PLEISTOCENE HISTORY OF THE BRITISH FLORA

by R. G. West

Subdepartment of Quaternary Research, Botany School, University of Cambridge

INTRODUCTION

In dealing with the vegetational history and environmental changes of the period since the last glaciation, we have a straightforward connection between past and present. Landscapes have changed little; basins of accumulation are recognizable and often still existent, and the vegetational changes are continuous and directly relative to present British vegetation and phytogeography. Naturally, therefore, it is this recent part of Pleistocene history which bears most interest for the ecologist and phytogeographer. Farther back in geological time, the changes in landscape consequent upon multiple glaciation, and the repeated and unknown number of climatic fluctuations in the Pleistocene, make it difficult to see any significance in the vegetational changes of those remoter times for the present British flora. What interest these periods lose for the ecologist, they gain for the geologist, for in recent years it has become obvious in north-west Europe, at least, that vegetational history can be the key for the unravelling of the Pleistocene sequence. But, on closer consideration, and in the wider context of the evolution of the flora and its response to environmental changes over a long period, the study of these older floras and their relation to the present flora on the one hand, and to the Pliocene flora on the other hand, can reveal overall patterns of migration and extinction of species, and patterns of aggregation and dispersion of species within vegetation types, which have an important bearing on the view we form of the interrelations of species of present plant communities, as well as of course providing the substantive evidence for the past history of the species.

Edward Forbes (1846) recognized at an early date the importance of climatic change, large enough to induce glaciation, for the history of the British flora. Thus he said that the glacial (arctic-alpine) element in the present flora appeared in Britain during the glacial epoch and had survived in favourable situations since that time. The biological importance of glaciation was recognized by Clement and Eleanor Reid (1915), who explained the depauperate nature of the Pleistocene flora, as compared with the Pliocene flora, as a result of climatic refrigeration and enforced migration acting in conjunction with barriers to migration formed, in Europe, by the predominantly west–east mountain chains—the Reids' ideas were based on the study of fossil floras of macroscopic plant remains. More recently, many more details of the Pleistocene history of the flora have been gained by studies of the microfossils, and the outline of the Pleistocene history of the flora is rather clear. But such studies have not only revealed the history of the flora. They have made possible a reconstruction in considerable detail of the sequence of climatic episodes, and of the environments against which the history of the flora must be viewed. It is the purpose of this essay to present such reconstructions that have been made, and to discuss what interest they hold for the botanist and geologist, and what may be expected in the future exploration of this field of study.

ENVIRONMENTAL DIVERSITY AND THE RELATION BETWEEN CLIMATE AND FLORA IN THE PLEISTOCENE

We can usefully distinguish in the Pleistocene three major divisions of environment—the glacial environment, the periglacial environment and the non-glacial environment. With the first we are not concerned, even though it is the environment in which is produced the thick glacial deposits which characterize the Pleistocene over much of north-west Europe. The periglacial environments can be considered as the dominant form of environment during the glaciations in non-glacierized areas. As far as can be seen it is a tundra-like environment of open vegetation and low mean temperatures, though the details vary according to climatic variation with time and with latitude and longitude. At some times and in some places permafrost may develop with indications of considerable continentality of climate; at other times and places more oceanic conditions may ameliorate the climate.

The non-glacial environment, transitional from and to the periglacial environment, shows the development of more temperate floras in the intervals between glacial advances. Physical evidence suggests a mean temperature difference of some 5–7 °C between the cold and temperate extremes. The type of vegetation developed depends on the length of the non-glacial period and the degree of climatic amelioration manifested. If, in a cycle of climatic change within a non-glacial period, the time or the degree of climatic amelioration only permits the development of boreal forest, the period is termed interstadial. If time and climatic amelioration allows the development of temperate deciduous forest, of a kind characterizing the Flandrian (Post-glacial) climatic optimum, then the period is termed interglacial. These definitions are not expected to be clear cut, for both latitude and longitude will play a part in determining non-glacial vegetational sequences, as will the relation of the periglacial to the non-glacial floras in particular areas. For example, we might envisage as a possibility the situation where a flora described as interglacial in an area of continental climate, where a rich periglacial flora survived, might be of the same age as a flora described as interstadial in an oceanic area distant from the glacial refuges of the thermophilous species required to transform it to an interglacial.

However, the concept of interstadial and interglacial ameliorations is useful in our area of the British Isles in categorizing the type of vegetational history to be found in non-glacial intervals.

These categories of climatic change, defined by vegetational change, are of course very broad. They concern on the one hand regional aspects of vegetation, and on the other hand the gross climatic effects on this vegetation. The details of seasonal distribution of temperature and rainfall and the extremes of variation in microhabitat tend to escape us. Yet from the point of view of vegetational history it is just these facts that we should wish to know in assessing the importance of climatic variations for plant distribution in the past. We should, for example, like to know the mosaic of communities which characterized the periglacial flora at any one time. Such investigations require the study of fossil floras known to be synchronous, and living under different microhabitats and differing edaphic conditions. The possibilities of diversity will be seen to be enormous and are well illustrated by the great diversity of treeless vegetation types in northern Eurasia at the present time. This complicated nature of the full-glacial flora, with its many phytogeographical elements, contrasts with the more easily explicable and uniform floras of the warmer episodes, with their variation in microhabitat muted by a more uniform forest cover.

