Available online at www.sciencedirect.com

SCIENCE DIRECT®

Review of Palaeobotany and Palynology 134 (2005) 185–196

Review of Palaeobotany & Palynology

www.elsevier.com/locate/revpalbo

Modelling pollen dispersal and deposition using HUMPOL software, including simulating windroses and irregular lakes

M. Jane Bunting*, Dick Middleton

Department of Geography, University of Hull, Cottingham Road, Hull, HU6 7RX, UK

Received 1 July 2004; accepted 15 December 2004

Abstract

This paper introduces a suite of software (HUMPOL) for modelling pollen dispersal and deposition. The suite uses a standard algorithm, the Sutton equation, to model pollen dispersal from vegetation sources and pollen deposition at a sampling location but handles vegetation data more flexibly than existing software packages. The suite is designed as a platform for development of new models of pollen dispersal and deposition, and the production of simulated pollen data from maps of real landscapes for empirical tests of the model. Results are shown to be comparable with those produced by existing software. We also present a simple variation on the standard algorithm which simulates a variable windrose (current models assume uniform wind distribution around the compass) and show that this can reproduce the main features of empirical data.

Keywords: Delphi; pollen–vegetation relationship; Prentice model; Sutton equation; Windows; windrose

1. Introduction

Quantitative reconstruction of past plant abundance and distribution from fossil pollen records has been the goal of palynological research since the earliest days (e.g. Von Post's 1916 lecture; Von Post, 1967) yet remains elusive. Palynologists argue among themselves over interpretation of pollen assemblages and some non-palynologists doubt or dismiss the findings of palaeoecologists. Utilising the full potential of the pollen record, and developing a quantifiable understanding of its precision and limitations, is an increasingly urgent need if palynologists are to participate fully in current debates and research agendas, such as the response of vegetation to future environmental change (Sugita, 1994; Birks, 1996).

The pollen dispersal and deposition system is highly complex and investigations have been helped by the creation of a sequence of models which can replicate the major features of the system (Davis, 1963; Tauber, 1965; Kabailiene, 1969; Andersen, 1970; Jacobson and Bradshaw, 1981; Prentice, 1985; Prentice et al., 1987; Jackson, 1994; Sugita, 1994; Sugita et al., 1999). Simplification via modelling is a

* Corresponding author. Fax: +1482 466340.
E-mail addresses: m.j.bunting@hull.ac.uk (M.J. Bunting), r.middleton@hull.ac.uk (D. Middleton).

0034-6667/$ - see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.revpalbo.2004.12.009

useful approach to developing a better understanding of complex systems, since model systems can be controlled, manipulated, and measured, and experiments are fully replicable, properties singularly lacking in the 'real world'. Relatively rapid experiments with a large number of possible input scenarios can both give insight into the real-world system and act as a valuable tool in the design of empirical experiments or, in the case of palaeoecology, the interpretation of empirical measurements (i.e. pollen assemblages from past sediments). This approach has proved effective in enabling the development of other scientific fields dealing with hugely complex systems such as ecology, hydrology and meteorology.

In this paper, we summarise existing models of pollen dispersal and deposition, and explore the assumptions they require. We then present a new software package, HUMPOL, which enables the models to be applied with fewer assumptions, and discuss the possible applications.

1.1. The Prentice model

The Prentice model (Prentice, 1985) is probably the most widely used of the pollen dispersal and deposition models currently available. The model simulates the pollen loading (y_{ik}) from species i at the surface of a basin at site k originating from plants of taxon i positioned in the surrounding landscape. The pollen loading at the centre of a basin is described by the following model (Prentice, 1985, 1988):

$$y_{ik} = \alpha_i \int_R^{Z_C} x_{ik}(z) g_i(z) dz + \omega_{ik} \tag{1}$$

where; α_i=taxon-specific relative pollen productivity estimate; $x_{ik}(z)$=the mean plant abundance of taxon i at distance z from the centre of the basin; $g_i(z)$=a pollen dispersal and deposition function for taxon i located at distance z from the centre of the basin, based on Sutton's ground source model of particle dispersal (Sutton, 1953; Prentice, 1988); R=radius of the basin; Z_C=distance from centre of basin to outer limit of vegetation survey; ω_{ik}=background pollen component of taxon i at site k (a constant).

Simple predictions such as variations in source area with basin size have been tested against empirical data successfully (see e.g. Jackson, 1990; Calcote, 1995). The model has been used to simulate and explore the behaviour of a variety of landscape pollen signals (e.g. Sugita, 1994; Sugita et al., 1997; Sugita et al., 1999). It also forms the basis of the 'Landscape Reconstruction Algorithm' approach to quantitative reconstruction of past vegetation assemblages (Broström, 2002; Sugita, S., personal communication, 2003), which has been successfully compared with empirical data (Sugita, S., personal communication, 2003; Nielsen, A.B., 2003). Forms of this model lie at the centre of the POLLSCAPE simulation approach and software suite, developed by Shinya Sugita (e.g. Sugita, 1993, 1994; Sugita et al., 1997, 1999; Broström, 2002).

The Prentice model, as described above, is based on the assumption that pollen is deposited at a single point and then not reworked, which is reasonable for a vegetated surface such as a moss polster, or a pollen trap. However, pollen deposited onto the surface of a lake is unlikely to simply sink and be incorporated into the sediment below without at least some mixing. Sugita (1993, 1994) presents an alternative version of the model, referred to in this paper as the Prentice–Sugita model, which takes into account the pollen loading across an entire lake surface. He effectively assumes total mixing of pollen throughout the water body between deposition on the surface and final incorporation into the sediment. Using the Prentice–Sugita approach, the pollen assemblage incorporated into the sediment below the central point on the lake surface is simulated as an average of the pollen loading across the entire lake surface.

