

Accepted Manuscript

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PII: S0034-6667(16)30070-7
DOI: doi: [10.1016/j.revpalbo.2016.04.009](https://doi.org/10.1016/j.revpalbo.2016.04.009)
Reference: PALBO 3747

To appear in: *Review of Palaeobotany and Palynology*

Received date: 9 May 2015
Revised date: 4 November 2015
Accepted date: 13 April 2016



Please cite this article as: Farrell, Michelle, Bunting, M. Jane, Middleton, Richard, Replicability of data collected for empirical estimation of Relative Pollen Productivity, *Review of Palaeobotany and Palynology* (2016), doi: [10.1016/j.revpalbo.2016.04.009](https://doi.org/10.1016/j.revpalbo.2016.04.009)

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Replicability of data collected for empirical estimation of Relative Pollen Productivity

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Abstract

The effects of repeated survey and fieldwork timing on data derived from a recently proposed standard field methodology for empirical estimation of Relative Pollen Productivity have been tested. Seasonal variations in vegetation and associated pollen assemblages were studied in three contrasting cultural habitat types; semi-natural ancient woodlands, lowland heaths, and unimproved, traditionally managed hay meadows. Results show that in woodlands and heathlands the standard method generates vegetation data with a reasonable degree of similarity throughout the field season, though in some instances additional recording of woodland canopy cover should be undertaken, and differences were greater for woodland understorey taxa than for arboreal taxa. Large differences in vegetation cover were observed over the field season in the grassland community, and matching the phenological timing of surveys within and between studies is clearly important if RPP estimates from these sites are to be comparable. Pollen assemblages from closely co-located moss polsters collected on different visits are shown to be variable in all communities, to a greater degree than can be explained by the sampling error associated with pollen counting, and further study of moss polsters as pollen traps is recommended.

Keywords: distance-weighted plant abundance; moss polsters; plant phenology; pollen analysis; relative pollen productivity; vegetation survey

1. Introduction

In recent years attempts to quantitatively reconstruct past vegetation cover based on pollen data have become increasingly widespread. Current methods of quantitative reconstruction such as the Landscape Reconstruction Algorithm (LRA: Sugita 2007a, 2007b) and the Multiple Scenario Approach (MSA: Bunting and Middleton, 2009) assume that properties such as the amount of pollen produced by a given taxon per unit area of vegetation, generally expressed as a relative pollen productivity (RPP) ratio, are constant in space and time.

A recent review (Broström *et al.*, 2008) reported a wide range of RPP values for single taxa from different studies. Estimates of RPP are obtained by comparing modern pollen assemblages from moss polsters (e.g. Andersen, 1970; Hjelle, 1998; Broström *et al.*, 2004; Bunting *et al.*, 2005; Mazier *et al.*, 2008; von Stedingk *et al.*, 2008), pollen traps (e.g. Sugita *et al.*, 2010; Mazier *et al.*, 2012), or lake surface sediments (e.g. Soepboer *et al.*, 2007; Poska *et al.*, 2011; Hjelle and Sugita, 2012; Matthias *et al.*, 2012) with the vegetation around the sampling point. The studies reviewed by Broström *et al.* (2008) used different methods of vegetation survey so it is unclear whether the assumption of constant RPP is in error or whether different methods lead to systematically different values. Bunting and Hjelle (2010) have shown that vegetation data collection method can have a marked effect on the RPP estimates obtained.

To allow the assumption of constant RPP to be tested, Bunting *et al.* (2013) presented a vegetation survey and moss collection protocol for RPP analysis which was developed through a practitioner workshop, and represented an agreed compromise between existing

methods which, it was hoped, balanced efficiency and data quality. Three nested levels of vegetation survey are carried out around the sampled moss, defined by radial distances. The inner 10 m (zone A) is recorded using a standard array of 1 m² quadrats, 21 in total, oriented to compass bearings to reduce subjective bias in placement of the array. The 10-100 m zone (zone B) is first mapped in the field to identify the main communities present, then a small number of randomly located quadrats are recorded in each community (1 m² in open communities, 6 m radius circular quadrats in tall shrub and woodland communities). The vegetation in the area beyond 100 m (zone C) is quantified from existing data sources, such as published maps, aerial photography or remotely sensed data; the distribution of communities is digitised, then community composition defined where possible by extrapolation from the mapped zone B communities, by additional field recording, or from existing studies or databases.

