The fossil plant record and global climatic change

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Abstract

The generally sedentary character of terrestrial plants gives them a special dependence on their adaptation to the climate under which they live. As a consequence, plants normally show structural adaptations which are characteristic of their habitat, and fossil plants constitute particularly sensitive palaeoenvironmental indicators. In Quaternary pollen analysis the assumption is generally made that the species recognised as pollen had the same climatic constraints as their present-day representatives. As we go back through Tertiary time, and extant species become progressively rarer, we seek the nearest living relatives of the plant fossils as a basis for palaeoclimatic interpretation. This approach relies on the accuracy of the taxonomic assignment of the fossil material. Various 'non-taxonomic' features of Tertiary fossils have also been used in attempts to read a 'palaeoclimatic signal', independent of the correctness of the taxonomic assignment. These include most notably leaf physiognomy, and growth responses to seasonality such as growth rings in fossil wood. When we look to Palaeozoic plants, even leaf physiognomic features are of limited value, but fossil plants of this age can still give us significant information about their palaeoenvironment. The presence of charcoal (fusain) produced by wildfire puts a constraint on the level of oxygen in the palaeoatmosphere. Stomatal density and index may be used to give a proxy measure of palaeo-CO_2 levels. The realisation of the link between the carbon-dioxide greenhouse phenomenon and climate makes the use of stomatal data from fossil plants of particular relevance to palaeoclimatic interpretation. Our results from a study of stomatal index in plants from the Devonian to Permian interval are consistent with evidence from physical sources of major changes in global CO_2 levels through that period.

1. Introduction

Geologists have recognised for over a century that there have been major changes in the pattern of the Earth's climate through the course of geological history. Perhaps the most revolutionary change in geological thought about past climates came with the recognition of the occurrence of the Pleistocene glaciations that affected high latitudes through the

last two million years (see Hallam, 1989). This led to the realisation that a similar phenomenon was involved in the Carboniferous–Permian glaciation of Gondwana. In hindsight it seems a little odd that the wide recognition of what is now referred to as Global Environmental Change (GEC) has come so late to the political and economic agendas of the world's governments.

GEC extends beyond purely climatic processes, and has come to include many interlinked phenomena, from predicted global warming produced by an enhanced greenhouse effect, and ensuing sea-level rise, to increased UV-B radiation produced

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by localised thinning of the stratospheric ozone layer. In its present usage, GEC usually carries an emphasis on causality associated with the activities of mankind—the enhanced greenhouse effect resulting from fossil fuel burning, and the effect that ensuing climatic change may have on the growth of plants and global agriculture.

The current concern with mankind's role in global change has given a new interest in the geological record of similar changes having occurred in the remote past. It is in this context that we attempt here to assess the role of fossil plants in giving a picture of past climatic change. Rather than considering the well-worked ground of Tertiary plant/climate interactions (see e.g., Boulter and Fisher, 1994), we concentrate on what can be deduced about Palaeozoic climate from plant fossils of that age. We also hope that this is more appropriate for a volume dedicated to Dr. W.A. Bell, who contributed so much to our understanding of Canadian Carboniferous plant assemblages.

First we shall review the use of Quaternary and Tertiary plant fossils as climatic indicators, in order to explore how far that methodology is applicable to earlier geological periods. We shall then consider the attempts that have been made to interpret Palaeozoic climates from fossil plant evidence. Finally, we examine the use of stomatal density in Palaeozoic plants, presenting some new evidence concerning the relationship between stomatal density and greenhouse-driven climate at that time.

2. Fossil plants as climatic indicators

Terrestrial plants have a unique degree of dependence on the environment to which they are committed by their sedentary habit. In very simplistic terms it might be said that while plants are directly dependent on the vagaries of climate, the animals within a community are adapted to the environment dictated by the vegetation. The distribution of the Earth's major biomes is manifestly governed by the global climatic pattern; the life forms of the plants which characterise each biome are in turn adapted to that climate. It is no whim of botanists that designations of biomes from tundra to rainforest relate to vegetation types rather than the fauna

which inhabit them. Thus plants have a 'special relationship' with climate that gives them a particular value as palaeoclimatic indicators. This was recognised over a hundred years ago by A.C. Seward (1892) who reviewed the role of fossil plants as 'tests of climate'. He summarised what was then known of the features of fossil plants, from their taxonomic assignment to structural attributes such as growth rings in permineralised wood, that indicated the climate under which they had grown.

