Holocene isochrone maps and patterns of tree-spreading in the British Isles

H. J. B. BIRKS *Botanical Institute, University of Bergen, Allégaten 41, N-5007 Bergen, Norway*

Abstract. Isochrone maps for *Betula* L., *Corylus avellana* L., *Ulmus* L., *Quercus* L., *Pinus sylvestris* L., *Alnus glutinosa* (L.) Gaertn., *Tilia* L., *Fraxinus excelsior* L. and *Fagus sylvatica* L. in the Holocene of the British Isles, constructed from 135 radiocarbon-dated pollen diagrams, provide a basis for studying the patterns of tree spread. They highlight the strongly individualistic behaviour of each taxon in its arrival areas, directions, timings, rates of spread, and attainment of broad-scale range limits. The biological processes that enable forest trees to spread at rates of 500 m yr^{-1} or more have implications for palae-oecological and palaeoclimatic reconstructions. Numerical results from models of Holocene biological invasions provide a background against which rates of recent invasion can be assessed.

Key words. Range dynamics, vegetational history, tree invasions, Holocene, dispersal, pollen analysis, British Isles.

INTRODUCTION

Pollen-analytical data can be displayed and interpreted in many ways depending upon the aims and interests of the study. Emphasis is commonly placed on temporal variations in pollen assemblages and the data are most frequently displayed as stratigraphical diagrams. In the Holocene (=Flandrian, post-glacial) and Devensian late-glacial, radiocarbon dating can provide, in theory at least, a chronology with a temporal precision fine enough so that correlations and comparisons between sites are reliable and independent of pollen-stratigraphical chronologies. This allows geographical patterns to be explored within palynological data.

Modern plant-distribution patterns are most conveniently displayed as distribution or range-limit maps. Interpretation of modern distributions, however, often requires a historical perspective (e.g. Pigott & Huntley, 1980). Past distributions, changing range-limits, and rates and directions of spread in time and space can be reconstructed by mapping independently dated contemporaneous plant-macrofossil data. However, because of the scarcity of well-dated macrofossil records, reconstructions of changing distribution patterns over large geographical areas such as countries or subcontinents, and long time periods (up to 10,000 years) must rely heavily on pollen-stratigraphical data.

Of the various approaches to mapping pollen-analytical data (Huntley & Birks, 1983; Birks, 1985a), most common are isopollen and isochrone mapping. Szafer (1935) first constructed isopollen or pollen-contour maps in which pollen frequencies within a specific geographical area at selected time intervals were mapped and contours or 'iso-

polls' drawn to connect sites with similar pollen percentages (see also Firbas, 1949). Since then, radiocarbon correlations have been used to construct isopollen maps at selected time intervals in, for example, Finland (Birks & Saarnisto, 1975), the British Isles (Birks, Deacon & Peglar, 1975), Poland (Ralska-Jasiewiczowa, 1983), Europe other than the Soviet Union (Huntley & Birks, 1983), and eastern North America (e.g. Bernabo & Webb, 1977; Webb, Richard & Mott, 1983a; Jacobson, Webb & Grimm, 1987). A disadvantage of isopollen maps is that many maps are required to display temporal as well as spatial variations, because a single isopollen map can only represent data for one taxon at one point in time.

Isochrone maps display both spatial and temporal patterns in pollen data. The contours, or isochrones, join sites at which similar pollen-stratigraphical events occurred at the same time. For example, ages of the first rise in values of a particular pollen type within an area of interest can be mapped and contoured to display spatial and temporal variations of this event on a single map. Such maps have been used to detect directions and rates of spread of trees in Europe, particularly Fennoscandia (e.g. Aario, 1965; Aartolahti, 1966, 1967; Moe, 1970; Persson, 1975; Tolonen & Ruuhijärvi, 1976; Høeg, 1978; Tolonen, 1983) and Russia (Serebryanny, 1971, 1973) and, more recently, in North America (e.g. Moran, 1973; Davis, 1976, 1981, 1983, 1987; Jacobson, 1979; Webb *et al.*, 1983a; Webb, Cushing & Wright, 1983b; Davis & Jacobson, 1985; Gaudreau & Webb, 1985; Björck, 1985; Davis *et al.*, 1986).

The criteria for constructing isochrone maps must be carefully considered, so that, for example, the first expansion of a taxon in pollen diagrams is consistently defined (Bennett, 1985, 1986a, 1988a; Davis & Jacobson, 1985.

Such maps, if critically and consistently constructed for an area, can provide a spatial and temporal synthesis of important pollen-stratigraphical events. For example, when first expansions are mapped, a geographical summary is obtained of the spatial dynamics of changing range-limits through time. Such patterns reflect plant spread, an important but poorly understood process in Quaternary vegetational history and dynamic plant geography.

This paper presents isochrone maps of the first Holocene rise in pollen values of the major tree taxa within the British Isles in 135 radiocarbon-dated pollen diagrams. The first rise provides minimal age estimates for the first unambiguous arrival of these taxa. The maps illustrate the individualistic behaviour of the major trees in the Holocene by revealing their different colonization patterns and rates of range expansion. The palaeoecological and biogeographical implications of these patterns suggest possible underlying causal processes and mechanisms of tree spread at the relevant spatial and temporal scales.

Preliminary versions of these maps based on sites 1–42 (Fig. 1 and Appendix 1) were presented in July 1981 at the Løvenholm symposium on the glacial refugia and migration routes of central and north European trees (Andersen, 1981). Versions based on sites 1–88 were discussed at the Quaternary Research Association symposium on 'Pollen Analysis and Quaternary Palaeoecology: Recent Developments' in January 1982 (Birks, 1981a). The maps presented here are based on a presumed unbiased sample of 135 sites, namely all radiocarbon-dated sites that I know of (as of 1 January 1988) with pollen-analytical data published in sufficient detail to permit mapping. The maps are a contribution to the 'international cooperation' that Andersen (1981) suggests is required to expand our knowledge and understanding of directions, routes, and rates of spread of European trees in the Holocene.

Following Bennett (1985), 'spread' is used to describe the process of establishment and directional movement of a taxon into new geographical areas, often over many generations. The more widely used term 'migration' (e.g. Davis, 1976; Huntley & Birks, 1983) should be restricted to 'those movements which have a specific goal, and are usually accomplished in entirety by each individual' (Bennett, 1985) and is thus inappropriate to describe plant spread. Mason (1954) discusses the concept of migration and distinguishes three types of movement – seasonal migration by animals, sporadic migration by animals (e.g. lemmings), and secular migration by animals or plants in evolutionary time with associated genetic differentiation. Plant spread and range expansion over the time-scales of Quaternary interglacials do not correspond to any of Mason's categories, although, as Pielou (1979) notes, rapid secular migration can overlap with slow spread. The terms spread (Bennett, 1985), range-expansion (Schaeffer, 1977) and dispersal (Armstrong, 1977) are preferable and are used more or less synonymously here. Platnick's (1976) term dispersion to describe movements within the historical geographical range of a taxon is avoided, as dispersion commonly refers to the spatial *pattern* resulting from dispersal processes (Armstrong, 1977; Pielou, 1979) rather than the *process* of spread.

PREPARATION AND INTERPRETATION OF ISOCHRONE MAPS

Of the 135 pollen sites used to prepare the isochrone maps (Fig. 1, Appendix 1), not all are used for each map as some sites do not cover the entire Holocene. All sites used have, satisfactory radiocarbon chronologies for the time intervals considered. They provide an average density of about one site per 2500 km² and a good geographical coverage except for southern and central England, parts of Ireland, and southern Scotland.

For each site I estimated by linear interpolation or extrapolation from radiocarbon dates the age (to within 100 radiocarbon years) at which the observed pollen percentages or pollen-accumulation rates provide unambiguous evidence for the earliest local presence of the taxon in question. There is clearly a subjective element in deciding what values indicate the presence of particular tree taxa (Davis, 1976; Davis & Jacobson, 1985; Bennett, 1985; Ritchie & MacDonald, 1986). It is essential to define the criteria of first local presence as exactly and as consistently as possible. For trees with a high pollen representation relative to *Fagus sylvatica* (e.g. *Betula, Pinus* L., *Quercus, Ulmus, Alnus* Mill., *Corylus* L., Andersen, 1970) I use the rational-limit (*sensu* Smith & Pilcher, 1973), which is the point at which the pollen curve begins to rise to sustained high values. For trees with a relative pollen representation equal to or less than *Fagus* (e.g. *Tilia, Fraxinus* L., *Fagus* L., Andersen, 1970) I use the empirical-limit (*sensu* Smith & Pilcher, 1973), which is the point at which pollen of the taxon first becomes consistently present in consecutive samples. One disadvantage of using the empirical-limit is that its position depends on the number of pollen grains counted (Tallantire, 1972). The rational-limit is not so count-dependent. At most sites (Fig. 1), the pollen sum is generally between 250 and 500 grains per sample. Thus the potential source of error in using empirical-limits is reduced by the use of more or less comparable pollen sums. At some sites, however, pollen sums exceed 1000 grains (e.g. Bennett, 1983a), thereby increasing the probability of finding rare pollen types and hence of extending empirical-limits backwards in time.

Despite these limitations, the use of rational and empirical limits is preferred to the use of 'critical pollen percentages' (e.g. Davis & Jacobson, 1985; Webb *et al.*, 1983a, b) for evaluating presence or absence of trees. Pollen percentages, however defined, are influenced by other taxa contributing to the pollen sum *and* by their absolute abundances and relative pollen representation (Andersen, 1980). As vegetation composition and tree abundance have changed with time, critical percentages defined on the basis of modern pollen spectra may have limited quantitative robustness in time or space. Empirical and rational limits are qualitative characteristics of the *shape* of a pollen curve and are thus largely invariant to the constraints imposed by pollen percentages.

Godwin (1975; see also Tallantire, 1972; Pennington, 1981; Birks, 1986) emphasizes the important ecological distinction between tree arrival (advent), establishment, and expansion, and he discusses the need to distinguish
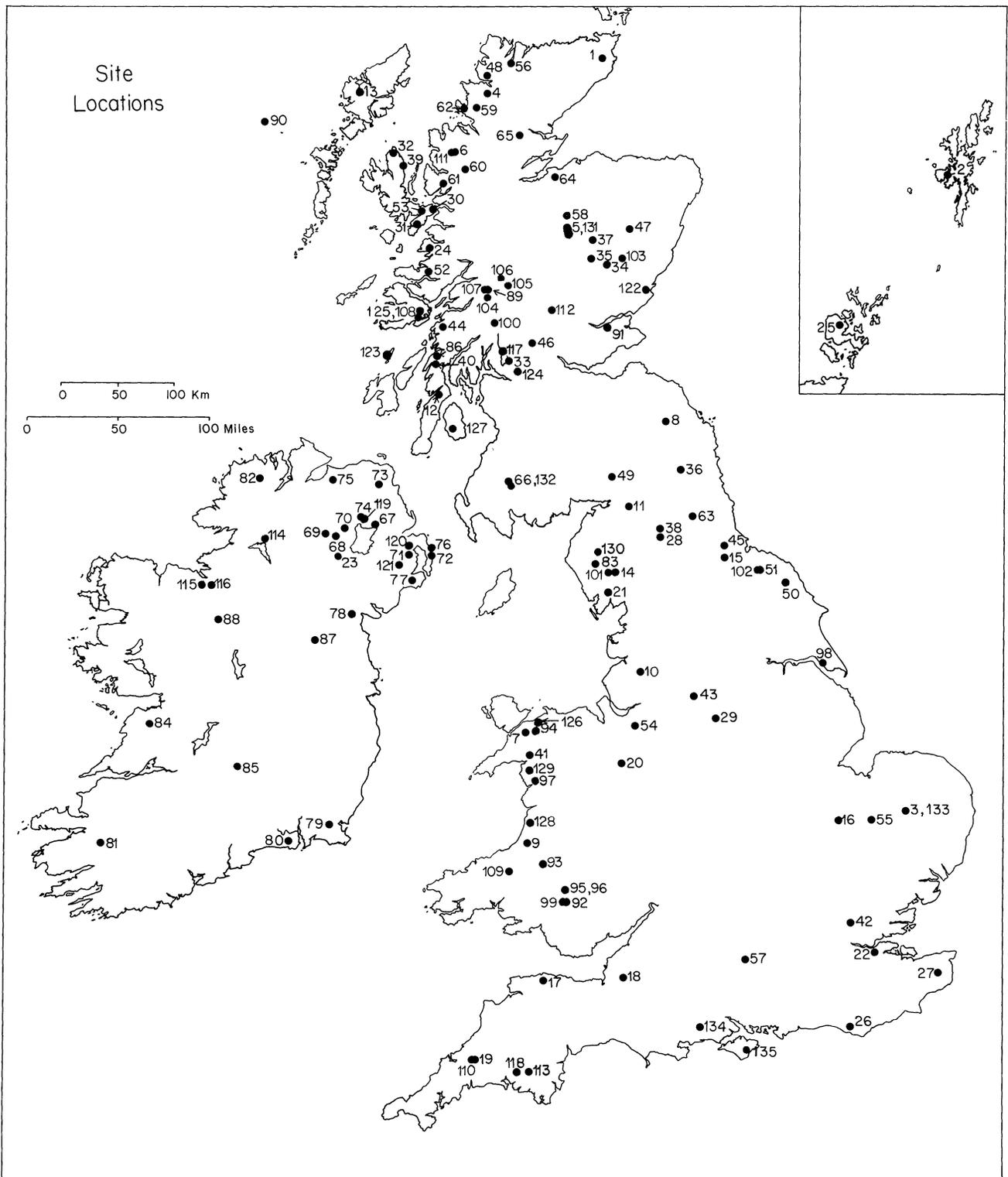
FIG. 1. Outline map of the British Isles showing the location of sites used in the construction of Figs. 2–10. The sites are numbered 1–135, and details of the sites are given in Appendix 1.

these successive phases within palynological data. Bennett (1985, 1986a, 1988a, c) discusses problems of determining from palynological data the first arrivals of trees, particularly those with low pollen representation such as *Tilia* or *Fagus*. He suggests that low sporadic pollen frequencies commonly found prior to the first continuous values (empirical-limit) may reflect local presence of small populations rather than, as is commonly supposed, distant transport of pollen from extra-regional populations. With a simple model, Bennett (1985) shows that small populations (density <1 tree ha^{-1}) within the pollen-source area of a site can easily go unrecorded in a sample pollen count. He suggests (1986a, 1988a, c)) that trees may have been locally present in low densities before the time of the empirical limit. Thus the 'migration rates' proposed by Davis (1981) and Huntley & Birks (1983) may not really reflect rates of spread but are estimates of rates of population increase to a critical local density, above which the taxon's pollen is consistently detectable in sample pollen-counts. Bennett (1983b, 1985, 1986a, 1988a, c) proposes that, as the first exponential or logistic rise of almost all pollen curves coincides with the empirical limit, the earlier phases of arrrival and population establishment (see Watts, 1973; Birks, 1986: Fig. 1.5) are undetected (and largely undetectable) palynologically (see also Green, 1987). Isochrone and isopollen maps may thus primarily reflect patterns of tree expansion rather than tree arrival. Bennett (1988a) argues that there has been 'a failure to separate rates of change of distribution from rates of change of abundance' and that Godwin's (1975) distinction between arrival, establishment and expansion has not been made in recent studies. I thus use the term 'spread' to refer to the geographical movement of tree populations of sufficient size into an area to be recorded palynologically as either empirical or rational limits.

If one assumes that the time of expansion to such a population size is related to the time of arrival of the first individuals, and that this time lag is relatively constant over the geographical area being considered, then the rate of spread of first expansion-times can be taken as an indirect reflection of the rate of spread of first arrivals. However, this assumption is not necessarily valid, as small populations may have occurred for varying times prior to expansion (e.g. *Alnus*; Bush & Hall, 1987). Isochrone maps based on pollen data can thus only provide *minimal* estimates for the timing of tree arrival following deglaciation.

With these problems in mind, I assume, following Ritchie & MacDonald (1986), that the age of the first rise in pollen values provides a minimal date for the earliest Holocene presence of the tree at a particular site. The maps presented here (Figs. 2–10) are interpreted to show the spatial and temporal patterns of these minimal estimates for the first unambiguous palynological evidence for local tree presence near the sites in question. Clearly, in light of Bennett's hypothesis, trees may have been present locally as small populations, undetected palynologically, considerably earlier than is shown on the maps. As first arrivals are, in practice, undetectable palynologically (Bennett, 1985, 1988c; Green, 1987), such minimal estimates are all that are attainable from existing pollen data.

In order to maintain consistency in deciding the age for first local presence, I have only used radiocarbon ages associated with detailed pollen diagrams. Ages reported in *Radiocarbon*, without diagrams, have not been used.

After the ages for particular pollen-stratigraphical events at individual sites were determined, the dates were mapped and contours drawn by hand, to show the positions of the taxon's presence at 250–1000 radiocarbon-year intervals. Isochrones can easily give the impression of increasing the number of data points (Davis, 1976; cf. Watts, 1979). The contours presented on Figs. 2–10 attempt to reflect the age patterns as accurately and as parsimoniously as possible, even if the resulting contour-patterns are complex and difficult to comprehend (e.g. Figs. 2, 6 and 7). Accurate contouring is, however, essential to a true representation of the data. Simplification is misleading (Ritchie, 1987); for example on the *Quercus* map for eastern North America (Davis, 1981: Fig. 10.8) eighteen of the thirty-seven plotted points do not correspond to the isochrone contours.

Contours are drawn at equal time-intervals of 250, 500 or 1000 years. Where data points are sparse, contours are broken (e.g. Figs. 2, 5 and 6). Approximate rates of spread (m yr^{-1}) are calculated from the average distances between contours of known age, and directions and routes of spread are inferred from the contour orientations.

A potentially important source of error in preparing these maps arises from the errors inherent in radiocarbon-dating of different organic sediments (e.g. Olsson, 1986). No rigorous attempt was made to assess the reliability of a given radiocarbon date because, as Tipping (1987) discusses, the information required to gauge the reliability is rarely if ever available. The temporal resolution of the maps (250–1000 years) should be achieved, in most instances, by radiocarbon dates from Holocene sediments.

An important feature of the maps presented here is their scale and the resultant spatial resolution they display. The maps cover the whole of the British Isles and display patterns discernible at that scale. Thus they cannot portray fine-scale patterns within topographically or geologically diverse areas where pollen data are available from many sites within a small area, such as the Lake District (Pennington, 1970) or northern Pennines (Turner *et al.*, 1973; Turner & Hodgson, 1979, 1981, 1983). Tallantire (1972) provides a critical discussion of the limitations of isochrone maps and of the problems in their construction.