Bunting et al. (2013) present an empirical test of the effects of different recording methods within zone A, which confirms that the array chosen produces statistically identical results to a more time-consuming complete survey using the 'ring method' (e.g. Broström et al., 2004), but did not investigate replicability of zones B and C. This paper presents a small-scale investigation of the possible effects of the timing of fieldwork on the datasets generated for zones A and B.

It is well known that the number of plant species that are recordable varies throughout the year, and some species show marked differences in their conspicuousness or abundance over the growing season (Hope-Simpson, 1940; Usher, 1980; Martínková et al., 2002).

Estimates of percentage cover, upon which survey methods for RPP estimates rely heavily

(e.g. Sugita et al., 1999; Broström et al., 2004; Räsänen et al., 2007; Mazier et al., 2008; von Stedingk et al., 2008; Abraham and Kozáková, 2012; Twiddle et al., 2012), vary throughout the growing season in hay meadows (Losvik, 1991; Martínková et al., 2002). In woodlands too there are large seasonal differences in the frequency with which some species are recorded, because they are either more abundant or more easily identified at a particular time of year (Kirby et al., 1986).

To test the assumption of constant RPP it is also necessary to apply a standardised method for collection of pollen data. Pollen trap studies show significant interannual variations in pollen production of individual species, in part caused by differences in seasonal temperature and precipitation (e.g. Andersen, 1974; Hicks, 2001; Autio and Hicks, 2004; Huusko and Hicks, 2009; Kuoppamaa et al., 2009; Nielsen et al., 2010; Donders et al., 2014). To avoid problems associated with this variation in the estimation of RPP, moss polsters are often used as pollen traps since they are generally thought to preserve and integrate several years of pollen rain (Andersen, 1970; Bradshaw, 1981; Caseldine, 1981; Mulder and Janssen, 1998; 1999), although some studies indicate that they represent little more than a single growing season (Räsänen *et al.*, 2004; Pardoe et al., 2010). In the proposed standard protocol, a single moss polster is collected and defines the central point of the vegetation survey (Bunting et al., 2013).

Seasonal differences between pollen assemblages also occur and are closely linked to flowering times (Bonny, 1980; Cundill, 1985; Hicks, 1985; Ribeiro and Abreu, 2014; Tosunoglu and Bicakci, 2015), so it is necessary to ensure that the full year's assemblage is represented in order to reduce the risk of biasing in favour of early-flowering species. Strong

seasonal variations have been recorded in pollen traps in Finland, with the majority of pollen being deposited in the summer when most plants were flowering. Autumn pollen assemblages comprised pollen from late-flowering plants, as well as redeposited pollen from the early-flowering taxa, and winter pollen assemblages consisted mainly of redeposited pollen along with some pollen from the earliest flowering taxa (Hicks, 1985). The source of the redeposited component is pollen moving through the trunk space, as well as that which has been filtered out by vegetation and later washed to the ground by precipitation (Tauber, 1965; 1967). Similar seasonal variations in pollen assemblages from Tauber traps have been recorded in Denmark (Andersen, 1974), Switzerland (Markgraf, 1980) and England (Bonny, 1980). Studies comparing moss polsters with other types of pollen trap such as Tauber traps, soils and lake surface sediments (Räsänen et al., 2004; Wilmshurst and McGlone, 2005; Pardoe et al., 2010; Lisitsyna et al., 2012) have found significant differences in their respective pollen assemblages, though they compare samples from two or more different traps taken at the same time and are therefore not useful for considering seasonal differences.

If the assumption that moss polsters preserve several years' worth of pollen rain proves to be false, pollen assemblages should ideally be collected at the end of the flowering season in order to avoid seasonal biases. The vegetation survey should be conducted at an earlier date so that the maximum possible number of species is recorded. The Crackles Bequest Project aims to compare estimates of RPP for common taxa from several sites in north-west Europe using the standard method proposed by Bunting et al. (2013). It was not possible within the confines of a three-year research project to survey all sites at the optimum time for vegetation recording and to return to each location to collect the pollen assemblage at

the end of the flowering season, therefore in this project pollen sampling was completed at the same time as vegetation survey, and fieldwork took place in early to mid summer whenever possible.

This paper presents a limited investigation of the possible effects of the timing of fieldwork on the datasets generated. Three sites were chosen to represent the three main cultural habitat types studied by the Crackles Bequest Project; semi-natural ancient woodlands, lowland heaths, and unimproved, traditionally managed hay meadows. Moss polsters were collected and vegetation surveys undertaken at each site in spring (May), summer (late June) and late summer/early autumn (September) in order to address the following research questions:

- 1) After vegetation data have been processed for RPP analysis, do statistically distinct differences remain between repeat surveys at the same site? Can these differences be explained by seasonal variations in plant recordability?
- 2) Does the timing of moss polster collection systematically affect the pollen assemblage recovered from the moss, and if so do those differences reflect seasonal patterns?