1.2. Assumptions underlying POLLSCAPE

Vegetation is essentially treated as one-dimensional in the form of the model presented by Prentice (1985) and in the 'ring source' approach used in POLLSCAPE (Sugita, 1993, 1994). In POLLSCAPE, mean vegetation composition is calculated for a series of incremental rings around the sampling point (see Fig. 1a). Each ring is then represented in the model as a single point source located at the appropriate radial distance from the sample location (a series of values of $x_{ik}(z)$ for incremental z values from R to Z_C). By expressing vegetation composition in this way, the modeller assumes that wind direction is evenly distributed around the compass.

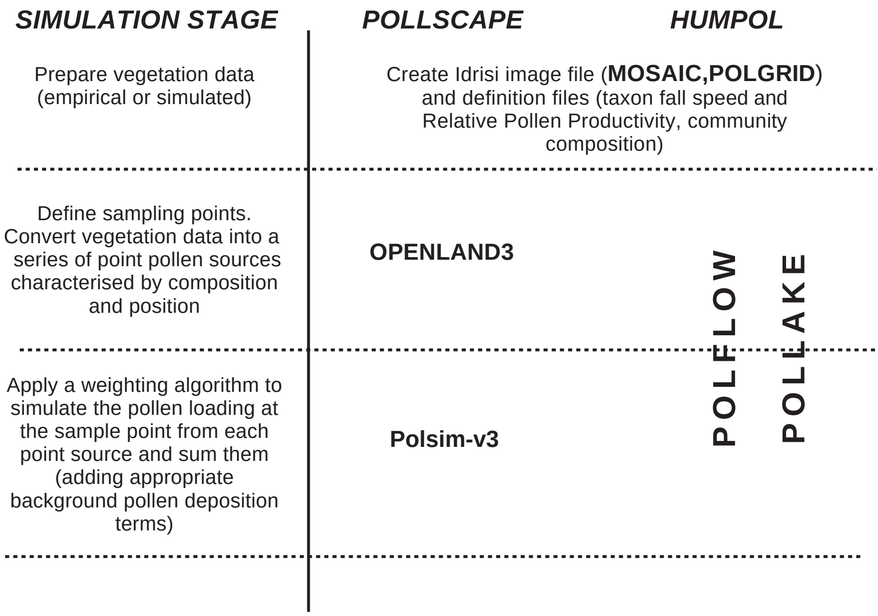

Fig. 1. Schematic of the conversion of vegetation data into pollen sources a) under the ring source model (Sugita, 1993) and b) under the multiple-cell source model (this paper).

The POLLSCAPE approach also requires the assumption that the site receiving the pollen is a circular opening in a closed vegetation canopy and simulates pollen loading at a single point at the centre of such an opening. When used to simulate the pollen assemblage predicted from empirical vegetation maps, non-circular lakes are approximated to circular by various means. OPENLAND3 (Eklöf et al., 2004), a package designed to prepare ring source data for use in Sugita's POLLSCAPE programs, defines basin size by fitting the largest possible circle centred on the sampling point that is entirely contained within the actual lake. Because basin size is a prime determinant of pollen source area (e.g. Prentice, 1985, 1988; Sugita, 1994), this may lead to some errors when compared with empirical data, since if the mapped lake departs strongly from the circular, the actual size may be substantially different to that modelled.

In the Prentice form, no subsequent movement of pollen is allowed for, which seems reasonable for bogs and mires where limited post-depositional pollen movement is anticipated. In lakes, the Prentice–Sugita form of the model assumes total mixing of pollen between deposition on the surface and final incorporation into the sediment. The pollen assemblage incorporated into the sediment below the central point on the lake surface is simulated as an average of the pollen loading across the lake surface for circular basins, or across the circular approximation of the basin shape where the basin outline is irregular. The Prentice–Sugita model assumption of total mixing of pollen arriving at the lake surface throughout the water body before deposition into the sediment may not be appropriate for non-circular (or indeed circular) water bodies. Especially where the size of the 'fitted circle' produced by OPENLAND3 and used as the basin surface in other POLLSCAPE components differs markedly from the actual basin area, the simulation cannot be expected to produce appropriate values for these situations and may therefore be misleading.

Thirdly, the landscape composition is assumed to be uniform to a considerable distance beyond the area studied (i.e. the background pollen component is calculated from the composition of the vegetation within the landscape unit modelled) (Sugita, 1993, 1994; Sugita et al., 1999). This is appropriate for the initial simple models or for work in areas where the assumption of uniform topography, climate, soils, disturbance regime and thus vegetation over large distances is valid. However, for studies of cultural landscapes, or landscapes with strong regional variation in vegetation over distances of 10–100 km (see e.g. the reconstruction of British woodland composition at 5000 radiocarbon years B.P. by Bennett (1989)), this assumption could be problematic.

These assumptions aided the development of POLLSCAPE and enabled computational simulation of pollen dispersal and deposition when computers were considerably less powerful than they are today. In this form, the Prentice and Prentice–Sugita models have produced predictions which accord well with empirical datasets (e.g. Prentice et al., 1987; Jackson, 1990; Calcote, 1995) and acted as a useful stimulus and aid in the quest for quantification.

