PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Use of Climate Response Surfaces to Reconstruct Palaeoclimate from Quaternary Pollen and Plant Macrofossil Data [and Discussion]

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Phil. Trans. R. Soc. Lond. B 1993 **341**, 215-224
doi: 10.1098/rstb.1993.0106

The use of climate response surfaces to reconstruct palaeoclimate from Quaternary pollen and plant macrofossil data

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SUMMARY

Climate response surfaces are described and their advantages for palaeoclimate studies discussed; their potential for bi-directional application is emphasized. The principal assumptions made when reconstructing past climates from plant fossils are then discussed and the essential attributes of a technique for quantitatively reconstructing palaeoclimate from plant fossil data are outlined. Examples of palaeoclimate reconstructions are described and some of the limitations of pollen data are introduced. Current initiatives aiming to overcome these limitations and difficulties are outlined. Finally, observations are made on the applicability of these techniques to Mesozoic palaeoclimate reconstruction.

1. INTRODUCTION

Quaternary scientists infer past climates from sediments and the fossils they contain, as well as from geomorphic features recording past sea levels, glacial activity, etc. Although qualitative or comparative inferences, arrived at upon the basis of subjective analyses of the evidence, are most frequent, efforts have increasingly been made to develop more objective analytical tools and to quantify the inferred conditions. However they are made, palaeoclimate inferences generally depend upon calibrations obtained from modern observations. It is extremely difficult to escape from this 'uniformitarian' approach and from the limitations that it imposes. Recent advances in understanding of past environments (see, for example, Bradley 1991) and recent syntheses of Quaternary fossil evidence (Huntley & Birks 1983; Jacobson *et al.* 1987; Huntley & Webb 1988; Graham & Grimm 1990), however, show past conditions often are not analogous to any modern conditions (Overpeck *et al.* 1985; Anderson *et al.* 1989; Huntley 1990*a*). This renders quantitative palaeoclimate reconstruction particularly challenging (Huntley 1990*b*).

This problem has become a research imperative as we have to seek improvements in our understanding of the dynamics of the global system. If we are accurately to forecast the environmental consequences of the changes being wrought by human society then simulation models of the global system are needed. These models may incorporate knowledge gained from palaeoclimate studies and also may be validated using independent palaeoclimate inferences (Webb *et al.* 1985, 1987*a*). For these purposes, palaeoclimate reconstructions must be quantitative and use analytical tools that are as objective and repeatable as possible, enabling large-scale syntheses of data from many localities. Only such extensive syntheses can reveal changes in atmospheric general circulation that determine regional climatic changes. Validating the simulation of these large-scale atmospheric features is essential if the overall performance of atmospheric general circulation models is to be validated (COHMAP Members 1988).

Whereas ocean records provide evidence of past global ice volume, of changes in ocean circulation and in sea-ice cover and of other climate-related variables, only terrestrial records can reveal many features of past atmospheric general circulation. Patterns of seasonal temperature extremes, drought, growing-season temperature sums and continental precipitation distribution all reflect general circulation features. These variables can be reconstructed from evidence preserved in continental deposits. Fossil evidence of past biota is the greatest potential source of palaeoclimatic information because it is multivariate and because different taxa respond individualistically (Huntley 1988, 1991). Of those organisms whose identifiable fossil remains are found in Quaternary deposits the most widely represented and most frequently investigated are the higher plants. Fossil pollen grains and spores are preserved in a wide range of sediments and frequently are accompanied by identifiable macrofossil remains of seeds, fruits and vegetative fragments of individual species. The assemblage of plant micro- and macrofossils recovered from a Quaternary sediment indicates the nature of both the vegetation and the environment surrounding that locality at the time of sediment deposition.

Quantitative palaeoclimate reconstructions require

Phil. Trans. R. Soc. Lond. B (1993) **341,** 215–224
Printed in Great Britain

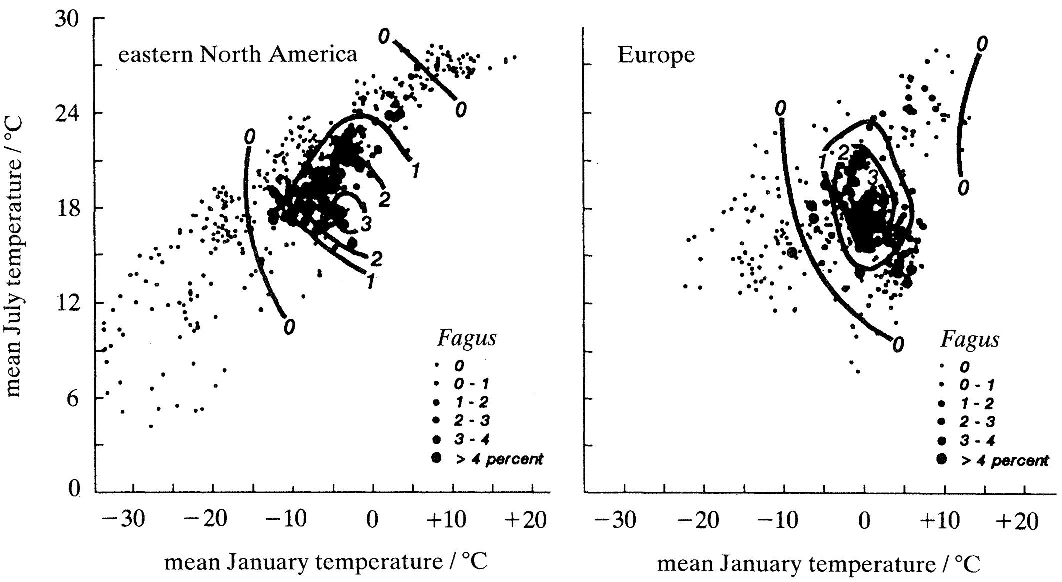

Figure 1. *Fagus* response surfaces for Europe and eastern North America (redrawn after Huntley *et al.* 1989).

appropriate methods that relate modern pollen rain or contemporary species distribution patterns to present climate. Bartlein *et al.* (1986) proposed the use of pollen–climate response surfaces that relate the abundance patterns of pollen taxa in surface samples to the values of a small number of climate variables. Prentice *et al.* (1991) applied this technique to the late Quaternary pollen record from eastern North America. A similar approach can be applied to relate species' distribution patterns to climate (P. J. Bartlein *et al.*, unpublished results; B. Huntley, unpublished results). Such climate response surfaces can be used bi-directionally either to reconstruct the climate at any point in time and space from the fossil plant assemblage or to predict the assemblage of plants expected under given climate conditions. This makes climate response surfaces powerful tools for evaluating alternate atmospheric general circulation model climate simulations (Webb *et al.* 1987*b*; Huntley 1992).

