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Introduction

Palaeoecology aims to study the ecology of past times: how to work out, from the geological record, the relation between plants and animals and their environment at particular times in the past. Palaeoecology gives the fourth dimension of time to ecology, and the necessity of its study for understanding present-day plant and animal communities and how they came about is obvious. Yet many books on ecology take only a present-day view of life on earth. They may stress the importance of the study of the dynamics of communities in the short-term view imposed by human life, but much less so the longer term view derived from the geological record. The recent and widespread recognition of global climatic change has now placed palaeoecology in a very significant position, able to provide evidence of past climates and of the biota which have preceded today's flora and fauna. So they provide information on how changing climates might affect today's flora and fauna.

Our present geological era, the Quaternary Era, began over a million years ago, and is characterised by marked cyclic climatic change, in contrast to the rather more stable climates of the Tertiary. The nature of this climatic change varies from region to region, as does climate naturally today. In north-west Europe, the area that concerns us, the changes are seen as alternations of temperate climate with forest vegetation and cold or severe climate with a lack of trees and presence of herb vegetation. These broad vegetation types thus characterise temperate and cold stages of the Quaternary, with cold stages occupying the major part of the time. At present we are in a temperate stage (post-glacial, Holocene Epoch or Flandrian Stage), which began only some 10,000 years ago, and succeeded a cold stage (Devensian Stage) which lasted at least 100,000 years. Unlike those of the earlier temperate stages, the post-glacial forests have been decimated by agricultural activities in the last 5000 years.

The great ice advances of the Quaternary, the reason for giving the period the epithet 'Great Ice Age', took place during the cold stages. Each ice advance did not occupy the total time of the cold stage in which it occurred, and there may have been more than one ice advance in each cold stage. Within each cold stage there may also have been periods of climatic amelioration, as well as the variations which led to ice advances at particular times. Cold stage climates were evidently complex, in apparent contrast to the temperate stages, which show the invasion and development of forest vegetation. For the reason that cold stages are characterised by periods of glaciation, they have been called glaciations or glacial stages, with the intervening temperate periods termed interglacial stages. Such points of nomenclature are discussed later.

Since the food chain for our biota starts with plants, it follows that the study of past floras and plant communities is absolutely essential as a basis for understanding past biota as a whole. Investigation of flora and vegetation of the cold (or so-called glacial) stages, which occupy a major part of Quaternary time, thus provides a necessary background for understanding the faunas of these times of what we would call severe climate, as well as how the flora and fauna relate to those of the present day.

The identification of Quaternary plant remains began to be taken seriously in the latter half of the last century by palaeobotanists mainly working on the floras of older rocks. The early investigators in north-west Europe, such as A.G. Nathorst, N. Hartz and C. Reid, were concerned with the identification of macroscopic plant remains in both temperate and cold stage sediments, at a time when the knowledge of Quaternary stratigraphy was in its infancy. In the early part of this century analysis of pollen and spores (palynology) developed as a technique, and its potential as a means of investigating vegetational history in the Quaternary was immediately recognised, to a degree eclipsing the study of macroscopic plant remains. Godwin (1968) has described the history of this application of palynology to Quaternary vegetational history in the British Isles.

A very large number of palynological studies of vegetational history of the last 10,000–13,000 years in our area has been published, covering the latest part (late-glacial) of the last cold stage (Devensian Stage) and its replacement 10,000 years ago by the present temperate stage (Flandrian Stage) (Birks 1996; Chambers 1996; Greig 1996; Mitchell *et al.* 1996). The European Pollen Data Base has been compiled to make these data accessible (de Beaulieu 1996). The result is a very detailed knowledge of vegetational history in north-west Europe in this period, with the study of events and correlations facilitated by the application of radiocarbon dating.

Thus it has been possible to construct maps showing the timing of the migration of forest trees and their expansion, expressed by isopolls (lines of equal pollen representation) for particular pollen taxa, often genera in the case of trees (e.g. Huntley & Birks 1983). Using these changes in distribution in time of particular trees, together with estimations of the climatic controls of the same tree at the present time and the relation between present-day forest composition and pollen deposition, transfer functions (climatic response surfaces) have been used to reconstruct climatic change in the past (Huntley 1993).

