

## A mutual climatic range method for reconstructing palaeoclimate from plant remains

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**Abstract:** The mutual climatic range (MCR) technique for reconstructing palaeoclimate relies on establishing the present-day climatic tolerance ranges of living species which are also found as fossils in Quaternary deposits. The palaeoclimate under which the species in a fossil assemblage co-existed can be inferred to lie within the intersection of the individual species' tolerance ranges. This paper describes a factor analysis of modern European climate data to determine two compound variables that describe the main features of the climate: 'summer warmth and dryness' and 'wetness and winter warmth'. Distribution maps of 80 plants from *Atlas Florae Europaeae* were combined with the climate data to determine each species' climatic range in factor space. MCRs were determined for two living plant assemblages from southeast England and found to give a reliable, although rather imprecise, reconstruction of the true thermal and precipitation climate. Reconstructions for two plant macro-fossil assemblages from Devensian gravels at Earith, Cambridgeshire, demonstrated palaeoclimates that were colder and more continental than the present, but with similar total amounts of precipitation. The study demonstrates the potential of the MCR method for use with Quaternary macrofossil plant remains, although there are methodological drawbacks in employing a climate-space defined by factor analysis.

**Keywords:** Quaternary, plants, climate, palaeoclimatology.

Sub-fossil fauna and flora preserved in Quaternary sediments often provide a detailed picture of the plants and animals that existed in the vicinity of a site and the surrounding region. Because the Quaternary is the most recent geological period the great majority of species recorded among the plants and invertebrates are still living today. This paper describes a means of using this evidence to make detailed quantitative reconstructions of climate using the mutual climatic range (MCR) method. This technique was first presented by Atkinson *et al.* (1986, 1987) although there were forerunners in work by Iversen (1944) and Grichuk (1969). It has since been widely applied using fossil beetles from Quaternary deposits (Elias *et al.* 1996). Most other methods for reconstructing terrestrial climate from biota, such as transfer functions (Sachs *et al.* 1977), bio-climatic analogues (Guiot 1990; Guiot *et al.* 1993), and pollen response surfaces (Huntley 1993) use relative abundance of pollen grains as their primary data. In contrast the MCR method resembles the climatic indicator approach (Zagwijn 1994) in employing only the known *presence* of a number of species. It is therefore well suited to assemblages in which each species may be represented by very few individuals, as is common for plant and insect macrofossils. The taphonomy of most macrofossil accumulations ensures that the living creatures dwelt near their site of preservation, whereas pollen of some wind-pollinated taxa may be derived from distances over 1000 km away. Additionally, many macrofossils can be identified to species level, which is essential for the MCR method, whereas most pollen taxa correspond to plant genera. However, there is no reason in principle why species-level pollens should not be used for MCR reconstructions, provided the investigator can be confident that the pollen was derived from plants growing near the site.

The purpose of this paper is to describe an extension of the MCR method to fossil plants, and to demonstrate its potential by reconstructing the modern climate for two sites in southeast

England, and palaeoclimates for two plant macrofossil assemblages from Devensian fluvial deposits at Earith, also in eastern England.

### Principles of the MCR method

The principles of the MCR method were outlined by Atkinson *et al.* (1986, 1987). The biological unit employed is the species and the method must be conducted with a target group of species, in this case the higher plants. The basic method is illustrated in Fig. 1 and rests upon the tenet that each species has a known climatic tolerance range. If a particular species, 'A', was present at a site in the past then the climate at that site must have lain within its tolerance limits. Likewise, if several species A, B, C . . . N all coexisted at the same place and time, the palaeoclimate must have lain within the overlap of their tolerance ranges, i.e. the *mutual climatic range* of the N species.

Development of the MCR method for any target group therefore falls into three stages.

(i) Determination of climatic tolerance ranges for a suitable number of species. These constitute the database of *species climatic ranges* on which the method is based. Preparing this database involves two sub-stages:

- (a) identification of the *key variables* which limit the ranges of most species in the target group, and which will form the axes of a *climate-space* like that in Fig. 1;
- (b) acquisition of data in the form of distribution maps and other information which allow the envelope bounding the species climatic range for each species to be drawn.

(ii) Testing and validation of the method and data-base of species climatic ranges using modern assemblages to make climate reconstructions and comparing them with the recorded climate for their localities.

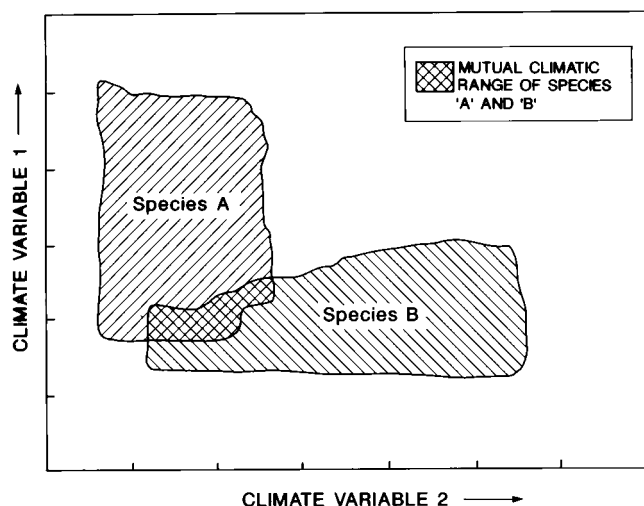


Fig. 1. The basic principle of the MCR method for palaeoclimatic reconstruction. Each species climatic tolerance range is mapped in a space defined by climatic variables. If several species are known to have been present simultaneously at a site, then the palaeoclimate must have lain within their mutual climatic range.

(iii) Application of the method to Quaternary assemblages to reconstruct palaeoclimate.

### Climatic reconstruction using the MCR method on plant species

#### *Choice of key variables for the climate space*

*Plant-climate interactions.* The physiology and life cycles of plant species are affected by the climatic regimes of temperature and moisture. These are linked through the dominant control that temperature exerts on *potential evapotranspiration*, i.e. the meteorologically determined capacity for evapotranspiration from moist ground and green leaves to which plants must respond, either passively or actively. Thus, the key variables chosen to define plants' species climatic ranges must reflect temperature and moisture variables.

The broad relationships between climate and plant physiology have been carefully and stimulatingly reviewed by Woodward (1987). He has shown that the physiognomy of vegetation (*not* individual species distributions) can be explained geographically by the interaction of climate with four physiological or developmental functions in plants. These are: competition for light; leaf area development; avoidance of desiccation due to drought; avoidance of tissue death due to chilling or freezing.

Competition for light involves the development of the most complex and structured vegetation that is possible, given the limitations of other factors. In vegetation with a high degree of competition for light, the overall leaf area index (LAI) is very high, as much as 9 in broadleaved evergreen forest in the tropics. However, greater leaf area allows greater evaporation losses from plants. The requirement that soil water budgets be sustainable as a repeated yearly cycle means that each climatic regime, expressed as the monthly march of temperature, potential evapotranspiration and rainfall, imposes a maximum LAI on the vegetation. Woodward (1987) shows that for many areas of the world, theoretical maximum values of LAI are

close to actual values. Where there is a discrepancy, this appears to be due to the interaction of the other processes listed above.

Seasonally dry climates present a risk of desiccation to evergreen plants. The adaptation to this among perennials is to become drought-deciduous, and among annuals and tuberose plants to survive the season in a state of dormancy. A combination of long dry seasons with high potential evapotranspiration leads to a reduction in LAI combined with drought-deciduous behaviour, exemplified progressively in savannah woodland, xerophytic scrub and grassland.

Both of these interactions, which were convincingly modelled by Woodward (1987), show the crucial control over vegetation exerted by water balance, especially in the dryer and/or warmer parts of the year.

Temperature appears to exert equally important controls on vegetation through two further climatic/physiological interactions. Plant survival through cold, in which cells are killed by chilling or freezing, favours the winter-deciduous behaviour seen in temperate broadleaved forests. The anti-freezing mechanisms of woody tissue in most hardwoods is less efficient than those of evergreen conifers, however, so the latter dominate the boreal forests found in the regions of coldest winters. Deciduous conifers (*Larix*) are important components of the most northerly forests of all. Thus the *minimum temperatures* of winter exert important controls on vegetation type.

Vegetation cannot be self-sustaining unless it can photosynthesize sufficient stores of energy to propagate itself. The minimum requirement, even for purely vegetative survival under the most adverse conditions, must be full leaf development. Climate influences this through ambient temperatures in summer, especially the number of growing degree-days. From the small amount of data available, Woodward (1987) argued that broadleaved tundra species require a minimum of 200–250 degree-days ( $^{\circ}\text{C}$ ), deciduous conifers 600 and evergreen conifers 900 degree-days. These summer temperature requirements, he argues, fix the boundaries between tundra, deciduous conifer woodland, and boreal forest.

The final climatic control on vegetation identified by Woodward (1987) is the insulating effect of snow and its influence on minimum temperatures experienced by small plants buried beneath the snow-pack. It is this factor, he suggests, which allows the survival of low, woody perennial shrubs as part of tundra vegetation in areas of extremely cold winters.