1.3. Limitations of POLLSCAPE

These assumptions restrict the flexibility of POLLSCAPE simulations. Developing alternative algorithms or variations on the Prentice and Prentice–Sugita models to treat the pollen sources in two or even three dimensions (e.g. in order to simulate variable windroses and/or aspects of topography) is not possible within POLLSCAPE software packages. The assumption of a wider landscape beyond the area studied with different vegetation composition can be partially allowed for by specifying the actual values for the background pollen component as part of the input to the latest versions of POLLSCAPE (polsim-v3.exe; Sugita, S., personal communication, 2002). This approach still requires the assumption that some sensible estimates of the background pollen component can be made by the modeller, which is not always the case.

1.4. HUMPOL: a new software approach

In this paper we present an alternative software suite for simulating pollen dispersal and deposition, also based on the Prentice model. In order to easily refer to the suite as a whole, we have nicknamed it 'HUMPOL' (HUll Method of POLlen simulation) to distinguish it from POLLSCAPE. Increased personal computer power makes it possible to handle many more point sources of pollen within the simulated landscape without excessive time or memory costs. Four aspects of the modelling approach encoded in HUMPOL, the software suite presented here, vary significantly from the approach encoded by Sugita in POLLSCAPE (Sugita, 1994; Broström, 2002):

(1) The distribution of pollen sources in the landscape is treated as two-dimensional rather than one-dimensional by replacing the ring source approach with a cellular source approach (see Fig. 1).

(2) The landscape is defined by a series of vegetation maps, with different extent and resolution, 'nested' together so that variation in vegetation composition at a range of scales can be incorporated into the simulation.

(3) The system allows an additional weighting factor to be applied to each source cell, varying according to its orientation relative to the deposition target, which enables inclusion in the simulation of environmental factors such as a variable windrose.

(4) The amount of pollen reaching a lake surface is computed by taking the centre of each cell of the water surface as a deposition target. Output from this approach currently produces two simulations of pollen deposition, the first (after Prentice, 1985) lists the values at the centre of each cell and the second (after Sugita, 1993) gives a single assemblage found by averaging across the whole lake surface. The resulting data are generated in an appropriate format for input to other models.

We discuss each of these points further below and compare the results of simulations from HUMPOL with those obtained from the existing POLLSCAPE suite (e.g. Sugita et al., 1999; Broström, 2002).

2. The simulation process

The HUMPOL suite has been developed using BORLAND's DELPHI 6 on a Windows 2000 platform. Wherever practicable the same file formats have been adopted as those used in the POLLSCAPE suite.

The general approach to simulation of pollen assemblages is summarised in Fig. 2, which also shows the software modules involved in the various steps in each software suite. This paper concentrates on the function of the POLFLOW (simulation of pollen assemblages at single points) and POLLAKE

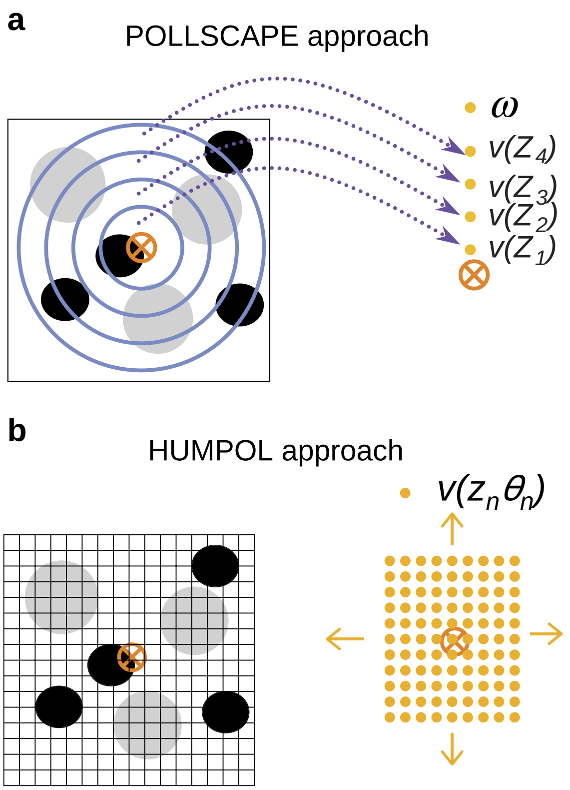

Fig. 2. Schematic of the steps in the simulation of pollen dispersal and deposition under POLLSCAPE and HUMPOL.

(simulating pollen assemblages across lake surfaces) elements of HUMPOL.

2.1. Preparing the vegetation data

Pollen assemblages are derived from the distribution of plants in the wider landscape around the sampling point. The vegetation composition and distribution used within the model can either be based on empirical data or be a simulated landscape scenario. The vegetation data are defined by three components:

- Maps defining the distribution of plant communities.
- The taxon composition of each community.
- Taxon-specific information.

A regional map, at low resolution, will usually be combined with a high resolution map of the vicinity of the target sampling points. For example, a piece of a national vegetation map, 100×100 km, with 100 m cells, could be used as context for a more detailed vegetation map obtained for a specific site (e.g. 1×1 km, 5 m cells). By nesting a series of grids, whether empirical or simulated, pollen dispersal and deposition can be modelled within a large and variable landscape without having to make any simplifying assumptions about the background pollen rain (point 2 above). To maintain compatibility with the POLLSCAPE suite categories 0 and 1 are reserved for bare ground and water, respectively. Other communities are defined by the user (the programme currently permits up to 48 communities to be defined).