Climate response surfaces and the procedure used to fit them will be described and the advantages stemming from their bi-directionality discussed. The principal assumptions made when reconstructing past climates from fossil evidence then will be outlined and the features desirable in a reconstruction technique briefly described. Some examples of Quaternary climate reconstructions made using response surfaces will be presented. Finally, some problems encountered in making these reconstructions, and research initiatives aiming to overcome these, will be discussed.

2. CLIMATE RESPONSE SURFACES

Maps portraying species' abundance or likelihood of occurrence by means of contours or differential shading are a familiar means of communicating biogeographical information. Isopoll maps portraying pollen taxon abundance patterns have also become familiar (Bernabo & Webb 1977; Huntley & Birks 1983; Huntley 1988; Webb 1988; Huntley & Webb 1989). Iversen (1944) depicted the range limits of three taxa (*Hedera*, *Viscum* and *Ilex*) with respect to axes of warmest and coldest month mean temperature, thus transforming a map of their geographical range limits into a 'map' of their range limits in 'climate space'. Hintikka (1963) made similar mappings into climate space for many species. Both, however, mapped only presence or absence so as to draw range limits in climate space. Bartlein *et al.* (1986) mapped pollen abundance values into climate space and for two-dimensional climate spaces summarized the patterns using pollen abundance isolines analogous to isopolls drawn upon pollen maps. These isolines depict a surface, the elevation of which at any point in climate space reflects abundance of the pollen taxon. This surface is the 'pollen–climate response surface' for that taxon with respect to those climate variables (Bartlein *et al.* 1986; Huntley *et al.* 1989; Huntley 1990*c*, 1992; Prentice *et al.* 1991) (figure 1).

Although they cannot readily be visualized, such surfaces can be constructed for higher dimensional climate spaces. Most work to date has employed a three-dimensional climate space (figure 2). Analogous surfaces can be constructed in which elevation reflects likelihood of occurrence of a species at that location in climate space.

Although such surfaces can be fitted using various approaches, the technique selected must satisfy several requirements (see below). Locally weighted regression (Cleveland & Devlin 1988) is employed using a tricube weighting function. Resulting surfaces are 'faithful' to the data; fitted values smooth the data while values interpolated across 'holes' in the data lie within the range of the values surrounding the 'hole' and extrapolated values are asymptotic to the marginal data values. This technique neither assumes nor provides any simple mathematical description of the fitted surface; thus the value at any location in climate space can be determined only using the surrounding data values. For reconstruction purposes values are

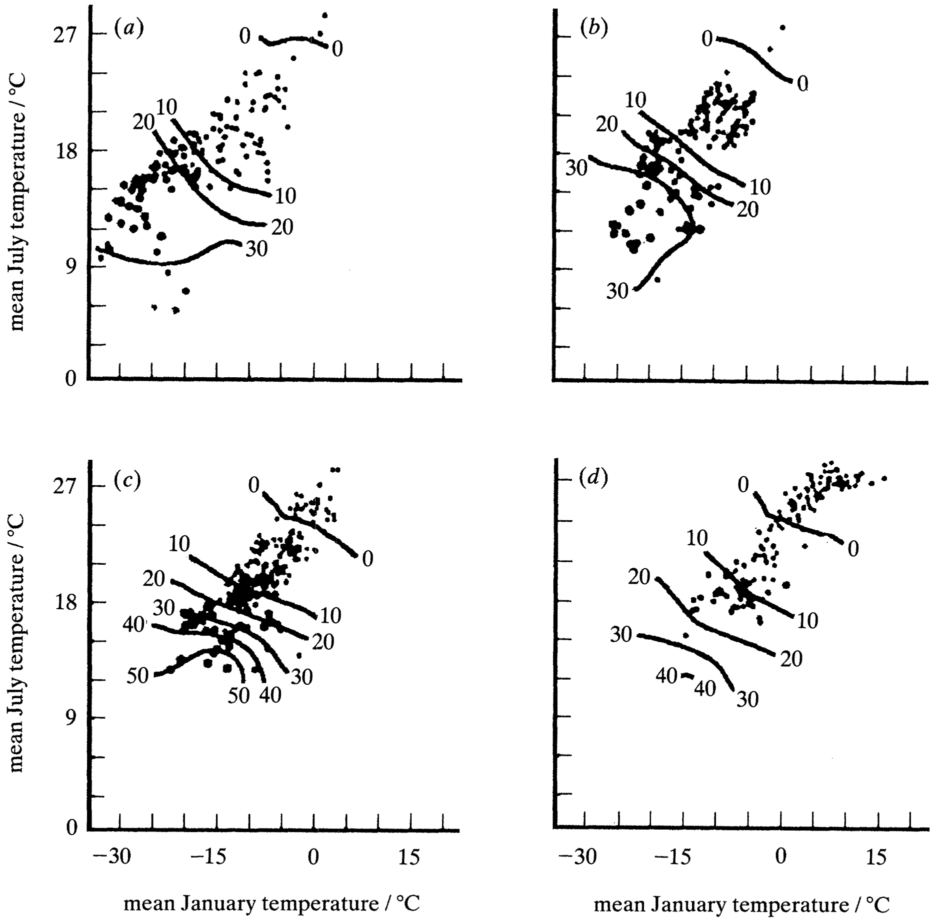

Figure 2. *Picea* response surface for eastern North America (redrawn after Prentice *et al.* 1991). Isolines are % pollen frequency. Annual precipitation: (*a*) 350 mm; (*b*) 650 mm; (*c*) 950 mm; and (*d*) 1250 mm.

evaluated and stored for a regular grid in climate space.

Climate response surfaces are fitted separately for each pollen taxon or species. The stored grid-point values from surfaces for a series of pollen taxa are combined to provide a fitted pollen spectrum for each grid point in climate space. These spectra then are the potential analogues for fossil spectra when making climate reconstructions. The climate associated with any fossil pollen spectrum is reconstructed by seeking its closest analogue(s) among the grid-point spectra (Prentice *et al.* 1991; Huntley 1992). Analogy is measured using the chord distance (Overpeck *et al.* 1985; Huntley 1990*a*). Where constraints are applied they are used to limit the range of possible analogues that may be considered (Huntley 1993).

Climate response surfaces also are bi-directional; not only can they be used to reconstruct climate from fossil pollen spectra, but also to predict, or simulate, pollen spectra expected under given climate conditions. Predicted values are obtained analogously to fitted grid-point values using locally weighted regression. In this way response surfaces can provide simulations of pollen abundance patterns corresponding to given climate scenarios. Applied to atmospheric general circulation model palaeoclimate simulations they provide a means of validating these simulations by comparing predicted pollen abundance patterns with those observed in the fossil record (Webb *et al.* 1987*b*; Huntley 1992).