Woodward's analysis is of climatic controls on *vegetation*. While he identifies limiting values of both temperature (winter minimum and summer degree-days of thaw) and moisture balance (via LAI and the requirement of cyclical closure for the average annual water budget of the soil), he is at pains to point out that these are not threshold values for individual species. Rather they represent the extremes of adaptation which can be achieved. Woodward's (1987) review of evidence for climatic control over distributions at the species level reveals much more idiosyncratic behaviour from species to species. Some are governed by threshold effects in which certain stages of the life cycle simply will not occur (or if they occur, will not be completed) unless a certain ambient temperature is reached. Others may show trigger effects, in which the conditions for a process (such as growth initiation, or flowering) to be successful may exist, but the process itself will not take place unless some prior climatic trigger has been experienced. This is often winter chilling, but could also be

wetting, for instance in seed germination. Finally, plants may simply be limited in their distribution by low chances of overall success in passing through all stages of their life cycle. Each stage of life cycle may be regarded as having a finite probability,  $p$ , of successful conclusion under prevailing conditions. In a stand of  $N$  plants,  $p \times N$  individuals will successfully complete a given stage. If there are  $n$  stages in the life cycle, then the probable number of plants of each generation propagating successfully will be the product of the proportions completing each stage, multiplied by the number of progeny per plant,  $k$ , i.e.  $k[N \times \prod_{i=1}^{i=n} p_i]$ . If, due to climatic conditions, this value is less than  $N$ , the population will decline and eventually die out. Thus the climatic tolerance range of a plant may be determined not so much by any one individual climatic factor as by a variety of factors and their cumulative effect on the survival chances of a local population.

This view of the climatic tolerance range of a species as being the expression of a probabilistic process explains why it is often possible to grow and propagate a species in gardens well outside its natural range. Gardeners take active measures to alter survival probabilities by insulating frost-sensitive plants or through careful selection of microclimate and position. It also explains why it is possible to transplant some species outside their normal range and for individuals to survive for many years before finally succumbing to extirpation. Thus, the climatic range of some species is probably intrinsically fuzzy at the edges, and can only be determined through observation over time of the species as a whole.

Climatic factors are not the sole determinants of plant distributions. Other abiotic factors such as soil type, base status and available water capacity, or hydrology and drainage exert a profound influence at a local scale. In addition many forms of interaction between species may exert influence, such as competition for limited resources of light, nutrients or water, allelopathy and disease, symbiosis, parasitism and selective pressures from phytophage animals. Each of these biotic factors may alter the lifetime probability of survival and propagation for individual local populations of a species.

Many botanists view competition as the most important biotic factor and some might regard it as more important than climate. At a local scale this is undoubtedly true, and for some species it may also be true at a wider scale. Much probably depends on the diversity or 'graininess' of local habitat variety compared with the regional habitat variations that are linked with regional climatic gradients. If local habitats show large diversity over relatively short distances, then it is likely that a species will find at least some localities in which it can form small but viable populations close to its tolerance limit, i.e. the limiting climate in which the survival probability product  $k \times \prod_{i=1}^{i=n} p_i$  is less than unity even in the absence of competition. The closeness with which such populations approach the climatic limit will depend on the matrix of competing species. From this it is clear that if we wish to establish the widest possible estimate of a species' climatic tolerance range, we must examine its distribution on a regional-to-global scale and pay particular attention to isolated occurrences of the plant beyond the main range as these will best approximate its true climatic limit. Even then, it is probably wise to regard the true limit in the absence of competition as lying somewhat beyond the most extreme occurrence of the plant. This is a point which has to be borne in mind in deducing species climatic ranges from geographical distributions. It is a corollary of the 'epidemic' model of species dispersal put forward by Carter & Prince (1981).

From the above considerations of the relationships between vegetation, plant physiology and climate, we can identify four types of climatic variables which are likely to govern plant distributions. These are:

- the warmth of summer;
- the availability of moisture (i.e. the precipitation–evaporation–soil water balance);
- the minimum temperature of winter;
- the insulating effects of snow.

We should expect there to be much interspecific variation in threshold values of these climatic variables, and indeed a considerable variation in the exact nature of the limiting variables for each species. Many species may not be limited so much by specific variables as by combinations. Moreover, a threshold value of a single variable may limit a species on one side of its geographical range, while a combination of different variables may limit it on the other side (Jeffree & Jeffree 1994). One way to deal with this uncertainty is to map plants' species climatic ranges into a climate space defined by generalized variables that express the character of the climate along the lines of the four types identified above. This approach requires a statistical analysis of present-day climate which is presented in the next section.

#### *Climate data and definition of key variables by factor analysis.*

The basic climatological data used in this study were a gridded set of monthly mean temperature and precipitation values for Europe as far east as the Urals (25°W to 60°E, and 35°N to 75°N). The data are mean values for 1951–80, based on 271 stations for temperature and 537 for precipitation. The station data were interpolated and gridded values derived for 1° longitude by 0.5° latitude cells using procedures described by Marsh (1990). Temperatures were reduced from each station altitude to sea level with a lapse rate of 6°C km<sup>-1</sup>, then interpolated to the centre of each grid cell before re-elevation to the average altitude of the cell using digital topography from FNOC (1992). Precipitation data was interpolated without altitudinal adjustment. Interpolation was by a standard inverse-distance weighting method employing all stations within a geographical radius of 9° from the grid cell concerned. A small land area in northernmost Russia could not be interpolated because there were not enough temperature stations within 9°. Most subsequent manipulation and analyses of data were performed using a geographical information system (ARC/INFO). Any climate grid cells which lay completely over sea, and all land-based cells that lay outside the area covered by the plant distribution maps in *Atlas Florae Europaeae* (Jalas & Suominen 1972–86; see below) were removed.

The basic data set was used to calculate a further set of variables which reflect the hydro-meteorological aspects of climate that are most significant to plant growth. As an initial step, monthly temperatures were interpolated as shown in Fig. 2 to determine the lengths of seasons in which average temperatures were above zero or above 6°C, the latter being an accepted threshold temperature for growth of most temperate plants (Ford 1982). Also determined, by integration of a fitted sine function, was the number of degree-days above 0°C. The precipitation data was summed to give the total amounts of precipitation in each of these seasons and in the whole year (Fig. 2).

Moisture availability to plants depends on the balance of precipitation, evapotranspiration and storage in the soil. A

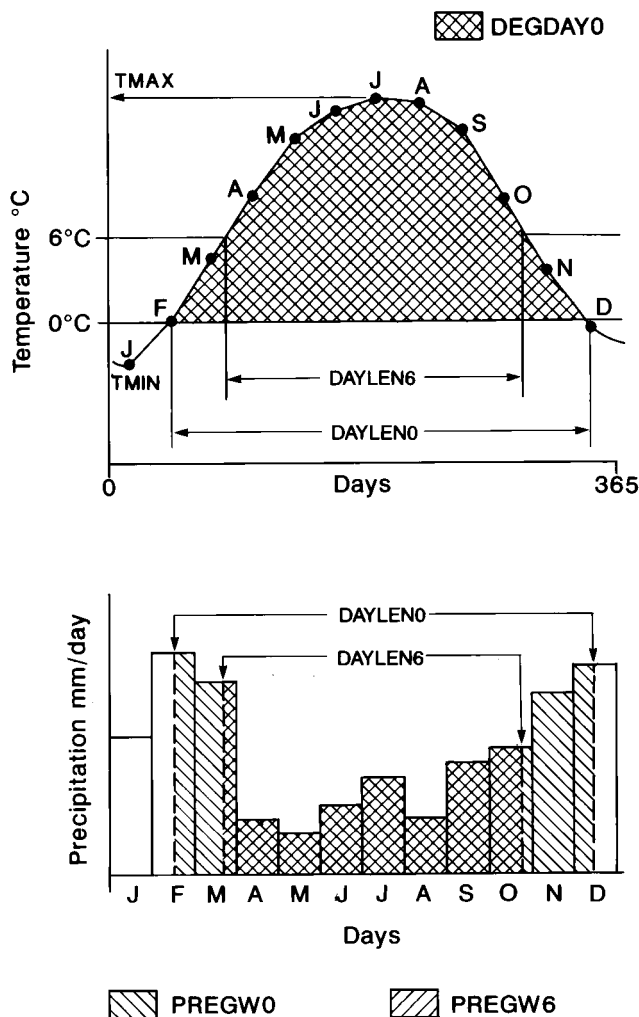


Fig. 2. Methods of determining temperature and precipitation variables from monthly mean values.