Subsequently, the growth of Pleistocene palynology, and particularly the science of 'pollen analysis' pioneered by Von Post (1944) has given a firm foundation to our understanding of the response of global vegetation to the oscillations of Quaternary climate. To a lesser extent, the study of Tertiary plants and their changing distribution has contributed to our understanding of the impact of climatic change of the last 70 million years on the pattern of global vegetation. (For a recent review, see Boulter and Fisher, 1994.) However, as we go back in time, the strength and nature of the 'climatic signal' that can be read from fossil plants become weaker (Chaloner and Creber, 1989).

3. Taxonomic and non-taxonomic methods

The underlying principle in Quaternary palynology ('pollen analysis') has been to use the present distribution of taxa (normally genera or species) to interpret observed pollen changes in terms of a response to climatic change. In recent years this methodology has been refined by combining the records of the climatic range (especially the mean July temperature plotted against the mean January temperature) for any given species of plant, with the abundance of the modern pollen representation within the 'climate space' that that species will tolerate. This produces a 'pollen abundance response surface' which shows in effect the climatic environment which will maximise the contribution of that species to the total pollen assemblage (see Huntley, 1993). That author gives a very perceptive analysis of the assumptions that underlie climate reconstructions based on fossil plant records. They

are worth repeating, as they are as pertinent to palaeoclimatic interpretation of Palaeozoic plants as they are to those of the Quaternary. (But it must be acknowledged that the margin of error is unfortunately materially greater in the former context!) Huntley's assumptions are:

(1) That a plant species' abundance and distribution are largely controlled by climate.

(2) That the relevant modern species' distribution is in equilibrium with the climate.

(3) That the fossil species under consideration was itself in equilibrium with the palaeoclimate under which it was growing.

(4) A sufficiently close biological analogue exists from which to infer the climate represented by a given assemblage or even individual species from past time.

As Huntley points out, there are suggestions that even within the Quaternary interval there are pollen spectra which have no close counterpart in any present-day environment. Clearly, this problem increases the further we go back in time. The existence of such 'unmatched' fossil plant/palaeoclimate relationships in Tertiary and Mesozoic times is further discussed in Wing and Greenwood (1993) and Spicer et al. (1993).

The methodology of Quaternary palynologists in using modern climatic patterns of plant taxa to interpret palaeoclimates has been extended back in time to interpret Tertiary fossil plant assemblages in terms of the 'nearest living relative' (NLR). This involves the assumption that the NLR of a given Tertiary fossil plant will show a climatic tolerance approximating to that of the fossil. If this can be done with a sizeable assemblage of fossil taxa, the mean result from their combined NLRs will give a higher level of confidence to the interpretation. There are a number of problems innate in this approach. Firstly, it is far more likely for Tertiary fossil plants than for Quaternary records that the NLR of a given fossil species will have undergone evolutionary change in the course of tens of millions of years, possibly changing its climatic tolerance to a significant degree. It is also evident that certain climatic conditions (such as Tertiary temperate environments within the polar circles) have no counterpart in today's 'icehouse world'. This represents an extreme case of the vulnerability of Huntley's fourth assumption. The

problems associated with the use of NLR within the Tertiary are further discussed in Boulter (1994), Chaloner (1994) and Collinson (1994).

As we go further back to early Mesozoic floras entirely lacking in angiosperms, it becomes clear that we cannot use the present-day distribution of their surviving 'nearest relatives' as any kind of guide to the palaeoclimate. The present-day distribution of those gymnosperm and free-sporing vascular plants ('pteridophytes') is a product of their having survived the onslaught of the angiosperms. It evidently bears little relationship to their range in the Mesozoic world, free from competition with that versatile group of ecologically aggressive plants. In the gymnosperm order of the Cycadales, for example, the present-day survivors are slow-growing pachycaul plants of tropical to sub-tropical frost-free habitats. But their pre-angiosperm representatives included deciduous forms which extended into high palaeolatitudes with a climate that must have been far beyond the tolerance of the present-day cycads (Spicer et al., 1993)

Even if pre-angiosperm fossil floras do not give us a direct proxy measure of any one climatic parameter, the global pattern of phytogeographic provinces gives clear indication of latitudinal zonation. This at least can show us the orientation of lines of palaeolatitude and the continuity (and separation) of land masses. This has been used for the Mesozoic (e.g., Vakhrameev, 1991) and for the Carboniferous–Permian (Chaloner and Creber, 1988). Ziegler et al. (1993) have taken this approach much further in analysing the likely climatic basis for the patterns seen in the phytogeographic provinces of the early Mesozoic. But inevitably floras of this age can only give a general picture of climatic parameters. Spicer et al. (1993) give a useful discussion of the limitations of this phytogeographic basis for palaeoclimate reconstruction.