3. QUANTITATIVE PALAEOCLIMATE RECONSTRUCTION FROM BIOLOGICAL EVIDENCE

Various authors have discussed the assumptions underlying climate reconstruction from fossil evidence (see, for example, Birks 1981). The extent to which these assumptions are met has been vigorously debated (Birks 1981, 1986, 1988; Webb 1986, 1988; Huntley 1988; Huntley & Webb 1989; Huntley *et al.* 1989). The principal assumptions are that: (i) species' distribution and abundance patterns are principally determined by macroclimate; (ii) present species' distribution and pollen abundance patterns are in equilibrium with climate; (iii) past species' distribution and pollen abundance patterns were in equilibrium with climate at the time for which reconstruction is being attempted; and (iv) a sufficiently close modern analogue exists from which to infer the climate represented by the fossil assemblage from which reconstruction is being attempted.

The validity of the first assumption critically depends upon the relationship between the geographical scales of the distribution patterns and of the climatic gradients. Nevertheless, a large body of experimental and physiological ecological evidence, including studies of long-lived trees (Pigott & Huntley 1981; Pigott 1981, 1991), implicates climate as the principal determinant of species' distribution and abundance patterns (Woodward 1987). Furthermore, Holten (1986; see also Holten & Carey 1992) identified fine-scale climatically determined species' distribution patterns along a 135 km transect in a region of steep climatic gradients in western Norway. Thus, although soil type, underlying geology and disturbance régime all determine fine-scale features of species' distribution and abundance patterns, they are secondary in importance to the macroclimate (Bradshaw & Zackrisson 1990; Bradshaw & Hannon 1992*a*,*b*; Davis *et al.* 1992).

Demonstrating equilibrium between climate and species' distribution and abundance patterns is difficult for two reasons. Firstly, as with all attempts to define an organism's niche, an almost limitless range of environmental factors might be considered. There is consequently a high probability that particular values of some subset of these might circumscribe the taxon's distribution without any causal relationship existing. The climate variables considered therefore should be limited to those having general roles in determining the growth and performance of the type of organism being examined. Three climate attributes have such general significance in the case of higher plants, namely degree of winter cold, growing season warmth and limitations upon soil moisture supply (Bartlein *et al.* 1986; Huntley *et al.* 1989; Prentice *et al.* 1992). Climate response surfaces have been fitted to variables that approximate these three factors.

Secondly, the equilibrium must be dynamic; species' range limits will track any change in the geographical positions of the climate thresholds by which they are determined. Documentary and instrumental records show substantial climate changes in recent centuries (Lamb 1982; Folland *et al.* 1990, 1992) paralleled by recent and ongoing changes in species' range limits (Davis *et al.* 1991; Bradshaw & Hannon 1992*a*,*b*; Bradshaw 1993). Nevertheless, demonstrating these changes are responses to climate change and maintain species' range limits in equilibrium with their climate thresholds is difficult. However, there are noticeable similarities between the climate responses surfaces of many equivalent eastern North American and European pollen taxa. Systematic comparison of the climate response of the pollen taxon *Fagus* in the two regions (Huntley *et al.* 1989) shows *Fagus* species occupy almost identical climate spaces with respect to seasonal temperatures in the two regions (figure 1). Because such a coincidence is extremely unlikely to arise by chance the most probable explanation is that *F. sylvatica* in Europe and *F. grandifolia* in North America each occupy a geographical range in equilibrium with climate. Although no other systematic comparisons have been made, the frequent similarity of the climate response of equivalent taxa in the two regions suggests that range limits are generally in equilibrium with climate.

Given the problems in demonstrating equilibrium between species' present range limits and climate, it is not surprising that demonstrating such equilibria in the past has been difficult. Various hypotheses have been advanced as to why past distributions might have been in disequilibrium with climate. The frequently advanced hypothesis of 'migrational lag' (Davies 1976; Birks 1981, 1986; Huntley & Birks 1983) proposes that the change from glacial to interglacial conditions between *ca.* 15 ka before present (BP) and *ca.* 6 ka BP took place in a small number of discrete large steps and that plant species' range limits responded slowly to these changes, attaining equilibrium with each new climate régime as much as several millennia after the régime became established (Birks 1981, 1986). A related hypothesis focuses upon rates of population growth rather than of migration (Bennett 1985, 1986, 1988), arguing that pollen records reflect species' abundance more accurately than they reflect their geographical range limits and proposing that increases in species' abundance following deglaciation lagged large step-like changes in climate by as much as several millennia. These hypotheses both invoke limitations in the species' biological characteristics that might limit their capacity to respond to rapid climate changes; firstly, propagule dispersal and secondly, the *per capita* production of offspring. Other hypotheses invoke environmental limitations apart from those imposed by climate, for example, pedogenic processes (Pennington 1986), to account for inferred disequilibrium between tree species' range limits and prevailing climate. The proposal that late Holocene changes in various European trees' range limits (e.g. *Fagus*, *Picea*) were a consequence primarily or solely of human activities (see, for example, Iversen 1973) implies that their previous range limits, prior to these late Holocene adjustments, were determined by non-climate factors and were in disequilibrium with climate.

These hypotheses share an assumption that climate changed in a small number of discrete large steps during the last deglaciation (and, by implication, during similar events earlier in the Quaternary). Although localized evidence of rapid climate change (see, for example, Dansgard *et al.* 1989) and evidence of rapid changes in North Atlantic surface temperature patterns (Ruddiman & McIntyre 1981) show that rapid changes did occur at some times and places and in some components of the climate system during the last deglaciation, it is also apparent that deglaciation extended over at least six millennia. Evidence of phases of more and less rapid rise of sea level (Fairbanks 1989) shows that major continental ice sheets did not decay at a uniform rate; nevertheless these decaying ice sheets had a persistent effect upon atmospheric circulation and climate, especially in the North Atlantic region (COHMAP Members 1988). Palaeoclimate reconstructions from fossil beetle assemblages indicate very rapid changes in climate during deglaciation (Coope 1977; Atkinson *et al.* 1987) and have been used to infer a disequilibrium, persisting for several millenia, between vegetation and climate. It is unlikely, however, that beetles and trees respond to the same components of climate (Huntley 1991) and other evidence suggests that the extent of any 'migrational lag' of trees behind climate change was rela-