simple method for calculating the soil moisture balance was presented by Penman (1949) and developed for agrometeorological use by Grindley (1967, 1969). The inputs to the Penman–Grindley method are daily, weekly or monthly values for precipitation and potential evapotranspiration. *Potential evapotranspiration* (PET) is the meteorologically determined amount of evaporation which will occur from a short, green grass crop for which water is freely available. In periods when PET exceeds rainfall, the vegetation draws upon the store of moisture in the soil. If this is depleted the flow of water from the soil to plant roots becomes restricted as pores dry out. Transpiration rates then decline to values less than the PET as plants respond by closing the stomata through which water evaporates from their leaves, or they respond by wilting. The Penman–Grindley model represents this process in terms of a parameter called the *root constant* and a variable known as the *soil moisture deficit* (SMD). The root constant is the amount of water (measured in mm of rainfall) which the soil can store in a form which is easily extracted by plant roots. For short-rooted crops (e.g. grass, herbaceous vegetation) a root constant of 75 mm is appropriate, whereas for deep-rooted species (e.g. many trees) 200 mm is used. The SMD is the amount of water (in mm) which must be added to a partially dried soil to bring its moisture content back to the state known as *field*

*capacity*, which is defined as the moisture content at which drainage from an initially saturated soil will cease. The Penman–Grindley model is essentially an accounting procedure which commences at a time when the soil can be assumed to be at field capacity. For each accounting period, an input of rainfall is added and an output of evapotranspiration is subtracted from the soil store to calculate the state of SMD at the end of the period. The evapotranspiration value used depends on the current state of SMD. If the SMD is less than a value equal to the root constant plus 25 mm, the figure used is the meteorologically determined PET. If the soil is drier than this, the *'actual' evapotranspiration* (AET) is less than PET by a ratio which depends on SMD, dropping linearly from a value of unity at  $SMD = (RC + 25) \text{ mm}$  to a value of 0.1 for  $SMD \geq (RC + 38) \text{ mm}$ . The output from this procedure consists of AET values and SMD for the end of each period. Further details can be found in Shaw (1988). For monthly data, Wigley & Atkinson (1977) showed that more accurate results were achieved by sub-dividing rainfall and PET evenly into ten equal periods for each month. We calculated SMD values using this procedure, including a further routine which stored precipitation as snow-pack in months with average temperature  $\leq -1^\circ\text{C}$ .

PET values required as input for the Penman–Grindley model were initially generated from the gridded monthly temperature data using Thornthwaite's formula (Thornthwaite 1948; Shaw 1988). The Penman formula (Penman 1948; Thom & Oliver 1977; Shaw 1988) gives a more accurate calculation of PET, being more closely based on the physics of the process, but it requires data other than temperature which was the only variable available in our climate data set. Penman and Thornthwaite values were compared at 61 European stations with adequate data and a regression equation derived to relate the two (Hulme *et al.* 1992). This was used to adjust the gridded data, giving monthly estimates of PET in approximate agreement with Penman values.

The above calculations produced a list of nine derived climate variables (Table 1) which contain enough information to encapsulate the whole of the bio-climatic regime.

As noted above the distributional limits of plant species are probably determined by combinations of temperatures and moisture availability. Practical difficulties of representing a plant's species climatic range in a nine-dimensional space led to the use of factor analysis to reduce the number of climatic variables, if possible to two. This statistical technique is a variation of the more widely-used principal components analysis (PCA) (Daultrey 1976) and was implemented using the SPSS computer package (Norusis 1988). In PCA the correlations between the variables are used to derive an equal number of new, compound variables called *principal components* which are orthogonal to one another. The principal components describe the original data exactly, and the values of the original variables for any data-point can be recovered from its coordinates (called *scores*) in principal component-space. However, whereas the total variance in the data set was evenly shared amongst the original variables, the PCA procedure is designed to assign the largest possible proportion of variance to the first component, as much of the residual as possible to the second, and so on. This maximization procedure results in most of the variance being described by the first few components, with the higher ones embodying the random aspects or 'uncorrelated noise' of the original data. The operator may choose to repeat the analysis, retaining only the first few principal components. This leads to the procedures of factor analysis, in which the

**Table 1.** Climate variables used in factor analysis

Variable name	Mean (units)	Standard deviation	Range	Definition
TMAX	18.83 (°C)	3.87	3.8–28.4	Mean temperature of warmest month
TMIN	–4.47 (°C)	7.44	–16.1–13.2	Mean temperature of coldest month
DAYLEN6	207.4 (days)	71.5	0–365	Length of the growing season ( $\geq 6^\circ\text{C}$ ), in days
DEGDAY0	3175 ( $^\circ\text{C} \cdot \text{day}$ )	1318	305–7019	Number of degree-days of thaw ( $>0^\circ\text{C}$ )
PET6	573 (mm)	313	0–1487	Total potential evapotranspiration during the growing season ( $\geq 6^\circ\text{C}$ )
PRECIP	628 (mm)	200	162–1903	Mean annual precipitation
PREGW0	518 (mm)	237	112–1903	Mean total precipitation during the thaw season ( $>0^\circ\text{C}$ )
PREGW6	400 (mm)	188	0–1903	Mean total precipitation during the growing season ( $\geq 6^\circ\text{C}$ )
SMMAXSHRT	83.7 (mm)	41.0	0–195	Maximum soil moisture deficit calculated by Penman–Grindley method for short-rooted vegetation

number of components (now called *factors*) extracted is specified by the operator. They are then subjected to a further rotation in the original variable-space to maximize the correlation between them and groups of original variables. Thus, factor analysis is a method of extracting associated groups of variables from the original data set and expressing the results in a smaller number of scores.

Factor analysis of the nine variables in Table 1 across 3244 climate grid cells showed that 92.2% of the original variance could be explained by two factors (Table 2). Table 3 shows the factor matrix scores (or *loadings*) after varimax rotation. A value of one in this table indicates perfect correlation between an original variable and a factor. Negative values indicate anti-correlation. Near-zero values show that there is negligible association between factor and variable. Factor I has high loading on the length of the growing season (DAYLEN6), the temperature of the warmest month (TMAX), the accumulated warmth of the period warmer than  $0^\circ\text{C}$  (DEGDAY0), the total potential evapotranspiration in the growing season (PET6), and the maximum soil moisture deficit (SMMAXSHRT). It therefore expresses ‘summer warmth and dryness’, i.e. the tendency for climates to be either hot and dry in the warmer part of the year or cooler but with greater soil moisture availability because of lower evapotranspiration. Factor II loads heavily on the temperature of the coldest month (TMIN)

**Table 2.** Total variance explained

Factor	Eigen value	% of total variance	Cumulative %
I	5.364	59.6	59.6
II	2.934	32.6	92.2

**Table 3.** Factor loadings after varimax rotation

Variable	Factor I	Factor II
TMAX	0.9492	–0.0379
DAYLEN6	0.8090	0.5562
DEGDAY0	0.9032	0.4080
PET6	0.9752	0.1119
SMMAXSHRT	0.8725	–0.2392
TMIN	0.5743	0.7275
PRECIP	–0.2871	0.9275
PREGW0	0.0120	0.9800
PREGW6	0.3190	0.9042

and the precipitation variables: annual total (PRECIP), precipitation in the period warmer than  $0^\circ\text{C}$  (PREGW0) and in the growing season (PREGW6). Localities with high scores on this factor tend to be wetter and/or have milder winters. Factor II therefore expresses ‘wetness and winter warmth’. Full details of the factor analysis are given in Sinka (1993).

Each climate grid cell can now be assigned two new variables which summarize its climate. These are the scores for that cell on Factors I and II, shown as contour maps in Fig. 3a and b. Figure 3c is a 2D plot of European climates in terms of the *key variables* of ‘summer warmth and dryness’ versus ‘wetness and winter warmth’ which were then used to define the species climatic ranges of individual plant species (see below).

Before ending this consideration of climate and key variables, it is appropriate to indicate how precisely and/or accurately the factor analysis model can be used to reconstruct the original nine variables. The analysis is performed on standardized values of the original variables, calculated by:

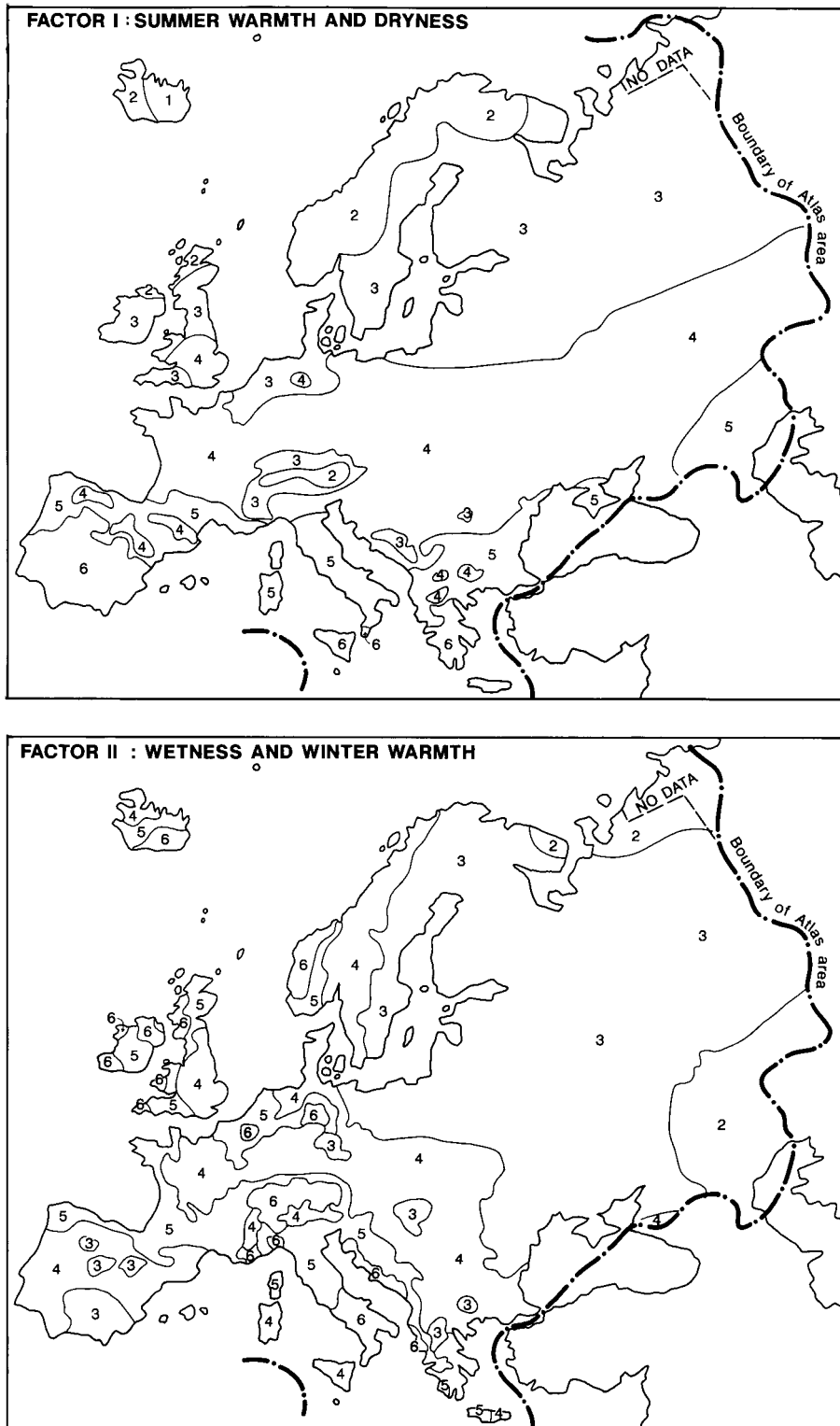
$$\text{value}_{(\text{standard})} = (\text{value}_{(\text{measured})} - \text{mean}) \div (\text{standard deviation}). \quad (1)$$

It follows that in their standardized form all of the original variables have means of zero and unit variance and standard deviation. The standardized values of variables can be reconstructed from factor scores by using the equation,

$$\text{VARIABLE}_{i(\text{Std})} = (\text{FACSCO1} \times \text{MATSCO1}_i) + (\text{FACSCO2} \times \text{MATSCO2}_i) \pm E_i. \quad (2)$$

in which the subscript *i* refers to the *i*th variable, FACSCO1 and FACSCO2 are factor scores (i.e. the coordinates of the point on Fig. 3c), and MATSCO1<sub>*i*</sub> and MATSCO2<sub>*i*</sub> are the factor matrix loadings of the *i*th variable on the two factors (Table 3). *E<sub>i</sub>* is a term to account for the fact that the model leaves some of the total variance in the original data unexplained by the first two factors. The division of unexplained variance among the original variables can be calculated and is shown in Table 4. For example, 9.8% of original variance in TMAX is unaccounted for by Factors I and II, and *E<sub>i</sub>* can be expressed as  $\pm \sqrt{(0.098)}$  or 0.31 standard deviation units. The reconstructed variable can be converted into measured units by rearrangement of Equation (1), while the error term *E<sub>i</sub>* must be multiplied by the *i*th variable’s standard deviation. Values of reconstructed variables and error terms are shown in Fig. 4.

A further source of error may arise because the factor analysis model assumes a linear relationship among all the original variables, which must also be approximately normally



**Fig. 3.** Results of factor analysis of European climate. (a) Generalized distribution of scores on Factor I—'summer warmth and dryness', across the *Atlas Florae Europaeae* (Jalas & Suominen 1972–86) area. (b) Generalized distribution of scores on Factor II—'wetness and winter warmth'. Key to map units in terms of factor-score values:

1	< -2	4	0 to 1
2	-2 to -1	5	1 to 2
3	-1 to 0	6	> 2

(c) Diagram of factor space with full scatter of European climates indicated, and some geographical areas identified.

distributed about their means. To the extent that these assumptions are untrue, a systematic inaccuracy may be introduced into the reconstructions in Fig. 4. This may be detected by looking for areas of climate space in which 'impossible' values or combinations are reconstructed, as shown by the shaded areas in the lowest panel on Fig. 4. Most of these lie

outside the bounds of the data, but it is notable that the linear model gives negative soil moisture deficits in areas with cool, wet summers combined with mild winters, such as Iceland or parts of Scotland and Norway, and reconstructs TMIN as larger than TMAX in areas such as some parts of Yugoslavia where winters are very mild and the growing season is long.

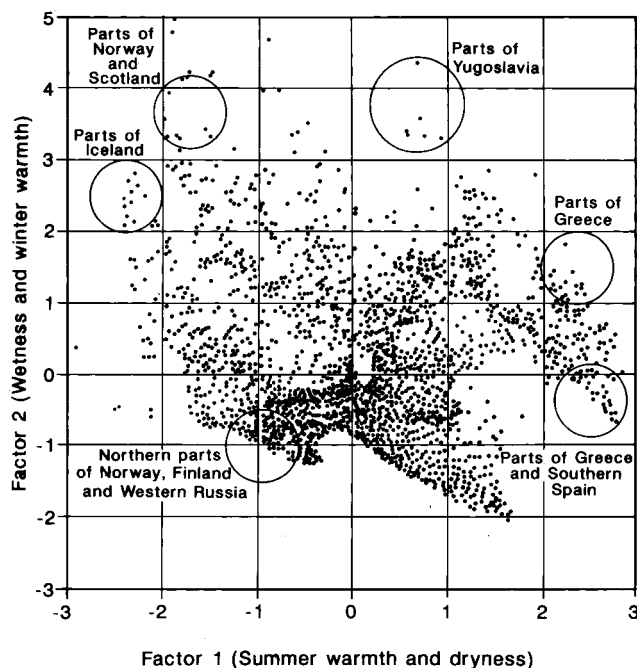


Fig. 3. (c).

**Table 4.** Community, or fraction of variance explained for each original variable

Variable	Community	Unexplained variance (%)
TMAX	0.9204	7.96
DAYLEN6	0.9639	3.61
DEGDAY0	0.9822	1.78
PET6	0.9636	3.64
SMMAXSHRT	0.8185	18.15
TMIN	0.8447	15.53
PRECIP	0.9427	5.73
PREGW0	0.9605	3.95
PREGW6	0.9193	8.07

Reconstructed climates that fall into or near these parts of the climate-space should be treated very cautiously.

#### Determination of climatic tolerance ranges

Broadly speaking there are three possible ways of determining a plant species' climatic tolerance range, in terms of numerical values of climate variables. The first is to experiment with growing the plant under different conditions. In general this is not a useful source of data for interpretation of Quaternary palaeoclimates. Woodward (1987) provides a detailed review of existing knowledge.

The second method is to study the reproductive and vegetative behaviour of stands of the species near the limit of its climatic or geographical range. By careful observation over a number of years, and comparison with the weather of those years, it may be possible to determine the precise climatic conditions which limit a plant's growth. This is very laborious although extremely rewarding in terms of the insights it may afford. An outstanding example is the Pigott & Huntley (1981)

study of the lime tree (*Tilia cordata*) which they showed to be limited in the range it could reproduce by the temperature of the few days of early summer in which fertilization took place. Trees outside this range could survive through vegetative propagation but could not disperse progeny to colonize new sites. Other examples are cited by Beerling (1993), Ford (1982) and Woodward (1990). Once again, this method has been applied to so few species that the results are of limited use in palaeoclimatic reconstruction. Moreover, the factors limiting a species distribution have normally been established at only one boundary of its range. Quite different factors may limit a plant at its southern or eastern range boundary from those operating in the cool, humid summers of its northwest limit in Britain. *Tilia cordata* again provides an example of this, being limited by different factors in Finland than in England (Pigott & Huntley 1981).

The third technique involves the comparison of a plant's geographical distribution with the geographical variations of climate. Most older studies of this genre (e.g. Dahl 1951; Conolly & Dahl 1970) compared maps of plant distribution with contoured maps of different climatic variables, seeking to identify a climatic contour which neatly bounded the plant's distribution. Such a contour, if it could be found, was inferred to be a threshold limiting factor for the plant's survival. This approach leads to the *indicator species* technique of palaeoclimate reconstruction, in which different species are used to infer that certain climatic variables lay above or below certain thresholds.