There is no doubt that the isochrone maps presented here will be modified in detail as additional data are obtained. However, they illustrate the general patterns and rates of tree spread discernible from existing pollen-stratigraphical data. They highlight areas where data are lacking (Fig. 1) and where future pollen-stratigraphical studies would yield valuable new data. For example, dated diagrams from the Isle of Wight (Scaife, 1982), and Sussex, Hampshire and Dorset (Waton, 1982, 1986), when published in full, will provide important additional data for southern England.

Macrofossil evidence for tree presence but lacking pollen-analytical data has not been used in map construction (cf. Bennett, 1984).
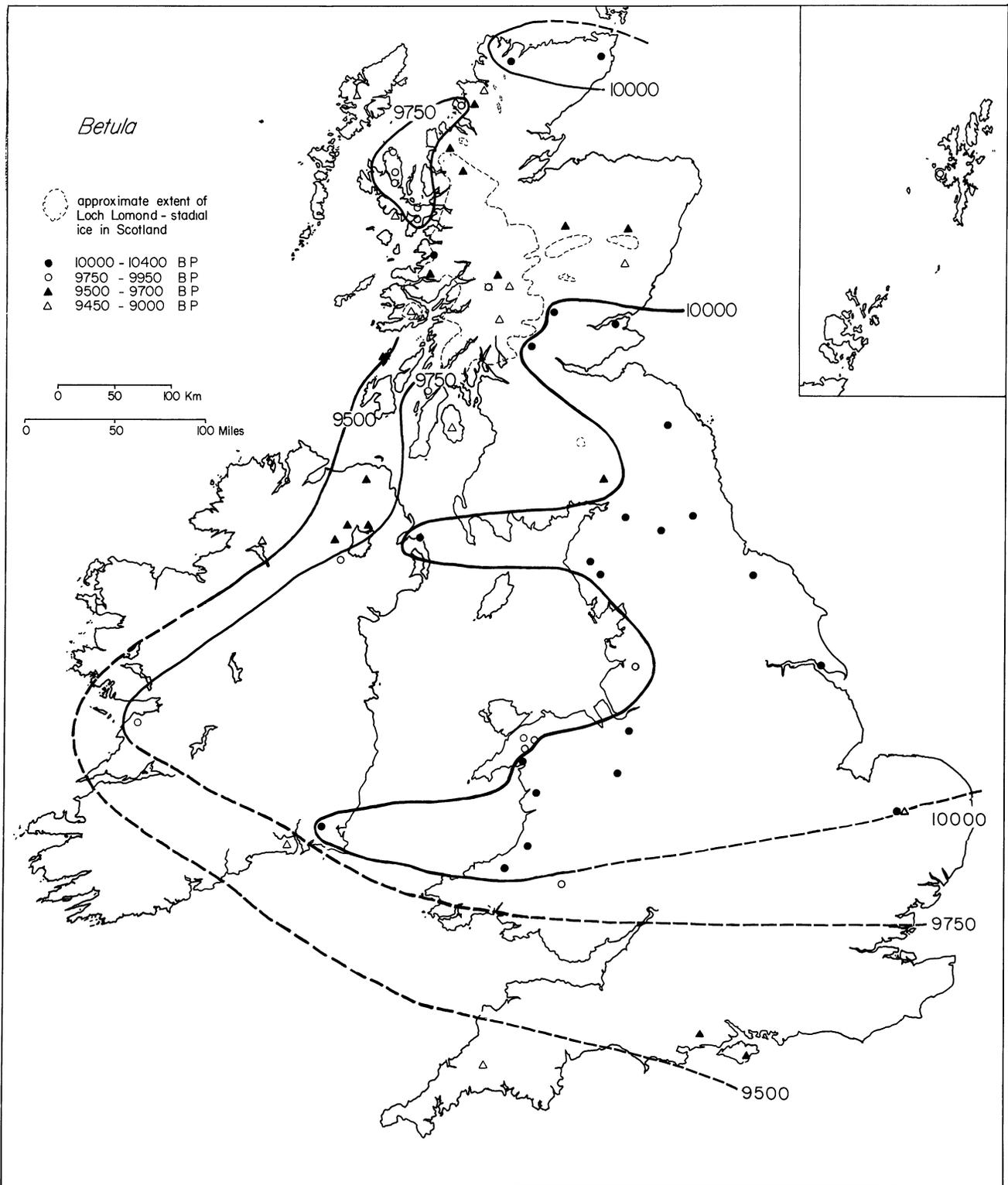
FIG. 2. Isochrone map of the rational limit of *Betula* pollen in the British Isles. The isochrones are based on data indicated by dots and triangles and are shown as radiocarbon years BP. The approximate extent of Loch Lomond Stadial ice in Scotland is also shown (mainly based on Sissons (1983) with minor additions from various other sources).

ISOCHRONE MAPS

Betula (tree birch) (Fig. 2)

Betula pubescens Ehrh. and *B. pendula* Roth. were locally present in the British Isles from about 13,500 BP (e.g. Pennington, 1981). Tree birch was locally abundant in the south and east, rare farther north and west, except in sheltered localities, and rare or even absent from much of Ireland. During the Loch Lomond Stadial (*c.* 11,000–10,200 BP) tree birch declined widely and possibly became extinct in much of the British Isles.

Fig. 2 shows the spatial pattern of *Betula*'s expansion following the climatic amelioration at the end of the Devensian late-glacial. This map with its isochrones for 250-year intervals should be viewed with caution. The available radiocarbon dates often have a large counting error, typically cover a long time span because of slow sedimentation rates in the early Holocene (Lowe, 1981), and are often subject to hard-water errors (Sutherland, 1980). With these caveats, it appears that before 10,000 BP *Betula* was well established in much of central and northern England, southern Scotland, and parts of Wales, and just extended into eastern Ireland. This pattern suggests spread from the east, probably from the then dry North Sea basin. By 9750 BP birch spread (*c.* 250 m yr^{-1}) and expanded in north Wales, Skye and the adjacent mainland, and central Ireland, and by 9500 BP it expanded in northern Ireland and parts of the Scottish Highlands. Expansion was delayed (to 9500–9000 BP) in areas of the Scottish Highlands that were glaciated during the Loch Lomond Stadial and on Bodmin Moor, presumably because of the time required for soil maturation following glaciation or periglaciation and because of soil instability and frost drought (Caseldine & Maguire, 1986).

In East Anglia, rapid rates of local population expansion (Bennett, 1983a, b) are not necessarily in the regions of first presumed arrival. This suggests that there may have been environmental constraints on local expansion but not on the regional spread of *Betula* in the early Holocene. On the sandy soils around Hockham Mere (Bennett, 1983a) its expansion was delayed compared to sites on more fertile soils nearby (Bennett, 1986b) and farther north and west. Factors such as temperature and precipitation may have had to attain higher levels than elsewhere before a critical local ecological threshold was passed (Bennett, 1983a, 1986b; Caseldine & Maguire, 1986).

Corylus avellana (hazel) (Fig. 3)

The *Corylus/Myrica* pollen type is almost entirely, if not exclusively, *Corylus avellana* in East Anglia (Bennett, 1983a), northern England, and western Scotland (Birks, 1973 and unpublished data; S. M. Peglar unpublished data; cf. Edwards, 1981). It is consistently present and first expands, often rapidly, in parts of coastal Wales, northwest England, western Scotland, and southern and northeastern Ireland by 9500 BP (shaded area on Fig. 3). However, it was not present in any abundance in the Devensian late-glacial in these areas (cf. Rymer, 1977). Occasional low (1–5%) values occur in several British late-glacial sites.

These cannot be attributed to definite local presence because of possibilities of distant transport, secondary redeposition, or contamination (Huntley & Birks, 1983).

Constructing reliable isochrones for the subsequent spread of *Corylus* is difficult because of limitations of the available radiocarbon dates. It appears to have spread (*c.* 500 m yr^{-1}) by 9000 BP into much of Ireland, Wales, England and Scotland (solid dots on Fig. 3). By 8500 BP it spread into central and eastern Scotland (open circles on Fig. 3), although there it never attained values as high as it did at this time farther south and west (e.g. Birks & Mathewes, 1978). This delay may be caused by the main Scottish mountains hindering the eastward spread of this frost-sensitive lowland shrub. The generally acid infertile soils and the relatively cool continental climate of the eastern Highlands may also have delayed its expansion and contributed to its limited success in this area.

An additional problem in constructing reliable isochrones arises from the difficulty of identifying and dating the empirical limit of *Corylus* pollen because its pollen curve often becomes continuous, rises initially, and then rises again to high values all within a very short stratigraphic interval. Fig. 3 is based on the initial rise (first rational limit). The conclusion of Boyd & Dickson (1986) about the late arrival of *Corylus* on the Isle of Arran, south-west Scotland is based on 'the *Corylus* rise' without stating which one. Judging from Robinson's (1983) diagram (see also Robinson & Dickson, 1988), the rise used appears to refer to the second, major one, although this diagram is complicated by the assignment of up to 35% total pollen as 'triporate', part of which may be derived from *Corylus*. Following Godwin's (1975) distinction between arrival, establishment and expansion, this second rise reflects the major expansion of *Corylus*, not its arrival and establishment, which I have taken to occur 30 cm lower than that of Boyd & Dickson (1986).

On the likely assumption that *Corylus* was absent from the British Isles during the Loch Lomond Stadial, the patterns (Fig. 3) suggest that hazel first became established in the British Isles around the Irish Sea basin and along the western seaboard of Scotland and subsequently spread inland eastwards and westwards. Possible dispersal agents for hazel nuts include animals (birds, rodents, etc.), accidental or deliberate spread by humans (Danielsen, 1970; Iversen, 1973) and water (Salmi, 1963). The idea that humans influenced the Holocene spread and/or increase of hazel (e.g. Danielsen, 1970; Smith, 1970; Kaland & Krzywinski, 1978; Boyd & Dickson, 1986) has little ecological evidence in its support (Rackham, 1980; Edwards, 1982; Edwards & Ralston, 1984). Smith's (1970) assertions that 'there is no doubt that the European *Corylus avellana* is fire resistant' and formed a 'fire climax' are challenged by Rackham (1980) because they refer to *C. cornuta* Marsh. and *C. americana* Walt. in the brush-prairie of Wisconsin (Chavannes, 1941) and not to *C. avellana* in Europe. Hazel nuts were important in the diet of Mesolithic people (e.g. Iversen, 1973; Godwin, 1975; Mellars, 1979), but this does not, of course, prove that the presence or abundance of hazel resulted from human activities, only that humans took advantage of the 'endless nut groves, a Garden of

FIG. 3. Isochrone map of the rational limit of *Corylus avellana* pollen in the British Isles. The isochrones are based on data from the sites indicated by the various types of dots and are shown as radiocarbon years BP. Sites where there is no pollen-analytical evidence for local presence are shown as open squares. The approximate area where *Corylus* was present before 9500 BP is shaded.
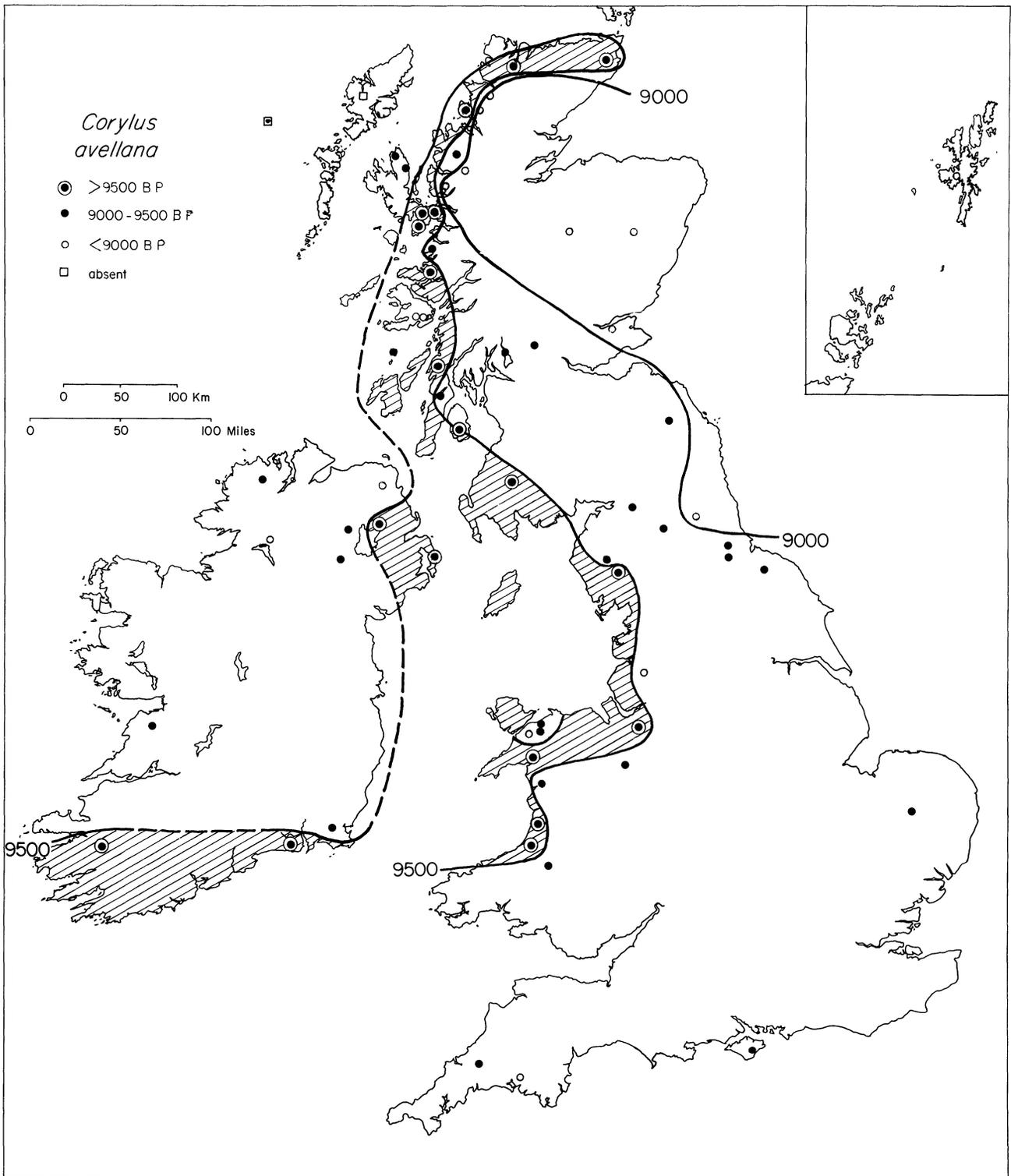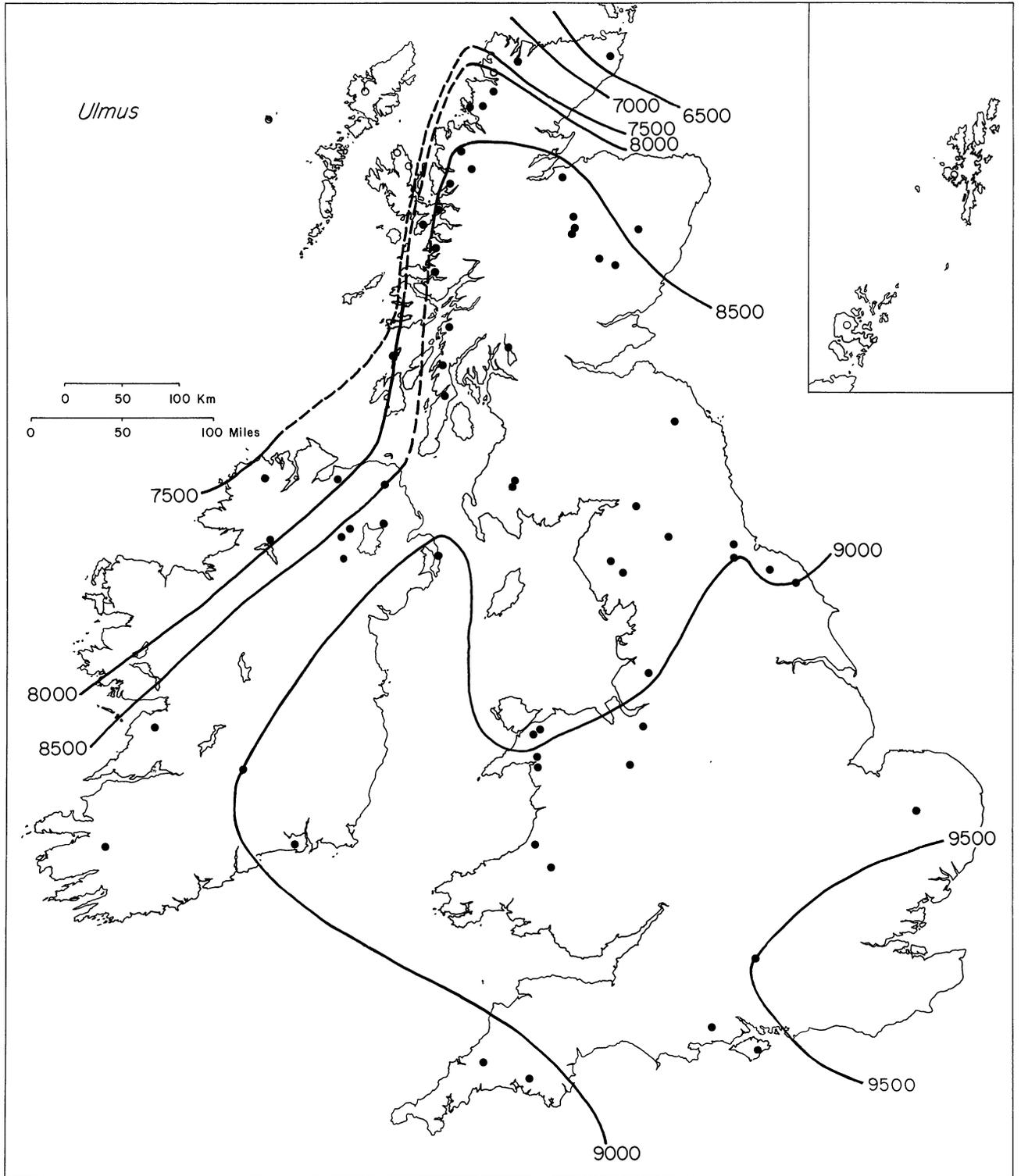
FIG. 4. Isochrone map of the rational limit of *Ulmus* pollen in the British Isles. The isochrones are based on data from the sites indicated by dots and are shown as radiocarbon years BP. Sites where there is no pollen-analytical evidence for local presence are shown as open circles.

