PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Rate of Spread and Population in Increase of Forest Trees During the Postglacial [and Discussion]

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Phil. Trans. R. Soc. Lond. B 1986 **314**, 523-531
doi: 10.1098/rstb.1986.0071

Phil. Trans. R. Soc. Lond. B **314**, 523–531 (1986)
Printed in Great Britain

The rate of spread and population increase of forest trees during the postglacial

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The last major ice-sheets in northern Europe and northern North America reached their maximum extent about 18000 years ago. With the retreat of the ice-sheets, changing climates permitted many plants to expand their ranges onto freshly deglaciated ground. The spread of these plants can be followed across continents by means of the pollen preserved in suitable sediments. Two aspects of this spread will be discussed. First, at individual sites, it is possible to compare the way in which the populations increase with theoretical models of population growth. It appears that, for forest trees, the populations increased exponentially, doubling every 20–500 years. Second, by estimating, from the pollen curve, when populations of each taxon began to increase at a series of sites across a continent, it is possible to estimate annual 'rates of spread'. These may be up to 2000 m a^{-1}, but it appears that spread may be achieved at population densities too low to be detected in the pollen record. The 'spread' observed may be due solely to the initial abundance/distance gradient and the rate of population increase.

1. Introduction

Observing changes of populations in undisturbed plant and animal communities is often difficult, even with short-lived organisms; any quantitative data is therefore invaluable. This paper describes how such data may be derived from the fossil pollen record of the changing abundances and distributions of tree populations following deglaciation in the northern hemisphere 10000 years ago. These changes provide an example of naturally occurring invasions on a timescale of thousands of years and over hundreds of kilometres in response to global climatic change (see Birks 1986). Such changes have occurred many times during the Pleistocene and must have been a major selective force in the evolution of present day taxa. It should be instructive to compare changes taking place on such long timescales with those taking place today.

2. Nature of the evidence

Reproductively active plants produce pollen, often in great abundance, which is preserved in suitable sediments that accumulate at the time of pollen release. Pollen is resistant to many forms of chemical attack, except oxidation. This limits 'suitable sediments' to anoxic environments, such as occur at the bottom of lakes. Analyses of the pollen content of cores from such sediments reveal changes in pollen content, through time, which can be related to changes in flora and vegetation of the area that contributed pollen to the sediment. Sediments of small (1–10 ha), deep (5–20 m) lakes are preferred because of their undisturbed sedimentary environments and limited pollen catchment areas relative to larger lakes (Jacobson & Bradshaw 1981).

Postglacial lake sediments of the temperate regions of the northern hemisphere are usually soft algal gyttja, easily cored with hand-operated apparatus, with high pollen content and excellent pollen preservation. Subsamples (*ca.* 1 cm^3) from the cores are processed to remove unwanted material: HF to remove silicates, HCl for carbonates, NaOH for humic acids, and a 9:1 acetic anhydride:sulphuric acid mixture for cellulosic components. Coarse material is removed by sieving with a 180 μm mesh. The residues are stained, dehydrated, and mounted in silicone oil for microscopic examination. Before the material is processed, a known quantity of an exotic pollen type (*Eucalyptus* or *Lycopodium*) is usually added to the measured sediment volume. It is then possible to estimate fossil pollen concentrations from the ratio of fossil pollen to exotic pollen (see Birks & Birks (1980) for methods in use). Pollen is identified, and the numbers of each type are counted at a magnification of about × 400, with × 1000 for critical identifications. This is the most time-consuming part of the whole process. Results are expressed, for each type at each level in the core, as percentages of the total pollen identified or as concentrations (numbers of grains cm^{-3}), plotted against depth. The organic sediment containing fossil pollen is readily dated by the radiocarbon method, thus providing a timescale for the changes in pollen content, and permitting calculation of pollen accumulation rates (grain $cm^{-2}\ a^{-1}$). Problems with variations between plant species in pollen production, dispersal and preservation, together with identification limitations, are discussed by Faegri & Iversen (1975), Birks & Birks (1980) and Bradley (1985).

Pollen diagrams have been obtained by these methods from hundreds of sites around the world over the last 60 years. The changing pollen content in cores, reflecting changing vegetation composition, has typically been interpreted in terms of shifting vegetation units during postglacial colonization; however, it is also possible to look at what is happening to individual taxa and the rates at which they change their distributions, from a purely population-ecology viewpoint (Watts 1973). The rest of this paper is about such studies.