The history of particular species will depend on climatic change, microhabitat diversity, reproductive ability and chance. In many examples we can trace the history of the species throughout the Pleistocene, noting their disappearance or appearance in cold or temperate conditions, as will be shown subsequently. It would be satisfactory if we could use the present distribution of such species as closer indicators of climate and environment in the past. But usually too little is known of the autecology of the species concerned or of their behaviour in communities, so that only broad generalizations about the environment can be made. It might be hoped that the history of the flora in the last few centuries, combined with our knowledge of climatic change within that time, might be used as a basis for extrapolating backwards in time on the relation between vegetation and climate. But the anthropogenic factor here confuses the relation.

The importance of relating known climatic change to known floristic change cannot be overstressed; only in this way will we be able to interpret the details of past climatic change and the effects of the present climatic tendencies.

VEGETATIONAL HISTORY OF THE PLEISTOCENE

Units of vegetational history

The biostratigraphical units which comprise vegetational history are pollen zones. These are assemblage zones, typified by dominant regional genera of the pollen spectrum. The pollen zones of the cold or glacial stages are divisible into full-glacial and interstadial types. The former show the prevalence of open vegetation, the latter the presence of trees of present boreal distribution. There is yet insufficient evidence for the erection of long sequences of pollen zones in the cold stages, though variations are seen in the full-glacial spectra, in particular in the diversity of taxa recorded. On the other hand, during the temperate interglacial stages, the marked vegetational changes give rise to sequences of pollen zones (Turner & West, 1968). In general, during these temperate stages, four major assemblage zones may be discerned, typified as follows (the youngest first):

Cambridge University Press
978-0-521-11201-7 - Studies in the Vegetational History of the British Isles: Essays in Honour of Harry Godwin
Edited by D. Walker and R. G. West
Excerpt
More information

ZONE IV (post-temperate zone). Amongst the trees, the dominant genera are boreal—*Betula*, *Pinus*, *Picea*. There is a thinning of the forest and non-tree pollen types are frequent, particular pollen of Ericales, associated with damp heathland.

ZONE III (late-temperate zone). The zone is characterized by the expansion of forest trees not abundant earlier in the stage—*Carpinus*, *Abies*, *Picea*, and perhaps *Tsuga*—at the expense of mixed oak forest genera already present.

ZONE II (early temperate zone). This zone is dominated by forest trees of the mixed oak forest—*Quercus*, *Ulmus*, *Fraxinus*, *Corylus*.

ZONE I (pre-temperate zone). This zone is characterized by the presence of boreal trees, *Betula* and *Pinus*, accompanied by significant quantities of pollen-types of light-demanding shrubs and herbs.

This sequence of zones is found in the temperate Pastonian, Cromerian, Hoxnian and Ipswichian stages, though in each sequence there are minor differences which permit distinctions to be drawn between each of them. The zones of the different stages can be conveniently signified by pre-fixing the initial letter of the stage to the zone (table 1).

In building up our sequence of assemblage zones, we have finally to draw a boundary between the cold or glacial stages and the temperate stages. The lower boundary of a temperate stage may be placed at the point where the tree-pollen percentages consistently exceed those of non-tree pollen, signifying the change from open vegetation to (boreal) forest. A similar definition, but reversed, can be used for the temperate/cold stage boundary, though this is more difficult to apply as the change is a more gradual one.

THE PLEISTOCENE SEQUENCE

Figure 1 summarizes the sequence of stages now known from the British Pleistocene. The extent of the fossil record in relation to these stages is also shown in the figure. It will be seen that there is a record, at one place or another in Britain, over much of the Pleistocene. Much of the record comes from sites in East Anglia. Regional variation at one time, however, is hardly known, because of the low total number of sites studied, except of course in the Flandrian. The curve shown in the figure is not to be taken as a complete expression of climatic change, but is inserted merely to give some kind of scale to the type of flora recorded and the approximate extent in relative time covered by the fossil floras.