In the cold stages, however, we are concerned with long periods of time in which vegetation of low stature, mainly herbaceous and locally very variable in character, was prevalent. Changes in mainly herbaceous pollen spectra arising from such vegetation are far more difficult to interpret than changes associated with forest history. In addition, the vegetation cannot necessarily be paralleled at present, as discussed later. Many analyses of pollen deposition in areas of present-day tundra vegetation have been made and related to the parent plant formation (e.g. Ritchie *et al.* 1987). These have been used to attempt reconstruction of cold stage vegetation and palaeoclimates, as with the use of the forest pollen analyses described above (Guiot 1990; Seret *et al.* 1992). These attempts, however, are more difficult with the cold stage pollen data for two reasons. Modern analogues are difficult or impossible to find, and the taxa represented in the fossil assemblages can usually be only identified to families or genera, each of which may be rich in species of varying environmental requirements. Records of macroscopic plant remains, more readily identifiable to a specific level, would enhance such approaches to past plant communities and climates in cold stages.

It is the possibility of combining the evidence for past floras from pollen and macroscopic identifications which gives an added dimension to the study of cold stage floras, a dimension which has not generally been exploited in the study of forest history of temperate stages or of long records of vegetational history from deep lakes.

The compilation of a cold stage flora database of higher plants for the British Isles is an attempt to provide a basis for an improved interpretation of cold stage vegetation and climates, using records of both pollen and macroscopic plant remains. Each of these two categories of fossils makes its own significant but different contribution to the interpretation, both in regard to the constitution of the vegetation and to the climatic interpretation.

These are the kind of questions we might wish to be answerable from such a database:

In regard to flora and vegetation:

What taxa grew where and when, and how abundantly?
What can be said about the representation of taxa as pollen or macro remains or both?
What is the present distribution of species found in cold stages?
What is the nature of the flora as a whole, in terms of biological properties, such as life form, life span, variation?
How far can plant communities be identified in the fossil record (a much more complex problem than with forest history in temperate stages)?
What species are found in both cold and temperate stages (i.e. appear to have climatic tolerance)?

In regard to taphonomy:

What are the complexities of fossil input into cold stage sediments and how do these affect interpretation of the fossil assemblages?

In regard to environment:

What can be said about climate and soil conditions from the plant fossil record?
Can variations in cold stage climate be detected in the plant fossil record or can they be expected to be detected?

The database should also make the cold stage fossil record much more easily accessible, for example, to those interested in proxy data for climatic reconstruction, phytogeographers who want to know the history of a species, taxonomists who are involved in working out variation in species, and palaeontologists who are interested in geological and evolutionary aspects of the subject. The analysis and discussion to follow are intended to illustrate principles and problems of the interpretation of the cold stage flora. Further analyses may be made by specialists, and data can be added as new sites are investigated. The richness of the fossil record may not have been widely appreciated. Nevertheless, the corpus of records must be regarded as very incomplete. Many more data are required for the study of regional vegetation and climates across the British Isles and the north-west European continent.

Consideration of the data in the following chapters is not meant to be an essay on arctic floras and vegetation. Rather it is meant to relate cold stage floras and vegetation to what is presently seen in northern lands, and to underline the problems which beset such a comparison. A perspective is taken which views the present arctic flora as derivative from the cold stage flora, a hardy remnant of the more southern and widespread cold stage flora of the Quaternary, which could spread far north as climate ameliorated in the temperate stages, leaving behind other species which could accommodate themselves to temperate conditions or to suitable refuges in mountains or elsewhere.

But before describing the database in more detail, it will be useful to give a brief historical survey of the subject, and to discuss two aspects of the study which can give rise to problems, such as the definition of terms and the question of analogues.