Eden where one could reap without having sown' (Iversen, 1973).

It seems more likely that *Corylus* nuts were dispersed by water currents from the west European coastal fringe where hazel was present prior to 9500 BP (see Huntley & Birks, 1983). Guppy (in Praeger, 1913) and Salmi (1963) demonstrated that hazel nuts can float for at least 30 days in fresh- or sea-water and retain viability, showing the feasibility of water currents as a long-distance dispersal agent. Iversen (1973) and Linnman (1981) discuss the favourable ecological setting for the early colonization of hazel that may have prevailed in the early Holocene, such as fertile soils with mull humus, mild climate, absence of competition from other trees, and rapid land-uplift.

For the British Isles the simplest explanation is that hazel arrived in the Irish Sea area by water transport (Fig. 3), that it rapidly expanded on fertile soils in coastal areas, and then spread inland and became locally abundant, except in eastern Scotland, forming a hazel-dominated landscape that persisted for over 1000 years in the absence of competition from taller, long-lived, dense-shade-producing trees (e.g. *Tilia*: Iversen, 1973; Bennett, 1983a). Interestingly, hazel was absent from the Rhine Basin at 10,000 BP (Huntley & Birks, 1983), possibly explaining why water transport by north European rivers was ineffective in dispersing hazel nuts to eastern Britain.

Ulmus (elm) (Fig. 4)

Pore-number frequencies of *Ulmus* pollen (Stockmarr, 1970) in early-Holocene sediments in northern England and western Scotland (H. J. B. Birks and S. M. Peglar, unpublished data) suggest that *U. glabra* Huds. was the major, probably sole, species of elm in the north and west. In East Anglia, pore-number frequencies suggest that *U. glabra* and *U. carpinifolia* Gleditsch were present in the early Holocene, although *U. glabra* probably predominated (Bennett, 1983a, b).

Ulmus was present in southern England by 9500 BP and it spread rapidly (500–600 m yr⁻¹) through central England and much of Wales and reached eastern Ireland by 9000 BP. It continued to spread rapidly through northern England, much of Scotland, and southern and eastern Ireland until 8500 BP. It did not reach north-west Ireland until 7700 BP. After 8500 BP its spread and associated local expansion in northern Scotland slowed dramatically (*c.* 100 m yr⁻¹), perhaps because of predominantly acid soils, or, more likely, unfavourable climate, with high winds and exposure. It reached northernmost Scotland by 6200 BP, although it was never an important component in the scrub and small woodland areas of Caithness (Peglar, 1979). The elm populations of the British Isles, as elsewhere in north-west Europe (Huntley & Birks, 1983), underwent a dramatic decrease (the 'elm decline') between 5000 and 5500 BP. This population crash, however, did not lead to any significant contraction in the range of elm within the British Isles.

Quercus (oak) (Fig. 5)

There is unfortunately no indication which oak species was initially present in the British Isles (cf. Simmons, 1965).

Oak was present in south-west England by 9500 BP and south-east Ireland by 9400 BP, following its rapid spread up the western seaboard of Europe since 10,500 BP (Huntley & Birks, 1983). Oak then spread at a rate of 350–500 m yr⁻¹ through England, Wales, central Ireland and southern Scotland until about 8000 BP. Its rate of spread then slowed considerably to about 50 m yr⁻¹, possibly because of climatic factors such as low summer temperatures. Also, the Scottish mountains acted as a barrier to its northward spread. Oak finally reached its northern limit as an important forest component in Scotland by 6000 BP. Small scattered oak populations may have occurred north of this limit in parts of Wester Ross, Sutherland and Inverness-shire, but the pollen values there are so low that it is difficult to distinguish confidently between local but rare presence and distant pollen transport from areas to the south (Birks, 1972; H. H. Birks unpublished data; Kerslake, 1982).

The estimated rates of spread of 350–500 m yr⁻¹ in the British Isles before 8000 BP and of 150–500 m yr⁻¹ on the European mainland (Huntley & Birks, 1983) are of considerable interest when compared with theoretical rates of spread of oak estimated mathematically by Skellam (1951) on the basis of a diffusion model of random dispersal of acorns. Skellam addressed the problem that Clement Reid (1899) raised about rates of spread of trees when Reid (1899: p. 25) wrote 'Though the Post-glacial period counts its thousands of years, it was not indefinitely long, and few plants that merely scatter their seed could advance more than a yard in a year, for though the seed might be thrown further, it would be several seasons before an oak for instance would be sufficiently grown to form a fresh starting point. The oak, to gain its present most northerly position in North Britain after being driven out by the cold, probably had to travel fully six hundred miles, and this without external aid would take something like a million years.' Skellam (1951) calculated that oak would have only travelled about 135 km (85 miles) within the 10,000 years of the Holocene (i.e. a rate of spread of 13.5 m yr⁻¹). The observed rates (350–500 m yr⁻¹) in the early Holocene falsify the hypothesis that the Holocene spread of oak conformed to a model of random dispersal of acorns. Birds such as jays (*Garrulus glandarius* L.), rooks (*Corvus frugilegus* L.) and wood pigeons (*Columbaria palumbus* L.) may have played a major role in its spread (e.g. Chettleburgh, 1952; Jones, 1959; Mellanby, 1968; Bossema, 1979).

Pinus sylvestris (pine) (Fig. 6)

Before 9000 BP pine was present widely but locally in southern England (Bennett, 1984). Between 9000 and 8500 BP it spread (*c.* 300–700 m yr⁻¹) to central England, the southern Lake District and the northern Pennines. It was also present in the southern North Sea basin at this time (Godwin, 1975; Devoy, 1982). In addition it was present in southern and western Ireland before 8800 BP (e.g. Craig, 1978; Watts, 1984) even though pine did not expand into Wales until 8400–8100 BP. This suggests that the Irish populations may have had an independent origin and were not necessarily derived from the early-Holocene populations of

FIG. 5. Isochrone map of the rational limit of *Quercus* pollen in the British Isles. The isochrones are based on data from the sites indicated by dots and are shown as radiocarbon years BP. Sites where there is no pollen-analytical evidence for local presence are shown as open circles.
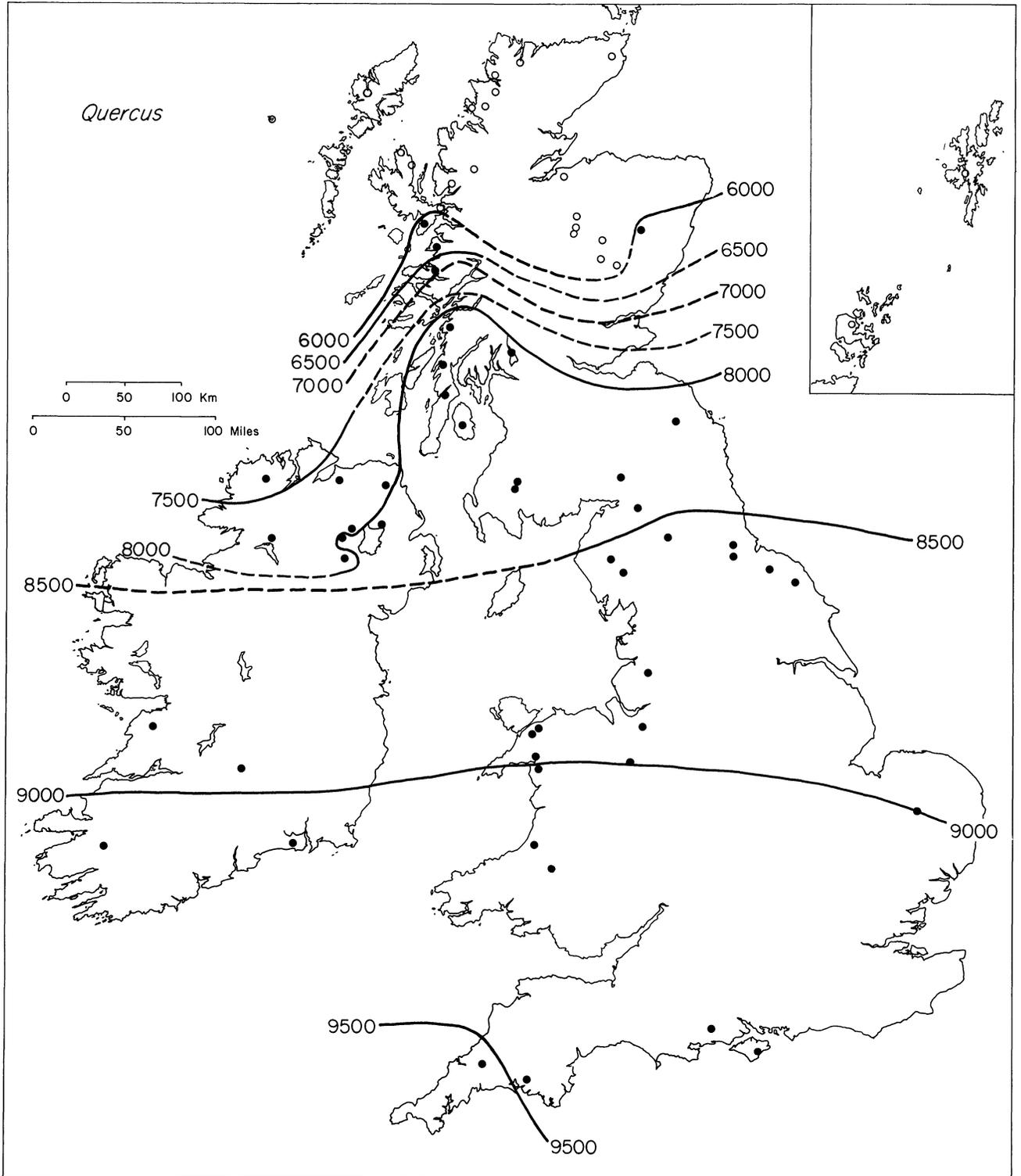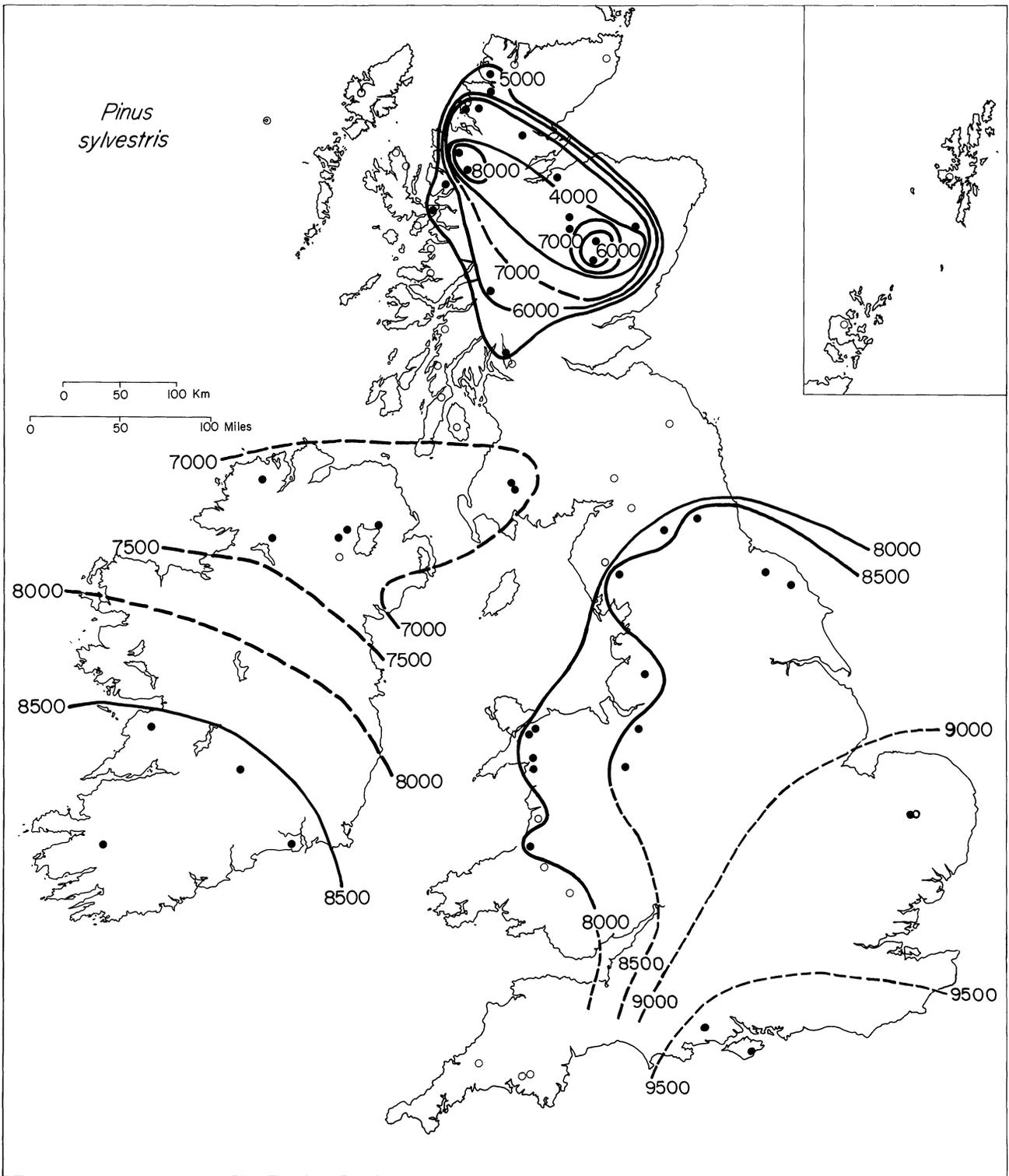
FIG. 6. Isochrone map of the rational limit of *Pinus sylvestris* pollen in the British Isles. The isochrones are based on data from the sites indicated by dots and are shown as radiocarbon years BP. Sites where there is no pollen-analytical evidence for local presence are shown as open circles.

eastern and central England. By 8000 BP the rate of spread decreased to 60–100 m yr^{-1} but pine continued to move into Wales, the Lancashire plain, and possibly central Ireland, and it was present in or near the Doggerbank area of the North Sea (Behre & Menke, 1969; Behre, Dörjes & Irion, 1984). It was absent or very rare, however, for the entire Holocene in south-west England (cf. Clarke, 1970) and much of the Cumberland lowland, lowland southern Scotland, lowland north-east England and southern Wales.

Pine appears to have expanded independently in north-west Scotland between 8500 and 8000 BP in the Loch Maree area (Birks, 1972; Kerslake, 1982) and at 7900 BP in the Loch Sionascaig area of Wester Ross (Pennington *et al.*, 1972). The origin of this apparently independent early pine expansion is unknown. One hypothesis (Huntley & Birks, 1983; Kinloch, Westfall & Forrest, 1986), proposes that *Pinus* grew in or near north-west Scotland during the last glacial stage, perhaps as small populations in sheltered localities. Although there is no unambiguous palynological evidence for the local presence of *Pinus* in north-west Scotland during the Devensian late-glacial (e.g. Pennington *et al.*, 1972), the detection of small localized populations is very difficult or even impossible. The glacial-survival hypothesis cannot be rejected on present evidence (Dahl, 1987), although on balance it seems unlikely, in view of Sutherland's (1984) detailed reconstruction of Devensian glaciation limits in Scotland.

A second hypothesis, unfortunately untestable, is distant, so-called jump dispersal (*sensu* Pielou, 1979) of pine seeds from southern Britain, mainland Europe, or the North Sea basin.

A third and testable hypothesis is that pine extended rapidly through western Ireland and south-western Scotland prior to 8500 BP (Forrest, 1982; Bennett, 1984) but that throughout this range it was extremely rare, being confined by competition to marginal habitats such as coastal sites, mires, high ground, river gravels, and dry limestone or sandy soils. In contrast, pine expanded regionally in north-west Scotland between 8500 and 8000 BP because of widespread poor soils and an absence of competition from deciduous trees such as oak, elm and hazel. An extremely localized but widespread former distribution can only be detected by local pollen diagrams or macrofossils from marginal habitats in several areas (see Walker (1966) and Turner *et al.* (1973) for examples). Bennett & Lamb (1984) tested this hypothesis by searching for pine-stumps in south-west Scotland. After extensive field-work, they concluded that pine did not spread into Kintyre, Islay, Jura or Arran (Bennett, 1984).

In Scotland pine moved eastwards (Fig. 6) between 8000 and 7500 BP to the area where today pine is prominent in the native forests of Upper Speyside and Upper Deeside. The available data indicate a regional expansion there at about 7500 BP (cf. O'Sullivan, 1977). By 6000 BP the northern, western and eastern margins of range in Scotland had stabilized, but the southern margin extended to the Rannoch Moor area. Pine also expanded altitudinally at this time in the Cairngorms and eastern Grampians (Dubois & Ferguson, 1985). By 5000 BP pine had expanded northwards into Sutherland and westwards to eastern Skye. Between 5000

and 4500 BP pine filled McVean & Ratcliffe's (1962) region of potential 'pine forest with birch' and extended northward, southward and westward beyond it. Macrofossil evidence indicates that pine also grew locally in Caithness and parts of the Outer Hebrides at about this time (Wilkins, 1984; Bennett, 1984).

In Ireland pine, possibly of different genetic stock, spread to the north between 7000 and 7500 BP. Interestingly, this is the same time that pine became established in the Galloway Hills of south-west Scotland (Birks, 1975). Pollen data from adjacent areas in north-west England (Walker, 1966) and southern Scotland (Birks, 1977) suggest that the English pine populations did not reach Galloway and that the Scottish pine populations did not expand southward to Galloway. The simplest and thus the preferred hypothesis is that the Galloway pine populations originated from distant (100 km) seed-dispersal from north-east Ireland, although the possibility of distant seed-dispersal from northern England cannot be discounted. The probability of such jump-dispersal events occurring during several hundreds of years (Simpson, 1962; Gretener, 1967; Pielou, 1979) is such that the hypothesis of dispersal from northern Ireland becomes increasingly more probable if enough attempts are made. Several plants that grow in south-west Scotland appear from their present-day distributions to have reached Scotland via Ireland rather than from England (e.g. *Cirsium dissectum* (L.) Hill, *Lathyrus palustris* L., *Ceterach officinarum* DC, *Trichomanes speciosum* Willd., *Cyclodictyon laetevirens* (Hook. & Tayl.) Mitt., *Dumortiera hirsuta* (Sw.) Nees.). Pine appears to have been absent from the lowlands of Wigtownshire west of Galloway (Moar, 1969b), perhaps due to competition and edaphic factors, although it was present locally at Bowness Common (Walker, 1966), on the south side of the Solway, where it grew on coastal sand and gravel deposits.