To maintain compatibility with POLLSCAPE, the vegetation community map is saved in IDRISI format. Each image consists of two files, a byte-binary grid of cells in which each cell being assigned a value representing a plant community and a text file containing the cell size, array dimensions and georeferencing information. The composition of each community defined in the landscape maps is specified in a separate input file. Another definition file contains the fall speed (sedimentation velocity) and the Estimated Relative Pollen Productivity for each plant taxon. Empirical estimates of these values have been published for most major tree taxa and some herbs (see e.g. Jackson and Lyford, 1999; Sugita et al., 1999; Broström et al., 2004). Both definition files are identical in format to those used in the POLLSCAPE suite.

IDRISI format map files can be prepared using a variety of computer applications, including two within HUMPOL: POLGRID (Middleton, unpublished) converts image files from a range of standard GIS formats to the IDRISI format required, and MOSAIC (Middleton and Bunting, 2004) enables the creation of landscape scenario images for use in simulation experiments.

2.2. Simulating the pollen assemblage deposited at a single point

The original form of the Prentice model (Prentice, 1985, 1988) assumes that once pollen is deposited, it is not then reworked or transported further. This approximates to the situation on a mire surface, in a moss polster, or in a pollen trap. Single-point pollen assemblages are simulated within HUMPOL by POLFLOW. Each cell in the landscape maps is treated as a single point source located at the cell centre (except for the cell containing the sample point which is considered to be located no closer than one quarter of the cell diagonal from the sample point), giving a two-dimensional scatter of point sources around the sample location (Fig. 1b). The pollen productivity of each cell is also weighted by the area of the cell (where nested grids contain different cell sizes).

The position of each cell relative to the sample point is found and the distance-weighting algorithm is applied to the vegetation composition data in order to simulate the component of the pollen loading at the sample point originating from that cell. This operation is carried out for every cell in the vegetation maps, and the loading components accumulated to give the total pollen loading for the point. No additional background component is added in POLFLOW, unlike POLLSCAPE components such as polsim-v3.exe (Sugita, S., personal communication 2002), because it is already simulated from the larger scale vegetation maps.

The simulation of pollen loading at a single point in the landscape using the HUMPOL approach can be expressed mathematically as:

$$y_{ik} = \sum \alpha_i x_{ik}(z, \vartheta) g_i(z) \quad (2)$$

where: $x_{ik}(z,\theta)$=the plant abundance of taxon i in the cell located at distance z and angle θ relative to the sample point[1]; $g_i(z)$=pollen dispersal and deposition function for taxon i located at distance z from the sample point, based on Sutton's ground source model of particle dispersal (Sutton, 1953; Prentice, 1988). This model uses atmospheric parameters, which can vary. The default setting uses the values used by Prentice (1988), but the software is designed to allow the user to specify different values via a simple scripting function (see Jackson and Lyford, 1999). The software has been designed so that this function is a discrete programme module, making it easy to build alternative forms of the weighting term (e.g. (distance)$^{-2}$) into the package.

The weighting factor used in this algorithm only incorporates the distance component of the cell position. However, since the angular position is known, an additional weighting term can be incorporated into the calculation of pollen loading:

$$y_{ik} = \sum \alpha_i x_{ik}(z, \vartheta) g_i(z) h_i(z, \vartheta) \quad (3)$$

where: $h_i(z,\theta)$=weighting function for pollen loading from taxon i located at position (z,θ) relative to sample point k.

Alternatively, a weighting factor can be derived from an additional input file or grid and used to simulate the secondary effects of topography, run-off, or wind frequency on the pollen loading derived from each source. In this paper we present an example of the latter form of position weighting to simulate a variable windrose by weighting the pollen loading contribution from a point proportionate to the frequency of winds from that bearing.

2.3. Comparison of results from HUMPOL and POLLSCAPE

Using a single simple landscape scenario generated in MOSAIC (detailed in Table 1), pollen assemblages at a series of sample points within the landscape were simulated using polsim-v3 (POLLSCAPE: Prentice model option) and POLFLOW (HUMPOL). In this case, the two approaches should produce very similar results. The results will not be identical, given the

Table 1
Details of landscape scenario used for comparison of the two software packages (results plotted in Fig. 3)

Taxon	Landscape role	Fallspeed (ms^{-1})	RPP
Quercus	matrix	0.035	7.6
Ulmus	large patch (200 m radius circle)	0.032	0.8
Betula	small patch (50 m radius circle)	0.024	8.9

The simulated landscape had a total area of 10×10 km, divided into 10 m cells. Three taxa were distributed randomly within the landscape, each contributing about 33.3% total coverage.
Values for fallspeed and RPP (Relative Pollen Productivity) are taken from Sugita et al. (1999).
10 sample points were randomly located within the central 4×4 km square.

[1] The program actually handles the positional coordinates as (x,y) but in order to avoid confusion and use the same symbols as in the standard expression of the algorithm used in the Prentice model (Eq. 1) where x represents vegetation composition rather than Cartesian coordinates, we use polar coordinates in the equations presented here.

different methods of vegetation data handling used. A single-point pollen assemblage is expected to be highly sensitive to the details of the vegetation in its immediate locality (e.g. Jackson and Wong, 1994; Calcote, 1995; Jackson and Kearsley, 1998). The values for vegetation closest to the sample point calculated using the two methods will differ more than those for more distant vegetation (as the number of cells included in the POLLSCAPE ring source increases), therefore simulation results for point samples are expected to be more variable than those for lakes. Fig. 3 shows scatter plots comparing the results. The match between values is not perfect, as expected, but least-squares linear regression analysis produces an r^2 value in excess of 0.95 ($p<0.005$) for all three plots.