2. Methods

2.1 Study sites

Site locations are shown on Fig. 1. North Cliffe Wood is a 35 ha woodland situated on postglacial lacustrine sands which overlie Mercia Muds. Soils are acidic, and the site lies at an altitude of approximately 7 m OD at the eastern edge of the Vale of York. Low-lying wetter areas are dominated by *Salix* spp and *Betula pendula*, while drier areas support

Quercus robur. Typical woodland species including *Hyacinthoides non-scripta*, *Primula vulgaris*, *Oxalis acetosella* and *Mercurialis perennis* are abundant within the ground flora.

The centre of the survey was located at 53° 49' 26.10" N, 0° 41' 36.97" W.

Wheldrake Ings comprise c. 160 ha of unimproved, seasonally flooded, species-rich hay meadows under traditional management. The hay crop is cut in July, at the end of the flowering season, and the re-growth is grazed by livestock until late autumn. The meadows are then enriched with sediment during the winter floods and the hay crop begins to grow again during the spring. Typical species include *Filipendula ulmaria*, *Sanguisorba officinalis*, *Achillea ptarmica*, *Silaum silaus*, *Leucanthemum vulgare* and a wide range of grasses and sedges. The centre of the survey was located at 53° 53' 22.89" N, 0° 56' 22.19" W. This location was on slightly higher ground towards the margins of the Ings, which during a typical winter are not actually inundated, but experience a high soil water table. Within zone B a lower area of ground (apparently a palaeochannel) supports more hydrophilic taxa such as *Ranunculus flammula* and contains standing water during the winter. Because the moss sample location was not inundated, water-borne pollen is not considered to be a significant taphonomic component of the pollen assemblage.

Strensall Common is a 580 ha expanse of acidic lowland heath formed over glacial sands and supports a mosaic of wet and dry heath, mire, open water, woodland and acid grassland.

Several typical heathland species are present, including *Calluna vulgaris*, *Erica tetralix*, *Molinia caerulea* and *Potentilla erecta*, as well as rarer species such as *Genista anglica* and *Drosera intermedia*. Trees present include *Pinus sylvestris*, *Quercus robur* and *Betula pendula*. The survey was centred on 54° 2' 54.00" N, 0° 59' 55.48" W.

2.2 *Vegetation survey*

A sampling point was selected on the first visit to each site and relocated on subsequent visits using handheld GPS, markers and photographs taken on the previous visit. At Strensall Common, it was possible to take subsamples from the same moss polster on each visit, so the location used was identical. At North Cliffe Wood and Wheldrake Ings, where moss was less abundant, samples were taken within 0.5 m of each other. On each visit moss polsters were sampled immediately to avoid contamination by disturbance of local vegetation. Vegetation data was collected followed Bunting et al. (2013). Zone A (0-10 m) was recorded using a standard, compass-aligned array of 21 quadrats centred on the moss polster sampled. At North Cliffe Wood, the canopy above each quadrat was recorded as well as the ground flora. Vegetation communities in zone B (10-100 m) were mapped in the field and their composition recorded using standard methods for open, semi-open and tree-dominated community patches (see Bunting et al., 2013 for full details). All field recording was carried out by one of the authors (MF).

2.3 *Pollen assemblages*

At each site, the same moss species was collected on every visit for intra-site consistency. Only the green parts of the moss were sampled, due to concerns about contamination by sub-moss soil, and care was taken when subsampling for pollen extraction to take a mixture of moss strands, in case pollen adheres to the moss in a non-random pattern. Moss polsters were prepared for pollen analysis following standard procedures (e.g. Moore et al., 1991), including sieving through 100 µm mesh and acetolysis. Residues were stained using aqueous safranin and mounted on microscope slides in silicone oil, then counted at a magnification

of $\times 400$, with $\times 1000$ magnification and oil immersion used for critical identifications. A minimum of 1000 terrestrial pollen grains were counted per sample. Pollen and spores were identified using the keys of Moore et al. (1991) and Beug (2004) and the reference collections of the Department of Geography, Environment and Earth Sciences, University of Hull. Pollen taxonomy follows Bennett (1995).