Where the NLR method becomes inapplicable, we are driven to seeking broad correlation between features of plant structure and the climate to which they are adapted. The use of such features (e.g., the size and form of leaves, the character of growth rings in secondary wood, which can be measured without needing to identify the plant concerned) has been referred to as a 'non-taxonomic' basis for

assessing past climates. This is a useful label, implying that such features can be used without needing to assign the fossil to any particular taxon.

Even within this 'non-taxonomic' method there are some taxonomic constraints. The use of the 'physiognomy' of fossil leaves as a palaeoclimatic indicator, as developed by Chaney (1947) and recently refined by Wolfe (1993) is limited taxonomically in being applicable only to assemblages of angiosperm leaves. There are considerable problems in trying to read a 'climatic signal' from the leaf characters of gymnosperms or pteridophytic plants of the Mesozoic or Palaeozoic (but see Ziegler et al., 1993, and comments on Schopf, 1973, below). There are however other features such as growth rings that have climatic implications of seasonality which are largely independent of the affinity of the plant (see e.g., Chaloner and Creber, 1984; Chapman, 1994). Since the focus of this paper is on the use of plants in interpreting Palaeozoic climates, we concentrate in what follows on such 'non-taxonomic' characteristics as a means of interpreting palaeoclimates from plant fossils.

4. Fossil plants and Palaeozoic climates

Interest in the type of climate under which coal formation took place in the Carboniferous goes back well into the last century. J.M. Schopf (1973) gives a useful summary of some twenty features shown by Carboniferous fossil plants of the Euramerican coal swamp vegetation that have been suggested by earlier authors (notably H. Potonié and D. White—citations given in Schopf, 1973) as indicative of tropical or sub-tropical climate (Table 1). All of these but the last ('the presence of close relatives of modern types of tropical plants') are non-taxonomic in character. However, as Schopf acknowledges, 'a specific objection might be taken to nearly every item listed'. Some of the features that he enumerates are adaptations to anaerobic soils, such as occur in many wetland plants, regardless of climate (e.g., Schopf's items 4 and 18), so that these cannot be treated as indicators of tropical or sub-tropical climate per se. Others (Schopf's items 13, 14.) are associated with features of the life cycles of primitive vascular plants, rather than having any partic-

Table 1
Features shown by Carboniferous fossil plants of the Euramerican province that have been regarded by some authors as indicating a tropical or subtropical climate (after Schopf, 1973)

1. General luxuriance, size and abundance of vegetation
2. Succulent nature of many plants
3. Tissue with large cells and thin cell walls
4. Presence of large intercellular spaces and abundant lacunar tissue
5. General absence of growth rings in secondary wood
6. Large size of compound pinnate leaves (fronds)
7. Delicate foliage of climbers
8. Presence of aphlebiae (large persistent leaf stipules)
9. Large size and texture of some entire leaves
10. Occurrence of stomata in grooves
11. Presence of hydathodes (water discharge pores)
12. Profusion of large drooping fronds and pendant branches
13. Delayed fertilization (of seeds) and adaptations for seed flotation
14. Prevalence of free-sporing habit and dependence on water for reproduction
15. Cauliflory (inflorescences borne on central stems)
16. Presence of subaerial roots
17. Smoothness and thickness of bark
18. Occurrence of pneumatophores
19. Dilation of tree bases
20. Presence of close relatives of extant tropical plants

ular climatic association. Yet others, such as cauliflory (Schopf's item 15, the bearing of inflorescences directly on the trunk and main branches of trees) are at best ambiguous and at worst, misleading. In flowering plants there is indeed a correlation between caulifory and the humid tropical climate, but this is usually seen as an adaptation to assist insect pollination in that dense shade environment. To project that climatic correlation into spore-bearing plants, dependent on wind dispersal of their spores, seems inappropriate if caulifory is to be used as a climatic indicator.

In fact the twenty indicator features of Schopf (1973) which have been historically invoked come down to only three that can be seen as unambiguous non-taxonomic indicators: (1) large size of the biggest plants, and large frond size of the biggest leaves; (2) presence of subaerial roots in ferns and pteridosperms; (3) absence of growth rings in plants with secondary thickening of the vascular system.

The first of these may be seen as a Palaeozoic

extension of the general correlation of angiosperm large leaf size with a warm and humid climate. But even this must be tempered with the acceptance of a number of significant exceptions. For example the bracken fern, *Pteridium aquilinum*, of the Northern Hemisphere temperate zone has deeply divided compound pinnate leaves, commonly up to 3 m in length.

The occurrence of subaerial roots in tree ferns (as for example in the living fern *Cyathea* and the Carboniferous fossil *Psaronius*) is evidently part of a strategy of gaining height with an upright stem supported by a false trunk of adventitious roots. This appears to be the only way open to ferns to produce a tree without having the capacity to form secondary thickening of the vascular tissue or cortex. When this strategy is combined with the large apical meristem characteristic of such pachycaul plants, vulnerable to frost damage and to desiccation, then it seems to place a climatic constraint on this growth form which limits it to humid, frost-free environments.