2.4. Example of a HUMPOL simulation with a variable windrose

Empirical studies show that the pollen deposition around a discrete stand of vegetation is often not symmetrical (e.g. Turner, 1964; Tinsley and Smith, 1974; Janssen, 1984; Gearey and Gilbertson, 1997; Bunting, 2002). At least part of the variation is often attributed to wind direction, with a downwind 'tail' of pollen deposited to leeward of the prevailing wind direction during the flowering period. In order to see whether it was possible to simulate this uneven distribution of pollen using a simple model, another landscape scenario was created using MOSAIC. The landscape had a total area of 10×10 km and was divided into 10 m cells. The scenario consisted of a matrix of one taxon (taxon A: fallspeed 0.035 m s^{-1} and Relative Pollen Productivity 1.0) with a central circular patch of a second taxon (taxon B: fallspeed 0.035 m s^{-1} and Relative Pollen Productivity 1.0). A simple windrose was defined by assigning frequency values to eight cardinal points, with South=65 and all other directions set to 5. Pollen deposition was simulated for a series of points radiating out from this central stand.

A scatter plot of the results (Fig. 4) shows a very strong downwind (northwards) 'tail' of increased pollen proportions of taxon B. The overall pattern seen is comparable with that obtained from empirical studies of isolated woodland stands (e.g. Turner, 1964), even though the current algorithm assumes the vegetation canopy is of uniform height, which is not the case in the empirical studies cited above. The actual difference in values is greater in this simulation, which is to be expected since the windrose is more strongly biased in one direction than in a typical natural system.

In order to model natural systems, though, it will be important to understand how the windrose experienced by the vegetation stand is best defined. For example, pollen dispersal is probably mainly affected by the windrose during the flowering season, and samples collected from moss polsters average the pollen signal over several years, therefore a typical windrose summarising one year's monitoring data is

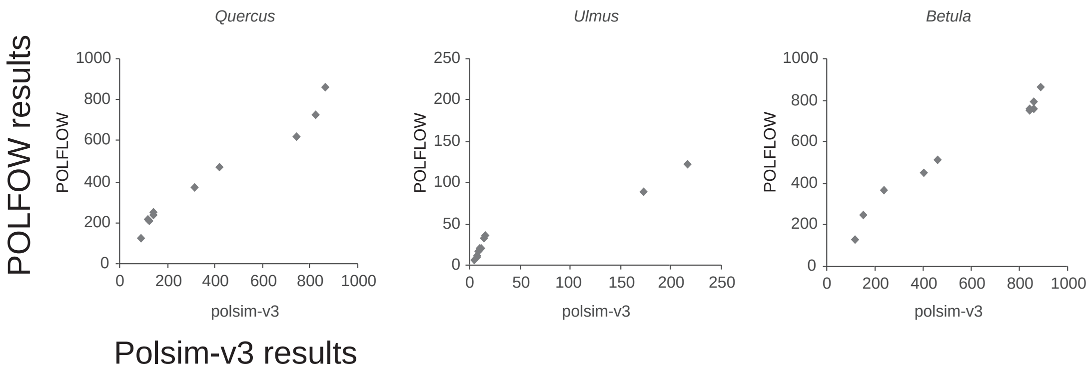

Fig. 3. Scatterplots of simulated pollen counts (base sum=1000 grains) produced by POLLSCAPE (using the Prentice model) against those produced by POLFLOW for a series of sample locations within the simple landscape specified in Table 1. Each scatterplot shows results for a single taxon, specified in the plot title. The x-axis shows the count of that taxon simulated by polsim-v3.exe and the y-axis shows the counts simulated by POLFLOW. Each dot represents a single specified location within the landscape scenario.

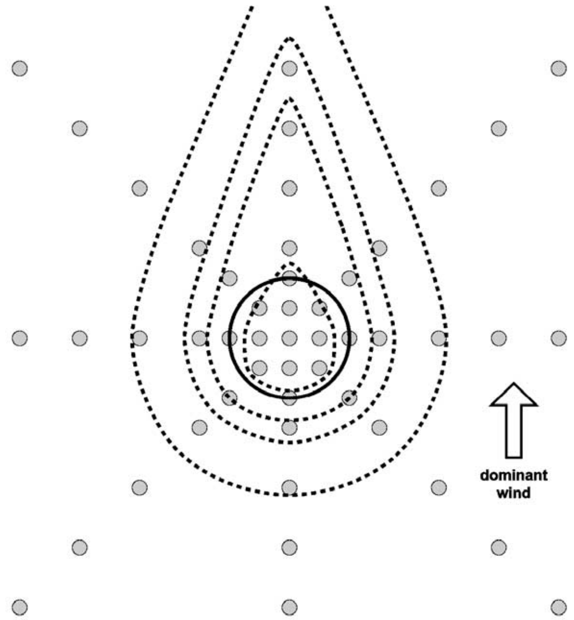

Fig. 4. Example showing changing proportion of taxon B (which occurs in the simulated landscape only as a central stand, indicated by the grey circle) with distance from the source plants simulated with a prevailing southerly wind included in the model (see text for details).

not going to be an accurate reflection of the wind component affecting pollen dispersal.