2.4 Data analysis

Data collection in zone A uses a standard, compass-oriented array of quadrats, therefore can be considered to be truly replicated between visits and any differences that occur are due to seasonal variation. In zone B, the community maps did not change significantly between visits, but since quadrats were randomly located within each community, differences may reflect sampling, seasonal changes in composition, or both.

2.4.1 Data formats

The plant species recorded were grouped into palynological equivalents (pe) then their abundances distance-weighted using the Sutton-Prentice model (Bunting et al., 2013). Distance-weighted plant abundance was cumulated to 10 m (dwpa(10) – where variations are expected to be purely due to seasonal changes) and to 100 m (dwpa(100) – where variations are expected to be due to both sampling effects and seasonal changes) and expressed as proportions (e.g. %dwpa(100)) for analysis. Pollen proportions were calculated as percentages of total land pollen and spores.

2.4.2 Comparison of sampling events

In order to compare values between different survey visits, the Bray-Curtis Index (Bray and Curtis, 1957; Kindt and Coe, 2006) was used. This is a similarity metric widely used in ecology (Clarke et al., 2006; Kindt and Coe, 2006), and was chosen for this study because it is sensitive to both abundance and composition, and the output value is not affected by the numerical size of the input value(s). The equation used is:

$$I_B = 1 - \frac{\sum_1^j (|x_{ik} - x_{im}|)}{\sum_1^j (x_{ik} + x_{im})}$$

where I_B is the Bray-Curtis Index, x_{ik} is the measurement of interest for taxon i in sample k , k and m are the two samples being compared, and there are a total of j taxa in the combined taxon list of the two samples taken together. I_B values were calculated for both complete pe taxa lists (“all taxa”) and for lists consisting only of pe taxa found in both the list of pollen and spore types and the vegetation list for the given site (“shared taxa”).

A simulation method was used to determine what value of I_B was likely to indicate a difference between pollen assemblages which was larger than that occurring as a by-product of the counting process. We generated sets of ten simulated pollen assemblages of specified count size using two actual assemblages as the probability distributions, one with high diversity (North Cliffe Wood, May) and one with low diversity (Strensall Common, April), then calculated I_B for each of the 45 possible pairs of samples. I_B values obtained are summarised in Fig. 2, which shows greater similarities between the simulated assemblages derived from the same underlying distribution with higher pollen counts and with lower taxonomic diversity, as expected. Since the results presented here all have a minimum pollen and spore count between 500 and 1000 grains, we use the results for simulated counts of that size from North Cliffe Wood to propose that an I_B value below 0.90 is

sufficient to indicate that there is a statistically meaningful difference between the underlying pollen distributions of the compared samples, not just differences due to counting errors.

3. Results

Summaries of plant and pollen data for each site are given in Tables 1a-c and Figs. 3a-c, and Bray-Curtis Indices are presented in Tables 2a-c.

3.1 North Cliffe Wood

Table 1a summarises the plant and pollen data from North Cliffe Wood. A total of 58 different plant types were recorded over the course of three visits, representing 42 pe plant types, and 36 distinct pollen and spore types were recorded across the three moss samples. Of these taxa, only 16 were present in both datasets, less than half of the total diversity of either group. The 16 shared pe taxa make up the majority of %dwpa(10), %dwpa(100) and pollen assemblages on every visit; Fig. 3a shows that proportions of the 'missing' taxa make up less than 15% of the pollen assemblage but around 20% of %dwpa(10) and 25% of %dwpa(100). This is partly due to the up-weighting of local understorey taxa in %dwpa, and probably also reflects background pollen contributions from beyond the survey area of some of the minor pollen taxa. All tree taxa in the vegetation within 100 m of the sampling point are recorded in the pollen and spore assemblages (hereafter pollen assemblages; Table 1a).

The pollen assemblages from North Cliffe Wood are dominated by tree pollen types, with only a small proportion of pe types which originate from plant taxa not found within the

100m survey area. The vegetation survey data (%dwp(10) and %dwp(100)) also show a preponderance of trees (Fig. 3a). As expected, tree pollen types make up a larger proportion of the pollen assemblage than of %dwp. Fig. 3a shows consistent over-representation of *Alnus glutinosa* and *Betula* in the pollen rain (that is, the proportion in the pollen assemblage is greater than the %dwp of those taxa).

