in a cooling over a large part of the western region of the continent. Moore et al. (1992b) also showed important differences in the simulations depending on the palaeotopography which was used, although their choice of palaeotopography is not the same as ours.

In the vicinity of the southern Gondwanan seaway this simulation is indeed less extreme than that of Valdes (1994). This is particularly noticeable for the summer since temperatures do not become anywhere near as high as in the previous simulation. In winter, the differences are more subtle since the effect of high orography over South Africa is important. However a difference map (not shown) does reveal a warming of up to 10°C in coastal regions. In other regions, the simulation is broadly similar to that of Valdes (1994). The tropical regions can reach temperatures as high as 40°C during parts of the summer months. The cool winter temperatures in North America are somewhat more severe than previously and, again, this can largely be explained by enhanced orography in this region.

Temperature is not the only aspect of the simulation that is important when making comparisons with geological data; moisture availability is also vital. Figure 10 shows the simulated seasonal precipitation. There are heavy bands of rainfall over the tropics, as well as in mid-latitudes; these are very similar to those described by Valdes (1994). During the Southern Hemisphere summer, there is a very strong monsoonal-type precipitation extending over the whole South American/African continent. However, in the corresponding winter season, the precipitation has completely disappeared and is replaced by marked drought conditions. The model predicts rainfall amounts near to zero. In mid-latitudes, the rainfall belts correlate closely with the model's simulation of storm tracks (not shown). In the winter season, there is a clear band of precipitation at approximately 40°S and 40°N . This

corresponds well with locations of the winter-wet biome. There is a substantial change compared to the previous simulation due to the southern seaway. This region is much wetter in the new simulation and therefore agrees better with the observed biomes. In addition to precipitation, another important indicator of hydrological conditions is the surface soil moisture content. This shows (Fig. 11) the amount of moisture in the soil, expressed as a percentage of the maximum allowed. It is effectively a balance between the total precipitation and the total evaporation, which is largely controlled by the temperature and moisture availability. Although the patterns of soil moisture mimic the precipitation patterns, there is a considerable amount of small-scale variability. This is in part the result of orography; elevated surfaces are cooler and hence there is less evaporation.

The maps of temperature, precipitation and soil moisture give a clear idea as to the type of biomes that are expected. However, for a more rigorous comparison between the model and data, it is useful to compute the Walter biomes based on the monthly mean temperatures and monthly mean precipitation values. Our procedure is identical to that shown in Kutzbach and Ziegler (1994). The resulting prediction of Walter biome/climate zones for the Late Jurassic is shown in Figure 12, and can be compared directly with the data-derived biome map shown in Figure 7C.

Overall comparison between the data and model is encouraging, maintaining the broad pattern of summerwet equatorial regions, succeeded polewards by desert then warm and cool temperate biomes. In the tropics, there are a few grid points predicting tropical rainforest type biomes, but there are no data near any of these grid points and so the model could be correct. The rest of the tropics are predicted to be summerwet, which is generally in good agreement with the data. The model predicts that this summer wet region (which is part of the tropical summer monsoon) extends into the Arabian region and up to 30°S. This is in direct conflict with the evaporite and aeolian sand data; the reason for this discrepancy is not clear, although the lithological distributions may represent too broad a time interval (i.e. correlations may not be sufficiently precise). Small changes in orography and sea surface temperature could influence the latitudinal extent but the disagreement is greater than 20 degrees of latitude, which is more than could simply be accounted for by the presently-available data.

In mid- to high latitudes, the most striking feature of the Northern Hemisphere is that the model predicts more extensive regions of winterwet climates and more restricted regions of warm temperate climates. In some senses, the distinction between these climates is relatively subtle and so perhaps the model error is correspondingly small here. Nonetheless, the model is somewhat too cool at these latitudes. The tendency of the model to be too cool is more striking in the Southern

Hemisphere. The data and model results agree on the southern side of the African/South American continent, and indicate a mixture of winterwet and warm temperate type climates. One exception is that the model predicts much cooler conditions over the orography, which is as one would expect. We performed an additional calculation by converting the surface temperatures into mean sea level temperatures, by assuming a uniform change of temperature with height of 6.5°C per 1000m of elevation. This converted the cool and cold temperate climates into a mixture of warm and winter wet climates. Nevertheless, overall data and model agreement at high latitudes on the Gondwanan continent is poor. On the coast itself, the agreement is reasonable and it can be argued that this suggests that our choice of sea surface temperatures is acceptable. However, in the southern interior of the continent the model is predicting a mixture of cool and cold temperate climates and very few areas of warm temperate climates. As with northern high latitudes, the model is clearly predicting temperatures which are too cold. Using mean sea level temperatures does reduce the regions of cold temperate climates, but does not help greatly since the temperatures remain substantially colder than indicated by the geological data.