Both the Irish (Smith & Pilcher, 1973) and the west Scottish (Pennington *et al.*, 1972; Birks, 1972; Birks, 1977; Bennett, 1984) pine populations underwent massive and rapid declines just before 4000 BP, leading to a major contraction in the range of pine in western Scotland and ultimately to its extinction in Ireland between about 2000 and 1000 BP (Watts, 1984; Bennett, 1984; Bradshaw & Browne, 1987). However, no decline occurred in its abundance or distribution in the eastern Highlands where large natural or semi-natural pine-forests persist to the present day. The causes of the pine decline in the west are unclear but may have included changes in precipitation, wind intensity, and the influence of prehistoric people, all of which could have resulted in a decline in tree growth, the spread of blanket-bog, and the reduction of pine on poorly drained sites (Birks, 1977).

The isochrone map (Fig. 6) suggests that there were probably two and possibly three independent centres of origin of pine within the British Isles. This is of considerable interest, as taxonomists and foresters frequently recognize a distinct taxon, *Pinus sylvestris* var. *scotica* (Schott.) E. F. Warb. (Steven & Carlisle, 1969; Tutin *et al.*, 1964), on the basis of morphological, physiological and growth characterstics. Var. *scotica* is today confined to native Scottish pinewoods. The English and Scottish pine populations were

probably separated by a large geographical gap (150–250 km) for at least 8000 years. The native Irish pine populations are now extinct, so unfortunately there is no means of knowing whether they differed from the English and Scottish populations.

Forrest (1980; see also Forrest, 1982) and Kinloch *et al.* (1986) show from monoterpene and isozyme analysis of populations from presumed native pinewoods in Scotland that the north-west Scottish populations are heterogeneous but very distinct genetically from other Scottish and European populations. They suggest that the history of pine in the north-west was different from other areas in the Highlands, and that pine possibly originated 'endemically from more than one refugium after the last glaciation' (Kinloch *et al.*, 1986). The isochrone map clearly indicates that the Holocene history of pine was different in these areas. Unfortunately, it does not provide any firm insights into how pine was able to expand so early in north-west Scotland.

Alnus glutinosa (alder) (Fig. 7)

Alder was present and locally abundant along the mid-Wales coast by 8900 BP, in inland areas near Harlech by 8500 BP, in East Anglia and the Thames estuary by 8200 BP, and in southern Argyll (site 40, Fig. 1) by 7900 BP. It was probably locally abundant not only in inland valley and basin mires (e.g. Rymer, 1974; Chambers & Price, 1985) and but also in coastal woodlands developed on marine alluvium (e.g. Heyworth, Kidson & Wilks, 1985), as suggested by Oldfield (1960). Ranwell (1974) describes one of the few extensive coastal alder woods surviving in Britain today which 'has similar characteristics to those described . . . for the ancient coastal forests' and which is a possible modern analogue for the early-Holocene habitats of *Alnus* in Britain. Alder is also recorded inland in Yorkshire at 10,500–9500 BP as wood and catkins (Bush & Hall, 1987) and at 8600±600 BP as leaf impressions in tufa (Pentecost, 1985). As Fig. 7 is based on pollen-analytical data only, these early macrofossil occurrences are not mapped. Before 8000 BP, alder may have been widely distributed throughout all or part of the British Isles but in small amounts and hence poorly recorded palynologically at most sites, and only abundant and hence well recorded palynologically at a few localities. This hypothesis has been proposed by Godwin (1966, 1975) and, in different contexts, by Bennett (1985, 1986a, 1988a, c). An alternative but untestable hypothesis proposes that these scattered early local occurrences reflect chance dispersal of alder fruits by water, and its subsequent establishment and expansion in widely separated parts of the British Isles. Guppy (in Praeger, 1913) has shown that alder fruits float and remain viable for over a year, and water currents are often proposed as their dispersal mechanism (e.g. Firbas, 1949; McVean, 1956a).

By 7500 BP *Alnus* had expanded inland in England and Wales. It should be noted, however, that this isochrone is based on very few sites because of absence of data from much of southern and central England. Alder was also well established in parts of north-west England and in or near

coastal areas of north-east Ireland and south-west Scotland at this time. By 7000 BP it was abundant throughout England (except the extreme south-west and parts of the northern Pennines) and, except at high altitudes, Wales and southern Scotland. In Ireland it was still confined to the north-east. By this time alder probably occupied the wide range of habitats in which it grows today (McVean, 1955, 1956b; Fremstad, 1983) and was no longer restricted to coastal or mire habitats.

Between 7000 and 6000 BP alder spread (*c.* 150 m yr^{-1}) through central and southern Ireland, into south-west England and south Wales, up the west coast of Scotland, and into central and eastern Scotland. It also expanded altitudinally in the northern Pennines (Turner *et al.*, 1973), south Wales (Chambers, 1983a) and southern Scotland (Stewart, 1983) to at least 400 m elevation. Today seed formation does not occur above 305 m (McVean, 1955, 1956a). Alder's expansion in upland areas is consistently younger than in the adjacent lowlands (e.g. Pilcher & Larmour, 1982). The high mountain areas of central and eastern Scotland, with their predominantly west–east-running valleys and generally unfavourable climate probably delayed the spread of alder into the central Highlands. An untested hypothesis is that alder spread around the main mountain barriers and colonized the eastern and central Highlands from the lowlands to the east. The few available radiocarbon dates for the arrival and expansion of alder in these lowlands and in the eastern valleys are consistently older than dates from the central Highlands.

After 6000 BP the rate of spread of alder slowed to less than 100 m yr^{-1}, and it finally reached the extreme north of Scotland, possibly including Orkney Mainland by 5300 BP (cf. Keatinge & Dickson, 1979). The slowing of its rate of spread in the west from 400–500 m yr^{-1} to less than 100 m yr^{-1} is unlikely to have resulted from a shortage of suitable moist habitats but is more likely to be a response to the strong, cool winds of these highly oceanic areas. High winds at flowering-time reduce fruit formation by desiccation (McVean, 1955, 1956a).

The ecological interpretation of the *Alnus* isochrone map is difficult. There is considerable variation in the shape and size of *Alnus* pollen curves, varying from curves with a sharp, well-marked, rapid rise from near zero to high percentages to curves with a long 'tail' of low values and a gradual rise (see Beckett (1981a) for contrasting curves from nearby sites). This makes it difficult to use the first continuous pollen values, the first rise, or the first major expansion to determine consistently the first unambiguous presence. Different events in the history of *Alnus* may thus have been mapped on Fig. 7. These difficulties could contribute to the different interpretations of much of the same data by Huntley & Birks (1983), Smith (1984), Chambers & Price (1985) and the present paper.

There is increasing evidence to indicate that alder was present in northern and western Britain well before its pollen values increased to high percentages in the south and east, suggesting its spread and expansion did not follow any simple south-to-north pattern. Expansion occurred at various times after its arrival. Low population levels persisted until changes in local ecological factors allowed its expan-

FIG. 7. Isochrone map of the rational limit of *Alnus glutinosa* pollen in the British Isles. The isochrones are based on data from the sites indicated by dots and are shown as radiocarbon years BP. Sites where there is no pollen-analytical evidence for local presence are shown as open circles. The question mark at the east side of Loch Lomond reflects the uncertainty of this date due to a possible 'discontinuity in both sedimentation rate and the sediment' (Stewart *et al.*, 1984) at Dubh Lochan.

sion. Bennett (1983b) concluded that there was a 'long period of low, variable values which cannot be attributed to early stages of population build up . . . the data suggest a continuous low population level before the expansion began', and suggested, as others have (e.g. Iversen, 1960, 1973), that the expansion was a response to local changes in water-table. Rising water-tables would have allowed alder to expand into habitats previously too dry for it, whereas a drop would have enabled alder to colonize habitats previously too wet (Firbas, 1949; Iversen, 1950 – see Oldfield (1965) for examples of contrasting local changes and alder expansions within a small area). Because of differences in altitude, topography and climate, local hydrological thresholds, and chance factors influencing seedling establishment (McVean, 1956c), the observed patterns of regional spread and expansion of alder are in all probability a function of a series of local, site-dependent events. Its detailed history is probably even more complex than the general patterns (Fig. 7) suggest (e.g. Bush & Hall, 1987).

The hypothesis of 'human influence in the expansion of alder' through burning and clearance (McVean, 1956a; Smith, 1970, 1984) requires critical testing in relation to all the available data on the timing, nature and rates of alder's expansion, and not just on selected data as in Smith (1984). Similarly the hypothesis of beaver activity facilitating the establishment of inland alder populations (Chambers & Price, 1985) requires critical evaluation. Quantitative analysis of the various phases in the initial pollen curves of *Alnus* (e.g. Bennett, 1983b) and subsequent synthesis and mapping of their timings are required before the Holocene patterns of alder in the British Isles can be more fully evaluated in terms of ecological processes operative over the spatial scale of the British Isles.

Tilia (lime, linden) (Fig. 8)

Tilia, mainly *T. cordata* Mill. but with some *T. platyphyllos* Scop. (Godwin, 1975; Pigott, 1981) was present in southern England by 7500 BP. It then spread (c. 400–500 m yr^{-1}) into central England and parts of Wales. Transformation of its observed pollen values by appropriate representation factors (Bradshaw, 1981; Greig, 1982) indicates that it was probably a major, if not a dominant, component of the forests, as it was on the European mainland (Huntley & Birks, 1983). *Tilia* never reached the extreme south-west of England. Its rate of spread after 7000 BP slowed dramatically to 100 m yr^{-1} or less. It reached its northernmost Holocene limit in the central Lake District and north-east England by 5500 BP (cf. Pigott & Huntley, 1980). This corresponds closely to the present northern limit of apparently native populations of *T. cordata* (Pigott & Huntley, 1978), where it survives, often as old multistemmed trees, in steep, rocky situations. It rarely sets fertile seed at these northern sites today, because mean summer temperatures are rarely high enough for successful pollen tube growth and fertilization (Pigott & Huntley, 1981). The relict northern England populations have probably persisted from mid-Holocene times by vegetative regrowth rather than by regeneration from seed, restricted to rocky situations that have probably never been entirely cleared of

trees by humans. The spread of *T. cordata* to northern England, however, must have involved fertile seed production and successful establishment, suggesting that, between 6000 and 5500 BP, July and August mean temperatures may have been 2–3°C higher than today (Pigott & Huntley, 1980, 1981).

Fraxinus excelsior (ash) (Fig. 9)

Fraxinus excelsior pollen was present in low but consistent amounts in southern and central England between 7000 and 6000 BP. Ash was presumably growing at this time in lightly shaded enclaves on seasonally wet basic soils within mixed-deciduous forests and in drier parts of fen-carr woods. *Fraxinus* spread slowly (c. 75 m yr^{-1}) into parts of northern England after 6000 BP and at an increased rate (c. 200 m yr^{-1}) into southern Scotland, much of Ireland, and parts of south-west England after 5000 BP. Its pollen values also increased after 5000 BP throughout much of its British range at this time, probably because of expansion into forest clearings created by prehistoric people. Between 4000 and 3000 BP it spread slowly (c. 50 m yr^{-1}) into northern Ireland.

The ash-dominated woods on the Carboniferous limestones of the Pennines, the Mendips, and parts of western Ireland are probably unique to the British Isles, although they almost certainly have an anthropogenic origin (Pigott & Pigott, 1963; Pigott, 1969; Merton, 1970). However, ash was undoubtedly a native but local component within the mixed-deciduous forests of England and Wales long before 5000 BP (Birks, 1982a; Bennett, 1983a).

Fagus sylvatica (beech) (Fig. 10)

There are, unfortunately, very few reliably dated pollen diagrams published from southern and central England from which to construct isochrone maps for *Fagus*. Available palynological data suggest that beech was present in the south-east by at least 3000 BP continuing its spread across north-west Europe since 5000 BP (see Huntley & Birks, 1983). It then spread fairly rapidly (100–200 m yr^{-1}) by 2000 BP into East Anglia and Somerset and by 1000 BP into Wales and Derbyshire. Godwin (1966, 1975) suggests that shifts in arable cultivation on to deeper, heavier soils associated with improved ploughing techniques in the Iron Age resulted in previously cleared areas on shallow, well-drained soils becoming derelict and hence open to colonization by *F. sylvatica* (see also Thorley, 1981; Baker, Moxey & Oxford, 1978).