Zone B in North Cliffe Wood did not show any clear community differentiation, therefore was recorded using four randomly placed 6 m radius circular quadrats, meaning less than 2% of the total area of zone B was actively recorded. Clear differences between visits in %dwp(100) data (e.g. presence/absence of *Alnus glutinosa*, see Fig. 3a) show that differences in the positioning of these quadrats has a marked effect on %dwp(100), and that the sampling strategy is insufficient for this situation.

Table 2a summarises the Bray-Curtis Indices for pair-wise comparison of sampling dates at North Cliffe Wood. The similarity in %dwp(10) between visits ranged between 86% and 96%, with 1-2% improvement when only shared taxa were considered. As expected, the lowest similarity was between the May and September surveys, though similarity between the May and June surveys was only marginally higher. If trees are removed from the dataset, the similarities between the May survey and the others fall sharply to 63% and 59%.

Similarity in %dwp(100) between visits is lower, ranging from 83% to 89%, again with very little difference in values seen when only shared taxa are considered. As expected, the lowest similarity was between the May and September surveys. Comparison of pollen

proportions found similarities between 80% and 89%, again with little change in similarity when only shared taxa were considered, suggesting that statistically significant differences exist between most of the underlying pollen assemblages.

3.2 Wheldrake Ings

At Wheldrake Ings 28 pe plant types were recorded (Table 1b) and 42 pollen types. Of these, 15 types were present in both datasets. Fig. 3b shows that over 50% of the pollen assemblage could have come from plants within 10 or 100 m of the sampling point. A large proportion of the pe taxa not recorded within the survey area are from trees and shrubs. A narrow marginal belt of trees surrounds the site, and the nearest tree is at least 160 m away from the sampling point. In September, pollen types from non-local herb species also make up a substantial fraction of the assemblage, particularly Chenopodiaceae and Rosaceae. The vegetation data also include a substantial proportion of taxa not registered in the pollen assemblages (Fig. 3b), mainly *Sanguisorba officinalis*; and the decrease in recording of this taxon on the September visit is the main cause of the reduction in this category. *Rumex acetosa* is consistently under-represented in the pollen assemblages compared to %dwpa at either distance.

Table 2b summarises the Bray-Curtis Indices for pair-wise comparison of sampling dates at Wheldrake Ings. When all taxa are considered, similarities range from 60% to 74% for %dwpa(10) with some improvement for %dwpa(100) (66-75%). When only shared taxa are considered, which removes *Sanguisorba officinalis* and other palynologically invisible taxa from consideration, similarities between the September survey and the others increase, but the similarity between the May and June surveys decreases, at both survey distances. The

general improvement in similarities noted on comparison of %dwpa(100) probably reflects the comparative stability of the main communities recorded in terms of the spatial extent and position, and suggests that averaging several quadrats within each to estimate composition smoothed out some of the local-scale heterogeneity.

Comparison of pollen proportions found similarities between 54% and 65%, with improvements in similarity when only shared taxa were considered, suggesting that statistically significant differences exist between the pollen assemblages. Note that there was no change in the shared taxon list between the two survey areas, therefore the pollen proportion similarities are identical. Since moss was comparatively sparse in the grassland, sample points were separated by a few tens of cm between visits; given the highly heterogeneous nature of grassland at the zone A scale in both space and time, even these small spatial differences could account for a substantial part of the variation seen.

3.3 Strensall Common

Nine pe plant types were recorded in the surveys at Strensall Common (Table 1c; Fig. 3c), along with seedlings of three arboreal taxa. All apart from Juncaceae and *Campanula*-type were represented in the pollen assemblages. The pollen assemblages contained a large proportion of tree pollen (Fig. 3c), sourced from beyond the 100 m survey area, and a total of 33 pollen types were recorded across the four sample visits. Poaceae and *Vaccinium*-type are noticeably under-represented in the pollen samples compared with the %dwpa (Fig. 3c).

Table 2c summarises the Bray-Curtis Indices for pair-wise comparison of sampling dates at Strensall Common. The similarity in %dwpa(10/100) between visits ranged from 72% to

94%, with a general improvement in values seen when only shared taxa were considered, and the lowest similarity was between the early summer visits and the September surveys. Comparison of pollen proportions found similarities between 52% and 86%. Again similarities between September samples and the others were markedly lower, reflecting a shift in the *Calluna*:Poaceae ratio in the assemblages. These findings suggest that statistically significant differences exist between the underlying pollen assemblages, even though samples were collected from the same moss polster and therefore only a few cm apart spatially.

4. Discussion

4.1 After vegetation data have been processed for RPP analysis, do statistically distinct differences remain between repeat surveys at the same site? Can these differences be explained by seasonal variations in plant recordability?