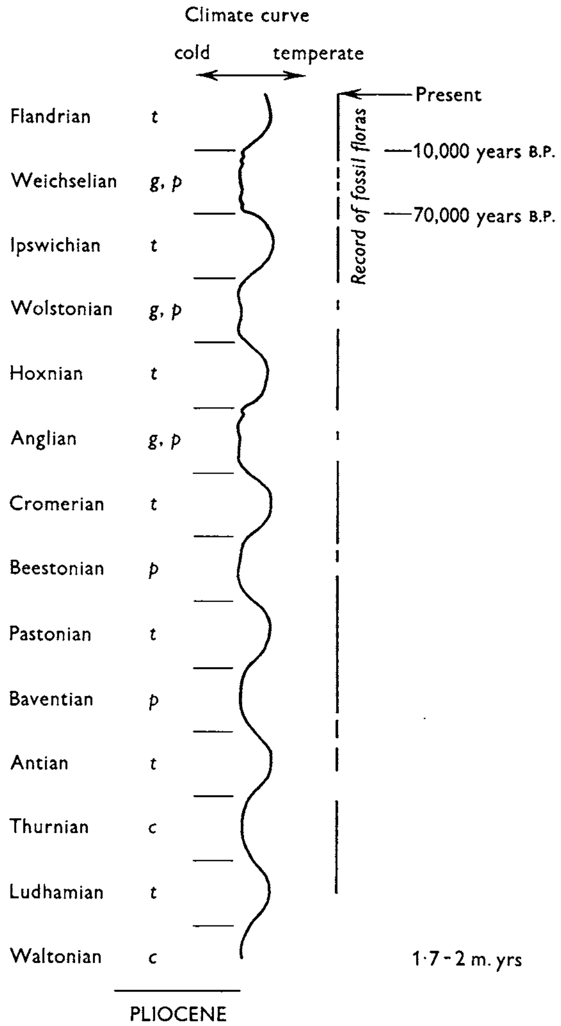

Figure 1. The sequence of Pleistocene stages in relation to climatic change and the fossil record. *t*, temperate; *g*, glacial; *p*, permafrost; *c*, other evidence of cold conditions.

PREGLACIAL VEGETATIONAL HISTORY

We consider first the vegetational history of pre-Anglian times, that is before the first great glaciation of midland Britain. Here the record is confined to East Anglia. Unfortunately there are not yet any certain records of the Pliocene flora in Britain, though on the continent there are rich fossil floras of Late Tertiary age. These show that the Pliocene flora of continental Europe was characterized by a considerable number of exotic genera, many now native in eastern Asia and north America. Such genera as *Sequoia*, *Tsuga*, *Carya*, and *Nyssa* are commonly found. This exotic element forms part of the circumboreal so-called Arcto–Tertiary flora of the northern Hemisphere. At the onset of the Pleistocene climatic deterioration, the exotic temperate genera must have been forced out from north-west Europe, and on the return of a temperate climate after the first cold stage (Pretiglian of the Netherlands) many did not reappear, and thus became extinct in north-west Europe as a result of climatic change. C. and E. M. Reid (1915) spoke of barriers to migration in the form of west–east oriented mountain ranges, and the Mediterranean, in western Eurasia, whereas in eastern Asia and north America the diversity of habitats given by the altitudinal range of the mountains and their alignment allowed the survival of the Arcto–Tertiary flora during the cold stages. The explanation is a very reasonable one. It must then be presumed that the surviving genera in western Europe were particularly hardy or were rich enough in biotypes to find suitable perglacial refugia.

In Britain few sites of Lower Pleistocene age have been studied, but there is a satisfactory long record from one or two boreholes. The pollen diagrams from these boreholes show fluctuations in vegetation, with mixed oak forest genera and *Tsuga* characterizing the temperate stages (Ludhamian, Antian) and higher percentages of non-tree pollen, principally Ericales, and boreal trees characterizing the cooler stages (Thurnian, Baventian) (West, 1961).

As there is no record of Pliocene flora we cannot say what effect the earliest cold period (Waltonian?) had on the Pliocene flora. But if the Ludhamian is equivalent in age to the Tiglian flora of the Netherlands, as seems likely, it follows that the flora of East Anglia was far poorer in exotic species than the continental flora, for there is a considerable percentage of exotic pollen types in the Tiglian flora, whereas only *Tsuga* is represented abundantly as a widespread exotic genus in East Anglia. Perhaps some of this difference may be a consequence of the fact that the Tiglian flora is a freshwater one whereas the pre-Baventian pollen floras of East Anglia are found only in marine deposits; but the magnitude of the contrast suggests that there is indeed a real difference, and that west European vegetation was clearly differentiated across the lines of longitude, more so perhaps than today.

The marine deposits of the pre-Pastonian cool stages (Baventian, Antian) are characterized by high percentages of Ericales pollen, much of it of *Empetrum*-type, while Baventian freshwater sediments show a contrast, with high percentages of non-tree pollen giving a true full-glacial aspect to the flora. This contrast between the two types of pollen flora results from differential transport according to environment, at present being investigated, and the meaning of the difference in regional vegetational terms is not clear. At any rate, between the forested stages there are clearly cooler and perhaps wetter intervals characterized by open vegetation and heath.

The Pastonian temperate stage, in contrast to the earlier temperate stages, shows a characteristic interglacial-type sequence of pollen zones, with very low frequencies of *Tsuga* confined to Zone P III. It is remarkable also in showing *Carpinus* present in Zone P II, in the mixed oak forest pollen flora. The full-glacial floras of the Beestonian are similar to those of the later glaciations. The Cromerian vegetational history is again a typical interglacial sequence. *Tsuga* is absent. *Carpinus* and *Abies* appear in Zone C III, as in the Hoxnian temperate stage. The flora of the Cromerian is remarkable in showing so few non-British species, even though it predates the earliest glacial deposits of East Anglia. In fact all Cromerian species known are either British or occur in later interglacial floras (e.g. *Salvinia natans*, *Azolla filiculoides*, *Trapa natans*).