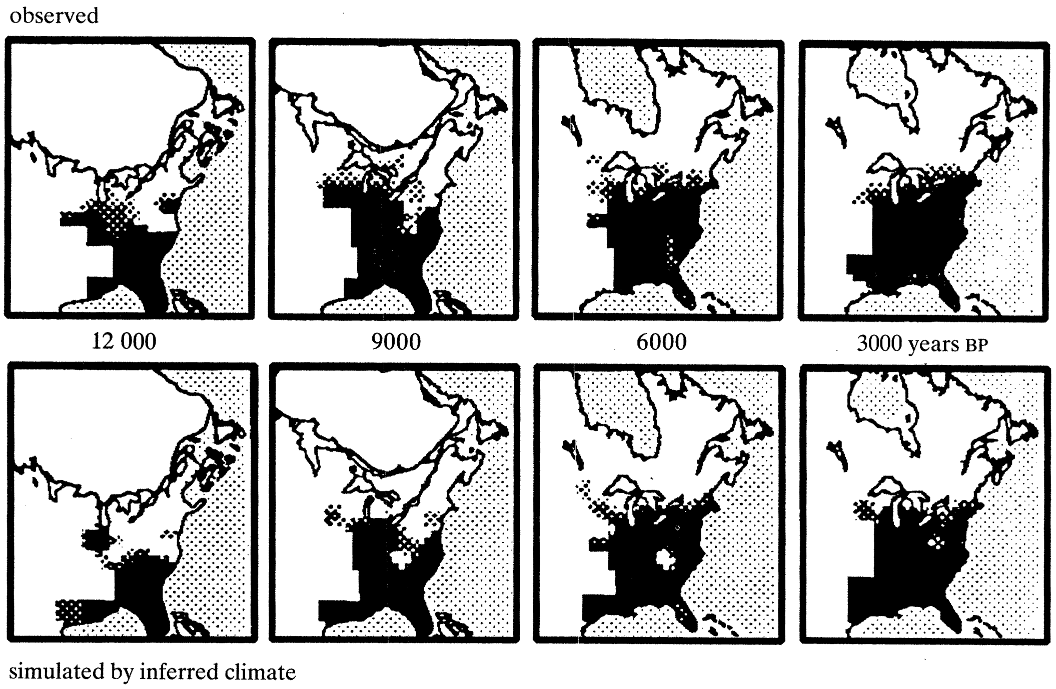

Figure 3. Observed and simulated Holocene history of *Carya* in eastern North America (redrawn after Prentice *et al.* 1991). Shading levels (light, medium and dark) signify pollen abundances greater than 1, 5 and 20% respectively.

tively slight (Webb 1986; Huntley & Webb 1989; Prentice *et al.* 1991).

The most convincing demonstration of equilibrium between tree species' range limits and Holocene climate is provided by Prentice *et al.* (1991). They show that the Holocene ranges of several eastern North American trees previously hypothesised to exhibit 'migrational lag' (Davis 1976) can be simulated using the climate response surfaces of these taxa and a climate history reconstructed using response surfaces of an independent suite of taxa (figure 3).

The final assumption, that a modern analogue can be found from which to infer the past climate, often cannot fully be satisfied. Studies of analogy between fossil and modern pollen spectra show the extent of this problem (Overpeck *et al.* 1985; Anderson *et al.* 1989; Huntley 1990*a*). Fossil pollen spectra from glacial stages most frequently have a low analogy with the most similar modern spectra. This parallels 'disharmonious assemblages' of beetles (Coope, 1977) and vertebrates (Stuart 1982; Graham & Grimm 1990) found in glacial stages and is to be expected given the no-analogue combinations of solar radiation, atmospheric composition, ice-sheet extent and sea-surface temperatures that then prevailed. Although the problem may never be completely overcome, incorporating a measure of analogy into palaeoclimate reconstruction methods provides an indication of the reliability of their results. Furthermore, calibration of the reconstruction technique using modern pollen spectra from as diverse a range of climate conditions as possible will minimize errors resulting from such lack of analogy.

Reconstruction techniques should not assume any particular mathematical form for the relationship between pollen abundance and climate variables; techniques using conventional regression analysis (Huntley & Prentice 1988) therefore should be avoided. Reconstruction techniques should allow some limited interpolation and extrapolation but must perform these conservatively; polynomial regressions are notorious for their unreliable behaviour beyond the limits of the domain within which they were fitted and should be avoided. The pollen values of all major taxa should be used to derive the reconstruction, thus utilizing most of the evidence provided by the fossil pollen spectrum. Recent experience shows also that it is often necessary independently to constrain the climate values that may be reconstructed (Guiot *et al.* 1993; Huntley 1993; J. Guiot & B. Huntley, unpublished results; P. J. Bartlein, personal communication). Such constraints may derive either from the pollen spectra themselves, for example by the prior assignment of spectra to broadly defined 'biomes' using a rule-based model (J. Guiot & B. Huntley, unpublished results), from complementary palaeovegetation evidence provided by plant macrofossils (Huntley 1993), or else from independent evidence such as fossil beetle assemblages (J. Guiot & P. Ponel, unpublished results) or past lake-levels (Guiot *et al.* 1993).

4. POLLEN- AND PLANT MACROFOSSIL-BASED RECONSTRUCTIONS OF QUATERNARY PALAEOCLIMATE MADE USING CLIMATE RESPONSE SURFACES

Although a number of studies are underway (Huntley 1993; B. Huntley, I. C. Prentice & P. J. Bartlein, unpublished results; J. Guiot & B. Huntley, unpublished results) only a limited number of published palaeoclimate reconstructions have used climate response surfaces (Kelly & Huntley 1991; Prentice *et al.* 1991). These studies fall into two categories; firstly, reconstructions for single, or small numbers of, localities using stratigraphic sequences of fossil samples (Kelly & Huntley 1991; Huntley 1993; J. Guiot & B. Huntley, unpublished results), and secondly, reconstructions of palaeoclimate patterns at particular times using fossils samples from many localities (Prentice *et al.* 1991; B. Huntley, I. C. Prentice & P. J. Bartlein, unpublished results).

Kelly & Huntley (1991) used 22 pollen–climate response surfaces fitted to mean January and July temperatures and mean annual precipitation. They used the pollen–climate dataset described by Huntley *et al.* (1989) and fossil data from a lake in central Italy (Lago di Martignano, Latium; 42°7′N, 12°20′E, 200 m a.s.l.). Their results show marked and independent Holocene variations in the climate variables, with evidence of periodic variations of precipitation. Although good analogues were found for the oldest pollen samples, the reconstructed extremely low mean January temperature conflicts with evidence elsewhere in the Mediterranean region indicating frost-sensitive sclerophyllous taxa present during the Weichselian (Watts 1985; Pons 1981).