3. Phases of increase

The plot for any type in a pollen diagram often shows a period when the taxon is absent, a period when its pollen frequencies are increasing, and a later period of more or less stable values. Watts (1973) pointed out that this sequence resembled the classic S-shaped curve of population ecology, and suggested that attempts should be made to see if such sequences were exponential or logistic increases. This can be done simply by plotting the logarithm of pollen accumulation rate against sample age; a linear plot demonstrates exponential increase. Logarithmic plots of this type also serve the function of displaying simply the increase phase over many orders of magnitude, because no more than two or three orders can be easily comprehended on a linear scale plot. A typical small lake could have 10^6 trees within 2 km of it, at a density of 1000 trees ha^{-1} (Bennett 1985). First arrival and the beginning of increase starts with one or two trees in that area, comprising 1 in 10^6 of the forest. Increase from that level to, say, 20%, simply cannot be demonstrated with linear-scale plotting, but is easily revealed on a logarithmic-scale plot. Any study of first arrival and increase phases must encompass the whole range of the phenomenon, or as much of it as possible.

Tsukada (1980, 1982*a*, *b*, *c*, 1983), Tsukada & Sugita (1982) and Bennett (1983) have recently shown that the increasing phases of pollen curves are exponential, and, moreover, that the phase of increase has already begun at the lowest levels of the pollen detectable. Routine pollen counts rarely exceed 1000 grains per sample, so abundances of less than 0.1 % are not normally measurable. As we have seen, this is already three orders of magnitude above a possible minimum abundance. Recent efforts to trace the increase phase below 0.1 % have found that exponential growth of the population is occurring from at least one order of magnitude lower (K. D. Bennett, unpublished data).

Because pollen accumulation rates, and hence tree populations, are increasing exponentially, we can obtain a doubling time, in radiocarbon years, for each taxon (table 1), which may be compared with values for doubling times obtained from increasing populations in present day forests (table 2; see also Piñero *et al.* (1984) for details). The data sets agree in showing tree populations doubling on timescales of 10–10^3 years, mostly about 10^2 years. The fossil data are for increasing populations averaged over large areas (up to 10 km^2, perhaps), and over long periods of time (more than 10^3 years), whereas the modern data comes from very much smaller

Table 1. Rates of increase of tree populations: fossil pollen data

taxon	doubling time* ^{14}C years	reference
Pinus contorta	107, 173	Tsukada & Sugita (1982)
Pseudotsuga menziesii	52	Tsukada & Sugita (1982)
	171, 365	Tsukada (1982*c*)
Abies	408	Tsukada & Sugita (1982)
Picea	35, 178	Tsukada & Sugita (1982)
Tsuga mertensiana	31, 462	Tsukada & Sugita (1982)
Thuja plicata	224, 231, 239	Tsukada & Sugita (1982)
Alnus rubra	112, 178	Tsukada & Sugita (1982)
Salix	204	Tsukada & Sugita (1982)
Fagus	187	Tsukada (1982*b*)
Betula	59	Bennett (1983)
Pinus sylvestris	73	Bennett (1983)
Corylus avellana	46, 45	Bennett (1983, 1986)
Ulmus	67, 29	Bennett (1983, 1986)
Quercus	141, 78	Bennett (1983, 1986)
Tilia cordata	99	Bennett (1983)
Alnus glutinosa	174, 268	Bennett (1983, 1986)

* Calculated from ln $(2/r)$, where r is the gradient of a regression of pollen accumulation rate (grains cm^{-2} a^{-1}) against age (^{14}C years).

Table 2. Rates of increase of tree populations: observational data

taxon	doubling time* years	reference
Araucaria hunsteinii	8	Enright & Ogden (1979)
	13	Enright (1982)
Astrocaryum mexicanum	18	Piñero *et al.* (1984)
Nothofagus fusca	25	Enright & Ogden (1979)
Araucaria cunninghamii	34	Enright & Ogden (1979)
Podococcus barteri	56	Bullock (1980)
Sequoia sempervirens	164	Namkoong & Roberds (1974)
Pentaclethra macroloba	347	Hartshorn (1975)

* Calculated from the eigenvalue (λ) of the transition matrix. ln $\lambda = r$, doubling time = ln $(2/r)$ (see Piñero *et al.* 1984). Where authors give a range of estimates for λ, the most rapid is used here.

experimental plots, and over much shorter periods of time. Given these differences in the nature of the data, there is an encouraging resemblance between the figures for population growth rate of modern and fossil populations. Some of the authors of the data in table 1 (see, for example, Hartshorn 1975) consider that the population growth rates they obtain are so low as to be indistinguishable from zero, so that populations are effectively stable. The fossil data show that such low growth rates can be maintained for long periods of time (longer than 10^3 years) and result ultimately in significant changes in species abundances.