What evidence we have, therefore, suggests that even before the time of the earliest known glacial advance into East Anglia a flora resembling the modern British flora was present in East Anglia, that modification of the flora from a possibly rich Pliocene flora occurred at the beginning of the Pleistocene, with *Tsuga* the only characteristic survivor into the Lower Pleistocene, and that a difference existed between the British Lower Pleistocene flora and the synchronous European flora.

The glacial stages

The floras of the glacial stages are divisible into full-glacial floras and interstadial floras. The full-glacial floras are characterized by high proportions of non-tree pollen, with a varying diversity of pollen types. The vegetation indicated by the plant remains is open and a mixture of plants of many ecological and geographical categories is usually present, e.g. northern and montane plants, halophytes, and other maritime plants, many plants of wide distribution, often 'weeds', and a few species of more southern distribution, often aquatics and marsh plants. Species in these groups were listed by Godwin (1956), but many more records have accumulated since then, and we are in need of a detailed re-assessment of the full-glacial flora.

A few of the more characteristic species may be mentioned:

Northern and montane plants: *Salix herbacea*, *Dryas octopetala*, *Draba incana*, *Thalictrum alpinum*, *Saxifraga oppositifolia*.

TABLE 1. *Zone characters of temperate stages (the frequency references ase to pollen percentages)*

	Pastonian		Cromerian		Hoxnian		Ipswichian		Flandrian	
	e Be		e A		e Wo		e We			
IV	P IV	*Pinus*, *Picea*, *Betula*, *Alnus*, Ericales	C IV	*Pinus*, *Picea*, *Betula*, *Alnus*, Ericales	H IV	*Pinus*, *Betula* N.A.P. higher	I IV	*Pinus*, N.A.P. higher		—
III	P III	M.o.f., *Carpinus*, *Picea*, *Tsuga*	C III	M.o.f., *Abies*, *Carpinus*	H III	M.o.f., *Abies*, *Carpinus*	I III	*Carpinus*		
II	P II	M.o.f., low *Carpinus*, *Picea*, and *Corylus*	C II	M.o.f., high *Ulmus*, low *Corylus*	H II	M.o.f., *Taxus*, *Corylus*	I II	M.o.f., *Pinus*, *Acer*, high *Corylus*	F II	M.o.f.
I	P I	*Pinus*, *Betula*	C I	*Pinus*, *Betula*	H I	*Betula*, *Pinus*	I I	*Betula*, *Pinus*	F I	*Betula*, *Pinus*, *Corylus*
	l Ba	—	l Be	—	l A	(*Hippophaë*)	l Wo	—	l We	—

Ba, Baventian; e, early; l, late; C. Cromerian; Be, Beestonian; P, Pastonian; Wo, Wolstonian; H, Hoxnian; A, Anglian; F, Flandrian; We, Weichselian; I, Ipswichian

Maritime plants: *Armeria maritima*, *Atriplex hastata*, *Plantago maritima*, *Sueda maritima*.

Weeds: *Polygonum aviculare*, *Potentilla anserina*, *Ranunculus repens*.

Plants of a more southern distribution: *Potamogeton crispus*, *P. densus*, *Ranunculus sceleratus*.

This type of plant list is recorded from floras of Beestonian, Anglian, Wolstonian and Weichselian age, and the assemblage recurs in Pleistocene time. The mixed assemblages must derive from the diversity of habitat and microclimate of the periglacial area, with its possibilities for permafrost, waterlogged soil, sunny banks, solifluction slopes and so on; and perhaps from minor climatic fluctuations in the periglacial area which affected the constitution of the assemblages. The considerable increase in knowledge of full-glacial floras in recent years must lead to a much more detailed knowledge of the species concerned and how they combined into communities. Studies of the macroscopic plant remains in conjunction with studies of pollen, local sediment and surrounding soil types should lead to a greater understanding of the peculiar full-glacial flora.

Interstadial floras, showing evidence for boreal forested conditions during glacial stages, are very few. The best known is the Chelford interstadial (Simpson & West, 1958) from the last (Weichselian) glaciation, where *Betula–Pinus–Picea* forest was the dominant local vegetation. If the Chelford interstadial is the same age as the Brørup interstadial of continental north-west Europe, it appears that the *Picea omorikoides* recorded from the continent at this time did not reach this country. On the other hand, *Picea abies* is represented. This species did not reach Britain in the Ipswichian, although characteristic of the later part of the equivalent Eemian interglacial on the continent.

There is some evidence for interstadial conditions at some time during the Wolstonian glacial stage at Mildenhall, with boreal forest present. On the other hand the only flora known from between the two ice advances of the Anglian glaciation, at Lowestoft, is of a glacial type, and was probably formed during an adjustment of ice sheets rather than during a definite climatic amelioration (West & Wilson, 1968).

INTERGLACIAL AND OTHER TEMPERATE STAGES

The interglacial deposits found in Britain may be referred to the Hoxnian or Ipswichian interglacial stages. The outline of forest history is shown in table 1, which tabulates the zones. The Flandrian (Postglacial) is also shown in this table, as well as two earlier temperate stages which have clear zonations.