2.5. Handling output data

POLFLOW produces a single output file in a simple text format from an analysis run. To assist in the extraction of relevant parts of the data, the application POLLOG has been developed, which selects and displays different parts of the file. These sections can then easily be copied into word processor or spreadsheet files for further manipulation.

Extended *R*-Value (ERV) analysis (Parsons and Prentice 1981; Prentice and Parsons 1983; Sugita 1994) is often used as part of the simulation process to estimate the Relevant Source Area of Pollen (e.g. Sugita, 1994; Sugita et al., 1999; Broström, 2002; Bunting et al., 2004). POLLOG therefore also has the capacity to output data from the log file in the format required by the POLLSCAPE module (ERV-v6.exe) (Sugita et al., 1999; Broström, 2002; Broström et al., 2004) or by the HUMPOL module, POLERV (not discussed further here). Analyses in POLLSCAPE require vegetation data in the 'ring source' format. In HUMPOL, this is approximated by averaging the composition of all cells whose centre falls within a specified ring, but OPENLAND3 (Eklöf et al., 2004) divides cells between rings where the ring border cuts through a pixel. Therefore the ring composition values produced by the different software suites are not identical, but, where the cell size is substantially less than the ring width, these differences are negligible.

2.6. Simulating the pollen assemblage deposited on a lake surface

POLLAKE is a component within HUMPOL which is designed to simulate pollen deposition across a lake surface. A single sample point is specified to indicate the water body to be considered, and a flood-fill algorithm is then used to identify all orthogonally contiguous 'water' cells.

POLLAKE simulates the pollen loading for the centre of each identified 'water' cell using the same approach as described above for POLFLOW. The output file contains both an average value equivalent to the Prentice–Sugita model of total mixing in the

Table 2
Comparison of results of simulation of the pollen assemblage recovered from the lake centre (see Fig. 5) assuming total mixing of pollen within the water body between arrival at the lake surface and deposition to the sediment–water interface

	POLLAKE	POLLSCAPE background to 400 km	POLLSCAPE background to 5 km
Quercus	39.52	40.07	40.17
Ulmus	3.00	3.04	3.04
Betula	57.48	56.89	56.80

water body before deposition and the pollen loading at each individual cell (Prentice approach output for every single cell rather than just one central point). The individual point values may then be plotted, displaying the expected distribution of pollen within the sediment if no mixing occurred within the water column. Neither of these two extreme situations (no mixing or movement and total mixing) is likely to occur often in natural systems. Thus model output only provides an indication of the range of possible values. Since the distribution of each taxon across the whole lake surface is simulated, and a variable windrose can be incorporated, it will be possible to compare the distribution maps produced with empirical data from appropriate lakes. This distribution, coupled with existing data on the behaviour of pollen in water (e.g. Holmes, 1994), will provide a starting point for the development of a more realistic model of pollen sinking and mixing within a water body. This could then be applied to the surface deposition simulated by POLLAKE to generate pollen deposition maps for the base of the water column which

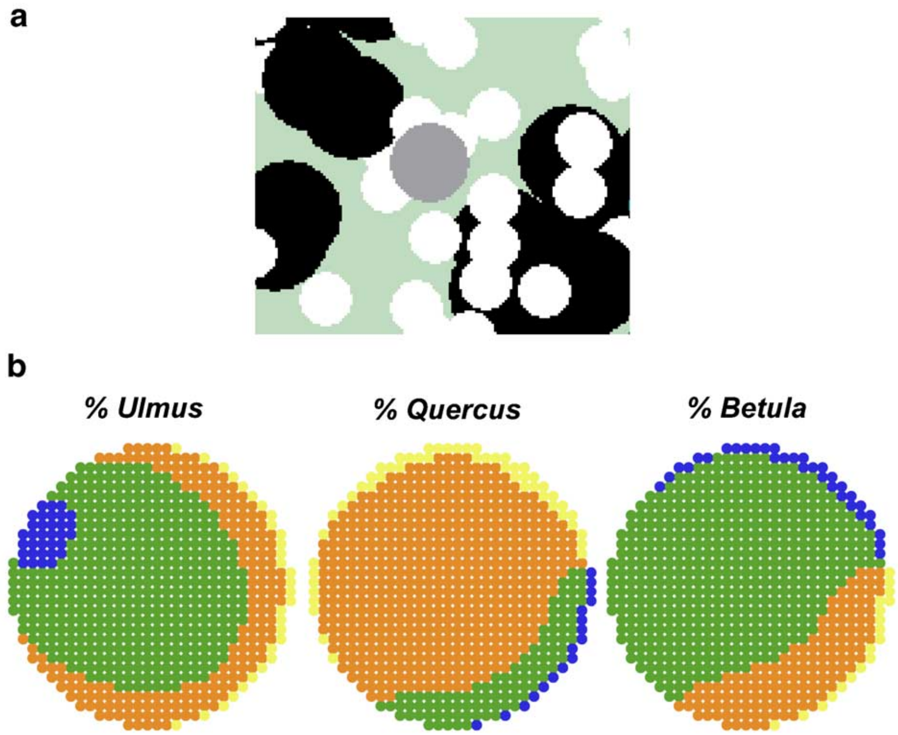

Fig. 5. (a) Part of the simulated landscape around the lake used to generate the pollen distributions shown in (b) and averages shown in Table 2. Pale grey represents *Quercus* (matrix), black *Ulmus* (large stands) and white *Betula* (small stands). The lake is indicated by the central darker grey circle. At this magnification the cellular structure of the simulated landscape is noticeable (each cell=10 m per side). (b) Distribution of the different pollen types deposited across the lake surface. The shading indicates a quartile rather than absolute scale (i.e. darkest shading represents pollen percentages in the upper quartile of the full range of percentages for that specific taxon).

allow for partial mixing and differential sedimentation rates.