Huntley (1993) uses a more extensive surface pollen dataset (J. Guiot, *et al.*, unpublished data) with climate conditions evaluated at each surface sample locality using spline surfaces fitted to modern meteorological data (Hutchinson 1991; W. Cramer & B. Huntley, unpublished results). He fits pollen-climate response surfaces in a space of coldest month mean temperature (°C), temperature sum above 5°C (day degrees) and actual to potential evapotranspiration ratio. These variables are derived using the BIOME model bioclimate generator of Prentice *et al.* (1992). Response surfaces for 28 taxa are applied to fossil spectra from a locality in Scotland (Morrone Birkwoods; 3°26′W, 57°0′N, 425 m a.s.l.) and attention focuses upon reconstructing Devensian lateglacial palaeoclimate. Analogues found for the lateglacial spectra come from a wide range of different climates and include spectra from areas of tundra, steppe and montane vegetation having in common modern spectra dominated by pollen of herbaceous taxa. The reconstructed values consequently have large uncertainties and vary markedly between stratigraphically adjacent samples.

The plant macrofossil record is used in an attempt to overcome this problem. Because most macrofossils can be identified to species level and are not transported over long distances, they can be used to identify components of the vegetation around the site of deposition. Most macrofossils in the Morrone Birkwoods' lateglacial sediments are of species that today exhibit Arctic–Alpine, Arctic–Sub-Arctic or Northern Montane distributions (Matthews 1937, 1955; see Huntley 1993) and occur together in Arctic and montane 'tundras'.

Constraints are derived using distribution maps of species whose macrofossils are found. Species' range limits are compared with maps of the climate variables used to fit the response surfaces. For each macrofossil assemblage, thresholds are determined for one or more climate variable(s); the most restrictive species' range limit determining each threshold. Although performed by visual inspection of the maps, this approach is analogous to the 'mutual climatic range' method applied by Atkinson *et al.* (1987) to beetle remains.

These constraints now limit the range of possible analogues considered for the fossil pollen spectra, excluding the 'inappropriate' analogues and giving palaeoclimate reconstructions that are less variable between samples and have smaller uncertainties. The results indicate a lateglacial climate in the eastern Highlands of Scotland characterized by a consistently low temperature sum above 5°C but with coldest month temperature, although always cooler than present (*ca.* 0°C), varying between a peak of *ca.* −5°C around 11.5 ka BP and a trough of *ca.* −16°C centred upon *ca.* 10 400 years BP (Huntley 1993).

Unfortunately parallel plant macrofossil records are not available from most pollen stratigraphically studied localities. An alternative approach to the derivation of constraints therefore is required. One possibility is the development of a rule-based model to assign pollen spectra to 'biomes' (J. Guiot & B. Huntley, unpublished results). Pollen taxa are grouped according to the 'plant functional type' (*sensu* Prentice *et al.* 1992) that they represent and threshold criteria derived by analysis of potential modern vegetation and surface pollen data. The climate tolerance rules developed by Prentice *et al.* (1992) for each plant functional type then provide the climatic constraints.

Prentice *et al.* (1991) present a series of reconstructions of palaeoclimate pattern for eastern North America since the last glacial maximum. They reconstruct independent spatial patterns of change for three climate variables and show how these reconstructions, based upon values for six major pollen taxa, can simulate the distribution and abundance history of seven minor taxa. Although similar reconstructions have been attempted for Europe (B. Huntley, I. C. Prentice & P. J. Bartlein, unpublished results) they have encountered more problems, as have parallel attempts using other reconstruction techniques (Guiot *et al.* 1993). Several differences between eastern North America and Europe potentially contribute to these problems; of these, the relatively greater climatic and topographic diversity and complexity of Europe probably is most important. This complexity is apparent when published reconstructions of mean July temperature at 6 ka BP made using transfer functions are compared (eastern North America, Bartlein & Webb 1985; Europe, Huntley & Prentice 1988). Ongoing work aims to overcome these problems.

5. DISCUSSION

Climate response surfaces provide both a convenient portrayal of the relationship between climate and taxon distribution or abundance patterns and a bidirectional tool for palaeoclimate reconstruction and for simulating distribution or abundance patterns corresponding to given climate scenarios. As tools for palaeoclimate reconstruction they have the desirable combination of attributes outlined above. Compared to conventional regression-analysis-based 'transfer-functions' they represent a substantial advance. The 'palaeobioclimate analogue' technique developed by Guiot (Guiot 1987, 1990, 1991; Guiot *et al.* 1989, 1991; Guiot & Couteaux 1992) also has the desirable attributes outlined above. The principal advantages of climate response surfaces over the palaeobioclimate analogue technique are: (i) smoothing of the data values reduces the likelihood of anomalous reconstructions from anomalous surface samples; and (ii) limited interpolation and extrapolation offers a more continuous domain of analogues than does the original data. Their bi-directionality and visual portrayal of the relationship between a taxon and climate are additional advantages of response surfaces. The palaeobioclimate analogue technique has complementary advantages: (i) selection of particular surface samples as analogues allows determination of both the geographical and climatic locations of the analogues; and (ii) because the data are not smoothed, the range of spectra encountered under given climate conditions remains available for matching. Recent work comparing the two techniques has shown them generally to give similar results (J. Guiot & B. Huntley, unpublished results).

Both approaches suffer from problems of lack of modern analogues or lack of the most appropriate modern analogues. These problems never may be overcome completely; some combinations of climate conditions prevailing in the past may occur nowhere today. However, the domain of possible analogues has conventionally been limited to surface samples from the same continental region as the fossil pollen site. Thus, Prentice *et al.* (1991) used surface pollen samples from east of *ca.* 110°W in the U.S.A. or Canada whereas Kelly & Huntley (1991) used surface samples from west of *ca.* 80°E in western Eurasia. However, biogeographically both regions are components of the Boreal Kingdom (*sensu* Good 1964) and many of the same pollen taxa are encountered in each. Furthermore, the climatic response of many shared taxa is very similar in the two regions and has been demonstrated to be almost identical in one case (Huntley *et al.* 1989). Although overlapping substantially, the overall climatic range encompassed by each region differs. The two regions together thus offer a wider range of potential analogues for past climates than does either region alone (Huntley *et al.* 1989). Work is in progress to develop a circum-boreal pollen surface sample dataset for climatic calibration. This may provide improved analogues for some European glacial and lateglacial spectra that apparently represent steppe-like vegetation under conditions of relatively cool summers and cold winters. Such cold steppes are not represented in surface sample data from western Eurasia but may be analogous to vegetation in parts of north-western North America or southern Central Asia.

Although these methods, developed for Quaternary palaeoclimate research, may be applicable to earlier geological periods such as the Mesozoic, such use is dependent upon two additional assumptions. Firstly, that taxa have not evolved changes in their climatic tolerances since the time being considered. Evidence supports this assumption for the Quaternary and late Tertiary (Huntley *et al.* 1989). However, the likelihood of significant evolved changes over timescales extending to the Mesozoic or beyond cannot be discounted. Secondly, an assumption that realized climatic ranges of taxa have not changed as a result of competition or other interactions with taxonomic groups that subsequently evolved. This assumption is difficult to sustain for geological periods prior to the evolution of tall, broad-leaved Angiosperm trees when taxa that today are subordinate to such trees played dominant roles under climate regimes where they are now excluded. Although the use of 'plant functional types' (*sensu* Prentice *et al.* 1992) rather than taxonomic entities offers potential to solve some such problems, it is likely that broadly constraining the range of possible climates may be the best that can be achieved for earlier geological periods.