We may briefly give the salient points which appear to characterize the different histories of the temperate stages as follows:

Flandrian: High *Corylus* frequencies in Zone F I.

Ipswichian: High *Corylus* early in Zone I II. Well-marked *Carpinus* zone (I III).

Hoxnian: High frequencies of *Hippophaë* pollen in the late glacial (l A).
Considerable *Tilia* frequencies in late Zone H II. *Corylus* maximum later in Zone H II. *Abies*, *Picea*, *Carpinus* and *Pterocarya* in Zone H III.

Cromerian: Low frequencies of *Corylus*. High frequencies of *Ulmus* in Zone C II, but *Tilia* low or absent. *Abies*, *Picea* and *Carpinus* occur in Zone C III.

Pastonian: *Carpinus* in Zones P II and P III. *Tsuga* in Zone P III. No or very low *Abies* in Zone P III.

The zonal sequence of the temperate stages

The sequence of four zones already outlined for the temperate stages must now be related to environmental changes forming the cycle of change during the stages. The fact that the four-zone system appears applicable to a number of temperate stages does support the idea that we are dealing with similar effects in each temperate stage. Zones I and II are clearly an expression of the early expansion of forest genera in the order boreal to temperate. Zone I is characterized by light-demanding genera, Zone II by the spreading of the temperate shade-giving genera, *Ulmus*, *Quercus*, *Alnus* and *Corylus*. This change must partly be a result of succession on soils improved from the raw immediately post-glacial state to richer mull soils, and partly a result of the times of immigration and expansion of genera.

The change from Zone II to Zone III is given by the expansion of genera, in particular *Carpinus*, *Abies*, and *Picea* at the expense of the mixed oak-forest genera. This expansion may be accompanied by an increase in Ericales pollen. Basically this change results from the expansion of genera either already present in low frequencies or because of late immigration (e.g. like that of *Picea* in north-west Europe during the late Flandrian). It is likely that soil development from a mull to a mor state is related to the expansion of certain of the genera (e.g. *Picea*) which are known to cause soil deterioration after their introduction (Andersen, 1966). The increased acidification of soils lead to expansion of conifers and often heathland. In Zone IV this expansion continued and is accompanied by a reduction in the number of thermophilous forest genera. It is probable here that climatic deterioration played a part in the restriction of the flora, as well as the increased soil deterioration.

It will be clear that the interactions of climate, soil and plants make it exceedingly difficult to disentangle the role of each in determining vegetational change. A possible scheme of such changes, outlined above, may be summarized as follows:

1 Climatic amelioration.
2 Expansion of light-demanding genera.
3 Soil improvement to mull condition and expansion of shade-giving forest genera.
4 Soil deterioration to mor condition and/or expansion of late-arriving genera.
5 Climatic deterioration, restriction of thermophilous genera, expansion of heathland.

This last episode gives way to the periglacial environment with its open vegetation and soils enriched by solifluction and freeze/thaw processes.

Distinctions between the zones of the different temperate stages

Though the zonal sequence of each temperate stage is similar, there are considerable differences between the zones of the several stages. Many factors can be involved in such differences. They include climatic differences between the stages, different barriers to migration during the stages, especially that formed by the present English Channel, differing distances of glacial refuges from which genera expanded, changes in ecological tolerance and variability within genera, and other changes consequent upon evolution or extinction. Again, it is most difficult to disentangle these factors. The difficulty of inferring climate from vegetation or flora records has been referred to many times. Perhaps a general trend of oceanicity or continentality may be discerned. For example, in the differences between the Hoxnian and Ipswichian interglacials: the former has an abundance of *Taxus*, *Ilex* and *Alnus* pollen less well represented in the latter, while the latter contains records of many continental thermophilous genera indicating higher summer temperatures than at present. Again this particular element in the Ipswichian flora is lacking in the Flandrian, which suggests that the Ipswichian climatic optimum may have been warmer than that of the Flandrian. But apart from these indications, it is difficult to draw further or close conclusions from analyses of fossil floras.

Some conclusions may perhaps be drawn regarding the persistence of the Channel barrier during the temperate stages. The resemblance of the Hoxnian of East Anglia and Holsteinian interglacial of continental Europe suggests no barrier between them in the early part of the interglacial. On the other hand, the considerable differences between the Ipswichian and Eemian (notably the lack of development in the Ipswichian of zones with *Tilia* and *Picea*) suggest a barrier early in the interglacial, perhaps formed by the connection through the Channel of the Eem Sea and the Atlantic. Such contrasts in the last two interglacials are in accord with marine mollusc faunas. The Eemian fauna has connections with the

Lusitanian fauna, while the Hoxnian fauna appears to have no such connection.

Differing distances of glacial refuges may account for the different behaviour of *Corylus* in the Hoxnian, Ipswichian and Flandrian stages. The notable difference is the progressively earlier time of expansion in England, late in the Hoxnian, at the time of the mixed oak forest in the Ipswichian, and before this in the Flandrian. This may be related to the increasing nearness of the glacial refuges to the ice-freed areas. If so, it may suggest a change in the ecological tolerances of *Corylus*, allowing it to survive in progressively nearer refuges, assuming that the intervening glacial climates were of a similar type. Here we come up against the question of changing biotypes or ecological tolerances within species and genera, which can more conveniently be dealt with separately below.