In contrast to the other trees mapped, the rate of spread of *Fagus* within Britain does not decrease with time, suggesting that by 1000 BP it had not reached its natural climatic limits and hence that its distribution was not in equilibrium with climate. Its present-day distribution has been greatly influenced by introductions and plantings. It thrives and regenerates far beyond its putative natural limit (Dierschke, 1985), supporting the view that there may be significant differences between its actual and potential native ranges.
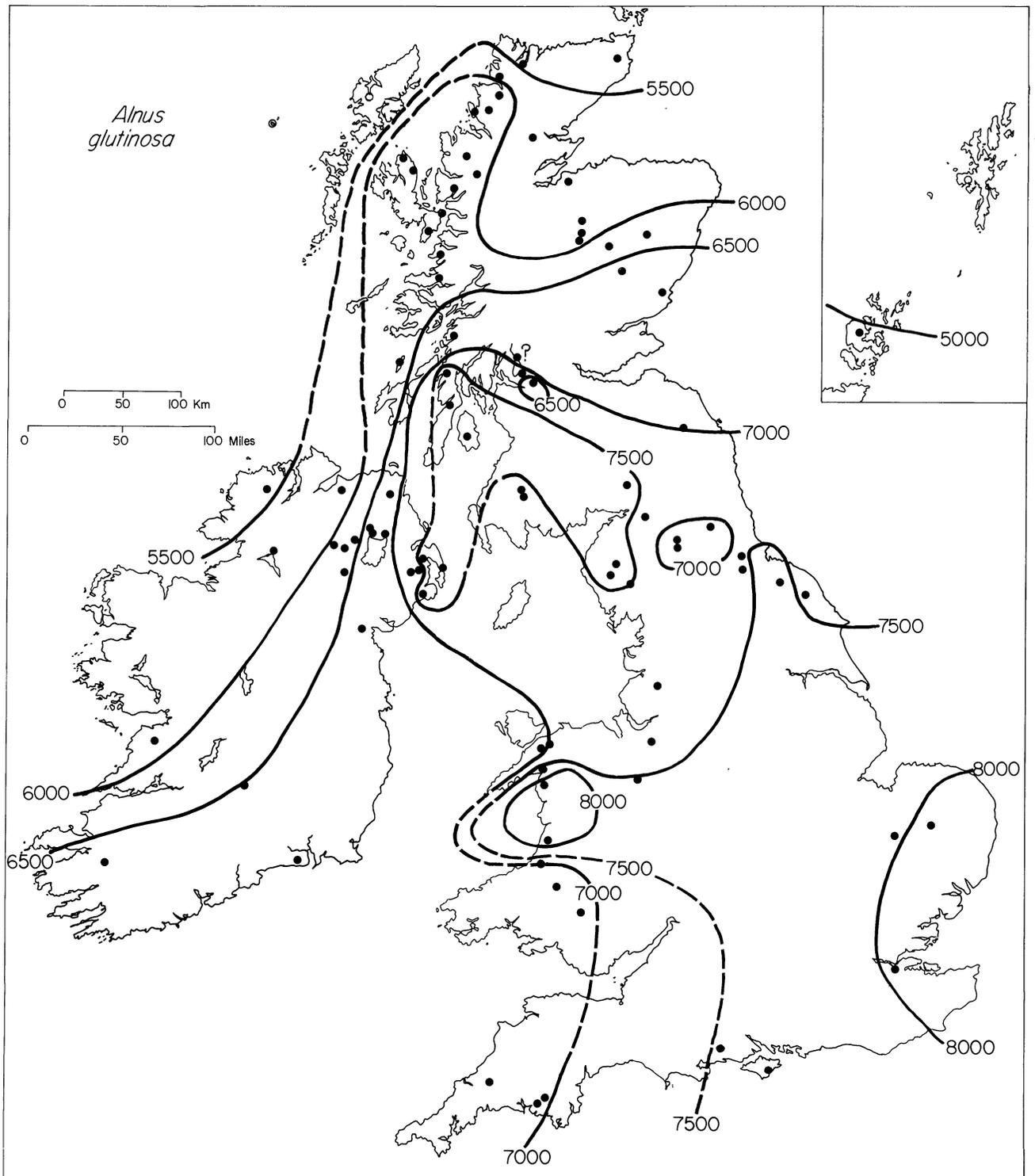
FIG. 8. Isochrone map of the empirical limit of *Tilia* pollen in the British Isles. The isochrones are based on data from the sites indicated by dots and are shown as radiocarbon years BP. Sites where there is no pollen-analytical evidence for local presence are shown as open circles.
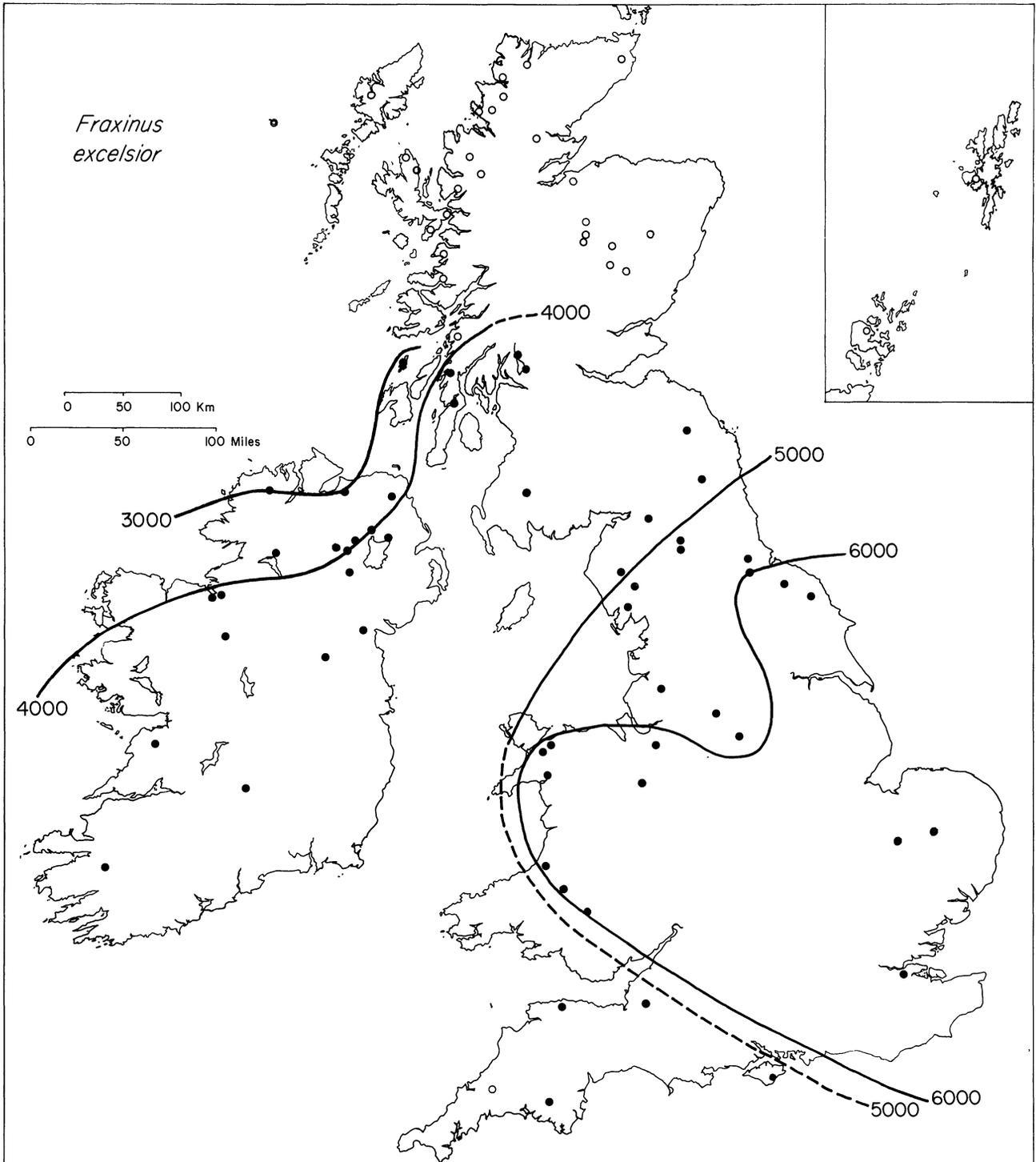
FIG. 9. Isochrone map of the empirical limit of *Fraxinus excelsior* pollen in the British Isles. The isochrones are based on data from the sites indicated by dots and are shown as radiocarbon years BP. Sites where there is no pollen-analytical evidence for local presence are shown as open circles.
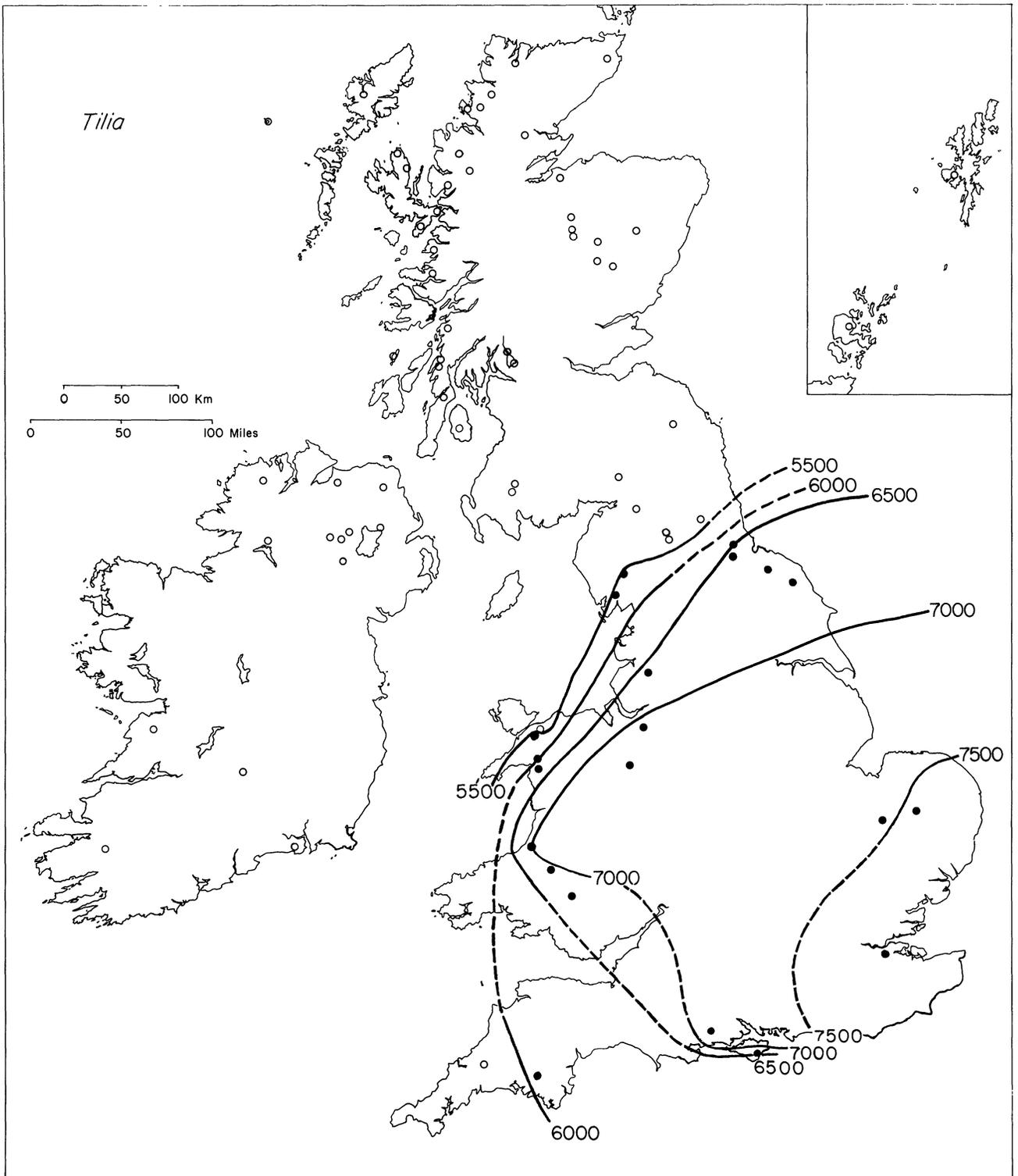
FIG. 10. Isochrone map of the rational limit of *Fagus sylvatica* pollen in the British Isles. The isochrones are based on data from the sites indicated by dots and are shown as radiocarbon years BP. Sites where there is no pollen-analytical evidence for local presence are shown as open circles.
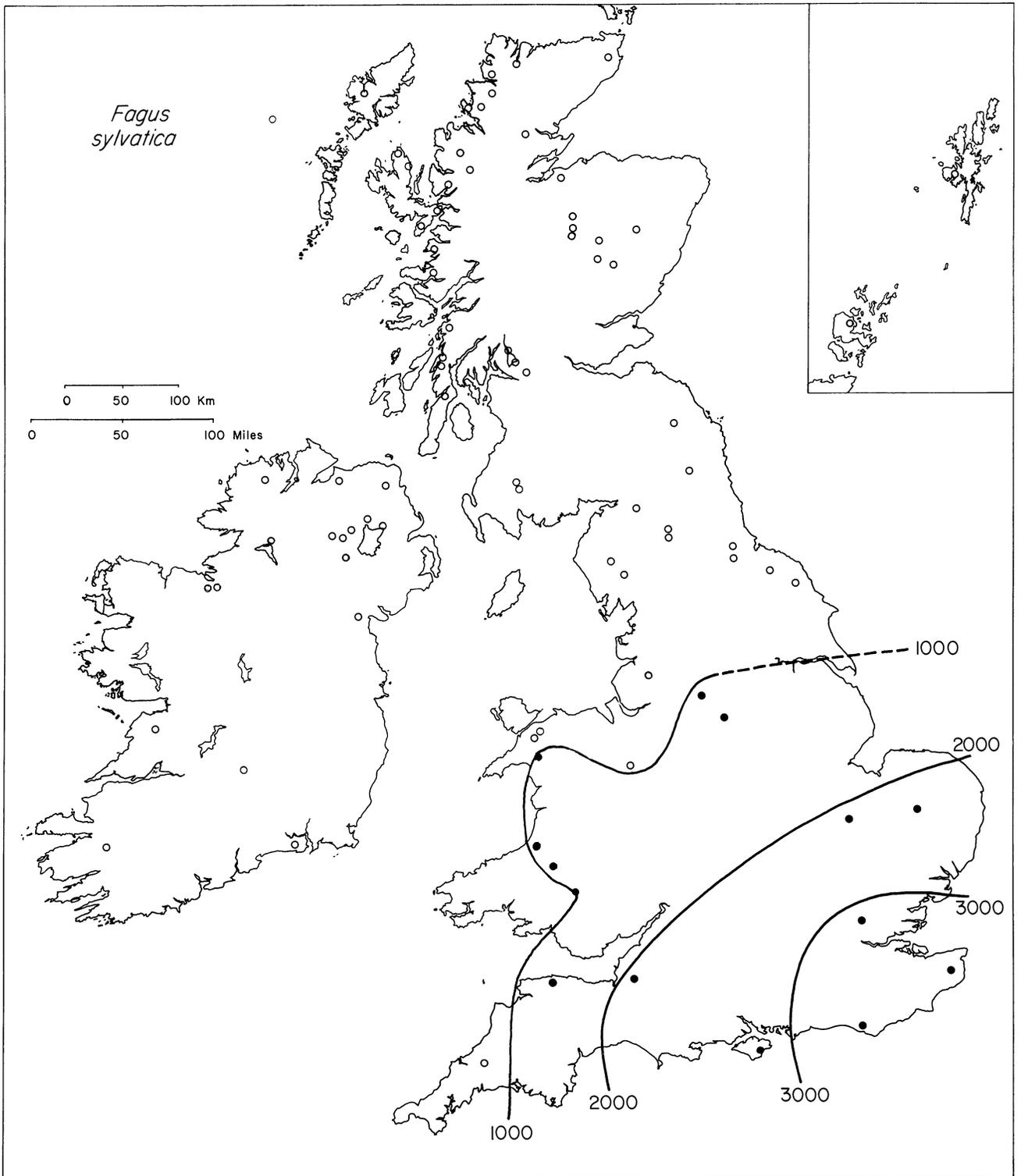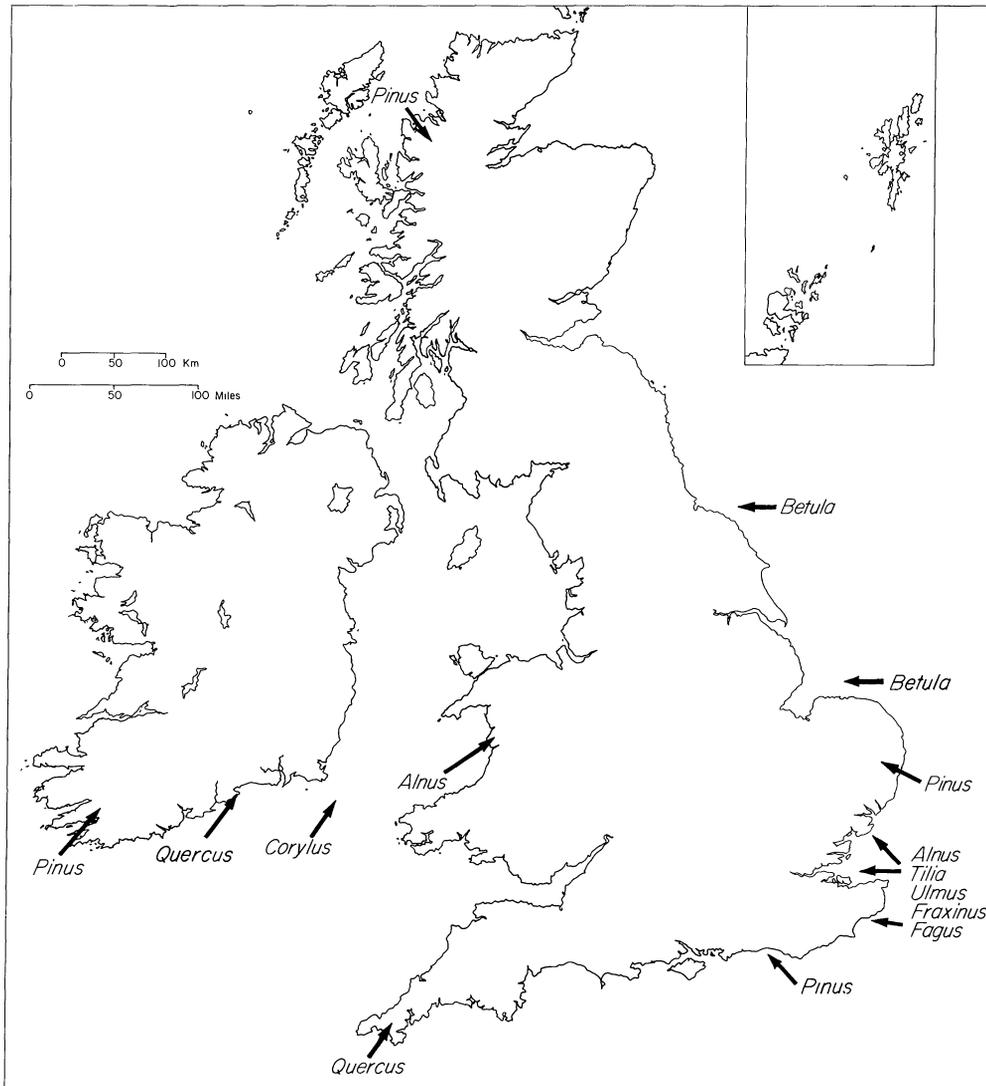
FIG. 11. Approximate directions of arrival of forest trees into the British Isles.

DISCUSSION

Although the distribution of sites is sparse in some areas (Fig. 1), and additional data may change the mapped patterns, at least in detail, several interesting and unsuspected features emerge about the timings, directions, and rates of tree spread within the British Isles. These patterns have implications for palaeoecology and vegetational history and for ecology, dispersal biology, and dynamic biogeography. Discussion is divided into these two broad but related subjects.

Palaeoecological implications

Individualistic behaviour. Taken as a whole, the most striking feature of the isochrone maps is the individualistic patterns and behaviour in time and space of each native tree in terms of (1) areas and timings of presumed first arrival or establishment and subsequent expansion, (2) directions and timings of spread, and (3) rates of spread during the

Holocene of the British Isles. No two tree taxa have identical patterns of arrival times and areas, or timings, directions, or rates of spread.

Assuming that sites where the earliest expansion occurs indicate the areas of first establishment within the British Isles following deglaciation, approximate arrival areas are proposed on Fig. 11. *Betula* appears to have arrived from the east, *Pinus, Ulmus, Alnus, Tilia, Fraxinus* and *Fagus* from the south-east, *Quercus, Alnus, Pinus* and *Corylus* from the south-west, and *Pinus* from the north-west. When viewed in the broader geographical context of Europe (Huntley & Birks, 1983) these arrival areas are largely predictable from the positions of the presumed glacial refugia. For example, last-glacial localities for *Corylus* and *Quercus* nearest to the British Isles were in south-west Europe, whereas those for *Tilia, Ulmus* and *Fagus* were in central, southern or south-east Europe.

The timings of presumed first arrivals range from 10,000 BP (*Betula*) to just before 3000 BP (*Fagus*). This range is also understandable in the broader context of
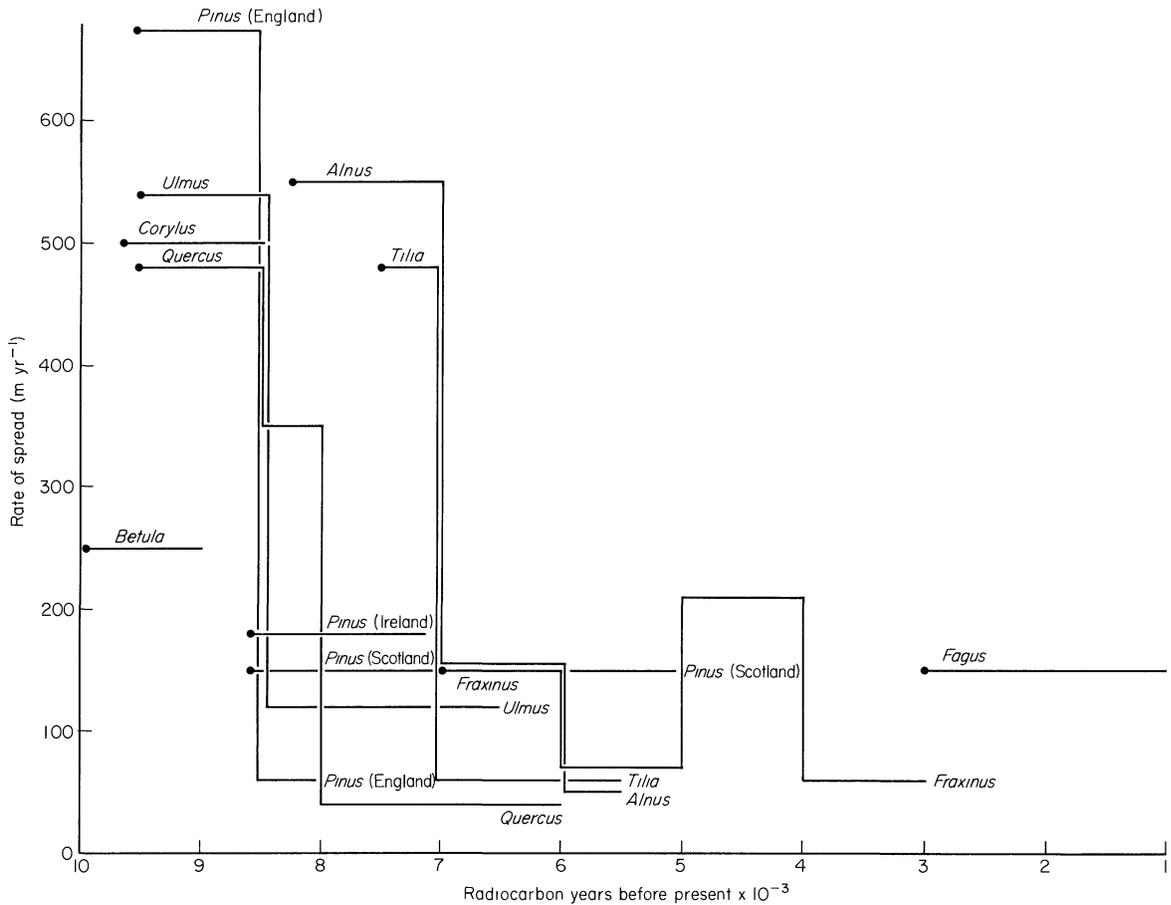
FIG. 12. Approximate rates of spread (m yr⁻¹) of forest trees in the British Isles at different times in the Holocene estimated from the isochrone contours in Figs. 2–10.