A brief historical survey

The development of phytogeography in the early part of the nineteenth century corresponded with increasing knowledge of recent geology. Edward Forbes (1846) realised the significance of the postulation of a widespread 'glacial sea', demonstrated by the occurrence of 'boulder clays and pleistocene drifts', for the presence of northern species of plants in the British Flora. He supposed that there was a spread of these plants around the margin of the 'glacial sea', but their distribution later became restricted to elevated mountain regions as climate ameliorated and the bed of the 'glacial sea' was uplifted. Darwin, in the *Origin of Species* (1859), devoted a lengthy section of his book to 'Disperal during the Glacial period', and largely followed Forbes' ideas in explaining the disjunct distribution of northern plants in the European mountains.

Later in the century, the Quaternary plant fossil record, termed by Godwin (1975) the factual basis for phytogeography, started to enlarge. For example, A.G. Nathorst, the Swedish 'hardrock' palaeobotanist, began to analyse (Late) Quaternary assemblages of macroscopic plant remains, which contained what he termed 'glacialpflanzen' or 'arktische pflanzenreste' (e.g. Nathorst 1914). Clement Reid (1899), in his book on the origin of the British Flora, identified many such plants from sites in Britain. As a result of these developments, the relation of phytogeography to the fossil record became a focus of study.

In 1936, a discussion was held at the Royal Society on the 'Origin and relationship of the British Flora'. A.C. Seward (1935), who introduced the discussion, referred to the controversial question of the effect of the Ice Age upon the plant world. Questions were raised about the survival of the British flora during the glacial periods and the relation of the present distribution of northern plants to climatic change: for example, whether the flora had been largely obliterated in the glacial stages (the *tabula rasa* hypothesis;

Reid 1911) or whether there had been perglacial survival on nunataks (Wilmott 1935).

By this time pollen analysis had become well established, complementing knowledge gained from macroscopic plant remains. But the state of Quaternary stratigraphy was much less well known, with far less information about the number of ice advances, the number of temperate (interglacial) stages and the detailed stratigraphy of the cold (glacial) stages in the glaciated and periglacial areas.

In recent years knowledge in all these areas has greatly increased, as has the fossil record. Since Bell's detailed account of last cold stage (Devensian) floras in Britain (Bell 1970) and Godwin's (1975) listing of fossil records to 1970, many more floras from the Devensian and earlier cold stages have been analysed. Godwin (1975) discussed the record and elaborated the relationship between phytogeography and stratigraphy in his classic book on the history of the British Flora. Dickson (1973) has treated the bryophytes likewise. Since that time much further knowledge has accrued, not only of fossils and stratigraphy, but also about present northern vegetation, proxy data for palaeoclimatology, interpretation of fossil assemblages in terms of present vegetation, the taphonomy of fossil assemblages, and absolute dating, especially radiocarbon dating. All these aspects have to be considered in relation to our interpretation of the fossil record, making the task of interpreting cold stage floras very different from the original simple and original 'Forbesian' statement about the relation between phytogeography and the 'glacial sea'.

The connection between geologically recent cold climates and the origin of the British Flora is one of the first areas in which phytogeography came to be seen as clearly related to geology. From this historical point of view, the present study is a development of the same thesis, attempting to take into account the vast geological and biological advances which have been made to the present. What is presented here may guide interest and activities in future studies, giving an idea of the problems and identification possibilities via pollen and macrosopic remains, and for interpreting cold stage environments, flora and fauna.

Definitions

It will be useful to discuss the definitions of some terms commonly used in Quaternary palaeoecology, since confusion often arises from their varied usage. The terms concern climate and vegetation, as at present and in the past. The problem is that the terms concerned naturally arise from what is seen at present. So there is a consequence that terms derived from present conditions are used to characterise past conditions, which may lead to incorrect conclusions, forcing past climates and vegetation into the likeness of present-day entities. With this problem in mind, we can first consider definition of present climatic conditions and vegetation.