The MCR method can be regarded in some respects as an extension of the indicator species technique. However, instead of trying to identify a single threshold value of a cardinal variable which controls each species' distribution, we instead try to define the *volume climate space* which the species can potentially occupy. The main difference is that in the MCR method we consider two or several climate variables together, rather than one variable at a time. In that respect the MCR method also differs from the climatic profile technique described by Kershaw & Nix (1988), while our procedures differ from those of Jeffree & Jeffree (1994) in that we do not specify the shape of the species climatic range in advance.

The data available for determining species climatic ranges is very limited for the majority of species likely to be of interest in European Quaternary studies. The most common data are in the form of geographical distribution maps. Ideally these should show the species' entire global range, or at least its range over a wide enough geographical area to encompass all or most of its probable species climatic range. This type of data can be supplemented by information from floras and naturalists' handbooks on the altitudinal distributions of species in defined regions (e.g. Slavic 1977; Polunin & Huxley 1965; Clapham *et al.* 1981; Fitter 1978), and also any other ecological requirements or preferences shown, for example for soil type, moisture status, light/shade etc., where these may have an effect on the species' rarity or abundance and perhaps exert a limit on its geographical range. These data may be supplemented in the cases of a few species by experimental or phenological data based on careful observation of the organism's response to climate.

The distribution maps chosen for this project were those in the *Atlas Florae Europaeae* (Jalas & Suominen 1972–86) which show presence/absence of a large number of species in 50 × 50 km squares, covering Europe as far east as the Ural mountains. Even this continental scale fails to encompass the full distributional range of many species and previous

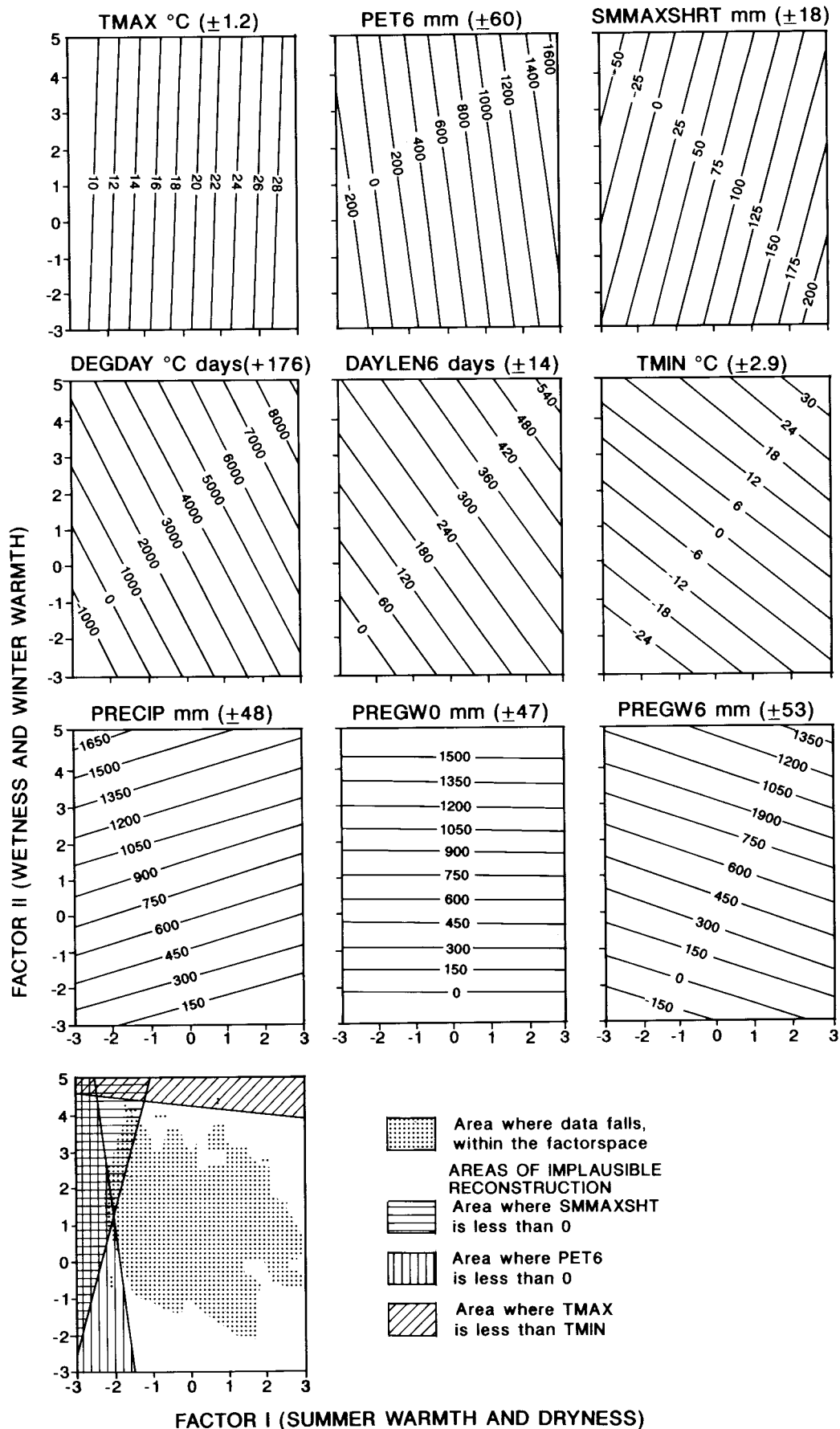


Fig. 4. Reconstruction of original climatic variables from first two factor-scores. Panels show factor space with contoured values of each variable. Note the areas of 'impossible' reconstructed climate in lowest panel. Figures in brackets above each panel show  $\pm 1$  s.d. error in reconstructed variables, calculated from unexplained variance (see text).



reconstructions using beetles with calibration over the whole Palaeo-arctic show that the coldest climates of Lateglacial Britain lay outside the range of thermal climates to be found within the *Atlas Florae Europaeae* area (Atkinson *et al.* 1987). Although circum-polar and hemispheric maps have been published for a number of species by Hulten (1970, 1971), Hulten & Fries (1986) and Meusel & Jaeger (1965–92), they vary greatly in detail, are on very small scales, and have unknown projections. The difficulties these factors cause in comparing mapped distributions with climate data suggested that for a pilot project it would be better to use the *Atlas Florae Europaeae* maps which could more easily be matched with the climate data-set.

An example of an *Atlas Florae Europaeae* distribution map for the pteridophyte *Selaginella selaginoides* is shown in Fig. 5a. For each of 80 species a similar map was digitized and overlaid on the coverages of gridded climate variables 'summer warmth and dryness' and 'wetness and winter warmth', using the Arc-Info GIS. Once the gridded data and distribution of the species had been matched, all grid cells that coincided with areas where the plant was present were identified and plotted in climate space, as shown in Fig. 5b. The remaining climate data, where the plant was absent, was also plotted, to ensure that boundaries to the distribution that were due to the edge of the data were not mis-identified as climatic limits. An envelope was then drawn around the 'presence' points to define the Species Climatic Range. The plot was then transformed into a numerical matrix by overlying a grid with elements of  $0.1 \times 0.1$  factor-score units, and assigning a value of 1 to elements within the species climatic range and zero to elements outside it. The matrix for *S. selaginoides* is shown in Fig. 5c.

Eighty species were selected because they occurred both in the *Atlas Florae Europaeae* and in one of four floral assemblages which had been chosen to try out the MCR method using plants. Two of these were from modern sites in southeast Britain and two were from organic layers in a sequence of Devensian gravels at Earith, described by Bell (1970). The next section describes the application of the MCR method to these sites.

### Reconstructions of modern and Pleistocene climates using floral evidence

#### *The sites*

The two modern sites selected to evaluate the MCR method were National Nature Reserves at Wicken Fen, Cambridgeshire and Stodmarsh, Kent (Fig. 6). Wicken Fen [TL 553 073] is a 225 ha area of fen and carr vegetation, one of the few surviving remnants of the Great Level of the East Anglian fens. The natural condition of this region was a very extensive swampy wetland, traversed by rivers which regularly flooded the surrounding marshlands. The region has undergone progressive stages of drainage since the seventeenth century, and is now traversed by a network of ditches and dykes from which water is pumped into rivers which flow between artificial levees, at a higher level than the surrounding fen. Much of the land has been converted to agricultural use and there are also extensive peat diggings. Wicken Fen is an island of semi-natural vegetation in this converted landscape. Water levels within the fen are maintained by pumping water into the reserve from the surrounding drainage ditches. The present vegetation remains similar to that of the formerly extensive

fenland marshes, with the water table everywhere within less than one metre of the surface of the peat soil. There are areas of carr woodland, reedbeds, sedge fen, ditches and open water, providing a variety of habitats. An extensive plant inventory is available, with 37 species included in the volumes of *Atlas Florae Europaeae* that had been published at the time of this study.