Europe (Huntley & Birks, 1983) and is presumably related to inherent differences in the rate and direction of spread of the trees across mainland Europe from their locations at the beginning of the Holocene (Iversen, 1960).

The varying directions of subsequent spread through the British Isles were controlled primarily by the location of first arrival, and secondarily by topography and climate, which created various barriers to further spread (e.g. mountains: *Alnus, Corylus*; Irish Sea; *Tilia*; natural climatic limits; *Quercus, Tilia, Alnus*). The timings of tree spread and the attainment of range limits near those of today vary considerably. Some trees (e.g. *Betula, Corylus*) attained such limits early in the Holocene, others (e.g. *Quercus, Ulmus, Tilia, Alnus*) in the mid-Holocene, and others (e.g. *Pinus* in Scotland, *Fagus*) in the late-Holocene.

Estimated rates of spread for British trees from the isochrones are summarized in Table 1 and compared with estimated rates for the European mainland (Huntley & Birks, 1983). Approximate rates of spread for 1000-year intervals within the British Isles are plotted in Fig. 12 to compare the changing rates of spread in time as estimated from the isochrone maps. Several points of interest emerge. First, rates are generally lower in the British Isles than on the European mainland (Table 1). Second, within the British Isles, rates of spread of many trees (e.g. *Pinus* in England, *Ulmus, Quercus, Alnus, Tilia*) decrease with time as

the trees approach their range limits (Fig. 12). Exceptions are *Fagus* and *Fraxinus*. Third, decreases in rates of spread occurred at different times for different trees, emphasizing further their individualistic behaviour (Fig. 12). Similar individualistic behaviour is found elsewhere in Europe (Huntley & Birks, 1983) and eastern North America (e.g. Davis, 1981; T. Webb, 1986). In view of the complex spatial and temporal patterns of first arrivals and the inherent differences between taxa in terms of demography, dispersal

TABLE 1. Estimated rates of spread (m yr⁻¹) of trees in the British Isles and on the European mainland (from Huntley & Birks, 1983).

	British Isles	European mainland
Betula	250	>2000
Corylus	500	1500
Ulmus	550 (100 near northern limit)	500–1000
Quercus	350–500 (50 near northern limit)	150–500
Pinus	<100–700 (England), 150 (Scotland), 150–200 (Ireland)	1500
Alnus	500–600 (50–150 year northern limit)	500–2000
Tilia	450–500 (50–100 near northern limit)	300–500
Fraxinus	50–200	200–500
Fagus	100–200	200–300

biology, and ecological tolerances, such individualistic behaviour is largely predictable (Chapin & Shaver, 1985; T. Webb, 1986). The observed changes form a 'temporal vegetational continuum' (Davis & Jacobson, 1985) analogous to a modern vegetational continuum along spatial gradients.

The general patterns of decreasing rates of spread as northern or western range-limits are approached results from at least two causes. First, the limited area of the British Isles and their shape impose physical constraints on plant spread. Because Britain tapers northwards, the same rate of spread would result in a decrease in the amount of new area occupied per unit time in the north compared with the south (R. Hengeveld, personal communication). Second, there is a general decrease in plant abundance, ecological tolerance, vitality, and reproductive potential towards range margins (e.g. Griggs, 1914; Kavanagh & Kellman, 1986). Hengeveld & Haeck (1981, 1982) discuss the distribution of abundance within geographical ranges and show as 'a general biogeographical rule' that higher abundances occur at range centres than at range margins (see also Brown, 1984). They suggest that ranges and abundance patterns within them are most usefully regarded as broad-scale optimum-response surfaces with gradients in ecological tolerances, vitality and reproduction declining from the range centre to its margins.

At the range margins, differences in fecundity become increasingly critical in influencing rates of spread, along with the number, availability and accessibility (*sensu* Heimans, 1954; Kellman, 1970) of sites suitable for colonization, as predicted from epidemic threshold theorems (Carter & Prince, 1981). Epidemic theory provides useful models for the processes of spread and invasion by metapopulations (*sensu* Levins, 1970), namely spatially separated populations that comprise the species presence in a geographical area. The theorems propose that in addition to numbers, dispersal, and establishment of propagules ('infection rate' or dissemination rate β), the number and availability of suitable but unoccupied 'susceptible sites' (x) and the numbers (y) and longevity or 'removal rate' (γ) of dissemination sources ('infective sites') are important parameters in influencing rates of spread. A threshold density of susceptible sites (x) is required to maintain or increase a metapopulation, with the numbers of susceptible sites (x) equal to or exceeding the relative removal rate (γ/β). Range limits are set when the relative removal rate exceeds the numbers of susceptible sites at a given time ($\gamma/\beta > x$). As abundance, vitality and demography all vary geographically, gradients in number of dissemination sources and susceptible sites and rates of extinction and dissemination will occur between range centres and margins. At range centres y is large and x is low, whereas at the margins x tends to be large and y is small (Hengeveld, 1985a). The dissemination rate β may be constant throughout the range or, more likely, decrease towards the range limits, and the removal rate γ may increase towards the range margins (Hengeveld, 1985a). The different rates of spread between the European mainland and the British Isles (Table 1) and within the British Isles (Fig. 12) are most simply interpreted as long-term, broad-scale responses to these gradients as the ranges of tree metapopulations

spread towards their presumed climatic limits. The threshold theorem suggests how relatively small changes in plant performance (fecundity or mortality, both of which may or may not be climatically controlled) can produce marked changes in rates of spread and distribution limits (e.g. Figs. 5 and 8). Carter & Prince (1981) show that increase in the number of susceptible sites near but outside a range limit, so that $x > \gamma/\beta$, can change the distribution limit *without* any change in climate. Small changes in the availability of suitable sites following gap creation independent of climatic change may thus have facilitated the accelerated rate of spread and range expansion of *Fraxinus* between 5000 and 4000 BP (Fig. 9).

The roughly constant rate of spread of *Fagus* in Britain (Figs. 10 and 12) suggests that none of the parameters of the threshold equation have attained limited values. The broad-scale spread of beech across central and western Europe in the last 5000 years (Huntley & Birks, 1983) may have resulted from an increased density of susceptible sites following forest disturbance and not necessarily from any climatic change. On the other hand, small changes in fecundity or mortality rate resulting from climatic change can lead to large changes in population size, particularly at or near range limits (Carter & Prince, 1981; Watkinson, 1985). This may have occurred in the western pine populations about 4000 BP (Fig. 6), causing their widespread decline.

The epidemic threshold theorems (Carter & Prince, 1981) in conjunction with Hengeveld & Haeck's (1981, 1982) 'general biogeographical rule' provide a useful conceptual model for broad-scale biogeographical dynamics, as reconstructed from synoptic pollen maps. Unfortunately many of the model's parameters cannot be estimated, thereby limiting its predictive abilities. Despite this, the model is useful and suggests that an interplay of several demographic and ecological factors is involved in range dynamics. Such interactions provide a caution against uncritically assuming that unidirectional, broad-scale expansions of range limits *must* result from broad-scale climatic change. The problem of inferring climatic change from broad-scale pollen-stratigraphical changes is discussed further below.

Tree-spreadings and climatic change. The progressive invasion of trees into an area during the Holocene produces a series of pollen-stratigraphical changes that are commonly used to delimit pollen zones. Zone boundaries so defined can only be of local chronostratigraphical value, as tree arrivals are time-transgressive over large areas (Smith, 1965; Birks, 1982b). Smith & Pilcher (1973) concluded that nearly all the major pollen-stratigraphical changes in the British and Irish Holocene are diachronous, a conclusion recently reiterated by Bennett (1988b). Such time-transgressive pollen-zone boundaries within an area as small the British Isles emphasize the impracticability of transforming the classical Blytt and Sernander pollen-zone terminology (Mangerud *et al.*, 1974) into a usable chronostratigraphical framework (Watson & Wright, 1980).

Trees arrived independently in different areas of the British Isles (Fig. 11) and spread at different rates within the British Isles (Fig. 12). It is therefore not surprising that

they arrived in a different order at separate localities. For example, oak arrived before elm in south-west England (Figs. 5 and 4), oak and elm expanded virtually together in northern England and southern Scotland, and oak expanded after elm in western Scotland. Similarly, alder expanded after oak (Figs. 5 and 7) in England, Wales and southern Scotland, but in western Scotland alder predated oak.

It may be argued that the steady northward movement of oak (Fig. 5), for example, was controlled by a corresponding northward climatic change. However, the simultaneous and independent diverse movements of other trees suggest that such a hypothesis of simple climatic control cannot suffice; complex climatic variations must therefore be invoked. These might include variations in seasonality, winter and summer temperature, and climatic anomaly and precipitation patterns, as well as unique combinations of, for example, temperature and precipitation conditions that no longer exist (e.g. Howe & Webb, 1983; Prentice, 1983, 1986; T. Webb, 1986). Such a complex hypothesis is unfortunately untestable at present, given the poor spatial precision of results from climatic simulations using general circulation models (e.g. Kutzbach & Guetter, 1986) and our current knowledge of Holocene climatic patterns at the scale of the British Isles (e.g. Huntley & Prentice, 1988). As Walker (1976: p. 26) has warned, it is possible to 'hazard climatic change as a reason for disappearances and appearances. Once in this frame of mind it is all too easy to become like a child with Christmas chocolates. We open the box of climatic Assorteds and take our pick of the seductive dainties inside: frosted springs, misty mornings, hot noons, or even glacier mints. Sometimes, with true experimental dash, we try something just because we have not tried it before'.

The simplest hypothesis to account for the observed diversity of patterns proposes that, after the major climatic changes associated with the beginning of the Holocene, there was chance dispersal of propagules and tree arrivals. Trees then spread from these arrival areas at their own individual rates wherever and whenever environmental and biotic conditions (e.g. climate, soil, competition) allowed. Both biotic (e.g. dispersal) and environmental (e.g. soil, climate) constraints may have been important in influencing the patterns of spread at different spatial and temporal scales. In the circumstances of this hypothesis, interactions among species would almost certainly have been different in the past in different areas and may have resulted in forest assemblages that have no modern counterparts (e.g. Bennett, 1983a, 1984). Therefore climatic reconstruction using present analogues is potentially fraught with difficulties (Birks, 1981b). Climatic reconstructions using present-day climatic responses of individual species (e.g. Bartlein, Prentice & Webb, 1986) avoid the 'no-analogue' assemblage problem but assume that species distributions are in dynamic equilibrium with climate today and were in the past at the relevant scales of space and time. The isochrone maps suggest that different trees may have attained broad-scale equilibrium with climate when their rates of spread fell to low (<100 m yr^{-1}) values (Fig. 12), but such equilibria were reached at different times during the Holocene.

Although range-limits of many but not all trees (e.g. *Fagus, Tilia*) may be in a dynamic equilibrium with climate today, the critical question for palaeoclimatic reconstructions based on individual response surfaces is whether such equilibria existed during the early or mid-Holocene when climatic changes may have been large (Kutzbach & Guetter, 1986; Kutzbach & Gallimore, 1988; Davis *et al.*, 1986). Were the distributions of, for example, *Corylus* at 9500 BP, *Ulmus* and *Quercus* at 9000 BP, *Pinus* at 8000 BP, *Alnus* and *Tilia* at 7000 BP or *Fraxinus* at 6000 BP in equilibrium with climate? At present, available evidence does not allow any firm conclusions to be drawn, at least at the meso-scale of the British Isles (cf. Silvertown, 1985; Prentice, 1986; T. Webb, 1986). The isochrone maps illustrate the complexity of the situation, and warn against any simple reconstruction of past climate *and* against any interpretation of the observed patterns solely in terms of simple climatic models at this scale.

Ecological and biogeographical implications

Despite the central role that tree spread plays in interglacial vegetational history, we are largely ignorant of the ecological mechanisms that enable trees to move at such surprisingly high rates (Pigott & Huntley, 1980; Walker, 1982; T. Webb, 1986), and of the processes that allow new tree species to invade and expand into existing forest vegetation (Watts, 1973; Walker, 1982). It is useful in discussing the ecological and biogeographical implications of the isochrone maps to consider separately the factors potentially important in influencing (1) the observed rates of spread and the processes operative in broad-scale changes in range-limits, and (2) forest invasion. In the third section I turn to tree-spreading as an example of long-term biological invasions.

Rates of spread. Estimates are shown in Table 2 of 'average spreading distances per generation' (Holland, 1981) (≡ 'minimal propagule dispersal distance', S. L. Webb, 1986). No obvious relationship is apparent (1) between estimated rates of spread (Table 1) or dispersal distance (Table 2) and

TABLE 2. Minimal propagule dispersal distances required to produce the observed rates of spread (Table 1).

	Dispersal distance (*sensu* S. L. Webb, 1986) (km generation^{-1})*	Dispersal agency and propagule type	
Betula	2.5	Wind	Winged nutlet
Corylus	7.5	Animal	Nut
Ulmus	8	Wind	Samara
Quercus	7–10	Animal	Acorn
Pinus	<1–7 (England)	Wind	Winged seed
	1.5 (Scotland)	Wind	Winged seed
	1.5–2 (Ireland)	Wind	Winged seed
Alnus	5–6	Water	Winged nutlet
Tilia	10	Wind	Winged nut
Fraxinus	1–3	Wind	Samara
Fagus	4–8	Animal	Nut

*Estimated from the spreading rates of Table 1 multiplied by the minimal age at which the tree commonly fruits (cf. S. L. Webb, 1986).

dispersal agency, or (2) between rates of spread within the British Isles and general ecological characteristics such as life-history, demographic or ecological traits, as defined by Birks (1986). Mean rate of spread for protocratic trees (*sensu* Birks, 1986) is 250 m yr^{-1}, mesocratic 450 m yr^{-1} and oligocratic 150 m yr^{-1}. Average dispersal distances are 2.5, 6.5 and 6 km generation^{-1}, respectively. There is no relationship with biological attributes such as propagule morphology (Table 2), weight or size, or numbers of propagules produced, or frequency of reproduction (cf. Howe & Smallwood, 1982; S. L. Webb, 1986). In general, the lowest minimal propagule dispersal distances per generation tend to be for trees with wind-dispersed propagules (e.g. *Fraxinus, Pinus, Betula*), whereas trees with animal-dispersed propagules (e.g. *Corylus, Quercus, Fagus*) require dispersal distances of 5 km or more per generation. The required dispersal distances (Table 2) may have been achieved by light, wind-dispersed fruits (e.g. *Betula, Ulmus*) or water-dispersed propagules (e.g. *Alnus*; McVean, 1956a) but are difficult to envisage for large, heavy propagules such as *Quercus* acorns or *Corylus* nuts. Although many fruits are eaten by jays (*Garrulus glandarius*), tits (Paridae L.) and small mammals (e.g. squirrels (*Sciurus* L. spp.)) or stored in caches (e.g. van der Pijl, 1972; Chettleburgh, 1952; Darley-Hill & Johnson, 1981; Jensen & Nielsen, 1986; S. L. Webb, 1986), this behaviour is unlikely to result in frequent dispersal over the distances required for the observed Holocene spreading rates. Moore (1987) proposes that mobile species such as the wood pigeon (*Columbaria palumbus*) extended the ranges of, for example, *Quercus, Corylus* and *Fagus* by chance dispersal of propagules over distances greater than 5 km sufficiently frequently to allow their rapid spreading rates, just as the now extinct passenger pigeon (*Ectopistes migratorius* L.) may have done in eastern North America (S. L. Webb, 1986). Problems with this hypothesis are (1) that although wood pigeons eat nuts and grind them in their powerful gizzards, the nuts are rarely carried or stored, and (2) that although birds migrate northwards in spring and southwards in the autumn, this is the opposite direction as far as tree spread is concerned. Birds will be flying towards the range centre during the fruiting season.

Prentice (1986) suggests that studies on Holocene vegetational dynamics provide a 'challenge which calls for simulation approaches to complement empirical studies.' Simulation models of wind and animal dispersal of propagules within a landscape of forested islands today (Johnson *et al.*, 1981) provide possible analogues for the early stages of tree-spreading during the Holocene. By modifying factors such as the number of entry points, population and reproductive biology of the trees concerned, and the physical environment, these and related spatial diffusion models can simulate dispersal over large geographical areas and long time spans (see Auld & Coote, 1980; Auld, Hosking & McFayden, 1983; Mack, 1985). Such simulations could provide useful extensions to Skellam's (1951) random-dispersal model and can generate predictions that can be potentially tested by comparisons with the observed Holocene rates of tree spread.

Additional biological limitations on rates of spread

include the frequency of propagule production, the age of first reproduction, the competitive ability of seedlings, and seedling growth in relation to climate, soil and biotic factors. These could determine the ability of different trees to exploit gaps in existing forests and to grow and reproduce under the environmental conditions within such gaps. The availability of gaps in time and space, produced by, for example, windthrow, fire, disease or natural death (Watts, 1973) may also be important. Unfortunately these factors are poorly understood ecologically and are difficult, if not impossible, to study in the predominantly cultural landscape of north-west Europe today.

The isochrone maps provide some evidence that natural barriers may also have influenced the rates of spread. For example, the Scottish Highland mountains slowed the spread northwards of *Quercus*, eastwards of *Corylus*, and northwards and eastwards of *Alnus*. Similarly the Irish Sea was a barrier to the westward spread of *Tilia* and *Fagus*. The area of deciduous forest of *Ulmus, Quercus* and *Corylus* in southern Scotland may have created a biotic barrier, through competition, to the spread of *Pinus* northwards. The observed mid-Holocene range-limits of *Pinus* (Fig. 6) cannot easily be interpreted in terms of climatic constraints influencing the northern limit of pine in England and its southern limit in Scotland, leaving a pine-free area of 150–250 km in between, unless there were ecotypes of contrasting climatic tolerances in the two areas of pine-dominance. A biotic barrier provides a simple explanation.