The simulated pollen loadings generated by POLLSCAPE (Sugita model) and HUMPOL (averaged value) for a single circular lake (50 m radius) placed into the landscape scenario outlined in Table 1 produced almost identical values (example shown in Table 2). Fig. 5 shows the spatial distribution of pollen from different taxa across the lake surface produced by HUMPOL before any mixing has taken place. This approach is not dependent on lake shape (see point 4 above) and therefore allows the total mixing model, or any other models developed, to be applied to irregular lakes.

3. Discussion and conclusions

The results presented here show that, although HUMPOL handles vegetation data in a different way than the already published POLLSCAPE approach, where the simulation experiment fulfils the assumptions of POLLSCAPE (e.g. even wind distribution, circular lake basin) then HUMPOL produces very similar simulated pollen loadings. This provides some validation of the HUMPOL approach to using the Prentice model and provides a firm basis for exploration of the effect on pollen loading distributions of simulating systems which do not fulfil the POLLSCAPE assumptions, and therefore better understand the complexity of the 'real-world' pollen–vegetation relationship.

HUMPOL is a user-friendly and relatively fast suite of applications for modelling pollen dispersal and deposition using the Prentice model (Sutton, 1953; Prentice, 1985; Sugita, 1993). It produces results which are essentially identical to those produced by Sugita's POLLSCAPE software suite (Sugita et al., 1997, 1999) but has much greater flexibility of data handling. HUMPOL provides a useful platform on which to carry out 'thought experiments' using existing algorithms and to develop alternative models of pollen dispersal and deposition suitable for a wider range of conditions. The literature already shows how combining simulation experiments and empirical testing can lead to improved interpretation of pollen diagrams and reconstructions of past environments (e.g. Jackson, 1994); HUMPOL, being quick, flexible and user-friendly, is a valuable tool for extending this line of research.

4. Planned developments

The development of the package is ongoing. Our current plans include:

- systematic exploration using simulations of the effect of varying lake shape on pollen assemblages;
- empirical testing of the actual distribution of pollen across lake sediment surfaces and the development of models of pollen sedimentation between lake surface and sediment (in collaboration with Tallinn Institute of Ecology);
- development of alternative pollen dispersal and deposition algorithms (different forms for $g_i(z)$ in Eqs. 2 and 3), including enabling the simpler but empirically effective z^{-2} option within HUMPOL (e.g. Calcote, 1995), and exploring the implications of the 'Bennett model' (Jackson, 1994) which argues that run-off within the hydrological catchment is an important source of pollen; and
- development of a version of POLLAKE for open basins with inflowing streams, which can contribute large amounts of pollen to the system (Peck, 1973; Pennington, 1979; Bonny, 1980).

5. Software availability

Anyone interested in using the software or in collaborating to incorporate new algorithms or carry out empirical tests is very welcome to contact the authors. We intend that the package will also be available via the POLLANDCAL website once it has been fully documented.

Acknowledgements

Thanks to members of the NorFA funded PolLandCal network (http://www.geog.ucl.ac.uk/ecrc/pollandcal/) for acting as guinea-pigs and bug-finders on different versions of the software applications, and for providing feedback and encouragement at every stage of the development process.

Especial thanks to Marie-José Gaillard for financial support and to Shinya Sugita for encouragement, mathematical debate and the use of the POLLSCAPE packages. Thanks also to Anne-Birgitte Neilsen, S.T. Jackson, T. Webb III, and two anonymous referees for comments on earlier versions of this manuscript.

References

Andersen, S., 1970. The relative pollen productivity and pollen representation of north European trees, and correction factors for tree pollen spectra. Dan. Geol. Unders., 2. Række 96, 1–96.

Bennett, K.D., 1989. A provisional map of forest types for the British Isles 5000 years ago. J. Quat. Sci. 4, 141–144.

Birks, H.J.B., 1996. Contributions of quaternary palaeoecology to nature conservation. J. Veg. Sci. 7, 89–98.

Bonny, A.P., 1980. Seasonal and annual variation over 5 years in contemporary airborne pollen trapped at a Cumbrian lake. J. Ecol. 68, 421–441.

Broström A. 2002. Estimating source area of pollen and pollen productivity in the cultural landscapes of southern Sweden—developing a palynological tool for quantifying past plant cover. LUNDQUA Thesis 46, Lund University.

Broström, A., Sugita, S., Gaillard, M.-J., 2004. Pollen productivity estimates for the reconstruction of past vegetation cover in the cultural landscape of southern Sweden. Holocene 14, 368–381.

Bunting, M.J., 2002. Detecting woodland remnants in cultural landscapes: modern pollen deposition around small woodlands in north-west Scotland. Holocene 12, 291–301.

Bunting, M.J., Gaillard, M.J., Sugita, S., Middleton, R., Broström, A., 2004. Vegetation structure and pollen source area. Holocene 14, 651–660.

Calcote, R., 1995. Pollen source area and pollen productivity: evidence from forest hollows. J. Ecol. 83, 591–602.

Davis, M.B., 1963. On the theory of pollen analysis. Am. J. Sci. 261, 897–912.