Stodmarsh [TL 229 601] is a 163 ha area of the floodplain of the River Stour, comprising meadow, reedbeds, shallow lagoons and alder carr woodland, with some areas of better drained woodland. There is thus a greater mixture of drainage conditions than at Wicken Fen, with some areas of wetland and others in which the soil is better drained than the peat soils of the Cambridgeshire site. A floral list is available for the site and 40 species were mapped in *Atlas Florae Europaeae*. The floral assemblage for Wicken Fen reflects almost entirely wetland habitats, whereas that for Stodmarsh contains species from both wetland and better drained sites.

The Pleistocene site at Earith [TL 388 764] was described by Bell (1970). It is located on a spread of gravels deposited by the River Ouse where it emerges into the Fen Basin from the plateau country to the west. A gravel pit exposed between 5 and 6.5 m thickness of stratified, cross-bedded fluvial gravels, resting on an eroded surface of Jurassic Amphill Clay at  $-1.5$  m OD. Within the gravel succession were lensoid beds of cross-bedded, finer-grained sediments containing abundant plant macrofossils and sparse pollen. Nine beds were numbered and investigated. Following deposition of the 'plant beds' ice wedge casts were developed in the gravels. In one case a wedge cast cuts a plant bed but without major disturbance. Involutions are also widespread in the succession, and some of the plant beds were disturbed by involutions formed during deposition of the succession as a whole. Thus, the sequence of events at the site appears to be one of an initial erosion into the Jurassic clay bedrock, then gravel deposition with finer grained 'plant beds' accumulating in backwaters, oxbow depressions or flood-plain ponds. During this time the sediments were involuted by cryoturbation from time to time, but ice wedge casts were not present. After the whole gravel sequence had accumulated, or perhaps during deposition of the upper part of the gravels, ice wedges formed beneath a relatively stable surface in a polygonal pattern which could be seen on aerial photographs. The age of the sediments is post-Ipswichian and there is a finite radiocarbon date of 42 ka BP on plant bed e7 (Birm.88, Bell 1970) and a second date of >45 ka BP on bed e9. Apart from this there are no constraints on the age of the deposits which are therefore best regarded as simply belonging to some period in the Early to Mid-Devensian. For the present study, species lists of plant macrofossils for plant beds e4 and e7 were used.

#### *Modern sites: Wicken Fen and Stodmarsh*

Of the 37 plants from Wicken Fen and 40 from Stodmarsh, only 20 species are common to both sites (Table 5). Figure 7 shows the MCR of each site in factor-score space, indicating the area of 100% species overlap and the position of the present-day climate as represented by the factor scores of the climatic grid-cell that contains each site. In terms of reconstruction of climate as an unknown factor from the evidence of the plant species alone, we can infer that the present climate of each site must lie within the MCR, which is in fact the case.

The factor-scores give a rather opaque measure of climate, but as explained above the original variables can be



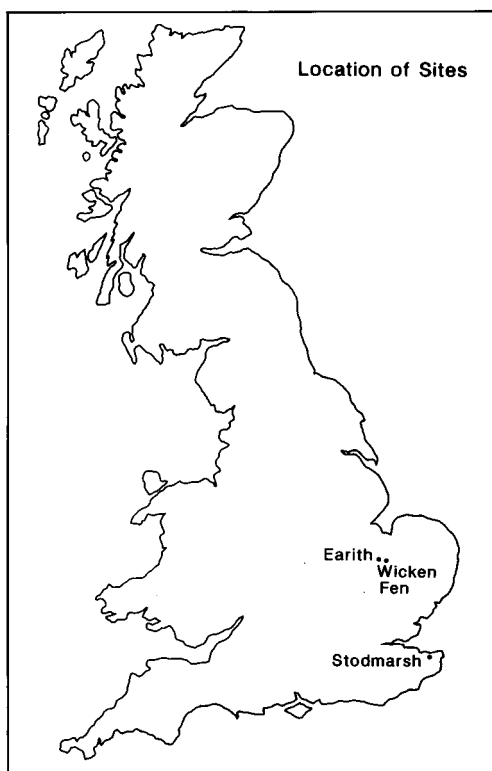


Fig. 6. Locations of Earith, Wicken Fen and Stodmarsh.

Wicken Fen is a groundwater-fed marsh, able to support wetland plants which would require a much wetter moisture balance to survive on a site fed only by direct rainfall. At Stodmarsh, which possesses a greater mixture of marsh and drier habitats, the actual values of all variables except TMAX lie within 1 s.d. of the MCR mean.

#### *Pleistocene floras: Earith Layers e4 and e7*

Although the above reconstructions of modern climates constitute a rather limited test of the methods employed, the results were encouraging enough to make an application to two Pleistocene floras seem worthwhile. At Earith layers e4 and e7 have rather similar flora, with the lists of species shown in Table 5. E4 is more restricted in the range of species for which distribution maps were available. Only one of the six species present was not also present among the 14 species in e7. None of the species in e4, and only 4 out of 14 in e7, is present at either Wicken Fen or Stodmarsh.

The MCRs for Earith are shown in Fig. 7. Both show wide ranges of 'wetness and winter warmth' which overlap the corresponding ranges for the modern sites but extend to lower values of Factor-score II, suggesting that while this aspect of the Devensian climate at Earith may have been similar to the present day, it is also possible that winters were colder and/or the precipitation was less than today. On the scale of 'summer warmth and dryness' both layers at Earith show a shift to lower values compared with the modern MCRs, indicating that summers were either cooler, shorter or wetter than today, or perhaps some combination of all three.

Figure 8 shows the ranges, standard deviations and means of the reconstructed original variables for the Earith floras. The true Pleistocene values at the site probably lay within the

ranges shown, although it must be borne in mind that the reconstruction has an intrinsic uncertainty that derives from the Factor Analysis model, as shown in Table 4 and Fig. 4.

#### *Comparison of modern and Pleistocene climates*

Bell (1970) found the floral elements at Earith to be largely common to all of the plant beds she studied. Bed e7 had the greatest floral diversity and most of the species identified from other beds could also be found there. Bell concluded that the vegetation was probably similar for all of the plant beds, and drew parallels with the modern climate and vegetation of the River Lena valley in Siberia. It should be noted, however, that G. R. Coope (pers. comm. 1991) dissents from this view as far as uniformity of palaeoclimate is concerned. In an unpublished study of fossil beetles in four of the plant beds at Earith, Coope finds evidence of distinct differences in climate among them. Beds e4 and e9 contained several species which no longer live in Britain but have modern distributions in exclusively cold and continental climates. These cold stenotherms are absent in beds e5 and e7, in which the coleopteran fauna is rather more temperate, containing many species native to Britain today and with an overall character typical of present day faunas in Finland or central Scandinavia.

Figure 8 compares the plant-based MCR climates for Earith with two measures of the modern climate in southeast England, firstly the values based on the instrumental record, and secondly the MCR estimates based on the modern floras. Taken at face value, the Earith MCR results indicate that the palaeoclimates of e4 and e7 lay somewhere within the ranges shown on Fig. 8. If we compare them with the instrumental values, it is clear that the growing season (DAYLEN6) was shorter and that there were fewer degree-days of thaw (DEGDAY0) in Devensian Earith than at nearby Wicken Fen today. The winter temperatures (TMIN) were also less, with the possibility of values as low as  $-10^{\circ}\text{C}$  for e7 and  $-17^{\circ}\text{C}$  for e4. Likewise, evapotranspiration in the growing season for e7 (PET6) was around half the modern value. This may have been due in part to a shorter growing season, but also to cooler temperatures in summer. The range of PET6 for bed e4 is broader and for this bed too there was a much lower evapotranspiration than today. A slight overlap with modern instrumental values is seen for both beds with respect to TMAX, indicating that summers might have been as warm as today, but were probably cooler. For e4 TMAX may have been as low as  $10^{\circ}\text{C}$ , whereas for e7 the MCR indicates that it exceeded  $13.7^{\circ}\text{C}$ . This result is in agreement with Coope's views of the differences in climate between the two beds, as noted above.