It remains a challenge to dispersal biology and ecology to interpret the high rates of spread and to explain the differential rates among taxa (Smith, 1978; Holland, 1981; Walker, 1982; Prentice, 1983, 1986; Bennett, 1986a; Moore, 1987). Webb (1985) proposes that 'among the biological changes controlled by climate are the differential migration rates'. As the rates of spread are so high compared with theoretical predictions based on abiotic random-dispersal models, one is forced to presume that chance dispersal by agents such as birds, small mammals, rivers, ocean currents, and possibly *Homo sapiens* were important. It is unclear how such events could be 'controlled by climate' (Webb, 1985), at least at the scales of interest here (cf. Axelrod, 1952). However, as in so much of historical biogeography, it is easier to hypothesize than to test! Discussion of rates and processes of tree spread is no exception.

Smith (1978) assesses the factors and mechanisms of dispersal biology and considers that chance colonizations may have been more important during the Holocene than the events of local propagule dispersal and seedling establishments near the parent tree, as predicted by random-dispersal models and by current concepts in dispersal biology (e.g. Berg, 1983; Howe & Smallwood, 1982). Romell (1938) discusses the evolutionary significance of dispersal mechanisms in relation to chance events and proposes that much of plant dispersal is really a problem in ornithology, meteorology and oceanography rather than in adaptation and co-evolution. Berg (1983) argues that there are three major modes of dispersal: specialized, generalized and chance. Specialized and generalized dispersal are important over ecological time-scales (1–100 years) (Birks, 1986),

whereas chance dispersal is effective over palaeoecological time-scales (100–10,000 years). The difficulty about invoking chance events in historical biogeography and palaeoecology is, as Smith (1978) emphasizes, 'distinguishing the impossible from the highly improbable, especially in the largely unknown conditions of the past'. S. L. Webb (1986, 1987) provides a convincing case for chance long-distance dispersal (over 100 km or more) of *Fagus grandifolia* Ehrh. from lower Michigan to eastern Wisconsin across either Lake Michigan or parts of the Illinois Prairie Peninsula to the south. The arrivals of *Pinus* in Scotland (Fig. 6) and *Alnus* in Wales (Fig. 7) are similarly most parsimoniously interpreted as resulting from chance jump-dispersal events.

So far, discussion has centred on dispersal. As 'transport without establishment has no significance' (Berg, 1983), I now turn to the processes of establishment and invasion and the possible role of chance events in establishment.

Processes of tree invasion and establishment. To spread, a tree species must not only disperse its propagules but also become established, invade, and expand into vegetation that lies beyond its range limits. However, the ecological processes by which trees accomplish invasion are poorly understood. Broad-scale isochrone maps give the impression that trees advance as a continuous front across the landscape and invade and occupy all suitable sites. At a finer scale this hypothesis is unlikely for many, if not all, trees (Watts, 1973). An alternative hypothesis (Godwin, 1966, 1975; Watts, 1973; Walker, 1982; Davis, 1987) is as follows. Chance long-distance dispersal of propagules into gaps and locally favourable sites beyond the range of the main population form small, outlying populations. These eventually expand, coalesce with the main population, and produce propagules, some of which are dispersed beyond the range limits into new gaps. The result is a discontinuous expansion of the range limit. However, this may appear as a continuous range-expansion at a broad-scale.

On this hypothesis, the rate of spread may be determined not only by (1) chance-dispersal factors but also by (2) the frequency and extent of gap production following unpredictable events such as windthrow, fire, disease and natural death, by (3) propagule production, seedling establishment and mortality and hence the ability of the tree to colonize and flourish in such gaps, and by (4) the intrinsic rate of population growth. Harper (1965) emphasizes the importance of seedling establishment in invasion; critical factors include seed characteristics, local climate and soils, predation and parasitism, and competition (see Smith, 1978).

Green (1982, 1987) shows in Nova Scotia that tree invasion and subsequent expansion coincide with extensive natural fires. He suggests that interference from established species may have been a more important determinant than dispersal rates on observed patterns of spread. Closed vegetation provides 'inertia' to invasion (Pearsall, 1959; Smith, 1965), and gaps created by periodic disturbance provide areas of reduced inertia ('susceptible sites' *sensu* Carter & Prince, 1981), which increase opportunities for invasion (see Miles (1975) for an experimental demonstration of the effects of reduced inertia on species establishment). Jacobson (1979) interprets the late-Holocene establishment and invasion of *Pinus strobus* L. into open *Quercus* savannas or

woodlands in Minnesota as a result of changes in the disturbance regime, in this case the fire cycle following regional climatic change. The spectacular spread and expansion of *Picea abies* (L.) Karst. into Fennoscandia may result, at least in part, from establishment in gaps created by forest clearance and agriculture (e.g. Huttunen, 1980).

Forest landscapes are dynamic and shifting mosaics of patches at different successional stages, which continuously vary in space and time. In this mosaic some opportunities will usually exist for invasion following disturbance, particularly as communities appear not to be 'saturated' and their richness is not determined by niche limitation (Simberloff, 1981; Wilson, Gitay & Agnew, 1987). Additional determinants of the rates of spread may include the time required for dispersal of propagules into available gaps and for attainment of reproductive maturity (Watts, 1973). It is possible, but largely untestable, that opportunities for invasion were greater in the early Holocene when forests were dominated by shade-intolerant, short-lived protocratic trees (e.g. *Betula, Populus, Pinus*), than in the mid-Holocene with shade-tolerant, longer-lived mesocratic trees such as *Corylus, Ulmus* and *Tilia* (Birks, 1986). In the late-Holocene human activities created many clearings, thereby increasing the potentialities for invasion. The changing rates of spread, which are assumed to be closely linked to invasion rates (Fig. 12) may be partly a result of changes in the ecological nature of the forests during the Holocene.

As more is discovered about the spatial and temporal patterns of tree establishment, invasion, and expansion within particular areas, it is becoming increasingly clear how complex the patterns are (e.g. Davis & Jacobson, 1985; S. L. Webb, 1987; Davis, 1987; Davis *et al.*, 1986; Green, 1987). Observed variations may be related in part to chance dispersal events (e.g. S. L. Webb, 1987; Davis, 1987) and in part to local site factors (e.g. Green, 1987) and soil and landscape differences (e.g. Van Leeuwarden & Janssen, 1987). In the last-named study, expansion consistently occurred 200–900 years earlier in lowland valleys than in the surrounding uplands. In south-east France, de Beaulieu *et al.* (1984) demonstrate very considerable variations in arrival and/or expansion times that do not appear to show any consistent ecological or geographical patterns. Perhaps the variations result from chance factors in dispersal and establishment *and* local site controls, producing complex and largely uninterpretable patterns. These examples and the spatial and temporal limitations of the isochrone maps for the British Isles strengthen Ritchie's (1987: p. 139) plea for the 'importance of precision in description because the coarse scale of the available . . . migration maps (Davis, 1981, 1983) appears to have generated misleading oversimplifications that influence paleoenvironmental inferences'.

Tree arrival, establishment and invasion in the past are notoriously difficult to study by pollen analysis alone (Bennett, 1985; Green, 1987). Co-ordinated studies are essential where close-interval pollen analyses using large pollen sums are combined with detailed macrofossil analyses not only of seeds, fruits or needles, but also of bud scales. Schneider & Tobolski's (1985) elegant investigations at Lago di Ganna

in northern Italy illustrate the potential of this approach in studying the establishment and subsequent expansion of *Fagus sylvatica*.

Modern analogues for these processes are, of course, very rare and difficult to study today. Fortunately the recent interest in biological invasions (e.g. Mack, 1985) is providing ecological insights into the invasion of established forests by other trees. Useful examples include studies on the invasion of *Pittosporum undulatum* Vent. into Australian eucalypt forests (Gleadow, 1982; Gleadow & Ashton, 1981), the invasion of *Pinus lutchuensis* Mayer into forests on Chichijima Island (Shimizu & Tabata, 1985), and the invasion of *Pinus radiata* D. Don into Australian eucalypt forests (Chilvers & Burdon, 1983). These studies all demonstrate the complexity of ecological invasions. They show, for example, the importance of gaps, of changes in the disturbance regime, and of chance dispersal for initial establishment, the role of environmental factors in influencing the rates of population expansion, and the clumped distribution of invaders within the established forests. Long-term monitoring of these 'natural experiments' could be of great value in understanding the processes important in Holocene tree invasions.

The main ecological implication to emerge from this discussion is that, just as in propagule dispersal, chance events were probably important in invasion and establishment of trees during the Holocene. Palmgren (1929), in considering plant distributions and colonizations, suggested that 'plant geography has doubtless been guilty of an omission by not taking into account chance as a real working factor . . . "chance" must be given a place amongst the biogeographically effective factors' (see also Romell (1938) and Simberloff (1978) for a more recent resurrection of chance as an alternative hypothesis in biogeography). Ecology, palaeoecology and historical biogeography have also tended to ignore the role of chance. Rowe (1966), in discussing range-limits, concluded that 'the ranges of plants frequently reflect a chance history of migration related to the vagaries of opportunity, competition, and disturbances.' Chance events in long-distance dispersal of propagules and in gap production and colonization may have played an important, even an essential, role in determining the order of arrival, facilitating the invasion, and influencing the rates of spread of forest trees, and hence in the broad-scale vegetation dynamics not only of the Holocene but also of earlier interglacials (Birks, 1986).

Tree spread and models of biological invasions. Many species' ranges are extremely dynamic over time-spans of hundred of years and spatial scales of $>10^3$–10^6 km² (e.g. Järvinen & Väisänen, 1979; Hengeveld, 1985b). Isochrone and isopollen maps provide unique insights into long-term dynamics of range boundaries and relative abundances of trees over thousands of years and areas of 10^5–10^9 km², insights that can have important biogeographical implications (e.g. Vuilleumier, 1987).

The isochrone maps depict tree colonization or invasion into the British Isles during the Holocene. A convenient summary of the rates and timings of these invasions is a plot of the cumulative area occupied by different trees through time (Fig. 13). These curves indicate contrasts in colon-

ization rates between the early arrivals (*Betula, Corylus, Ulmus, Quercus*) and the later colonizers (*Alnus, Tilia, Fraxinus, Fagus*). The contrasting rates for *Pinus* in England, Ireland and Scotland are particularly striking.

Logistic, S-shaped colonization curves such as in Fig. 13 are expected from a simple spatial diffusion process (Cliff *et al.*, 1981) involving contagious spread in a uniform environment. There is an initial primary or establishment phase, a diffusion phase resulting in rapid spread, a condensing phase, and a final saturation phase (Mack, 1985). Nearly all the curves in Fig. 13 follow this logistic pattern. The colonization of *Fagus* is clearly still in the diffusion phase, whereas all the other trees have reached the saturation phase but at different times in the Holocene. Interestingly the diffusion phases for *Alnus* and *Pinus* (England) are similar in slope to the diffusion phases of the early colonizers. The major differences between the early- and mid-Holocene colonizers¯ are in the length of the condensing phase (cf. *Corylus, Quercus, Alnus*). A logistic colonization model represents one of the simplest spatial diffusion processes and thus serves as a convenient 'null' model of spread in a uniform environment, against which observed patterns of colonization can be compared. If environmental factors (physical or biotic) have influenced the colonization process, deviations from a simple logistic curve could be expected. Such deviations are apparent in the *Fraxinus* and *Pinus* (Scotland) curves. Possible explanations for these deviations are presented above in the discussion of epidemic threshold theorems. Data of high spatial and temporal resolution could use this or related types of 'null' models to test competing hypotheses about the underlying causes of the observed tree patterns (e.g. T. Webb, 1986; Davis *et al.*, 1986; Prentice, 1986).

The recent upsurge of interest in the analysis of biological invasions (e.g. Drake & Williamson, 1986) has resulted in a series of mathematical models for invasions (e.g. Mollison, 1986; Hengeveld, 1989; Lubina & Levin, 1988). One of the most useful is Skellam's (1951, 1973) combined diffusion-growth model, developed in part from Fisher's (1937) genetic model for an advancing wave of advantageous genes. By combining spatial diffusion with exponential or logistic population growth, Skellam's model specifically regards invasion or range-spreading as a combined result of dispersal and arrival of propagules, establishment and growth, and population expansion. Bennett (1986a, 1988a, c) emphasizes the importance of identifying and considering the role of all these processes in determining observed rates of tree spread. Without local population growth, expansion, subsequent dispersal and further invasion, spreading could not occur.

Skellam's model assumes a homogeneous population invading a constant and homogeneous environment. It predicts that if an exponential increase in population coincides with an outward random dispersal of reproductive propagules (comparable to Brownian motion), a wave of population expansion will develop and spread at a constant radial rate. It also predicts that the rate of spatial advance of the range limit will be a linear function of the square root of the area occupied when plotted against time (see Skellam, 1951; Ammerman & Cavalli-Sforza, 1971; Williamson &
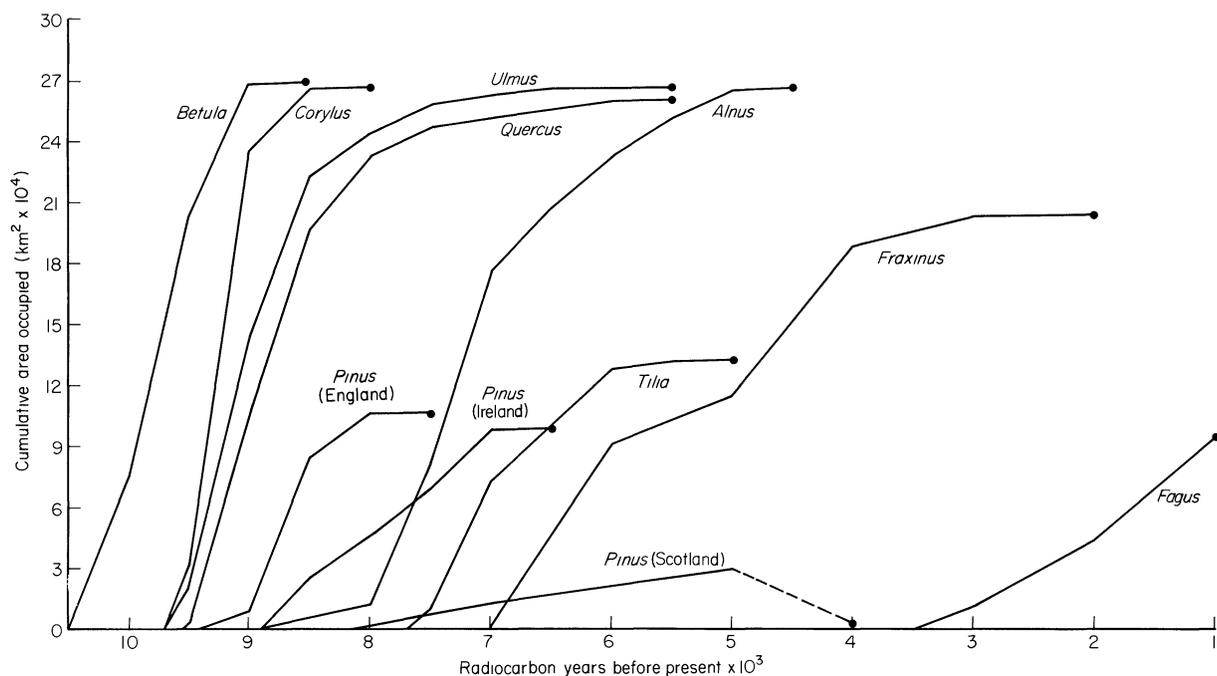
FIG. 13. Cumulative area ($km^2 \times 10^4$) occupied in the British Isles by the different forest trees during the Holocene plotted against radiocarbon years BP.

Brown, 1986; Hengeveld, 1988, 1989 for examples). Fig. 14 shows the square root of the cumulative-area data (Fig. 13) plotted against time. As Williamson & Brown (1986) discuss, the slope of the linear relationship is an estimate of $(rk)^{1/2}$ where r is the intrinsic rate of population increase and k is the mean square dispersion rate, diffusivity, or habitat-dependent diffusion constant (km^2 yr^{-1}). Estimates of the slope from least-squares regression are given in Table 3. The model is strictly concerned with advancing range limits, whereas the British data (Fig. 13) cover not only the diffusion phase but also the condensing and saturation phases (Cliff *et al.*, 1981). Slope estimates are given for the full data

sets of Fig. 14 and, in the cases of *Ulmus, Quercus* and *Tilia*, for the period prior to the saturation phase (9500–7000, 9500–7500 and 7500–6000 BP, respectively).