5. Growth rings in fossil wood

Fossil tree trunks formed of secondary wood, produced by the activity of a vascular cambium, carry one of the more persuasive of palaeoclimatic signals. Trees growing under a more or less seasonless climate, as in the humid tropics, generally show more or less uniform secondary wood, while trees in a seasonal (wet/dry or warm/cold) climate generally show seasonally controlled growth rings. With a number of provisos, observation of growth rings—and of their absence—in fossil woods is perhaps the most directly climate-controlled signal offered by fossil plants. The nature of these provisos and some of the pitfalls in ignoring them are discussed in Chaloner and Creber (1984) and Chapman (1994).

The massive stems of the arborescent lycopods, the seed ferns, the calamites and the cordaites of the Euramerican Carboniferous province generally show uniform growth of their secondary wood, with a complete lack of any growth rings. Taking this information at its face value, this points to their growth within the humid tropical belt of that time, which is consistent with the palaeomagnetic evidence for the continental positions at that time. It is a pity that we have far less evidence from permineralised wood from higher palaeolatitudes of the synchronous Angara floral province, where coal formation is now seen as extending into Carboniferous palaeolatitudes as high as 60°N (see e.g., Crowley, 1994).

There is a minor paradox in our understanding of this situation, in that lacking growth rings we cannot use the normal method of arriving at the age of these Carboniferous plants, by counting the annual growth increments in the wood. As a result we have very little direct evidence as to the age of any of the individual plants of the Carboniferous flora. However, the very size of the trees and the body of the secondary wood formed points to growth spanning many seasons.

With the Carboniferous North Pole lying some twenty degrees of palaeolatitude beyond the northern shore of Pangea, we have no picture of the polar environment from fossil wood in the Northern Hemisphere. In the Southern Hemisphere, it is not until Permian time that we have good records of permineralized tree trunks within the palaeo-Antarctic Circle. While these indicate a strong seasonality, seen by clearly defined growth rings (Schopf, 1973; Chaloner and Creber, 1984), they also show disconcertingly broad annual growth increments, unmatched in such high latitude sites in our contemporary 'icehouse' world. Conditions favouring tree growth close to the palaeopoles are clearly documented for Late Cretaceous and early Tertiary records, but these are generally interpreted in terms of a high carbon-dioxide 'greenhouse' world. The extent to which forests of *Glossopteris* spread into the South Polar (Antarctic) region following the close of the glaciation of Gondwana contrasts with the corresponding but much more limited spread of largely coniferous forests into high North Polar latitudes in Quaternary interglacial and post-glacial phases.

6. Plants, climate and the palaeoatmosphere

The relationship between atmospheric carbon-dioxide and climate has now become a key issue

in any consideration of global climatic change. Even so, as Worsley et al. (1994) remarked "the notion that atmospheric concentration of CO_2 dominates all other climate control variables ... has been slow to influence the Earth sciences".

Four key processes relate long-term atmospheric change, plants life and climate (Fig. 1):

(1) The photosynthetic fixation of atmospheric CO_2 by phytoplankton in the oceans and terrestrial vegetation is one of the two routes by which carbon may be drawn down from the atmosphere and deposited in the deep ocean. In the case of plankton, this can occur directly, in situ, while terrestrial organic matter has a more circuitous and varied route. In regions of high water table (whether for topographic or climatic reasons) peat may accumulate at the land surface. With change of base level, this may come to be buried, and converted to coal,

remaining as fixed carbon in continental sediments for many millions of years. Tectonic movement may cause eventual exposure of the coal at the land surface, resulting in its weathering and return to the atmosphere. Its use by mankind as fossil fuel achieves the same end more rapidly!

Some small fraction of terrestrial plant biomass may escape biodegradation outside the peat environment, as for example in coastal wetlands, being thence transported into the marine realm. These two pathways (oceanic and continental) result in draw-down of atmospheric carbon and its eventual incorporation in deeply buried sediments (Fig. 1, item 1 and d, k).