A further detailed discussion of the differences between the zones of the successive temperate stages would be out of place here. It will be apparent that much further information on the zones and their regional differentiation must be obtained before we can make more progress in disentangling the causes of the differences.

The behaviour of certain forest genera

The interpretation of past vegetation and its relation to climate is based on the present behaviour of genera or species. Convincing generalizations can be drawn because the parallel behaviour of different taxa in fossil sequences leads to reasonable environmental conclusions. If we examine the zones of the temperate stages we find little or no evidence to refute this view. The genera behave together as would be expected in a climatic cycle. But if we examine the history of each genus in more detail, we may discern that certain genera have a changing behaviour within climatic cycles assumed to be similar. Of course such changes may be the result of chance or other effects on distribution, and differences in the intensity of glaciation and climate of the cool stages. But because certain trends do emerge, it is possible that such effects do not have an overall importance, and we may then consider whether there is any evidence for evolutionary change.

Let us take certain temperate genera, and consider their behaviour in East Anglia during the temperate stages, summarized in figure 2. Some, like *Quercus* and *Ulmus*, occur consistently in each temperate stage. They are the earliest temperate forest genera to occur in each temperate cycle and expand as part of the temperate forest flora in Zones II and III. *Tilia* is not so consistently a part of the mixed oak forest. It is rare or absent in the Pastonian, Cromerian and Ipswichian, only forming an obvious forest component in the Hoxnian and the Flandrian. When present it is characteristic of Zone II. The behaviour of *Corylus* in the Flandrian, Ipswichian and Hoxnian has been mentioned already. In the Pastonian and Cromerian this genus plays a very minor part in the mixed oak forest. Figure 3 compares pollen curves for *Corylus* which have been found in East Anglia for the temperate stages. The change in time of the behaviour of this taxon shows that during the earlier stages its expansion corresponded with that of the mixed oak forest; but in the later temperate stages it may be suggested that there were changes in the biotypes which allowed it to survive in periglacial refuges in western Europe and to expand rapidly in the Flandrian before the expansion of the mixed oak forest and compete more effectively in the mixed oak forest.

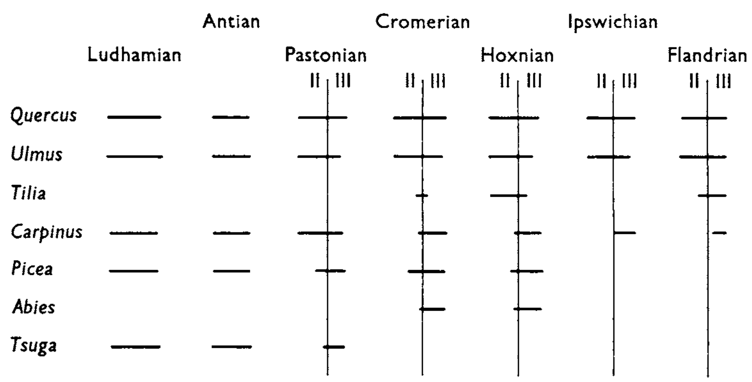

Figure 2. The occurrence of certain forest genera in East Anglia during the temperate stages of the Pleistocene.

Alternatively, chance survival or the differing extent of glaciation may have had similar effects on the perglacial survival of *Corylus*. A regional study of the behaviour of *Corylus* in the temperate stages over north-west Europe would be likely to lead to a solution of this problem.

Carpinus occurs in Zones II and III of the Pastonian, but only in Zone III of the Cromerian, Hoxnian and Ipswichian. Thus in these latter stages it shows a late expansion, small in the Cromerian and Hoxnian and Flandrian, but massive in the Ipswichian. This variation which only allowed it to survive in later glaciations at a distance which gave rise to late expansion in the temperate stages.

Picea, in the earlier temperate stages (Pastonian to Hoxnian), occurs in Zones II and III, though there is a tendency for expansion in Zone III. In the Ipswichian, no marked pollen frequencies occur; neither do they in the Flandrian. On the continent, in these two most recent stages, *Picea* shows late expansion. Thus the late immigration in these two stages did not allow spread to Britain, contrasted with its earlier appear-