4. SPREAD

The spread of taxa across continents has been traced using the pollen record by two distinct approaches. First, pollen frequencies for each taxon at selected time horizons have been plotted, giving, for each taxon, a series of maps showing how the distribution/abundance relation changes with time. These are called 'isopollen' maps, and the approach, pioneered by Szafer (1935), has now been refined by the advent of radiocarbon dating (see Ralska-Jasiewiczowa 1983; Webb *et al.* 1983*a*, *b*; Huntley & Birks 1983). The second approach, typified by Davis (1981), identifies a point on the increasing curve of pollen accumulation rates, where a 'sharp increase' or a 'ten-fold increase' (Davis 1983) is considered to begin, and plots, on one map for each taxon, the time when the 'sharp increase' commences. Such maps are called 'isochrone' maps. Smith & Pilcher (1973) had earlier separated the increasing pollen curve into two phases by a 'rational limit'; this is 'the point at which the pollen curve begins to rise to sustained high values' (Smith & Pilcher 1973, p. 904). Estimates of rates of spread have been made from both these approaches. Davis (1981) suggested that the tree species she considered in eastern North America were, during the early postglacial, spreading at rates of between 100 and 400 m a^{-1}; Huntley & Birks (1983) obtained rates of up to 2000 m a^{-1} for taxa in Europe. These figures can only be considered as estimates of postglacial rates of spread if tree populations spread at densities of more than one tree per hectare. Strictly, they should only be taken to represent the rate at which the area occupied by a taxon of greater than a certain density (this varies between taxa) is changing. It does not necessarily measure the rate of spread of the population margin.

There are considerable problems in estimating rates of spread from pollen data. As I have indicated, plant population densities vary over several orders of magnitude, and only the upper three orders are detectable by pollen analysis. We cannot trace plant population densities much less than 1 ha^{-1}, and are therefore unable to assess whether spread is actually taking place at lower densities. Traditionally, it has been supposed that postglacial spread of plant populations is limited by dispersal mechanisms, but it is equally possible that dispersal of propagules is very effective (witness the fact that oceanic islands have a flora at all), and the limiting factor is the ability to establish and increase populations in the presence of existing vegetation. Also, we simply do not know what cold stage distribution/abundance relations were really like. If some of the taxa currently abundant had widespread cold stage distributions but at densities below 1 ha^{-1}, they could have occurred much nearer ice margins than is often supposed, and this would obviously have considerable bearing on calculation of rates of spread onto the previously glaciated area. 'Thus every broad front of a climax formation is preceded by a fringe of outliers in favoured localities, so that territory is very quickly colonized when climate alters' (Godwin 1966, p. 6). Finally, as discussed earlier, there is actually no reason to suppose that the phase of increase of pollen curves is divisible into two phases as Smith & Pilcher (1973) and Davis (1981) suggest. The apparent 'sharp' or 'sudden' increase may be an artefact of plotting values that rise exponentially on a linear scale. These problems are discussed in more detail in Bennett (1985).

5. Combined effect: spread and increase

Figure 1 illustrates the combined result of the rates of population spread and increase discussed above. In this example, the taxon appears to be spreading at about 430 m a^{-1}, but this is due solely to the initial abundance/distance gradient and the rate of population increase. The actual rate of spread could be greater or less than this, but is undetectable because of the relatively high population densities needed before the taxon would be represented in the pollen rain. Probably only at very high rates of population increase (doubling every 10–20 years) will the apparent rate of spread be equal to the actual rate of spread. Populations are then establishing and increasing so rapidly that it is the rate of spread which is limiting, with maximum population densities being achieved shortly after dispersal into a new distribution area.