Though the plant-based MCR provides a fairly clear indication that the Devensian climates of Earith were cooler in summer and much colder in winter than their modern counterpart, the same cannot be said of precipitation. For all three precipitation variables (PRECIP, PREGW0 and PREGW6) the MCR bars are rather wide and overlap the instrumental values at both modern sites. Thus there is little indication that the amounts of precipitation were different from today, although a much higher proportion would have fallen as snow if winter temperatures were below zero, as is indicated by frost-generated involutions in the host sediments (Bell 1970). An aspect of the moisture regime at Earith which does appear to differ from the modern situation is the soil moisture. Lower evapotranspiration combined with similar precipitation levels imply that soil moisture deficits would have been less than

**Table 5.** Plant species used, by site, numbers of species and species common to pairs of sites

Species name	Sites				Species name	Sites			
	Wicken Fen (w)	Stodmarsh (s)	Earith e4	Earith e7		Wicken Fen (w)	Stodmarsh (s)	Earith e4	Earith e7
<i>Alnus glutinosa</i>	+	+			<i>Quercus robur</i>	+	+		
<i>Arenaria ciliata</i>				+	<i>Rumex acetosa</i>		+		
<i>Athyrium filix-femina</i>	+				<i>R. acetosella</i>	+	+		+
<i>Betula nana</i>				+	<i>R. conglomeratus</i>		+		
<i>B. pendula</i>		+			<i>R. crispus</i>		+		
<i>B. pubescens</i>	+				<i>R. hydrolapathum</i>	+	+		
<i>Carpinus betulus</i>		+			<i>R. maritimus</i>	+			
<i>Castanea sativa</i>		+			<i>R. obtusifolia</i>	+	+		
<i>Cerastium arvense</i>			+	+	<i>R. palustre</i>	+			
<i>C. fontanum</i>		+			<i>R. sanguineus</i>		+		
<i>Chenopodium album</i>	+				<i>Salix alba</i>	+	+		
<i>C. rubrum</i>	+	+			<i>S. atrocinerea</i>		+		
<i>Corylus avellana</i>		+			<i>S. cinerea</i>	+	+		
<i>Dryopteris carthusiana</i>	+				<i>S. fragilis</i>	+	+		
<i>D. dilatata</i>	+				<i>S. herbacea</i>			+	+
<i>D. filix-mas</i>	+				<i>S. pentandra</i>	+			
<i>Equisetum arvense</i>	+	+			<i>S. phlycifolia</i>			+	+
<i>E. fluviatile</i>	+	+			<i>S. polaris</i>			+	+
<i>E. palustre</i>		+			<i>S. purpurea</i>	+			
<i>Humulus lupulus</i>		+			<i>S. repens</i>	+			
<i>Lychnis alpina</i>			+	+	<i>S. viminalis</i>	+	+		+
<i>L. flos-cuculi</i>	+	+			<i>Silene dioica</i>		+		
<i>Minuartia rubella</i>			+		<i>S. vulgaris</i>				+
<i>Myosoton aquaticum</i>	+				<i>Stellaria graminea</i>		+		
<i>Myrica gale</i>	+				<i>S. holostea</i>		+		
<i>Ophioglossum vulgatum</i>	+				<i>S. media</i>	+	+		
<i>Pinus nigra</i>		+			<i>S. pallida</i>		+		
<i>P. sylvestris</i>	+	+			<i>S. palustris</i>		+		
<i>Polygonum amphibium</i>	+	+			<i>Suaeda maritima</i>				+
<i>P. aviculare</i>	+	+		+	<i>Thelypteris palustris</i>	+			
<i>P. hydro Piper</i>		+			<i>Urtica dioica</i>	+	+		+
<i>P. lapathifolium</i>	+	+							
<i>P. persicaria</i>	+	+			Wicken Fen	37			
<i>P. viviparum</i>				+	Stodmarsh 1	20	40		
<i>Populus alba</i>	+				Earith e4	0	0	6	
<i>P. tremula</i>	+				Earith e7	4	4	5	14
<i>Pteridium aquilinum</i>		+							

today, and the MCR bars for SMMAXSHRT confirm this, with upper limits to reconstructed SMD of 60 and 70 mm, compared with over 100 mm today. Thus soils were probably wetter and may even have remained near to saturation throughout most of the growing season, as can be seen from the extension of both SMMAXSHRT bars to zero (Fig. 8).

The differences between modern and Devensian conditions at Earith are fairly clear if we compare MCR reconstructions with instrumental values. However the interest of palaeoclimatologists is often focused on climatic changes through time as revealed in a geological record. For this it is necessary to compare MCR reconstructions with one another, without any instrumental data to guide the comparison. If we do this for the Earith climates and the two modern sites, we find that the MCRs of the two Earith assemblages do not overlap the modern sites' MCRs in factor-score space at all (Fig. 7), although their boundaries are contiguous over a short distance. This suggests that while the two sets of climates may overlap in respect of some attributes, they do not share any single set of values for all nine. This is confirmed by Fig. 8, which shows a degree of overlap in the ranges of all variables except DEGDAY0, for which the upper bounds of the Earith bars just reach the lower bounds of the bars for Wicken Fen

and Stodmarsh. For all of the other variables describing the thermal regime (TMAX, TMIN, DAYLEN6) the overlaps form a small proportion of the MCR bars in Fig. 8, with most of the ranges for Earith on the 'cold' side, whereas the greater parts of the modern ranges are on the 'warm' side of the overlap.

The best, *a priori* guess we may make of the likelihood of the true climate falling at any particular point in factor-score space is that it is uniform over all possible positions within the MCR, and zero for all positions outside it. This assumption allows the calculation of approximate likelihood that where two MCRs overlap the true climates of both fall within the region of overlap. For the two modern climates, this likelihood is 43%, i.e. there is 57% chance that one or both of the two climates lies outside the overlap. In fact, both lie within it. For the two Earith plant beds, there is only a 7% likelihood that both climates lie within the rather narrow area of overlap, and a 93% likelihood that one or both of them does not. Since the MCR for e7 is itself rather restricted and most of the area occupied by the MCR of e4 lies to the left of it on Fig. 7, this result may be interpreted as indicating that the e4 climate most likely has a lower score on Factor I than e7, i.e. e4 is probably colder in summer and/or has wetter soil. Reference to Fig. 8

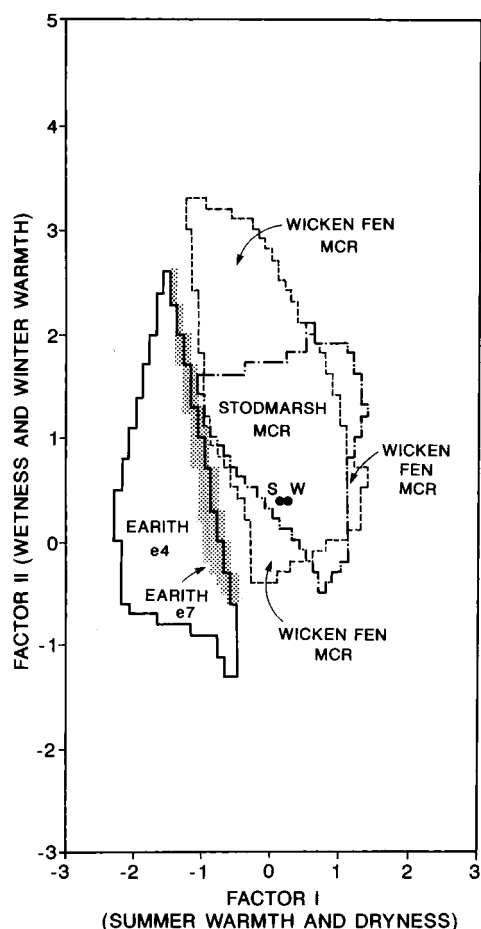


Fig. 7. Mutual climatic ranges in factor-score space for four plant assemblages. Actual climates of Wicken Fen (W) and Stodmarsh (S) also shown.

suggests that the differences between e4 and e7 may be greatest for variables whose bar for e4 is much longer and extends to lower values than e7. Such variables include TMAX, TMIN, DAYLEN6 and DEGDAY0, making it likely that the main difference between the e4 and e7 climates is cooler temperatures for e4.

To sum up, the MCRs of the modern sites suggest a moderately high likelihood that the climates of Wicken Fen and Stodmarsh are broadly similar, which is in fact the case, the main difference between the instrumental records being the greater precipitation at Stodmarsh. Both the modern climates can be distinguished from the Devensian palaeoclimates at Earith, as there is no overlap in their MCRs, even though they are contiguous over a small part of their boundaries. The Pleistocene climates were both apparently colder than their modern counterparts, more continental in terms of seasonal temperature range, and had lower evaporation and wetter soils. However, there was no definite difference in precipitation amounts. There is a high likelihood (>90%) that the climate of e4 was colder than that of e7, although they appear to have been similar in most other respects.

## Discussion

This paper has shown how the mutual climatic range method, which was originally used to derive palaeoclimate from beetle

fossils, can be adapted for use with plants. The results of this pilot study are promising, but it is nevertheless appropriate to list here some of the assumptions that are implicit in the methods used, and to discuss their validity.

The most basic assumption of the MCR method is that the species climatic ranges (SCRs) used are in fact correct representations of plants' actual tolerance ranges. The validity of this rests upon the method by which SCRs are deduced from plants' geographical distributions, remapped into climate variable space. It is important to note that this remapping allows us to avoid assuming that the realized geographical range fills the entire potential range that the species could occupy. Many parts of the potential geographical range may be empty and these places will appear in the SCR diagram as 'absent' points inside the SCR itself (compare Fig. 3c and Fig. 5b). The reasons why a plant is excluded from parts of its potential geographic range could be various and they need not concern us here. All that need be assumed for the purposes of drawing the SCR is that the species occurs at the limits of its climatic tolerance in enough places for the SCR envelope to be drawn accurately when the data is mapped into climate space. The number of such places need not be great, so long as they are sufficient to define the limits of the SCR on all its sides. This assumption cannot easily be tested except by the criterion of consistency in actual use. In our studies of beetles (Atkinson *et al.* 1986, 1987) it was found initially that some assemblages based on modern, living faunas failed to give a 100% overlap of all species, i.e. there was no wholly 'mutual' climatic range. Trial and error enabled us to identify a few species which were responsible for this situation. Their SCRs were re-examined and either revised in the light of additional distribution data (e.g. in North America) or the species concerned were removed from the library of SCRs. We have not yet gained enough experience with the present plant-based MCR method to identify whether there are 'rogue' SCRs in our library.