(2) The other route of carbon-dioxide drawdown into the oceans is by the weathering of silicate minerals by CO_2 dissolved in rainwater, resulting in bicarbonate ions, balanced by calcium
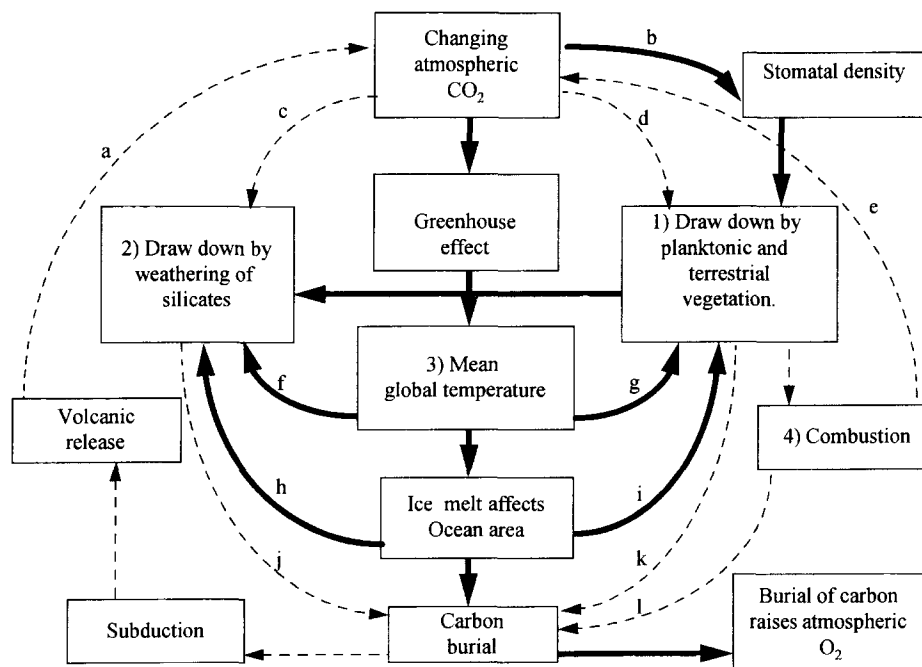

Fig. 1. A diagrammatic representation of the general relationship between atmospheric CO_2, photosynthesis, stomatal density, silicate weathering and global climate over geological time. The broken arrows indicate pathways of carbon flow; the solid bold arrows indicate indirect effects of the processes shown; a = volcanic release of CO_2 from subducted organic carbon and carbonate; b = stomatal density responding to changing atmospheric CO_2; c = rain washout of atmospheric CO_2; d = draw-down of atmospheric CO_2 by photosynthesis; e = release of CO_2 by wildfire; f = increased global temperature accelerates weathering, and (g) enhances biomass production; h = changing total global land area controls the area of silicate rock accessible to subaerial weathering, and (i) the total terrestrial biomass; j = HCO_3^- transported to the oceans; k = terrestrial burial of biomass (as peat) or transport of terrestrial biomass to the oceans; l = transport of charcoal from wildfire to continental or oceanic burial.

and other basic ions from the same source, passing into solution at the ground surface. In the form of these bicarbonate ions, the carbon is carried into the oceans to be used either in photosynthetic uptake, or precipitation as carbonate by either phyto- or zooplankton (Fig. 1, item 2 and c, j).

The rate of such weathering is strongly influenced by whether the rock surface is covered by soil and rooted vegetation, and of course the prevailing climate, particularly the temperature (Fig. 1, f). The net draw-down of carbon by this route is also then a function of the exposure of rock surfaces to weathering, and hence to the global sea level, which in turn governs the total area of exposed land surface (Fig. 1, h). In the long term, all such 'carbon burial' may be seen as leaving elemental oxygen in the atmosphere; the more carbon that is buried, the greater the amount of oxygen available in the atmosphere. Modelling of the balance between atmospheric oxygen and carbon burial plays a key role in estimating the changing oxygen content of the palaeoatmosphere (Berner and Canfield, 1989).

(3) The fact that these two routes (photosynthesis and weathering) of carbon draw down influence the concentration of the principal atmospheric greenhouse gas CO_2 links them with the mean global temperature (Fig. 1, item 3). The ensuing feedback mechanisms are undoubtedly a major feature of long-term global climatic change (see Berner, 1994; Worsley et al., 1994).

(4) There is a further link between plant life and the atmosphere in terms of the role of oxygen in the occurrence of wildfire. The combustion of plant biomass on land in naturally occurring fires is dependent on adequate oxygen in the atmosphere. Since fossil charcoal (fusain) which is produced by wildfire, has a more or less continuous record throughout the last 400 million years, it indicates that conditions have been favourable for wildfire throughout that period. This constrains the atmospheric level of oxygen to within both upper and lower limits—the 'fire window' of Jones and Chaloner (1991). These authors suggest that the fossil record of charcoal means that atmospheric oxygen has not fallen below 13% and not risen above 35% throughout the history of plant life on land. Charcoal is also largely unbiodegradable; the

most likely fate of any charcoal residue from forest fire is transport down the drainage system, and eventual burial, or if on a peat surface, incorporation within the peat (Fig. 1, item 4, e, 1).