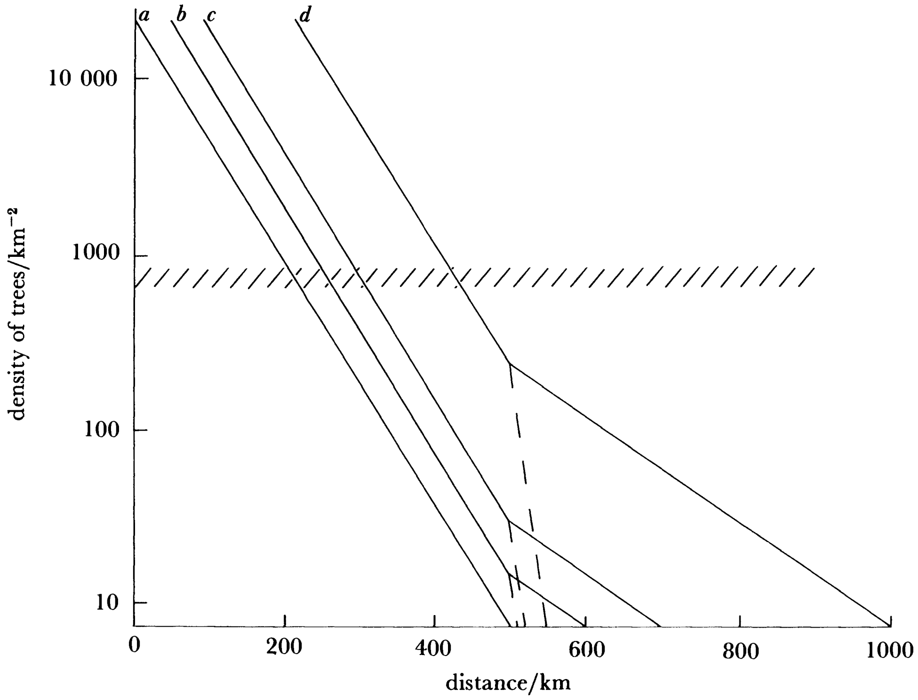

Figure 1. Hypothetical section across the margin of a species range. Abundance of the taxon is plotted on the ordinate (note the logarithmic scale), distance on the abscissa, for four time intervals as the species expands its range: $a = 0$, $b = 100$, $c = 200$, $d = 500$ years since expansion began. Population densities double every hundred years, while the margin of the range is advancing at 100 m a^{-1} (broken line) or 1000 m a^{-1} (solid line). The level of abundance at which the taxon would normally be detected by routine pollen analysis is shaded. In this example, the species appears to be spreading at about 430 m a^{-1}, but this is due to the abundance/distance gradient and the rate of population increase, rather than the rate of spread at the species range limit. The apparent rate of spread may be greater or less than the actual rate of spread. Note that, as the margin advances, the overall abundance/distance gradient could steepen, become more shallow, or remain constant, depending on the relations between initial abundance/distance gradient, rate of population increase, and rate of spread of margin.

6. CONCLUSION

Analysis of the increase phases of pollen curves shows that tree populations in the early postglacial increased with doubling times of around 100 years. The effect of this on initial distribution/abundance gradients is to produce apparent rates of spread of regions densely occupied by these taxa of up to 2000 m a^{-1}. Because of the high densities necessary for detection of taxa in the pollen record, we actually know little about dispersal rates of the various taxa, and hence cannot readily discuss this aspect in relation to known dispersal mechanisms.

However, the observed rates of increase are similar to those in operation today where tree populations are on the increase (tables 1 and 2). There would seem, therefore, to be no need to invoke mechanisms to explain postglacial spread and increase beyond those that can be observed today. A forest today will contain areas where any given taxon is increasing, decreasing, or stable, in a rough balance. When, in the early postglacial, a population was in the process of increase, there would initially have been few places where it occurred at all, and increase predominated. As its density increased, the possible factors that might cause decrease also became more probable, until a balance was reached. At this point we enter the realm of how and why rates of increase decrease. It is not clear what would be an appropriate model.

The potential of the fossil tree pollen record for investigating rates of change in undisturbed populations is clear. We probably owe the fact that there is such a record to the longevity of trees and their long pre-reproductive period. Plants with much shorter life spans can increase their populations much more rapidly (data in Sarukhán & Gadgil 1974; Law *et al.* 1977; Werner & Caswell 1977; Leverich & Levin 1979; Fetcher & Shaver 1983), and consequently their distribution changes after the climatic changes at the end of the last glaciation cannot be resolved in the pollen record.

I thank Dr L. C. Cwynar, Dr B. Huntley, Dr H. F. Lamb, Dr G. M. MacDonald, Professor W. A. Watts and Dr T. Webb, III, for helpful discussions of some of the topics raised in this paper, and Mrs A. M. Bennett, Dr P. L. Gibbard, Professor L. J. Maher, Jr, Mrs S. M. Peglar and Professor R. G. West, F.R.S., for advice and moral support following the Discussion Meeting. I am especially grateful to Dr H. J. B. Birks and Dr J. C. Ritchie for supervising me during the tenure of a NERC Research Studentship and a NSERCC Postdoctoral Fellowship, for discussions and support at every stage of my research, and encouragement to develop it along these lines.