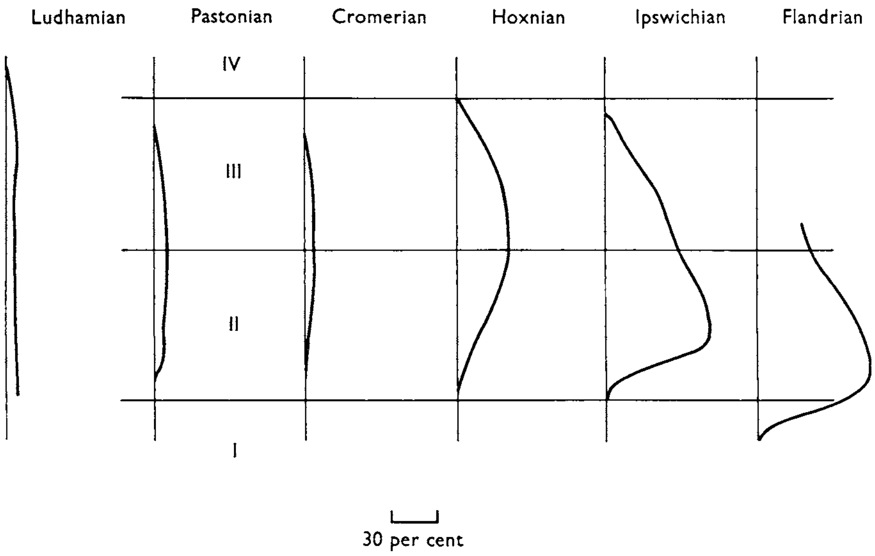

Figure 3. Schematic *Corylus* pollen curves for temperate stages in East Anglia, presented as percentages of total tree pollen and related to the zone system described in the text.

massive expansion contrasts with the less marked (Zone g) expansion on the continent, where it is accompanied by a rise in *Picea* pollen frequencies. We may suggest that the absence of *Picea* from the Ipswichian, perhaps a result of the absence of a land-bridge to the continent in the interglacial, allowed the unhindered expansion of *Carpinus*, while on the continent the spread of *Picea* favoured the podsolization of soils and limited conditions suitable for *Carpinus*. Likewise, the absence or rarity of heathland in Zone IV of the Ipswichian, compared with its presence in Zone IV of the previous temperate stages, might partly be related to a much reduced tendency to soil deterioration. In contrast, on the continent acidification of the soils towards the end of this interglacial does seem to have lead to the development of heathland.

The restriction of *Carpinus* to Zone III in the four latest stages (but not in the Pastonian) may suggest this genus has undergone a reduction in biotypic

ance in the older stages. We may perhaps conclude that the successive glaciations impoverished the biotypes of *Picea* in such a way that refugia in western Europe were not available in the last two glaciations, though they were in earlier cold stages.

Abies is a characteristic tree of Zone III in the Cromerian and Hoxnian, but not in the other temperate stages. On the continent in north-west Europe it is a late immigrant, occurring in Zone III in the Holsteinian (Hoxnian) and Eemian (Ipswichian). The sporadic appearance of this genus in our interglacials is probably related to its rather slow spread from continental refuges during the temperate stages. Thus in the Eemian it failed to reach Denmark and the present western seaboard.

Tsuga is a characteristic tree only of the Ludhamian and Antian temperate stages, though it also occurs in very low pollen frequencies in Zone III of the Pastonian. In later temperate stages it is absent. This behaviour is most easily explicable by considering

Tsuga as a late immigrant in the Pastonian, having suffered severe restriction in western Europe during the previous (Baventian) cold stage, then extinction in western Europe during the succeeding (Beestonian) cold stage. The genus was thus an early loss in the west European forest flora, though in southern Europe it may have survived into later temperate stages.

These remarks on the history of particular genera show how it may be possible in future to decipher in more detail the changing status of particular genera, and how each responded to environmental change. It would be of interest to relate the behaviour of these genera with their known taxonomic diversity. The Arcto-Tertiary flora will have contained genera in various states of evolution and biotypic variety, and it might be expected that extinction by environmental change in western Europe would affect most of those genera with minimum variation. Unfortunately the state of taxonomy of the major forest trees does not permit any correlation at present. In summary, figure 2 underlines the fact that those genera (*Quercus*, *Ulmus* and *Corylus*) which are most successful are those with a widespread distribution in western Europe, while others have suffered restriction in the course of time, perhaps caused by loss of biotypes (*Carpinus*, *Picea*, *Tsuga*), and yet others (*Tilia*, *Abies*) show an inconsistent behaviour more probably related to a combination of environmental effects and change in biotype content.

TABLE 2. *Some fossil occurrence of species in different phytogeographical elements of Matthews (1955)*

Oceanic southern	*Damasonium alisma*	Weichselian; periglacial
	Ranunculus parviflorus	Ipswichian; temperate, Zone I II
Oceanic west European	*Daboecia cantabrica*	Wolstonian; periglacial
	Erica mackaiana	Hoxnian (Gortian); temperate, Zone H III
Continental southern	*Buxus sempervirens*	Hoxnian; temperate, Zone H III
	Helianthemum canum	Weichselian; periglacial
Continental	*Carpinus betulus*	Ipswichian; temperate, Zone I III
	Ranunculus lingua	Weichselian; periglacial
	Stratiotes aloides	Beestonian; periglacial
Continental northern	*Cicuta virosa*	Cromerian; temperate, Zone C II
	Potamogeton praelongus	Weichselian; periglacial
Oceanic northern	*Armeria maritima*	Weichselian; periglacial
	Naias flexilis	Flandrian; temperate, Zone VI Weichselian; periglacial
North American	*Eriocaulon septangulare*	Flandrian; temperate, Zone VII a Wolstonian; periglacial