Bunting et al. (2013) tested the effectiveness of the quadrat-based grid used within zone A against complete recording, and found that after calculation of dwpa the two methods produced statistically comparable results, albeit from a small sample. Therefore differences between visits in %dwpa(10) observed in this study are considered to purely reflect seasonal differences and innate variability of the recording methodology, since the use of a common starting point and fixed, compass-aligned array of quadrats kept the location the same, and recording was carried out by the same person on all visits. Differences between visits in %dwpa(100) also include a random sampling factor, since although community maps were stable between visits, random quadrats were placed into the mapped communities for plant recording, and therefore positions varied between visits. The underlying rationale for

reduced sampling effort in zone B is that the down-weighting of this area compared to zone A reduces the precision of vegetation data required (Bunting et al., 2013).

4.1.1 Variations in *dwpa* between vegetation surveys in zone A (10 m radius)

At North Cliffe Wood, replicability between visits in zone A ranged from 86% to 96%. At this site, a strong seasonality signal in the ground flora component of the vegetation was anticipated. This is seen in the relatively low similarities between the May visit and later visits when only the non-tree taxa within zone A are considered; the effect is much reduced comparing the June and September visits.

The range of similarities of vegetation survey zone A of the grassland at Wheldrake Ings was 60-85%, varying with timing and with species list considered. Here differences were generally greater between the September visit and earlier ones when all taxa were considered. Once *Sanguisorba officinalis* and other minor palynologically invisible taxa were removed, the relatively greater abundance of grasses in June and September compared with May dominated the pattern. Seasonal variation in species abundance is likely to be compounded in grasslands by differences in the visibility and distinctiveness of taxa to the surveyor (Losvik, 1991; Martínková et al., 2002). Estimating vertical projections of cover is challenging especially later in the summer when the vegetation can be over 1 m tall; shorter taxa and shorter growth stages may be overlooked, and determining the proportions of grasses and sedges in particular can be influenced by the presence of identifiable flowers since the leaves and stems alone can be harder to distinguish with confidence.

Similarity between %dwpa(10) values from the heath at Strensall Common ranged from 72-93%, with markedly higher values in most cases once Juncaceae and other palynologically invisible elements were removed (88-96%). The high degrees of similarity between surveys at the site are attributable to the fact that coverage and identifiability of the major taxa associated with heathlands tend to remain fairly constant throughout the growing season.

Results from heathland and woodland with trees included were similar and suggest a reasonable level of replication between surveys despite seasonal changes, especially when only the shared taxa (those most likely to be relevant to RPP studies) are considered.

Woodland ground flora and grassland surveys showed greater variation between visits. In woodland, these seem to largely result from expected seasonal changes in the ground flora (e.g. Kirby et al., 1986) such as a decrease in the recorded abundance of *Hyacinthoides non-scripta* as the year progressed. In grassland, as well as the seasonal changes in vegetation abundance, the very high level of local heterogeneity may play a larger role; differences of a few tens of cm in moss location may also have affected the similarities.

4.1.2 Variations in dwpa between vegetation surveys in zones A and B (0-100 m radius)

At North Cliffe Wood, where a single woodland community is recorded in zone B, the sampling strategy of four, 6 m radius quadrats seems to be insufficient to record its diversity. The method for surveying tree cover in zone B proposed by Bunting et al. (2013) recommends mapping the main woodland community types and using a stratified random sampling approach which should increase the replicability between surveys. However, in woodlands like North Cliffe where clear patch structure is not visible, community mapping is not possible. For mixed woodland without clear communities, the approach proposed by

Bunting et al. (2013) samples less than 2% of the area of zone B. Alternative approaches to recording canopy in zone B such as using 100 m long canopy composition transects (e.g. Mazier et al., 2008) or recording the species of 50 randomly selected trees would sample a similarly small proportion of the canopy but are likely to intercept a larger number of individual trees, and therefore may give a better representation of the overall composition of the canopy. The circular quadrat method was adopted as best allowing rapid survey of both canopy and understorey elements in dense woodland, but these results suggest that supplementing it with wider recording of the proportions of tree species present or replacing it with intercept transects for canopy recording might be needed to give appropriate representation of the minor components of the canopy, which may still be making a substantial contribution to the pollen deposited at the sample point.