This paper was prepared at the invitation of the organizers of the Royal Society Discussion Meeting '*Palaeoclimates and their modelling with special reference to the Mesozoic era*'. Many stimulating discussions with Pat Bartlein, Joël Guiot, Colin Prentice and Tom Webb, among others, have helped develop the ideas presented. The Royal Society, COHMAP, EC (EPOCH 004), NERC (GST/02/523) and NATO (86/0800) have all supported the development of European pollen–climate response surfaces and their application to reconstruct palaeoclimates. The text benefitted from critical reading by Judy Allen, Jacqui Huntley, Bob Spicer and Alayne Street-Perrott.

REFERENCES

Anderson, P.M., Bartlein, P.J., Brubaker, L.B., Gajewski, K. & Ritchie, J.C. 1989 Modern analogues of late-Quaternary pollen spectra from the western interior of North America. *J. Biogeogr.* **16**, 573–596.

Atkinson, T.C., Briffa, K.R. & Coope, G.R. 1987 Seasonal temperatures in Britain during the past 22,000 years reconstructed using beetle remains. *Nature, Lond.* **325**, 587–593.

Bartlein, P.J., Prentice, I.C. & Webb, T., III 1986 Climatic response surfaces from pollen data for some eastern North American taxa. *J. Biogeogr.* **13**, 35–57.

Bartlein, P.J. & Webb, T., III 1985 Mean July temperature estimates for 6,000 yr B.P. in eastern North America; Regression equations for estimates from fossil-pollen data. In *Climatic change in Canada*, vol. 5 (ed. C. R. Harrington) (*Syllogeus* **55**), pp. 301–342.

Bennett, K.D. 1985 The spread of *Fagus grandifolia* across eastern North America during the last 18,000 years. *J. Biogeogr.* **12**, 147–164.

Bennett, K.D. 1986 The rate of spread and population increase of forest trees during the postglacial. *Phil. Trans. R. Soc. Lond.* B **314**, 523–531.

Bennett, K.D. 1988 Post-glacial vegetation history: ecological considerations. In *Vegetation history* (ed. B. Huntley & T. Webb III), pp. 699–725. Dordrecht: Kluwer Academic Publishers.

Bernabo, J.C. & Webb, T., III 1977 Changing patterns in the Holocene pollen record of northeastern North America: a mapped summary. *Quat. Res.* **8**, 64–96.

Birks, H.J.B. 1981 The use of pollen analysis in the reconstruction of past climates: a review. In *Climate and* *history* (ed. T. M. L. Wigley, M. J. Ingram & G. Farmer), pp. 111–138. Cambridge University Press.

Birks, H.J.B. 1986 Late-Quaternary biotic changes in terrestrial and lacustrine environments, with particular reference to north-west Europe. In *Handbook of Holocene palaeoecology and palaeohydrology* (ed. B. E. Berglund), pp. 3–65. New York: Wiley.

Birks, H.J.B. 1988 Long-term ecological change in the British uplands. In *Ecological change in the uplands* (ed. M. B. Usher & D. B. A. Thompson), pp. 37–56. Oxford: Blackwell Scientific Publications.

Bradley, R.S. (ed.) 1991 *Global changes of the past.* (514 pages.) Boulder, Colorado: UCAR/Office for Interdisciplinary Earth Studies.

Bradshaw, R.H.W. 1993 Forest response to Holocene climate change: equilibrium or non-equilibrium. In *Climate change and human impact on the landscape* (ed. F. M. Chambers), pp. 57–65. London: Chapman and Hall.

Bradshaw, R.H.W. & Hannon, G. 1992*a* The disturbance dynamics of Swedish boreal forest. In *Response of forest ecosystems to environmental changes* (ed. A. Teller, P. Mathy & J. N. R. Jeffers), pp. 528–535. London: Elsevier.

Bradshaw, R.H.W. & Hannon, G. 1992*b* Climatic change, human influence and disturbance regime in the control of vegetation dynamics within Fiby Forest, Sweden. *J. Ecol.* **80**, 625–632.

Bradshaw, R.H.W. & Zackrisson, O. 1990 A two thousand year history of a northern Swedish boreal forest stand. *J. veg. Sci.* **1**, 519–528.

Cleveland, W.S. & Devlin, S.J. 1988 Locally weighted regression: an approach to regression analysis by local fitting. *J. Am. Statist. Ass.* **83**, 596–610.

COHMAP Members 1988 Climatic changes of the last 18,000 years: observations and model simulations. *Science, Wash.* **241**, 1043–1052.

Coope, G.R. 1977 Fossil coleopteran assemblages as sensitive indicators of climatic changes during the Devensian (Last) cold stage. *Phil. Trans. R. Soc. Lond.* B **280**, 313–337.

Dansgaard, W., White, J.W.C. & Johnsen, S.J. 1989 The abrupt termination of the Younger Dryas climate event. *Nature, Lond.* **339**, 532–534.

Davis, M.B. 1976 Pleistocene biogeography of temperate deciduous forests. *Geosci. Man* **13**, 13–26.

Davis, M.B., Schwartz, M.M. & Woods, K. 1991 Detecting a species limit from pollen in sediments. *J. Biogeogr.* **18**, 653–668.

Davis, M.B., Sugita, S., Calcote, R.R. & Frelich, L. 1992 Effects of invasion by *Tsuga canadensis* on a North American forest ecosystem. In *Response of Forest Ecosystems to environmental changes* (ed. A. Teller, P. Mathy & J. N. R. Jeffers), pp. 34–44. London: Elsevier.

Fairbanks, R. 1989 A 17,000-year glacio-eustatic sea level record: influence of glacial melting rates on the Younger Dryas event and deep ocean circulation. *Nature, Lond.* **342**, 637–642.

Folland, C.K., Karl, T.R. & Vinnikov, K.Ya. 1990 Observed Climate Variations and Change. In *Climate change: the IPCC scientific assessment* (ed. J. T. Houghton, G. J. Jenkins & J. J. Ephraums), pp. 195–238. Cambridge University Press.

Folland, C.K., Karl, T.R., Nicholls, N., Nyenzi, B.S., Parker, D.E. & Vinnikov, K.Ya. 1992 Observed Climate Variability and Change. In *Climate change 1992: the Supplementary report to the IPCC scientific assessment* (ed. J. T. Houghton, B. A. Callender & S. K. Varney), pp. 135–170. Cambridge University Press.