As Fig. 14 and Table 3 are based on very few data points, these estimates and the ensuing discussion are very tentative. The main purpose of this analysis is to focus attention on possible parallels between Holocene tree spread and biological invasions. The slopes are estimates of $(rk)^{1/2}$. As V, the spreading rate (km yr^{-1})$=2(rk)^{1/2}$ (Lubina & Levin, 1988), the slopes multiplied by 2 are estimates of the mean rate of spread of the range limit. The highest rate of spread is shown by *Corylus*, followed by *Betula, Pinus* (England),

TABLE 3. Estimates of the slopes for data in Fig. 14, correlation coefficient, number of data points used in the estimates of spreading rate (V) and k (diffusion constant), and the time span on which the estimates are based.

|	Slope	Correlation coefficient	No. of data points	V (km yr^{-1})	k (km^2 yr^{-1})	Time span (10^3 years BP)
Betula	0.24	0.97	4	0.49	3.5	10.0–9.0
Corylus	0.35	0.90	3	0.69	7.8	9.5–8.5
Ulmus	0.13	0.84	6	0.26	1.7	9.5–7.0
	0.10	0.81	7	0.20	1.0	9.5–6.5
Quercus	0.21	0.89	5	0.42	9.1	9.5–7.5
	0.10	0.79	8	0.21	2.2	9.5–6.0
Pinus (England)	0.24	0.95	3	0.47	5.9	9.5–8.0
Pinus (Ireland)	0.10	0.99	4	0.21	–	8.5–7.0
Pinus (Scotland)	0.05	0.96	4	0.09	–	8.0–5.0
Alnus	0.12	0.90	7	0.25	3.8	8.0–5.0
Tilia	0.17	0.94	4	0.33	3.9	7.5–6.0
	0.12	0.90	5	0.25	2.2	7.5–5.5
Fraxinus	0.06	0.97	4	0.11	–	6.0–3.0
Fagus	0.10	0.99	3	0.20	–	3.0–1.0
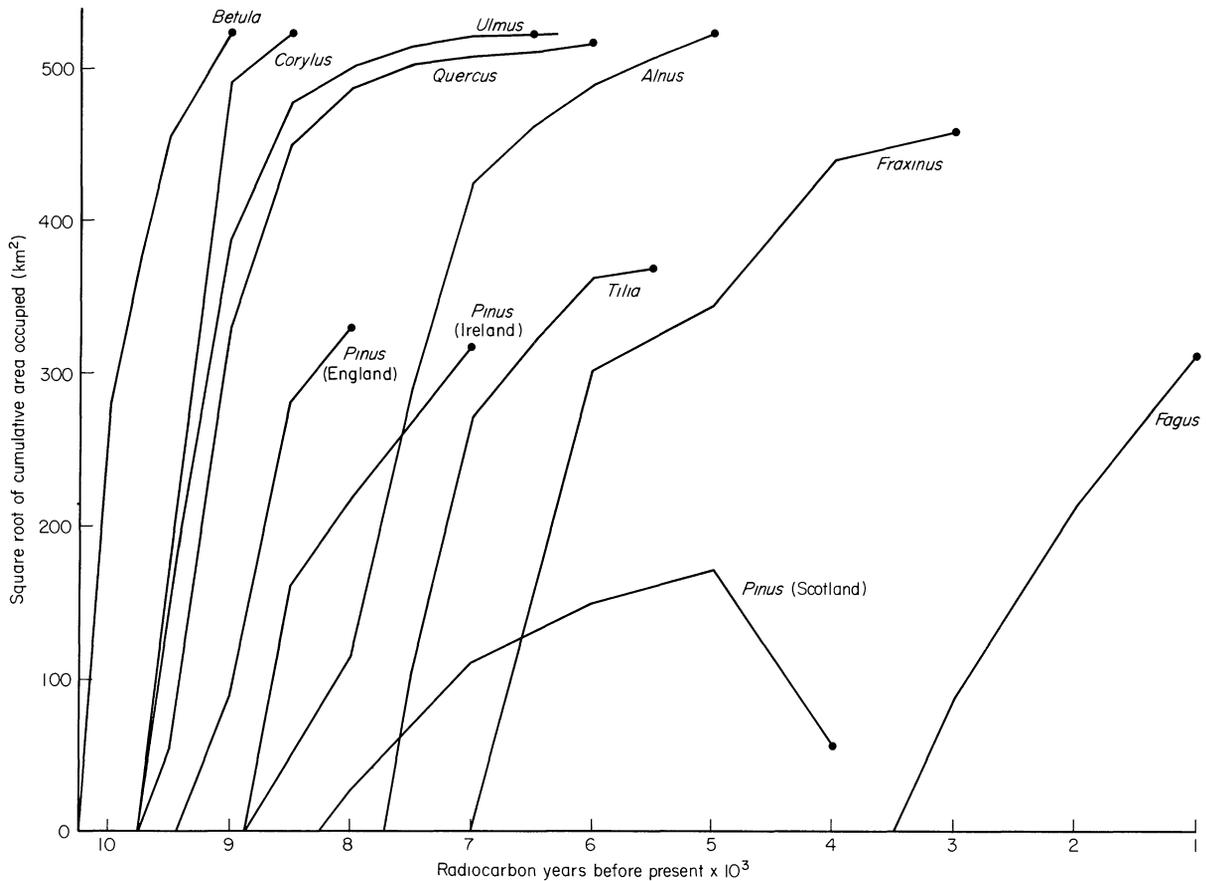
FIG. 14. Square root of the cumulative area (km²) occupied in the British Isles by the different forest trees during the Holocene plotted against radiocarbon years BP.

Quercus (9500–7500 BP), *Tilia* (7500–6000 BP), *Alnus*, *Pinus* (Ireland), *Fagus*, *Fraxinus* and *Pinus* (Scotland). These calculated mean rates of spread range from 690 m yr⁻¹ (*Corylus*) to 90 m yr⁻¹ (*Pinus* in Scotland) and contrast with the crude estimates on Table 1 and Fig. 12 that are based on rates of change of isochrones along one or two radii of the spreading patterns. If we knew the intrinsic rate of population increase, we could estimate k, the diffusion constant. Bennett (1983b) has estimated r for some of the trees mapped here on the basis of their Holocene population expansions at Hockham Mere (site 3 in Fig. 1). If, for purposes of discussion, we use these estimates, we can derive k, the diffusion constant (Table 3). These estimates are likely to be very approximate because r for a particular tree has probably varied geographically and temporally (Bennett, 1983a, c).

In the absence of related analyses from other areas it is not possible to evaluate these estimates of k. Given the intrinsic rates of population increase estimated by Bennett (1983b), they are estimates of the mean diffusion constant required to achieve the observed rates of invasion and occupancy of the areas colonized within the time periods during which the invasions actually occurred (Fig. 13). It should be emphasized that they are estimates of the mean rate of dispersion in all directions and that they are derived from the observed colonization patterns. For the trees for

which we have estimates of r, the order of mean rate of dispersion (k) is *Quercus, Corylus, Pinus* (England), *Tilia, Alnus, Betula* and *Ulmus*, the order of spreading rate (V) is *Corylus, Betula, Pinus* (England), *Quercus, Tilia, Ulmus* and *Alnus*, the order of intrinsic rate of population increase (r) is *Corylus, Betula, Ulmus, Pinus, Tilia, Quercus* and *Alnus*, and the order of arrival is *Betula, Corylus, Ulmus, Quercus, Pinus, Alnus* and *Tilia*. There is little correspondence among these orders. The reliability and implications of these estimates clearly require further research.

The diffusion model from which these surprisingly high rates of diffusion and spread are estimated assumes that the populations were invading areas where the tree was totally absent. Such high rates could be spurious because the model may be inappropriate or in error, the data may be in error, or the assumptions of the model are invalid for these data. If the trees were present over a large area in low amounts (and hence largely undetected palynologically; Bennett, 1985, 1988c; Green, 1987) prior to their expansion, the model would be inappropriate and the estimates would be a gross over-estimate. As Mack (1985) shows by simulation, each population or source accelerates the rate of invasion. The testing of Bennett's (1985, 1986a, 1988a, c) hypothesis of widespread populations but with very low densities throughout much of the range prior to the apparent 'arrival' or expansion times depicted in isochrone

maps would be an important step in resolving the mechanisms of tree spread and in understanding the estimated rates of spread. It will require very large pollen counts, reliable chronologies, and detailed macrofossil studies (e.g. Schneider & Tobolski, 1985) at many sites in critical areas near range limits (e.g. Davis *et al.*, 1986) and along presumed routes of spread (e.g. Hafsten, 1986). Small values and irregular occurrences of pollen types before their main expansion can perhaps be too readily dismissed as resulting from contamination or distant pollen transport, whereas they may reflect low local population densities, as predicted by Bennett's model. Such studies represent a challenge to current methodologies and interpretations.

In the context of recent discussions of biological invasions, it will be of interest to compare these estimates of *V* and *k* for long-term natural invasions with estimates for recent invasions by trees and with natural tree invasions in other areas during the Holocene. With such comparisons it will be possible to see if rates of past invasion are similar to present-day invasions, and hence provide a historical background against which to evaluate recent invasions. As Mack (1985) comments in his discussion of plant invasion, 'attempts to estimate population size with fossil pollen deal with a serious deficiency in plant population biology.'

CONCLUSIONS

The isochrone maps display the major patterns of tree-spreading in the British Isles during the Holocene. Analyses of these patterns in terms of the rates, timings, and directions of spread, the required propagule dispersal distances, the areas colonized, and the estimated mean rates of diffusion raise several questions in ecology, palaeoecology and biogeography. The maps clearly demonstrate the dynamic nature of range limits and highlight how little we understand about how they are controlled. The patterns of tree spread are diverse. They probably result from a mixture of chance factors and intrinsic biological factors interacting with external abiotic factors such as climate and soil. The patterns are interpreted here primarily in biological and stochastic terms, although alternative interpretations involving purely environmental controls are possible.

It is important to acknowledge that many of the explanations presented in the individual taxon accounts, such as the explanation for the early-Holocene spread and behaviour of hazel, are narrative in character (*sensu* Ball, 1975). They are largely untestable and are, at best, therefore pseudoscientific. This is a major limitation of much of historical biogeography and palaeoecology (Heck & McCoy, 1979; Simberloff, 1983; Ghiold & Hoffman, 1984; Birks, 1985b). Despite Popper's (1980) assertion that historical events are not precluded from falsifiable explanations, I concur with Simberloff's (1983) admission that 'we are propounding local narratives and not general theories' and Ghiold & Hoffman's (1984) conclusion that 'as frustrating as it may be, historical biogeography must remain a narrative science, with pluralistic methodology and using circumstantial evidence'.

These biological interpretations do, however, provide plausible and consistent explanations for the patterns

observed at the scale of the British Isles. These patterns are not so tractable solely in terms of broad-scale range-dynamics driven by continental-scale climatic change (e.g. Kutzbach & Guetter, 1986). Without independent data on past climate at the relevant spatial and temporal scales, maps such as these cannot contribute to the critical testing of competing hypotheses about climate ('equilibrium') and dispersal ('non-equilibrium') as factors controlling range limits in the past.

Prentice (1986) concluded that 'dynamic equilibrium may often be a reasonable approximation for the responses of the broadest continental-scale patterns to orbitally induced climatic change. But as spatial and temporal frames of observation are diminished and resolution increased, biotic processes must eventually come to dominate. At sufficiently fine scales the main observable phenomena are successional responses to natural disturbance events.' The challenge in interpreting maps such as these is that they represent spatial scales intermediate between 'continental-scale patterns' and 'fine scales' of individual forest stands. As we do not know at what scales 'biotic process . . . come to dominate', it is probable that both climatic and biotic factors have affected tree ranges at the scale of the British Isles, but it is difficult to sort out their relative roles. The isochrone maps provide a synthesis of numerous pollen-analytical studies within a relatively small area. The maps can be used to examine range-dynamics at a meso-scale and to interpret (or speculate) on the processes and factors controlling the patterns. Limitations in the interpretations are obvious and point the way to future directions of research in understanding the broad-scale patterns of tree dynamics in the Holocene of the British Isles.

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APPENDIX 1

Details of the sites shown in Fig. 1 and used in the construction of Figs. 2–10.

1. Loch of Winless	(Peglar, 1979)	22. World's End	(Devoy, 1979)
2. Murraster	(Johansen, 1975)	23. Killymaddy Lough	(Hirons, 1983)
3. Hockham Mere	(Bennett, 1983a)	24. Lochan Doilead	(Williams, 1977)
4. By Loch Assynt	(H. H. Birks unpubl.)	25. Glims Moss	(Keatinge & Dickson, 1979)
5. Abernethy Forest	(Birks & Mathewes, 1978)	26. Lewes II	(Thorley, 1981)
6. Loch Maree	(Birks, 1972)	27. Wingham	(Godwin, 1962)
7. Nant Ffrancon	(Hibbert & Switsur, 1976)	28. Valley Bog	(Chambers, 1978)
8. Din Moss	(Hibbert & Switsur, 1976)	29. Leash Fen	(Hicks, 1971)
9. Cors Tregaron	(Hibbert & Switsur, 1976; Turner, 1964)	30. Loch Ashik	(Williams, 1977; Birks & Williams, 1983)
10. Red Moss	(Hibbert, Switsur & West, 1971)	31. Loch Meodal	(Williams, 1977; Birks & Williams, 1983)
11. Scaleby Moss	(Godwin, Walker & Willis, 1957)	32. Loch Cleat	(Williams, 1977; Birks & Williams, 1983)
12. Loch Cill an Aonghais	(S. M. Peglar, unpubl.)	33. Loch Lomond	(Dickson *et al.*, 1978)
13. Little Loch Roag	(Birks & Madsen, 1979)	34. Coire Fee	(Huntley, 1981)
		35. Caenlochan Glen	(Huntley, 1981)
14. Blelham Tarn	(Pennington, 1965; Pennington *et al.*, 1976)	36. Steng Moss	(Davies & Turner, 1979)
15. Neasham Fen	(Bartley, Chambers & Hart-Jones, 1976)	37. Morrone Birkwoods	(Huntley, 1976)
		38. Weelhead Moss	(Turner *et al.*, 1973)
16. Holme Fen	(Godwin & Vishnu-Mittre, 1975)	39. Loch Cuithir	(Vasari & Vasari, 1968; Vasari, 1977)
17. The Chains	(Merryfield & Moore, 1974)	40. Drimnagall	(Rymer, 1974)
18. Somerset Levels	(Godwin, 1960; Beckett, 1979; Beckett & Hibbert, 1979)	41. Cors Dolfroig	(Edwards, 1980)
		42. Lodge Road Bog	(Baker *et al.*, 1978)
		43. Featherbed Moss	(Tallis & Switsur, 1973)
		44. Oban 1A	(Donner, 1957; W. Williams, unpubl.)
19. Dozmary Pool	(Brown, 1977)	45. Morden Carr	(Bartley *et al.*, 1976)
20. Crose Mere	(Beales, 1980)	47. Tynaspirit	(Lowe, 1978)
21. Roudsea Wood	(Birks, 1982a)	47. Braeroddach Loch	(Edwards & Rowntree, 1980)
		48. Duartbeg	(Moar, 1969a)
		49. Bigholm Burn	(Moar, 1969b)

50. Fen Bogs — (Atherden, 1976)
51. West House Moss — (Jones, 1977)
52. By Salen — (W. Williams, unpubl.)
53. Loch Cill Chriosd — (Birks, 1973)
54. Hatchmere — (H. J. B. Birks, unpubl.)
55. Shippea Hill — (Clark & Godwin, 1962)
56. An Druim, Eriboll — (H. H. Birks, unpubl.)
57. Thatcham — (Churchill, 1962)
58. Loch Pityoulish — (O'Sullivan, 1976)
59. Loch Sionascaig — (Pennington *et al.*, 1972)
60. Loch Clair — (Pennington *et al.*, 1972)
61. By Loch Coultrie — (H. H. Birks, unpubl.)
62. Lochan Dubh — (Kerslake, 1982)
63. Pow Hill — (Turner & Hodgson, 1981)
64. Allt na Feithe Sheilich — (Birks, 1975)
65. Coire Bog — (Birks, 1975)
66. Cooran Lane — (Birks, 1975)
67. Sluggan Bog — (I. C. Goddard, 1971; Smith & Pilcher, 1973)
68. Ballynagilly — (Pilcher & Smith, 1979)
69. Beaghmore — (Pilcher, 1969)
70. Slieve Gallion — (Pilcher, 1973)
71. Ringnell Quay — (Morrison, 1961)
72. Ballyhalbert — (Morrison & Stephens, 1960)
73. Altnahinch — (A. Goddard, 1971; Smith & Pilcher, 1973)
74. Ballyscullion — (Smith & Pilcher, 1973)
74. Gortcorbies — (I. C. Goddard, 1971; Smith & Pilcher, 1973)
76. Roddans Port — (Morrison & Stephens, 1965)
77. Woodgrange — (Singh & Smith, 1973)
78. Redbog — (Watts, 1985)
79. Coolteen — (Craig, 1978)
80. Belle Lake — (Craig, 1978)
81. Muckross — (E. Vokes and W. A. Watts, unpubl.)
82. Lough Nadourcon — (M. Telford and W. A. Watts, unpubl.)
83. Burnmoor Tarn — (Pennington, 1970)
84. Gortlacka — (Watts, 1984)
85. Littleton Bog — (Mitchell, 1965; W. A. Watts, unpubl.)
86. Lochan Taynish — (Rymer, 1974)
87. Clonsast — (Mitchell, 1955)
88. Treanscrabbagh — (W. A. Watts, unpubl.)

89. Rannoch Moor — (Birks, 1975)
90. Gleann Mor — (Walker, 1984)
91. Creich Castle — (Cundill & Whittington, 1983)
92. Coed Taf — (Chambers, 1983a)
93. Cefn Gwernffrwd — (Chambers, 1982, 1983b)
94. Cwm Gywion — (Ince, 1983)
95. Craig-y-Fro — (Walker, 1982a)
96. Craig Cerrig-gleisiad — (Walker, 1982a)
97. Llyn Gwernan — (Lowe, 1981)
98. The Bog, Roos — (Beckett, 1981a)
99. Traeth Mawr — (Walker, 1982b)
100. Tyndrum — (Lowe & Walker, 1981)
101. Blelham Bog — (Pennington & Bonny, 1970)
102. Kildale — (Jones, 1977)
103. Blackness — (Walker, 1975)
104. Clashgour — (Walker & Lowe, 1981)
105. Rannoch Station I and II — (Walker & Lowe, 1979)
106. Corrour 2 — (Walker & Lowe, 1979)
107. Kingshouse — (Walker & Lowe, 1977)
108. Coire Clachach — (Walker & Lowe, 1982, 1985)
109. Cledlyn Valley Pingo U — (Handa & Moore, 1976)
110. Hawks Tor — (Brown, 1977)
111. Subhainn Lochan — (Kerslake, 1982)
112. Amulree 2 — (Lowe & Walker, 1977)
113. Blacklane Brook M1 — (Simmons, Rand & Crabtree, 1983)
114. Meenadoan — (Pilcher & Larmour, 1982)
115. Carrowkeel — (Göransson, 1984)
116. Ballygawley Lough — (Göransson, 1984)
117. Dubh Lochan — (Stewart, Walker & Dickson, 1984)
118. Shaugh Moor — (Beckett, 1981b)
119. Newferry — (Smith, 1981, 1984)
120. Carrivnoragh — (S. M. Holland unpubl. in Smith, 1984)
121. Lackan I — (S. M. Holland unpubl. in Smith, 1984)
122. Fullerton — (Smith *et al.*, 1980)
123. Loch Cholla — (Andrews, 1987)
124. Craigbarnet Muir — (Stewart, 1983)
125. Torness — (Walker & Lowe, 1982, 1985)
126. Melynllyn — (Walker, 1978)
127. Machrie Moor — (Robinson, 1983; Robinson & Dickson, 1988)
128. Clarach Bay — (Heyworth *et al.*, 1985)
129. Moel y Gerddi — (Chambers & Price, 1985)

130. Johnny's Wood   (H. J. B. Birks, unpubl.)
131. Loch Garten   (O'Sullivan, 1974)
132. Loch Dungeon peat   (Birks, 1975)

133. The Mere, Stow Bedon   (Bennett, 1986b)
134. Cranes Moor   (Barber, 1987)
135. Gatcombe Withy Bed   (Barber, 1987)