Present climate: arctic and subarctic

A great variety of definitions have been proposed for these terms, which are used both capitalised and adjectivally without capitals. Polunin (1951) commented:

> A bad blot in the literature is the persistent vagueness surrounding the use of the term 'arctic', whether it be employed in the adjectival form . . . or as a substantive implying a region, viz., the Arctic. It is common for an author to term a plant (or its range) arctic when it reaches an area which according to his conception (or mere copying) constitutes part of the Arctic; but what this last is, or where it begins or ends, evidently varies greatly in different authors' minds.

Any student of the matter will agree with Polunin's sentiments. Generally, 'Arctic' is used to define a region, while 'arctic' refers to conditions associated with such a region. If required, a reasonable and clear definition of the terms as regional terrestrial entities, based on climate, would seem to be the definitions of Young (1989), based on summer temperatures, which are as follows:

Arctic – mean temperature of all months less than 10 °C, with at least one month below below freezing.

Subarctic – mean temperatures of no more than four months above 10 °C, and one or more below freezing.

Present vegetation

The Arctic is characterised by a lack of tree growth, in contrast to the coniferous forest of the Subarctic. The simple treeless character of the Arctic is balanced by the vast variety of vegetation which occurs in the area, promoted by the lack of a forest canopy. It has been divided into areas of High, Middle and Low Arctic on the basis of **bioclimate**, using differences in temperature and the length of growing season for plants, differentiating such features as plant cover percentage, the variety of herbaceous vegetation and the presence of shrub vegetation. Edlund (1987) and Ritchie (1987) have described the bioclimates of the Canadian north, the latter providing a range of climate diagrams for the diversity of conditions from temperate to arctic.

Tundra is the term most commonly used to describe the vegetation of the

Arctic. It is helpful to quote the *Shorter Oxford English Dictionary* (1947) on this term:

> 1841.(Lapp.) One of the vast, nearly level, treeless regions which make up the greater part of the north of Russia, resembling the *steppes*, but with Arctic climate and vegetation. Also applied to similar regions in Siberia and Alaska.

As will be discussed later in relation to the interpretation of cold stage floras and vegetation, the treelessness has been associated with low annual carbon gain of the vegetation, low soil temperatures and winter desiccation.

It is important to realise the complexities of the many vegetation units and plant communities of the Arctic, described by numerous authors (e.g. Batzli 1980; Andreev & Aleksandrova 1981; Bliss 1981a). Young (1989) has distinguished broad divisions as follows: sedge meadows, tussock tundra, wet tundra, mesic tundra, shrub tundra, fell fields, polar steppe and polar desert. Chapin and Shaver (1985) have described characteristics of major Arctic vegetation types in north America: the high Arctic polar desert and polar semidesert, and tundras typified as wet sedge-moss, tussock, low shrub, tall shrub and heath. In general terms, the shrubby tundras occur at lower Arctic latitudes, the other tundra types more frequently in the mid and high Arctic. The complexity of the vegetation is in contrast to the relative paucity of the Arctic flora. Young (1971), who divided the Arctic into four floristic rather than vegetation zones, commented that little more than a thousand species of vascular plants occur in the Arctic.

Communities with abundant grasses occur widely in the Arctic. If they were not in the Arctic they might be termed steppe communities. Nevertheless, polar steppe is a recognised vegetation type in the tundra. Grassland (see Bliss 1975) is a term which can be properly used to describe the floristic affinities of such vegetation, and which avoids a temperature connotation, though it does imply a continentality or aridity of climate, insufficient for tree growth, which may occur in the Arctic region (polar steppe) or to the south (steppe, prairie). The term steppe-tundra then signifies climatic conditions which promote grassland, but allow the growth of species nowadays considered Arctic or steppe, i.e. variation along gradients of annual and seasonal temperature and precipitation. If we find evidence for such communities in the cold stage flora, the ascription to a particular climate type must then be cautious.