HISTORY OF PHYTOGEOGRAPHICAL ELEMENTS

The British flora has been divided into a number of phytogeographical elements from the point of view of revealing the relations of the British flora to the European flora as a whole. Such geographical elements within the British flora were considered by Edward Forbes (1846) to relate to the origin of the flora in the sense that certain elements were of preglacial origin (Lusitanian, atlantic, southern continental), the arctic-alpine element appeared during the glacial period and the widespread 'Germanic' element was post-glacial in origin. Though each element is heterogeneous in that each species within it is likely to have had a different history, Forbes's deductions regarding the glacial and Lusitanian elements have support from fossil evidence. The earliest full-glacial floras (Baventian) are like those of the last glaciation and it is clear that in each of five cold stages a similar full-glacial flora was present. Presumably in each of the temperate stages this was dispersed to refugia as it is now. There is also fossil evidence for considering the Lusitanian element to contain species relict from Lower Pleistocene times in oceanic western Europe, though much more work needs to be done on the phytogeography of the Late Tertiary and Lower Pleistocene. Pliocene and Lower Pleistocene floras suggest considerable oceanicity in western Europe in those times, and it is probable that Lusitanian species were more widespread then.

It is more useful to discuss, though, the fossil history of particular species rather than of phytogeographical elements in the flora. There is a substantial record of species from nearly all the geographical categories named by Matthews (1955). Even a short list, such as that in table 2, shows that species in each category can have very different environments of fossil occurrence. We cannot therefore generalize from the history of particular species to the history of phytogeographical elements. Some species occur in both periglacial and temperate environments, others in periglacial environments only or temperate environments only. The reconstruction of the past history by the assembling of fossil records is the most important key to present distribution. A most striking example has been the finds of species (e.g. *Erica mackaiana*, *Daboecia cantabrica*) of the so-called 'Lusitanian' element in the Hoxnian (Gortian) interglacial of Ireland (Watts, 1959). Evidently these species have a long history in Ireland and further evidence may well demonstrate that some of these species were able to survive the periglacial environment.

CONCLUSIONS

We have considered in general terms the changing flora of Britain during the Pleistocene; such a general treatment is partly a result of the lack of knowledge of regional diversity of floras of the British Isles. While much is known of regional diversity, in terms of altitude, latitude and longitude and to some extent surface rock type, in the Flandrian and Late-Weichselian, hardly anything of this sort is known for early periods. Only in the Hoxnian interglacial (Gortian of Ireland) can it be said that regional variation is known to some extent, and that only in terms of longitudinal variation resulting from increased oceanicity in the west. Much more study is required of sites in Britain and Ireland, to detect regional trends and their relation to the continent. The relation of the Irish Pleistocene flora in other interglacials than the Hoxnian will be of particular interest, in view of the possibility that the Irish flora has occupied a very isolated position throughout the Pleistocene and perhaps Pliocene.

The regional variation of full-glacial floras, of obvious importance to problems of perglacial survival, is again unknown. One of the difficulties here is the necessity for comparison of floras known to be synchronous. To take full advantage of sites it is clearly necessary to carry out combined studies of macroscopic plant remains with pollen studies, to obtain evidence of regional and local vegetation. We may expect improved interpretation of fossil assemblages from the currently developing work and interest in recent pollen rain and sedimentation of macroscopic remains, and their relation to present plant communities. With this information available we may be able to say more of the process of build-up of communities in the temperate stages, of retrogressive succession in the latter parts of these stages, and of the selection and spread of the periglacial floras.

Since the publication of Professor Godwin's book on *The History of the British Flora* in 1956, fossil plant records have accumulated more and more rapidly, with the increased number of researchers in the field, both in respect of Flandrian times and the older Pleistocene stages. So much so that to make full use of the data for reconstruction of the history of the flora, it will be necessary to have some sort of data retrieval system whereby records for locality, age, and local environment for each species can be grouped, of the kind already started by Professor Godwin. The accumulation of records in the British Isles, where the variety of regional climates and rock types within a relatively small area, isolated from the continent, and with a satisfactory stratigraphical record in the Pleistocene, will be very great value in providing the data for interpretation of the effects of environmental changes on the evolution of floras, a subject which becomes increasingly more important as man's pressure on natural vegetation systems increases.

SUMMARY

The major Pleistocene environments, glacial, periglacial and non-glacial, are discussed with reference to their characteristic flora and vegetation. The extent of the Pleistocene fossil record is demonstrated. Preglacial, periglacial and temperate floras are described, and a general zonation applicable to temperate stages is described and its meaning discussed. Analogous zones in the successive temperate stages are compared with especial reference to the history of forest tree genera in East Anglia. The history of phytogeographical elements in the British flora is discussed.

I am pleased to acknowledge helpful discussions with Dr Charles Turner during the preparation of this essay.

REFERENCES

Andersen, S. Th. (1966). Interglacial vegetational succession and lake development in Denmark. *Palaeobotanist* **15**, 117–27.

Forbes, E. (1846). Of the connection between the distribution of the existing fauna and flora of the British Isles, and the geological changes which have affected their area, especially during the epoch of the Northern Drift. *Mem. Geol. Survey Gt. Britain* **1**, 336–432.

Godwin, H. (1956). *The History of the British Flora.* Cambridge University Press.

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