In drawing the envelopes of SCRs, we have intentionally erred on the side of making them a little larger than need be, except where there is a very clear boundary to the spread of 'presence' points. This practice reflects the intrinsic 'fuzziness' of species' distributions near the limits of their range. It is worth bearing in mind that the logical deduction which is made regarding climatic reconstruction is that *the palaeoclimate lay somewhere within the SCR as it has been defined*. Clearly, drawing the SCR slightly larger than the true tolerance range will not negate this statement, although if carried too far it will lead to loss of information content. To illustrate this latter point, one may think of cosmopolitan species whose presence tells us almost nothing about climate because their tolerance range is so wide. On the other hand, drawing the SCR unnecessarily widely will invalidate probabilistic arguments about the likelihood that the true climates related to two overlapping MCRs are in fact different. Thus, the art of drawing accurate SCRs rests both on the assumption that the realised climatic range adequately expresses the potential range, and on the judgement of the investigator. The envelope must be positioned widely enough to include climates near the boundaries where the plant is poorly represented, but not so widely that it includes climates where its survival would be impossible. Clearly, there is scope for applying rule-based 'fuzzy logic' techniques in further development (Bardossy & Duckstein 1995).

A feature of the present approach to plant-based SCRs is the use of factor-scores as key variables to define the climate-space. Though it can be justified partly by the fact that plants'

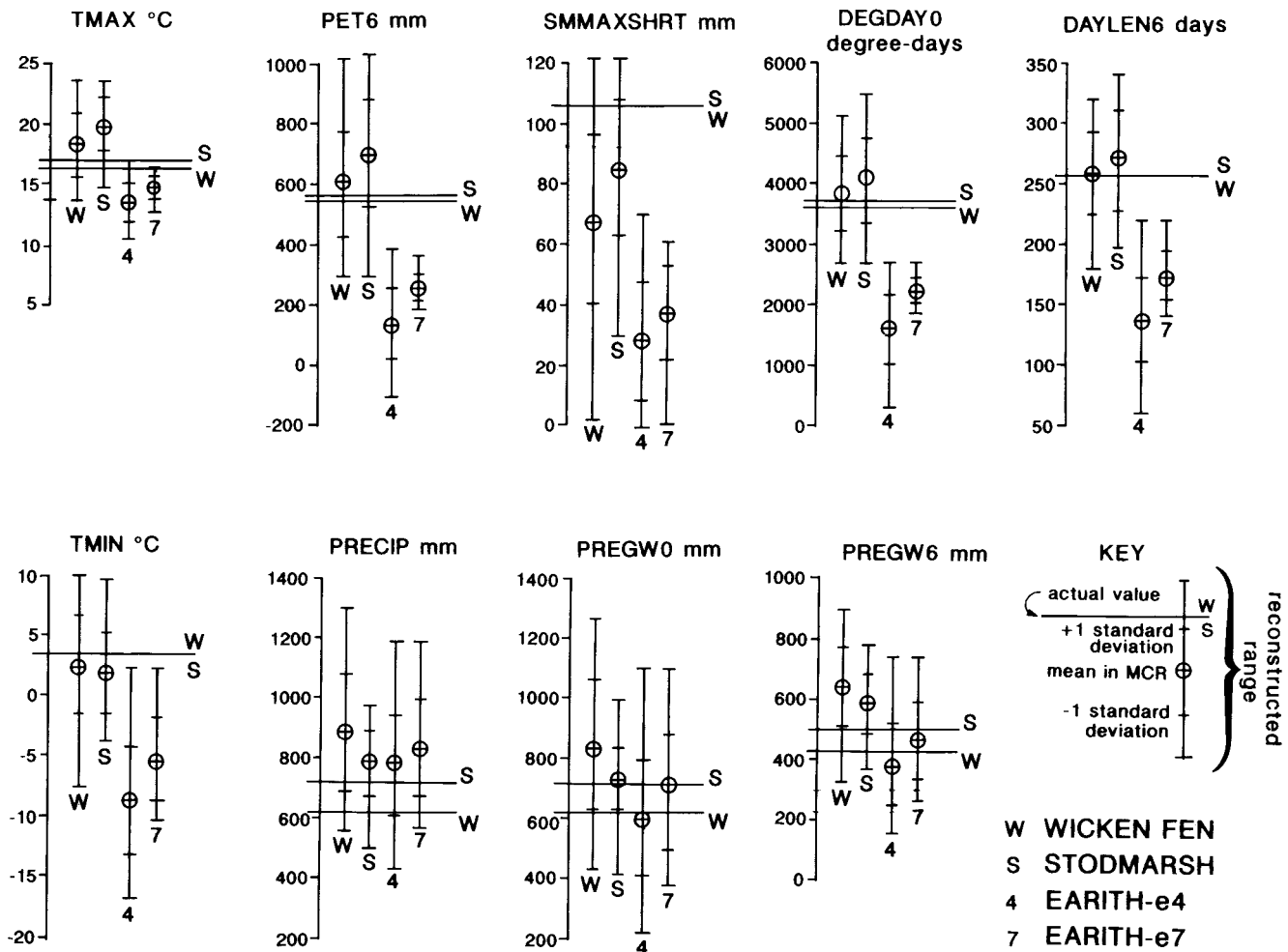


Fig. 8. Comparison of reconstructed original variables among the four sites, and with the measured climate for Wicken Fen and Stodmarsh.

distributions reflect complex combinations of the primary climatic variables of temperature and precipitation, and partly by the simple need to represent the climate space in just two dimensions, this approach has a number of methodological drawbacks. Foremost is the obvious influence of unexplained variance in the factor analysis model. For most of the original variables this amounts to around ten per cent of the whole variance in the calibration region (Tables 2–4). There is also the probability that the relationships between some original variables are somewhat non-linear, which invalidates the factor analysis model. The fact that the model predicts ‘impossible’ climates within part of the range of the calibration data (Fig. 4) is an indication that this limitation should be taken seriously. The variables most affected are PET6, which is derived from temperature data by the non-linear Thornthwaite formula (Thornthwaite 1948), and SMMAXSHRT which is derived from PET6. Part of the MCR of Earith bed e4 (Fig. 7) falls into this region.

A more fundamental methodological drawback of using factor analysis to define the climate-space is that the resultant factor-scores are not absolute attributes of climate but depend upon the data-set used. A factor analysis of climate over the whole palaeo-arctic would have resulted in different factor scores from those in this paper which are based on the more

restricted area of Europe alone. This does not matter in any practical sense if the MCR method is simply being used to reconstruct the modern climate for places within the climatic calibration region, since for these the factor-score values are valid by definition. However, when the method is applied to past climates, two new implicit assumptions creep in, which are methodologically undesirable. The first of these is that the palaeoclimate being reconstructed lay within the range of the calibration climates, both in terms of the absolute values of the various variables and in terms of the variety of ways in which their ranges are combined. The second is more subtle, in that the adoption of a factor analysis model based on the correlation matrix of modern climates implies the assumption that the contemporaneous palaeoclimates over a continental-scale region around the site being reconstructed shared the same correlation matrix. Since even today the correlation matrix can be altered by choosing a different geographical area for climatic calibration, this implicit assumption is very questionable indeed. In many respects other than the convenience of being able to represent a complex climate in 2D space, it would be desirable to abandon the factor analysis approach of the present study, in favour of a multi-dimensional climate space composed of actual climatic variables.

## Conclusions

Notwithstanding the methodological reservations expressed above, this study has shown that a factor-analysis-based climate space can be used for mapping plants' species climatic ranges. These in turn have been used to reconstruct the temperature and precipitation for two modern sites, with results that are accurate in that they include the measured climates but are rather imprecise in that for most of the nine variables the MCR embraces a fairly wide range of values, and gives little means of deciding *a priori* which is most likely to be the true value. In addition, the method has shown that the early or mid-Devensian climates as represented by the macrofossil floras in two plant beds at Earith were colder than the modern climate, but that precipitation totals were probably similar to today. This is an important advance, in that numerical reconstruction of the precipitation regimes of the past is a crucial problem in palaeoclimatology, which is as yet largely unsolved. In a future paper we shall show how the MCR method can be used with plant and beetle species simultaneously, both to identify parts of the plant-based MCR in which 'true' climate is most likely to lie, and to allow indicative reconstructions of seasonal water balance and hydrological regimes.

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