DISCUSSION

Despite the relatively subtle temperature gradients apparent in the Jurassic, floral variation does occur and can be employed to measure spatial and temporal climate changes. Individual leaf genera can occur in almost any floral list, but the climate signal is lodged in the sum total of the floral elements; our statistical approach at least provides an objective scale to compare the floras. It also highlights the scope for developing a more quantitative analysis of pre-angiosperm floras and palaeoclimate interpretation. Our approach has already been applied to Mesozoic floras from Eurasia (Spicer et al., 1994; Ziegler et al., 1994, 1996) and shows the potential of pre-angiosperm floras as at least semiquantitative indicators of palaeoclimate. Initial results from Cretaceous floral ordinations (Spicer et al., 1994) have demonstrated that the appearance of angiosperms did not significantly alter the relationship between non-angiosperm distributions, physiognomy and climate signals. It should therefore be possible to calibrate the climate signals derived from non-angiosperms against the quantitative signals obtained through studies of angiosperm leaf physiognomy (e.g. Wolfe, 1993).

It is the overall climate signal lodged in individual and collective floral assemblages which enables larger-scale interpretations of past climates. It should be

emphasised that this is only possible if all the plants in a fossil assemblage are described or listed, instead of just the well-preserved or biologically-interesting ones. Without this basic information the full potential of the plant fossil record to reveal past environmental and climate change cannot be exploited. Of course, this must be based primarily on accurate plant determinations, an appreciation of the limitations of the fossil plant data and the critical use, whenever possible, of independent age evidence. Despite the reasonable agreement between our data-derived climate map (Fig. 7C) and the modelled ones (Figs 8-12), our interpretations should still be regarded as preliminary. It is only by combining our data with that from other palaeobotanical (e.g. palynology and fossil wood), palaeosol and other lithological climate indicators, in addition to marine palaeontological and isotopic data, that we can understand Jurassic climates based upon all of the available geological evidence.

Previous Late Jurassic (Kimmeridgian) GCMs (e.g. Moore et al., 1992a; Valdes, 1994) match reasonably the global climate results from the new floral and lithological data, particularly for the Northern Hemisphere. There are some problems, however, particularly in southern Gondwana, where the models predict a cold temperate central core for the continent, precisely where geological data are absent. It should be noted that agreement between the new (Volgian) model and data on the southern edge of the African/South American continent is much better than with the original simulation of Valdes (1994). Thus, as well as providing an important test of the model, it could be argued that this provides further confirmation of the existence of a seaway in this region.

We suggest that, in some regions, the discrepancies between data and model results could be improved if mean sea level temperatures were used instead of surface temperatures (which could be greater than 2000m above sea level and hence more than 13°C cooler). This raises the issue of one potential preservational bias on fossil plants. It is more likely that a fossil plant assemblage will be preserved at the bottom of a valley than at the crest of a ridge or mountain. Therefore the assemblage may tend to indicate the valley bottom temperatures, which would be relatively warm. One means of reducing (though not overcoming) such bias is to use our 'whole flora' approach to data collection, so that even locally rare elements growing more distally to the depositional sites are included in the floral lists. Despite this, the palaeogeographic data and the model cannot really resolve valleys. Hence elevation in the model is considerably higher than the valley bottom and consequently the temperatures will be cooler. It can be argued that the correction to mean sea level provides a more realistic comparison between model and data. It is worth noting that such corrections are used routinely in weather forecasting; Salzburg, Austria, for example, is in a valley at approximately 300m whereas many weather forecast models

use a mean orography of more than 1000m since they cannot resolve the valley. Hence the raw weather forecasts from the models are much too cool and post-processing is applied to correct for the elevation difference.

The data/model comparison clearly suggests that the model is too cold at high latitudes in both hemispheres. Changing CO₂ levels and sea surface temperatures could make some difference, but is unlikely to completely resolve the problem. It appears to be another example of the 'equable climates' issue noted for the Cretaceous and Eocene (e.g. Sloan and Barron, 1990; Barron et al., 1994). Recent work (Dutton and Barron, 1996; DeConto this volume) has suggested that some of the disagreement can be reconciled by including feedbacks between the climate and vegetation. This effect is also likely to be important for the Jurassic and we are in the process of incorporating this in our simulations.

Although we apply terms such as cool temperate to describe high latitude Jurassic climates, it should be borne in mind that we are referring primarily to the length of plant growing season (4 to 6 months for the cool temperate biome). The main limitation on growing season length at such latitudes today is temperature, whereas in the Jurassic it was most probably light. So there is a difference, although many of the 'cool temperate' plants appear to respond in a similar fashion by shedding their leaves seasonally. The important point is that we are applying the biome label to introduce some consistency to the interpretation of past vegetation and climates and that this represents an initial attempt to interpret global patterns. It is the relative occurrence, abundance and degree of association of different fossil leaf genera that helps define these patterns. By conducting the exercise on a global scale and by applying statistical methods to arrange the plant data, we can produce 'biome/palaeobiome/climate/pattern' maps for intervals in the geological past which can be compared directly with the climate model results.