Good, R. 1964 *The geography of the flowering plants*, 3rd edn. (518 pages.) London: Longman.

Graham, R.W. & Grimm, E.C. 1990 Effects of global climate change on the patterns of terrestrial biological communities. *Trends Ecol. Evol.* **5**, 289–292.

Guiot, J. 1987 Late Quaternary climatic change in France estimated from multivariate pollen time-series. *Quat. Res.* **28**, 100–118.

Guiot, J. 1990 Methodology of the last climatic cycle reconstruction from pollen data. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **80**, 49–69.

Guiot, J. 1991 Structural characteristics of proxy data and methods for quantitative climate reconstructions. In *Evaluation of climate proxy data in relation to the European Holocene* (ed. B. Frenzel) (*Paläoklimaforschung/Palaeoclimate Res.* **6**, Special Issue: ESF-Project 'European Palaeoclimate and Man' **1**), pp. 271–284.

Guiot, J. & Couteaux, M. 1992 Quantitative climate reconstruction from pollen data in the Grand Duchy of Luxembourg since 15 000 yr BP. *J. Quat. Sci.* **7**, 303–309.

Guiot, J., Harrison, S.P. & Prentice, I.C. 1993 Reconstruction of the Holocene pattern of moisture in Europe using pollen and lake-level data. *Quat. Res.* (In the press.)

Guiot, J., Pons, A., Beaulieu, J.L. De & Reille, M. 1989 A 140,000-year continental climate reconstruction from two European pollen records. *Nature, Lond.* **338**, 309–313.

Guiot, J., Reille, M., Beaulieu, J.L. De and Pons, A. 1991 Calibration of the climatic signal in a new pollen sequence from La Grande Pile. *Climate Dyn.* **6**, 259–264.

Hintikka, V. 1963 Über das Grossklima einiger Pflanzenareale in zwei Klimakoordinatensystem Dargestellt. *Annls bot. Soc. zool. bot. fenn. Vanamo* **34** (5), 64 pp.

Holten, J.I. 1986 Autecological and phytogeographical investigations along a coast-inland transect at Nordmørem, central Norway. Ph.D. thesis, University of Trondheim.

Holten, J.I. & Carey, P.D. 1992 Responses of climate change on natural terrestrial ecosystems in Norway. *NINA Forskningsrapport* **29**, 1–59.

Huntley, B. 1988 Glacial and Holocene vegetation history: Europe. In *Vegetation history* (ed. B. Huntley & T. Webb III), pp. 341–383. Dordrecht: Kluwer Academic Publishers.

Huntley, B. 1990*a* Dissimilarity mapping between fossil and contemporary pollen spectra in Europe for the past 13,000 years. *Quat. Res.* **33**, 360–376.

Huntley, B. 1990*b* Studying global change: the contribution of Quaternary palynology. *Palaeogeogr. Palaeoclimatol. Palaeoecol. (Global and Planetary Change Section)* **82**, 53–61.

Huntley, B. 1990*c* European post-glacial forests: compositional changes in response to climatic change. *J. veg. Sci.* **1**, 507–518.

Huntley, B. 1991 How plants respond to climate change: Migration rates, individualism and the consequences for plant communities. *Annls Bot.* **67** (Suppl. 1), 15–22.

Huntley, B. 1992 Pollen-climate responses surfaces and the study of climate change. In *Applications of Quaternary research* (ed. J. M. Gray) (*Quat. Proc.* **2**), pp. 91–99.

Huntley, B. 1993 Late-Devensian and Holocene palaeoecology and palaeoenvironments of the Morrone Birkwoods, Aberdeenshire, Scotland. *J. Quat. Sci.* (Submitted.)

Huntley, B., Bartlein, P.J. & Prentice, I.C. 1989 Climatic control of the distribution and abundance of beech (*Fagus* L.) in Europe and North America. *J. Biogeogr.* **16**, 551–560.

Huntley, B. & Birks, H.J.B. 1983 *An atlas of past and present pollen maps for Europe: 0–13000 years ago.* (667 pages.) Cambridge University Press.

Huntley, B. & Prentice, I.C. 1988 July temperatures in Europe from pollen data, 6000 years before present. *Science, Wash.* **241**, 687–690.

Huntley, B. & Webb, T., III (eds) 1988 *Vegetation history*. (803 pages.) Dordrect: Kluwer Academic Publishers.

Huntley, B. & Webb, T., III 1989 Migration: species' response to climatic variations caused by changes in the earth's orbit. *J. Biogeogr.* **16**, 5–19.

Hutchinson, M.F. 1991 The application of thin plate smoothing splines to continent-wide data assimilation. In *Data assimilation systems* (ed. J. D. Jasper), pp. 104–113. Bureau of Meteorology, Melbourne: BMRC Research Report No. 27.

Iversen, J. 1944 *Viscum*, *Hedera*, and *Ilex* as climatic indicators. *Geol. För. Stockh. Förh.* **66**, 463–483.

Iversen, J. 1973 The development of Denmark's nature since the last glacial. *Danm. geol. Unders., series V* **7-C**, 126 pp.

Jacobson, G.L., Jr., Webb, T., III & Grimm, E.C. 1987 Patterns and rates of vegetation change during the deglaciation of eastern North America. In *The Geology of North America*, vol. K-3 (*North America and adjacent oceans during the last deglaciation*) (ed. W. F. Ruddiman & H. E. Wright Jr), pp. 277–288. Boulder, Colorado: Geological Society of America.

Kelly, M.G. & Huntley, B. 1991 An 11,000-year record of vegetation and environment from Lago di Martignano, Latium, Italy. *J. Quat. Sci.* **6**, 209–224.

Lamb, H.H. 1982 *Climate, history and the modern world*. (387 pages.) London: Methuen.

Matthews, J.R. 1937 Geographical relationships of the British flora. *J. Ecol.* **25**, 1–90.

Matthews, J.R. 1955 *Origin and distribution of the British flora*. London: Hutchinson.

Overpeck, J.T., Webb, T., III & Prentice, I.C. 1985 Quantitative interpretation of fossil pollen spectra: Dissimilarity coefficients and the method of modern analogs. *Quat. Res.* **23**, 87–108.

Pennington, W.A. 1986 Lags in adjustment of vegetation to climate caused by the pace of soil development. *Vegetatio* **67**, 105–118.

Pigott, C.D. 1981 Nature of seed sterility and natural regeneration of *Tilia cordata* near its northern limit in Finland. *Annls bot. fenn.* **18**, 255–263.

Pigott, C.D. 1991 *Tilia cordata* Miller. Biological Flora of the British Isles, No. 174. *J. Ecol.* **79**, 1147–1207.