Terrestrial plant life, the carbon-dioxide and oxygen in the atmosphere and the greenhouse control of the mean global temperature are all thus interlinked. Fig. 1 attempts to summarise their relationship in diagrammatic form.

7. Atmospheric carbon-dioxide and stomatal density

Woodward (1987) offered the first strong evidence that changes in the level of atmospheric CO_2 influence the density of stomata on the leaves of certain temperate deciduous trees. These observations have been extended to use changes in stomatal density in fossil leaves as a proxy measure of atmospheric CO_2 in Quaternary (Beerling, 1994; Beerling and Chaloner, 1994), Tertiary (Van der Burgh et al., 1993) and in Palaeozoic plants (McElwain and Chaloner, 1995). Work on extant plants and Quaternary fossil leaves shows that when the CO_2 has risen (as at the end of the last two glacials) stomatal density has fallen, as it has also done with the anthropogenic rise in CO_2 of the last two hundred years. The most likely explanation for this response is that the plants have opted to reduce transpirational loss through the stomata by reducing stomatal density, at the expense of limiting their maximum photosynthetic CO_2 uptake. In simplistic terms, the added CO_2 has made it possible for the plants to maintain their carbon uptake while reducing transpirational water loss. That is, they have increased their water use efficiency—the number of carbon atoms acquired for every water molecule lost by transpiration.

The measurement of stomatal density (the number of stomata per unit area of leaf) alone is susceptible to errors associated with the water relations of the plant. A preferable parameter is the stomatal index, the ratio of the number of stomata to non-stomatal epidermal cells (Salisbury, 1927). This ratio is fixed early in leaf development, and remains relatively unaffected by irregularities

in water availability during development. However, to measure stomatal index requires a clear view of the epidermal cell outlines as well as the number of stomata, and this is not always possible when dealing with fossil material.

This relationship between stomatal density and atmospheric CO_2 seems to be sustained across a time span extending back to the last glacial stage, where we have ice core evidence of the CO_2 level; Van der Burgh et al. (1993) show that it can be sustained as far back at the late Tertiary, using temperatures assessed from palynological data as a proxy for the CO_2 level. We have attempted elsewhere (McElwain and Chaloner, 1995) to test Berner's (Berner, 1994) Phanerozoic CO_2 curve by measuring stomatal density in much older fossil plants (see Fig. 2).

The interval that we have concentrated on is the Devonian to Permian, as this shows the greatest change from a Devonian high of some ten times the pre-industrial CO_2 level, to a value approaching that of the present by the end of Carboniferous time (Fig. 2). This of course correlates with the accelerated photosynthetic draw down of CO_2 associated with the build-up of global terrestrial vegetation through the Devonian and Carboniferous. This was then combined with massive carbon burial through the formation of extensive marine limestones (especially during the Early Carboniferous) and later Carboniferous bituminous coals. Other significant features of Berner's curve are that it is consistent with the warm 'greenhouse world' as exemplified by conditions during Old Red Sandstone time in the Northern palaeo-Hemisphere, followed by the 'icehouse world' of Carboniferous–Permian time, culminating in the glaciation of Gondwana at high southerly palaeolatitudes.

We were constrained in our choice of suitable fossil plant material for these Palaeozoic stomatal counts by the need to have a high quality of preservation to facilitate accurate replicated measures of stomatal density, and where possible, stomatal index. It was also necessary to have some living equivalent of the fossil plant with which to compare its stomatal numbers. The difficulty in achieving this gives our observations a lower resolution than that possible where the fossil is attribut-
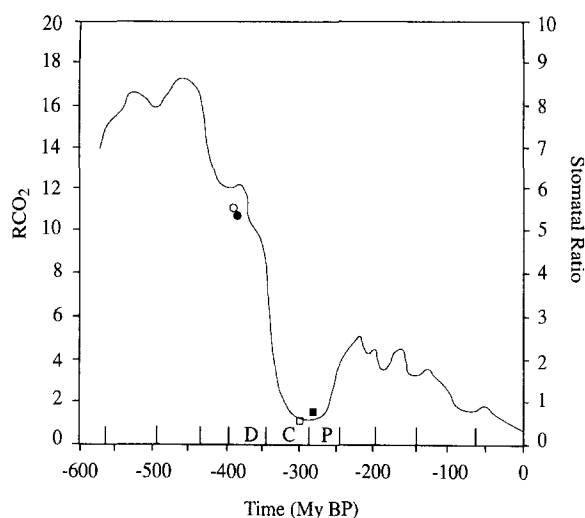