At Wheldrake Ings and Strensall Common, %dwpa(100) values were in general higher than the %dwpa(10) values for the same data pairs. The consistency over the recording visits in the position of the communities at the mapping scale used, and the use of multiple quadrats within each community, seems to provide relatively replicable results at these sites, although the area surveyed is still a small fraction of the total in the zone.

4.2 Does the timing of moss polster collection systematically affect the pollen assemblage recovered from the moss, and if so do those differences reflect seasonal patterns?

Moss polsters were collected from the same moss species at each site, although the species differ between sites. The species were not identified but it is possible to classify the mosses by growth-form (Gimingham and Birse, 1952). The samples from North Cliffe Wood were from a smooth mat (Ms) type, while those from Wheldrake Ings can be categorised as a tall

turf type with erect branches (Te). The samples from Strensall Common were all collected from the same *Sphagnum* moss polster, classified as a tall turf with divergent branches of limited growth (Td; Gimingham and Birse, 1952). The surface area of the polsters sampled should ideally have been recorded, since this is the effective determinant of the pollen trap size in the algorithm used for estimating RPP, and would have allowed analysis of pollen concentrations per unit area as well as proportions, enabling better comparison with other studies (e.g. Räsänen et al., 2004; Pardoe et al., 2010).

The Bray-Curtis Indices (Table 2a-c) show that differences in pollen assemblages between visits almost all exceed the level that could be explained by counting errors alone, based on the simulation presented in Fig. 2. Whilst this seems reasonable in the samples from Wheldrake Ings, given the high level of local vegetation heterogeneity and greater separation of moss samples, it is worrying in the samples from Strensall Common, which were collected from the same *Sphagnum* moss polster (a species generally considered to preserve pollen from multiple years) within a stable vegetation mosaic. The differences observed at Strensall are interpreted as reflecting either very local factors such as gravitic input of an anther to a single point, or a strong seasonal phenological influence on the forming pollen assemblage, suggesting that it is dominated by pollen deposited over the last few months, rather than over several years (e.g. Cundill, 1985).

Micro-scale variation in pollen assemblages has been little studied though it may be significant (Pardoe, 1996), especially where there is micro-topographical variation within the sampling site (Kitcher, 2014). Earlier studies have recommended an amalgam of mosses from multiple points within a small area (Broström et al., 2004; Räsänen et al., 2004; Mazier

et al., 2008), and although this has its own limitations (for example, in areas where mosses are sparse such as meadows multiple mosses will not occur in close proximity; ensuring sampling is unbiased both in the field and when subsampling for extraction requires extra time and care; a single outlying assemblage will raise the average of the taxa concerned in the mixed sample, and is less likely to be detected) it may give more representative results. This has been demonstrated for pollen assemblages from soil surface samples, where pollen preservation conditions are known to be problematic (Adam and Mehringer, 1975; Hill, 1996).

The use of a moss polster as a pollen trap assumes that the moss has been in existence for several years, that it has effectively trapped pollen input throughout those years, and that there is negligible loss of pollen through degradation *in situ* or through remobilisation of grains. If the assumption of multiple years of pollen influx is flawed, either due to losses following first deposition or due to short-lived mosses being selected, we might expect to see strong seasonal differences in assemblages from the same location. Losses following first deposition have two main possible causes, the action of transporting agents such as water flow through the polster into the soil or humus accumulating beneath it (e.g. Clymo and Mackay, 1987), or degradation of pollen *in situ*. The latter is considered relatively minor since the acidic and moist nature of moss surfaces provides a good microenvironment for preservation (Boyd, 1986) and the condition of pollen grains from moss polsters is generally excellent, with minimal signs of chemical damage typical of grains exposed to oxidising conditions or possible partial consumption by pollenivores (e.g. Goldstein, 1960; Havinga, 1984; Roulston and Cane, 2000). Moss growth-form may have an effect on the former; for example Boyd (1986) shows that tall turf mosses are least affected by differential loss of

pollen due to through wash and may therefore reflect the composition of the pollen rain more accurately than mat-forming mosses.