Eklöf, M., Broström, A., Gaillard, M.-J., Pilesjö, P., 2004. OPENLAND3: a computer program to estimate plant abundance around modern pollen sampling sites from vegetation maps. Rev. Palaeobot. Palynol. 132, 67–77.

Gearey, B., Gilbertson, D., 1997. Pollen taphonomy of trees in a windy climate: northbay plantation barra, outer hebrides Scottish. Geogr. Mag. 113, 113–120.

Holmes, P.L., 1994. The sorting of spores and pollen by water: experimental and field evidence. In: Traverse, A. (Ed.), Sedimentation of Organic Particles. Cambridge University Press, Cambridge, pp. 9–32.

Jackson, S.T., 1990. Pollen source area and representation in small lakes of the north-eastern United States. Rev. Palaeobot. Palynol. 63, 53–76.

Jackson, S.T., 1994. Pollen and spores in quaternary lake sediments as sensors of vegetation composition: theoretical models and empirical evidence. In: Traverse, A. (Ed.), Sedimentation of Organic Particles. Cambridge University Press, Cambridge, pp. 253–286.

Jackson, S.T., Wong, A., 1994. Using forest patchiness to determine pollen source areas of closed-canopy pollen assemblages. J. Ecol. 82, 89–100.

Jackson, S.T., Kearsley, J.B., 1998. Representation of local forest composition in moss-polster pollen assemblages. J. Ecol. 86, 474–490.

Jackson, S.T., Lyford, M.E., 1999. Pollen dispersal models in quaternary plant ecology: assumptions, parameters, and prescriptions. Bot. Rev. 65, 39–75.

Jacobson Jr., G.L., Bradshaw, R.H.W., 1981. The selection of sites for paleovegetational studies. Quat. Res. 16, 80–96.

Janssen, C.R., 1984. Modern pollen assemblages and vegetation in the Myrtle Lake Peatland, Minnesota. Ecol. Monogr. 54, 213–252.

Kabailiene, M.V., 1969. On formation of pollen spectra and restoration of vegetation. Trans. Inst. Geol. (Vilnius) 11, 1–148 (in Russian with English and Lithuanian summaries).

Middleton, R., Bunting, M.J., 2004. Mosaic v1.1: landscape scenario creation software for simulation of pollen dispersal and deposition. Rev. Palaeobot. Palynol. 132, 61–66.

Nielsen, A.B., 2003. Pollen based quantitative estimation of land cover—Relationships between pollen sedimentation in lakes and land cover as seen on historical maps in Denmark AD 1800. Ph.D. thesis, Institute of Geography, Faculty of Science, University of Copenhagen, and Geological Survey of Denmark and Greenland. Denmarks og Grønlands geologiske undersøgelse rapport 2003/57, 135 pp.

Parsons, R.W., Prentice, I.C., 1981. Statistical approaches to *R*-values and the pollen–vegetation relationship. Rev. Palaeobot. Palynol. 32, 127–152.

Peck, R.M., 1973. Pollen budget studies in a small Yorkshire catchment. In: Birks, H.J.B., West, R.G. (Eds.), Quaternary Plant Ecology. Blackwell, Oxford, pp. 79–104.

Pennington, W., 1979. The origin of pollen in lake sediments: an enclosed lake compared with one receiving inflow streams. New Phytol. 83, 189–213.

Prentice, I.C., 1985. Pollen representation, source area, and basin size: towards a unified theory of pollen analysis. Quat. Res. 23, 76–86.

Prentice, I.C., 1988. Records of vegetation in time and space: the principles of pollen analysis. In: Huntley, B., Webb III., T. (Eds.), Vegetation History. Kluwer Academic Publishers, Dordrecht, pp. 17–42.

Prentice, I.C., Parsons, R.W., 1983. Maximum likelihood linear calibration of pollen spectra in terms of forest composition. Biometrics 39, 1051–1057.

Prentice, I.C., Berglund, B.E., Olssen, T., 1987. Quantitative forest-composition sensing characteristics of pollen samples from Swedish lakes. Boreas 16, 43–54.

Sugita, S., 1993. A model of pollen source area for an entire lake surface. Quat. Res. 39, 239–244.

Sugita, S., 1994. Pollen representation of vegetation in quaternary sediments: theory and method in patchy vegetation. J. Ecol. 82, 881–897.

Sugita, S., MacDonald, G.M., Larsen, C.P.S., 1997. Reconstruction of fire disturbance and forest succession from fossil pollen in lake sediments: potential and limitations. In: Clark, J.S., Cachier, H., Goldammer, J.G., Stocks, B.J. (Eds.), Sediment Records of Biomass Burning and Global Change. Springer-Verlag, Berlin, pp. 384–412.

Sugita, S., Gaillard, M.-J., Broström, A., 1999. Landscape openness and pollen records: a simulation approach. Holocene 9, 409–421.

Sutton, O.G., 1953. Micrometeorology. McGraw-Hill, New York.

Tauber, H., 1965. Differential pollen dispersion and the interpretation of pollen diagrams. Dan. Geol. Unders., 2. Raekke, 89.

Tinsley, H.M., Smith, R.T., 1974. Surface pollen studies across a woodland/heath transition and their application in the interpretation of pollen diagrams. New Phytol. 73, 547–565.

Turner, J., 1964. Surface sample analyses from Ayrshire Scotland. Pollen Spores 6, 583–592.

Post, Von, 1967. Forest tree pollen in south Swedish peat bog deposits. Pollen Spores 9, 375–401 (Translation by M.B. Davis and K. Faegri, Introduction by K. Faegri and J. Iversen).