Fig. 2. Values for the stomatal ratios of four Palaeozoic plants superimposed on the mean value of Berner's (1994) Phanerozoic CO_2 curve. The stomatal ratio is the value of the stomatal index of the nearest living equivalent divided by that of the relevant fossil. The fossils shown, and their ages, are: *Aglaophyton major* (white circle), Siegenian/Emsian; *Sawdonia ornata* (black circle), Emsian; *Swillingtonia denticulata* (white square) Westphalian; '*Lebachia*' *frondosa* (black square), Early Permian. Each of these points is placed with respect to the horizontal (time) axis on the basis of their absolute age. The Devonian, Carboniferous and Permian Periods are shown as D, C and P, respectively. The time scale is in millions of years before present. The vertical axis at left (RCO₂) is the estimated ratio of the palaeo-CO_2 level to that of the pre-industrial level (from Berner, 1994). The scale of stomatal ratio (at right) has been set so as to bring the Carboniferous value approximately onto the CO_2 curve, and this choice has dictated the value of that scale.

able to a living species, as in the Quaternary and Late Tertiary material cited above.

For comparison with the stomatal densities of our Palaeozoic plants, we chose living plants which we regarded as their nearest ecological, systematic or structural equivalents. The two early Devonian plants for which we obtained stomatal data (*Aglaophyton* and *Sawdonia*) were compared with upright, terete photosynthetic structures in the form of *Juncus* leaves and the photosynthetic stems of *Psilotum*. These represent respectively what may be regarded as an ecological equivalent and as near a living relative as we have in the present flora. We also selected Upper Carboniferous and Lower Permian conifers, for which stomatal data

were readily obtained, choosing as a nearest living equivalent a small-leaved conifer, *Araucaria heterophylla*. Details of these choices, the sources of material and a discussion of this procedure are given in McElwain and Chaloner (1995).

The results of these Palaeozoic stomatal studies are summarised in Fig. 2. We plot the median values of Berner's 1994 CO_2 curve for the Phanerozoic, and superimpose on it the values of 'stomatal ratios' for the four Palaeozoic plants for which we have relevant data. The 'stomatal ratio' is the stomatal index of the nearest living equivalent divided by that of the fossil. For the two Devonian species, we have used the mean value of the two nearest living equivalent species cited above. The RCO_2 axis gives the values of the CO_2 level from Berner's data as a multiple of that of the pre-industrial level (see caption to Fig. 2 for further details).

Although we freely accept that this is at best only a first excursion into this interpretation of fossil plant stomatal data, we note that the Devonian, Carboniferous and Permian indices show at least the same trend as Berner's CO_2 model. Taken at face value, this means that the plants adapted to the falling CO_2 value through the late Palaeozoic by raising their stomatal density. This may have been accompanied by loss of water-use efficiency; that is, more water would have been lost by transpiration for each molecule of CO_2 fixed by photosynthesis than was possible under the Devonian CO_2 high. However, in the humid palaeo-Equatorial coal-forming swamps the near-saturated atmosphere may have minimised this impact of high stomatal densities. This rise of stomatal densities with falling CO_2 is of course the reverse of the process that has apparently taken place in dicotyledonous trees in response to the rising CO_2 of the last 2OO years (Woodward, 1987).

We believe that the stomatal data from fossil plants offer a potentially useful proxy measure of past CO_2 levels, and are pursuing this research with material from other ages. In view of the established relationship between the carbon-dioxide enhanced greenhouse effect and global climate, we anticipate that these data will contribute to our

understanding of the causality of climatic change in the past.

References

Beerling, D.J., 1994. Palaeo-ecophysiological studies on Cretaceous and Tertiary fossil floras. In: M.C. Boulter and H.C. Fisher (Editors), Cenozoic Plants and Climates of the Arctic. Springer, Berlin, pp. 23–33.

Beerling, D.J. and Chaloner, W.G., 1994. Atmospheric CO_2 changes since the last glacial maximum: evidence from the stomatal density record of fossil leaves. Rev. Palaeobot. Palynol., 81: 11–17.

Berner, R.A., 1994. 3Geocarb II: a revised model of atmospheric CO_2 over Phanerozoic time. Am. J. Sci., 291: 56–91.

Berner, R.A. and Canfield, D.E., 1989. A new model for atmospheric oxygen over Phanerozoic time. Am. J. Sci., 289: 333–361.

Boulter, M.C., 1994. Reconstruction of North Atlantic climate change over the last 70 million years using extinct plant taxa. In: M.C. Boulter and H.C. Fisher (Editors), Cenozoic Plants and Climates of the Arctic. Springer, Berlin, pp. 389–390.

Boulter, M.C. and Fisher, H.C. (Editors), 1994. Cenozoic Plants and Climates of the Arctic. Springer, Berlin, 401 pp.