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Discussion

SIR RICHARD SOUTHWOOD, F.R.S. (*Department of Zoology, South Parks Road, Oxford OX*1 3*PS, U.K.*). To what extent have the 'frontiers' of the invasion by trees kept a constant distance from the edge of the ice?

K. D. BENNETT. Some tree taxa, such as *Betula* in Europe and *Picea* in North America, probably did keep up with retreating ice margins, but other taxa spread at lower rates. The rate of retreat of ice margins must be some function of climate, whereas the rate of spread of tree taxa probably has more to do with their intrinsic reproductive properties. It would thus be surprising if there were much coincidence between the two, either in rate or direction.

J. H. Lawton (*Department of Biology, University of York, York YO1 5DD, U.K.*). I can understand how a wind-dispersed tree like *Betula* could advance several hundred metres a year, but I find it difficult to understand how those with much larger seeds, like *Fagus* or *Quercus*, could.

K. D. Bennett. I agree that it is puzzling. There appears to be no real distinction between taxa like *Fagus*, *Alnus* or *Corylus*, despite their different dispersal strategies. Animals may have been important agents in the spread of some trees.

A. Gibbs (*Research School of Biological Sciences, Australian National University, Box 475, P.O., Canberra City, A.C.T. 2601, Australia*). The genetics must also be interesting, in that some populations may be uniform while others are a mixture of fast- and slow-spreading types. Have the colonizers been compared with the source populations genetically?

K. D. Bennett. Results certainly support the view that one taxon can disperse significantly faster than another, and rates of spread differ at different margins of the distribution.

M. H. Williamson (*Department of Biology, University of York, York YO1 5DD, U.K.*). It is interesting to see the evidence of different rates of spreading in Europe and North America, where the species mix is different. Is there any information about the rate of movement of redwoods and hemlocks in North America? If *Acer* moved rapidly there, why did sycamore (*A. pseudoplatanus*) not colonize parts of Europe like the United Kingdom?

K. D. Bennett. North American *Acer* species are different ecologically and also in spreading rate from northern European *Acer* species. These appear to have spread slower than some other genera like *Corylus*. Intercontinental comparisons are not easy to make at the present time.

M. W. Holdgate (*Department of the Environment, 2 Marsham Street, London SW1P 3EB, UK.*). We know that forest composition was different in other interglacials, for example with greater prominence of genera like *Carpinus* in Britain. Does Dr Bennett have any data from the earlier interglacial periods to set against those in his paper?

K. D. Bennett. The pattern may well differ because different refugia were available. *Carpinus* was very prominent in the last interglacial, but invaded Britain only late in the current one. We do not have enough data to describe the details, especially because there is a lack of an independent timescale in previous interglacials.

W. D. Hamilton, F.R.S. Do Dr Bennett's results throw light on the status of *Fagus* in Britain?

K. D. Bennett. *Fagus* appears to have reached south-eastern Britain about 3000 years before present (Huntley & Birks 1983). *Carpinus*, on the other hand, probably colonized later (see Godwin 1975). The data seem to justify a claim for native status for the former, and I think the latter is also likely to be native but there are more grounds for uncertainty.

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G. R. Conway (*Imperial College Centre for Environmental Technology*, *48 Prince's Gardens*, *London SW7 1LU*, *U.K.*). I am interested in the movement of early crop plants. The postglacial expansion of *Quercus* in the eastern Mediterranean was accompanied by the wild wheats, emmer and einkorn. The conventional wisdom is that, once domesticated, these wheats were carried by hand through Europe. Referring to your maps of the spread of *Quercus* in Europe, is there any evidence of the accompanying natural spread of wild wheats? If so, the wild wheats could have been domesticated *in situ* in Europe. Could it also be possible that *Quercus* and other tree species were spread deliberately by man once the idea of cultivation had become common?

K. D. Bennett. The maps of Huntley & Birks (1983) suggest that *Quercus* spread across Europe more rapidly, and earlier in the postglacial, than cereals did. I cannot comment on the possibility of *in situ* domestication of wheat in Europe.

It is possible that *Quercus* and other tree species were spread deliberately by man, but this would have been before cultivation became common. There is no evidence that *Quercus* or any other tree species was spread by man, deliberately or accidentally, during the early postglacial. It seems unlikely in view of probable low human population densities, and the fact that sequences similar to those for the postglacial occur in previous interglacials.