Past climate

Since there are no measurements of past climate available, we have to use proxy data for their reconstruction. There is a wide array of geological and

Glacigenous or periglacial formations

Interstadial climatic development	Interglacial climatic development
	Arctic
Arctic	Subarctic
Subarctic	Boreal
Boreal; summer temepratures essentially lower than the climatic optimum of the post-glacial period	Temperate climate with a summer temperature at least as high as during the post-glacial climatic optimum of the area in question
Subarctic	Boreal
Arctic	Subarctic
	Arctic

Glacigenous formations

Figure 1.1. Climatic development of interstadials and interglacials according to Jessen & Milthers (1928).

biological sources of such proxy data, listed by Bradley (1985). We are concerned here particularly with the use of palaeobotanical data for the recognition of broad climatic events in the Quaternary. Jessen and Milthers (1928) distinguished **interglacial** events from **interstadial** events by the degree of climatic amelioration, determined from palaeobotanical data. Their scheme is shown in Figure 1.1. The terms, as used by Jessen and Milthers, might well be put in a category of **palaeobioclimatic** terms, identifying past climates from biological data. This usage would parallel the use of the term bioclimate to characterise present terrestrial climates, as with the subdivisions of the Arctic mentioned above.

In considering cold stage floras we are concerned with stadial and interstadial events. The 'stadial' terminology developed originally as a result of the subdivision of glacial stages into stadia, associated with periods of ice advance (see Nilsson 1983). However, with an increased knowledge of the periglacial environment and its history, it appears that glacial advance is not necessarily a concomitant to stadial periglacial conditions. This problem is avoided if we use the term pleniglacial, used by Van der Hammen (1951) to describe the non-interstadial parts of the Netherlands periglacial succession in the Tubantian (Last) Cold Stage of the Netherlands, prior to the Late-Glacial. Full-glacial is an alternative version of pleniglacial. Where the stadia of ice advances fit into the periglacial–pleniglacial succession is an important question, because it implies that pleniglacial climates are far from uniform.

In this account of the cold stage flora, the Jessen & Milthers (1928) definition of interstadial is used, based on degree of amelioration of summer temperature indicated by forest development. But it should be remembered that the presence of forest is also controlled by seasonal precipitation as well as temperature. The Early Devensian Chelford Interstadial is identified as an interstadial on the basis of the develpment of forest. 'Interstadial' is not used to identify geological events related to changes of sediment type, such as a bed of peat sandwiched between cover sands, which of itself need give no clear evidence of climatic change, though of course what may be termed **palaeolithoclimatic** units such as cover sand occur abundantly in the Quaternary. Thus the clay bed in the Corton Sands, which lies between two tills of Anglian age in East Anglia, is not interstadial using the Jessen & Milthers criteria. A most interesting problem for a palaeobioclimatic definition of interstadial arises when biological evidence for climatic amelioration taken from palaeobotanical and palaeozoological evidence is at variance, as occurs in the Middle Devensian Upton Warren Interstadial Complex. This very significant matter is discussed in Chapter 13.

As examples of the problems of definition we can refer to the use of 'Arctic' to describe plant beds, where fossil assemblages have been found to contain plants of arctic distribution, e.g. the Lea Valley Arctic Bed. As Wilmott (1935) pointed out, these assemblages may contain many other species which are now associated with temperate climates, and he questioned the use of the term 'Arctic'. The description of vegetation as tundra at lower latitudes in pleniglacial times is also questionable, in view of the vast difference in bioclimate between present Arctic tundra areas and lower latitudes.

Analogues

In the interpretation of cold stage floras and faunas, the search for present-day analogues has always presented an important problem. Are there indeed any present-day analogues? This question has long been discussed, especially in relation to tundra and steppe; for example, by Nehring (1890) in his classic *Ueber Tundren und Steppe der Jetzt- und Vorzeit* and by Grichuk & Grichuk (1960) in their work on Russian periglacial floras, in which they postulated tundra-steppe communities at the margin of ice sheets.

A discussion of present-day analogues for cold stage floras is essential for their understanding. Two elements of the discussion are involved. The first, and fundamental, one is the physical environmental element; the second,