The terminology we have adopted is arguably less important than the fact that our approach is more comprehensive and repeatable than any other that uses pre-angiosperm plant data. Ultimately, if all of the 'patterns' match between the data and model results, then we can use the parameters of the model to accurately define global patterns of temperature, precipitation and soil moisture. However, we can only be reasonably certain that the model is correct if we have a robust means of testing it initially. Our contribution represents just one example of ongoing studies aimed at testing, refining and improving feedbacks between the data and models.

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FIGURE CAPTIONS

Figure 1. Correspondence analysis (CA) axis 1/axis 2 plot for 57 Early Jurassic leaf genera from Northern Hemisphere localities. The genera have been assigned to the following broad morphological categories: microphyllous cycadophytes, microphyllous conifers and *Pachypteris* (large solid squares); macrophyllous cycadophytes (vertical crosses); ferns, sphenophytes and lycophytes (diagonal crosses); 'unassigned' conifers (small solid squares); macrophyllous conifers and ginkgophytes (open squares). Numbers refer to the following leaf genera: 1 *Zamites*, 2 *Otozamites*, 3 *Brachyphyllum*, 4 *Pachypteris*, 5 *Ptilophyllum*, 6 *Pagiophyllum*, 7 *Pterophyllum*, 8 *Taeniopteris*, 9 *Nilssonia*, 10 *Elatocladus*, 11 *Ctenis*, 12 *Podozamites*, 13 *Baiera*, 14 *Ginkgo*, 15 *Pityophyllum*, 16 *Sphenobaiera*, 17 *Czekanowskia*, 18 *Desmiophyllum*.

Figure 2. Early Jurassic CA axis 1/axis 2 plot for 196 Northern Hemisphere plant localities. Localities are coded according to palaeolatitude: 0° to 40°N (solid circles), 40° to 60°N (vertical crosses), 60° to 90°N (open circles).

Figure 3. Jurassic floral gradient, derived from the averaged axis 1 scores of genera common to J1, J2 and J3 floras. Five broad morphological categories ('morphocats') and their constituent genera are highlighted, showing the gradation from microphyllous forms to macrophyllous conifers and ginkgophytes.

Figure 4. Early Jurassic locality gradient score *vs.* palaeolatitude for Northern and Southern Hemispheres. Locality scores are derived from the scores of the constituent genera shown in Figure 3. Open circles represent small samples with 3, 4 or 5 genera present on the floral gradient, filled circles are larger samples with 6 or more gradient genera.

Figure 5. Distribution of Jurassic coals and evaporites by palaeolatitude. Occurrences of coals within a 10° latitudinal interval were calculated as a percentage of total coal occurrences. The same calculation was used for evaporite occurrences. Curves represent averages of Northern and Southern Hemisphere data, and shaded rectangles show the approximate latitudinal extent of East Antarctica, for which lithological data are absent.

Figure 6. Occurrences of Jurassic plant morphocats by palaeolatitude. Individual points represent total numbers of morphocats within each 10° interval, whereas the

curve represents an average of Northern and Southern Hemisphere data. Shaded areas represent the approximate latitudinal extent of East Antarctica, for which palaeobotanical data are absent.

Figure 7. New Early Jurassic (a), Middle Jurassic (b), and Late Jurassic (c) palaeogeographic maps, showing floral and lithological data as well as inferred biomes.

Figure 8. Comparison of (a) data-derived and (b) modelled palaeogeography (including topography).

Figure 9. Modelled Late Jurassic surface air temperatures for (a) Dec-Jan-Feb seasonal average (i.e. Northern Hemisphere winter and Southern Hemisphere summer), and (b) Jun-Jul-Aug (i.e. Northern Hemisphere summer and Southern Hemisphere winter). The contour interval is 4°C; areas warmer than 28°C are darkly shaded and areas colder than 0°C are lightly shaded.

Figure 10. Modelled seasonal precipitation, as in Figure 9. The contours are 0.5, 1, 2, 4, 8, and 16mm/day. Areas greater than 2mm/day are lightly shaded and areas greater than 8mm/day are darkly shaded.

Figure 11. Modelled surface soil moisture (in the first 7.5cm of the soil), as in Figure 9. Contours are every 25% of total soil water capacity, and shading is for areas in excess of 50%.

Figure 12. Predicted Walter biome/climate zones for the Late Jurassic (colour scheme as in Figure 7).