Chaloner, W.G., 1994. Fossil plants as palaeoenvironmental indicators. In: M.C. Boulter and H.C. Fisher (Editors), Cenozoic Plants and Climates of the Arctic. Spinger, Berlin, pp. 13– 20.

Chaloner, W.G. and Creber, G.T., 1984. Climatic indications from growth rings in fossil wood. In: P. Brenchley (Editor), Fossils and Climate. Geol. J. Spec. Iss., pp. 49–74.

Chaloner, W.G. and Creber, G.T., 1988. Fossil plants as indicators of late Palaeozoic plate positions. In: M.G. Audley-Charles and A. Hallam (Editors), Gondwana and Tethys. Geol. Soc. Spec. Publ., 37: 201–210.

Chaloner, W.G. and Creber, G.T., 1989. Do fossil plants give a climatic signal? J. Geol. Soc. London, 147: 343–350.

Chaney, R.W., 1947. Tertiary centres and migration routes. Ecol. Monogr., 17: 140–148.

Chapman, J., 1994. Distinguishing internal developmental characteristics from external palaeoenvironmental effects in fossil wood. Rev. Palaeobot. Palynol., 81: 19–32.

Collinson, M.E., 1994. Arcto-Tertiary '93: Perspectives and Prospects. In: M.C. Boulter and H.C. Fishers (Editors),

Cenozoic Plants and Climates of the Arctic. Springer, Berlin, pp. 383–388.

Crowley, T.J., 1994. Pangean Climates. In: G.D. Klein (Editor), Pangea. Geol. Soc. Am. Spec. Pap., 288: 25– 39.

Hallam, A., 1989. Great Geological Controversies. Oxford Univ. Press, Oxford, 244 pp.

Huntley, B., 1993. The use of climate response surfaces to reconstruct palaeoclimate from Quaternary pollen and plant macrofossil data. Philos. Trans. R. Soc. London B, 341: 215–224.

Jones, T.P. and Chaloner, W.G., 1991. Fossil charcoal, its recognition and palaeoatmospheric significance. Palaeogeogr. Palaeoclimatol. Palaeoecol. (Global Planet. Change Sect.), 97: 39–50.

McElwain, J. and Chaloner, W.G., 1995. Stomatal density and index of fossil plants track atmospheric carbon dioxide in the Palaeozoic. Ann. Bot., 76: 389–395.

Salisbury, E.J., 1927. On the causes and ecological significance of stomatal frequency, with special reference to the woodland flora. Philos. Trans. R. Soc. London B, 431: 1–65.

Schopf, J.M., 1973. Coal, climate and global tectonics. In: D.H. Tarling and S.K. Runcorn (Editors), Implications of Continental Drift for the Earth Sciences, 1. Academic, London, pp. 609–622.

Seward, A.C., 1892. Fossil Plants as Tests of Climate. Clay, London, 151 pp.

Spicer, R.A., Rees, P.M. and Chapman, J.L., 1993. Cretaceous phytogeography and climate signals. Philos. Trans. R. Soc. London B, 341: 277–286.

Vakhrameev, V.A., 1991. Jurassic and Cretaceous Floras and Climates of the Earth. Cambridge Univ. Press, Cambridge, 318 pp.

Van der Burgh, J., Visscher, H., Dilcher, D.L. and Kurschner, W.M., 1993. Paleoatmospheric signatures in Neogene fossil leaves. Science, 206: 1788–1790.

Von Post, L., 1944. The prospect for pollen analysis in the study of the earth's climatic history. New Phytol., 45: 193–217.

Wing, S.L. and Greenwood, D.R., 1993. Fossils and fossil climate: the case for equable continental interiors in the Eocene. Philos. Trans. R. Soc. London B, 341: 243–252.

Wolfe, J.A., 1993. A method of obtaining climatic parameters from leaf assemblages. US Geol. Surv. Bull., 2040, 71 pp.

Woodward, F.I., 1987. Stomatal numbers are sensitive to increases in CO_2 from pre-industrial levels. Nature, 327: 617–618.

Worsley, T.R., Moore, T.L., Fraticelli, C.M. and Scotese, C.R., 1994. Phanerozoic CO_2 levels and global temperatures inferred from changing paleogeography. In: G.D. Klein (Editor), Pangea. Geol. Soc. Am. Spec. Pap., 208: 57–74.

Ziegler, A.M., Parrish, J.M., Jiping, Y., Gyllenhaal, E.D., Rowley, D.B., Parrish, J.T., Shangyou, N., Bekker, A. and Hulver, M.L., 1993. Early Mesozoic phytogeography and climate. Philos. Trans. R. Soc. London B, 341(1297): 297–305.