Pigott, C.D. & Huntley, J.P. 1981 Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range. 3. Nature and causes of seed sterility. *New Phytol.* **87**, 817–839.

Pons, A. 1981 The history of Mediterranean-type shrublands. In *Ecosystems of the world. II. Mediterranean-type shrublands* (ed. F. di Costi, D. W. Goodall & R. L. Sprecht). Amsterdam: Elsevier.

Prentice, I.C., Bartlein, P.J. & Webb, T., III 1991 Vegetation and climate change in eastern North America since the last glacial maximum. *Ecology* **72**, 2038–2056.

Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A. & Solomon, A.M. 1992 A global biome model based on plant physiology and dominance, soil properties and climate. *J. Biogeogr.* **19**, 117–134.

Ruddiman, W.F. & McIntyre, A. 1981 The North Atlantic during the last deglaciation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **35**, 145–214.

Stuart, A.J. 1982 *Pleistocene vertebrates in the British Isles*. (212 pages.) London: Longman.

Watts, W.A. 1985 A long pollen record from Laghi di Monticchio, southern Italy: a preliminary account. *J. geol. Soc. Lond.* **142**, 491–499.

Webb, T., III 1986 Is vegetation in equilibrium with climate? How to interpret late-Quaternary pollen data. *Vegetatio* **67**, 75–91.

Webb, T., III 1988 Glacial and Holocene vegetation history: Eastern North America. In *Vegetation history* (ed. B. Huntley & T. Webb III), pp. 385–414. Dordrecht: Kluwer Academic Publishers.

Webb, T., III, Kutzbach, J.E. & Street-Perrott, F.A. 1985 20,000 years of global climatic change; Palaeoclimatic research plan. In *Global change* (ed. T. F. Malone & J. G. Roeder), pp. 182–218. International Council of Scientific Unions, Cambridge University Press.

Webb, T. III, Street-Perrott, F.A. & Kutzbach, J.E. 1987*a* Late-Quaternary paleoclimatic data and climate models. *Episodes* **10**, 4–6.

Webb, T., III, Bartlein, P.J. & Kutzbach, J.E. 1987*b* Climatic change in eastern North America during the past 18,000 years: comparisons of pollen data with model results. In *The geology of North America*, vol. K-3 (*North America and adjacent oceans during the last deglaciation* (ed. W. F. Ruddiman & H. E. Wright Jr), pp. 447–462. Boulder, Colorado: Geological Society of America.

Woodward, F.I. 1987 *Climate and plant distribution*. (174 pages.) Cambridge University Press.

Discussion

R. A. Spicer (*Department of Earth Sciences, University of Oxford, U.K.*). I am interested to know what account is taken of taphonomic variables in the establishment of (i) the modern day pollen data, and (ii) the palaeoassemblages when using the response surfaces technique. Holmes (1990) has demonstrated the heterogeneity of pollen and spore distribution in a small lake. Could not the taphonomic factors he observed affect substantially the use of response surfaces?

Reference

Holmes, P.L. 1990 An experimental approach to spore taphonomy. Ph.D. thesis, University of London.

B. Huntley. Quaternary palynologists have long been aware of the problems associated with the differing source areas for pollen recruitment into lake sediments; source areas differ according to lake size and morphometry, pollen taxon and the position within the lake basin from which sediment samples are obtained. In so far as it is possible, the effect of these taphonomic variables is minimized in the work using pollen–climate response surfaces by the use of pollen data from surface sediment samples and cores collected in the central parts of lake basins or treeless mires of moderate size (50 m–1 km in diameter). Although pollen data from smaller and/or larger lakes and mires are used to extend the geographical coverage into regions where no other data are available, the extreme effects of taphonomic variation are avoided by excluding data from very small basins that lie beneath a forest canopy. Given these precautions, the variations related to taphonomy are small in magnitude compared to the variations in pollen spectra that relate to climatic variation across the broad geographical area being examined.

W. G. Chaloner (*Biology Department, Royal Holloway and Bedford New College, University of London, U.K.*). Dr Huntley makes the point that to use response surfaces to reconstruct palaeoclimate he asumes that the vegetation is in equilibrium with the climate. At times of rapid climatic change, the capacity of any plant species to keep in equilibrium with the climate will surely depend on the rate at which it can migrate. Does this not in turn depend on its mobility, that is on its reproductive strategy? Might one not expect (to put it rather simplistically) that 'r-strategy' plants might be able to keep up with climate change more readily than those of 'K-strategy?' How far does this capacity of a species to migrate influence the validity of using its response surface as a basis for palaeoclimate reconstruction, under conditions of rapid climatic change?

B. Huntley. It does seem intuitively reasonable to suppose that, if climate changes occurred sufficiently rapidly, then plants with differing reproductive strategies might show differential rates of response of their range boundaries that would relate not to their climatic tolerances but to their reproductive strategies. The association of the attributes of an 'r-strategy' with a tendency to occur in the early stages of succession renders it more difficult to determine the extent to which rates of migration are related to reproductive strategy. However, Holocene pollen records from both Europe and eastern North America show relatively 'K-strategist' trees (e.g. *Quercus*) migrating rapidly following deglaciation and no apparently systematic relationship between the rate of migration and either reproductive strategy or the time of migration. It thus seems unlikely that reproductive strategy can have any significant effect upon palaeoclimate reconstructions that are often made at millennial intervals or even less frequently.

E. A. Jarzembowski (*P.R.I.S., University of Reading, U.K.*). Russell Coope (1979) has shown that beetles have a rapid response rate to climate change in the Quaternary. Please could Dr Huntley expand on the value of insects as independent constraints on plant-based palaeoclimatic reconstructions.

Reference

Coope, G.R. 1979 Late Cenozoic fossil Coleoptera: evolution, biogeography and ecology. *A. Rev. Ecol. System.* **10**, 247–267.

B. Huntley. Palaeoclimate reconstructions can be made from a variety of 'proxy' data; fossil beetles and plants represent just two of the possibilities. Each palaeoclimate proxy has its own distinct characteristics, including strengths and limitations. It is generally preferable to utilize data from different proxies to independently reconstruct palaeoclimate; the results can then be compared and may be used to provide cross-validation or to identify discrepancies between their palaeoclimate indications. The recent work of Guiot and his collaborators referred to above has adopted a different approach in which temperature reconstructions based upon beetle assemblages are used to constrain the range of analogues used in a pollen-based palaeoclimate reconstruction. The two reconstructions are, however, no longer independent and there is an underlying hypothesis that the beetle-based temperature reconstructions are more reliable than the unconstrained pollen-based reconstructions. Without independent evaluations this hypothesis remains untested. In my opinion, the primary value of fossil beetle data remains that of an independent palaeoclimate proxy and I favour a multi-proxy approach to the problems of understanding past climate changes.