If variations in moss polster pollen assemblages are dominated by pollen input from the current flowering season, then we might expect the changing composition of the assemblages over the year to reflect the flowering time of the pe types (e.g. Cundill, 1985). The link between flowering season and pollen influx is well documented in the aeropalynological literature (e.g. van Vliet et al., 2002; Ribeiro and Abreu, 2014; Tosunoglu and Bicakci, 2015; Ugolotti et al., 2015). Tauber trap studies aimed at improving interpretation of palaeoecological pollen assemblages also show variation in pollen production related to flowering season (Andersen, 1974; Bonny, 1980; Markgraf, 1980; Hicks, 1985). At North Cliffe Wood, the proportion of spring-flowering tree taxa (*Alnus glutinosa*, *Betula* sp., *Corylus avellana* and *Salix*) showed little variation. At Wheldrake Ings, Poaceae and other grassland plants are expected to be flowering most abundantly in summer, and seasonal differences in Poaceae pollen proportions, from around 25% in May and September to over 50% in June, may reflect differences in pollen production through the season. At Strensall Common Poaceae proportions are higher in the September sample, but *Calluna*, in full flower in September, had much lower proportions in this sample than earlier in the year. Temporary pollen traps deployed in a different heathland for another experiment during a sunny week with high levels of visibly flowering *Calluna* in August 2012 also recorded almost no *Calluna* pollen (Bunting and Farrell, unpublished data); it is plausible that 2012 was a poor pollen production year for the species, and the higher values in earlier samples show the influence of a better production year in 2011, subsequently diluted by Poaceae influx in 2012.

When estimating RPP, the relationship between pollen proportion and vegetation abundance is important, not the properties of the two datasets considered separately. Scatter-plots of pollen proportion against vegetation abundance are expected to show a generally monotonic relationship, modified by the interdependence of percentage data, and taxa are broadly described as over-represented if the proportion of the taxon within the pollen sum exceeds the proportion in the vegetation data, and under-represented where the opposite is the case. If differences between pollen assemblages are due to small changes in sample location, and the moss pollen assemblages are stable, season-independent measures of the local vegetation (i.e. are the average of multiple years, such that including only part of the present year's pollen input is only a minor factor in determining the overall proportion of a pollen type) we might expect the relationship between pollen proportion and vegetation proportion to be consistent – that is, if the proportion of type X in the vegetation falls between sample date 1 and sample date 2, then the proportion of type X in the pollen assemblages should fall, and in both samples the ratio of pollen to vegetation remain comparable. This is not seen in the data presented in Fig. 3, suggesting something more complex underlies the patterns observed.

The variations between moss pollen assemblages seen in this study do not make data already collected using a single-sample methodology meaningless, since the habitat sampled is always clear from the assemblages, and as multiple published RPP studies show, variations in vegetation composition are correlated with variations in single pollen assemblages (Räsänen et al., 2007; von Stedingk et al., 2008; Abraham and Kozáková, 2012). However, our results do suggest that at least some of the noise in those datasets, attributed

to the interdependence of pollen percentage data (the 'Fagerlind Effect'; Fagerlind, 1952), is actually due to highly local-scale variation in pollen assemblages at the sampling point, which may be responding to vegetation patterning at a finer spatial scale than that captured by the vegetation data used for RPPs, reflecting the contribution of different transport modes to the pollen assemblage (e.g. gravity deposition), or resulting from post-depositional processes within the moss trapping system. Description and quantification of this local-scale component, and development of a methodology which minimises its effect on RPP datasets, is clearly necessary.

4.3 Implications for field methodologies for RPP estimation

Vegetation survey using the Crackles Bequest Project method for RPP estimation (Bunting et al., 2013) appears to generate results with a reasonable degree of similarity throughout the field season within zone A. Matching the phenological timing of vegetation surveys within and between studies seems to be particularly important for grassland communities, where large differences in %dwpa(10) occurred over the study season. For woodlands, this is less important unless understorey taxa are of interest to the particular study, since these showed greater variation in %dwpa(10) than tree taxa. Similarities in %dwpa(10) from heathland surveys suggest a high level of replication despite seasonal changes.

Within zone B, the method achieves relatively replicable results between surveys in both grassland and heathland, despite the small proportion of the total area recorded. This appears to be due to consistency in the position of the different communities mapped. In woodlands, recording of tree species using the standard method proposed by Bunting et al. (2013) for zone B is insufficient to achieve replicability of minor canopy taxa, and in

woodlands where a clear community structure is not present in zone B allowing stratified random sampling, some supplementary recording of canopy cover should be undertaken. Additional research to determine the minimum number of quadrats required to characterise zone B vegetation in woodlands is required. Alternative survey methods such as drone photography may also be useful for recording woodland canopy cover.

In most cases, moss polsters do not provide a consistent pollen assemblage throughout the field season, with observed differences being larger than would be expected due to counting errors alone. Similarity between assemblages is greatest for mosses collected from the woodland. The lower similarity in the meadow assemblages is likely due to the samples being located slightly further apart than at other sites, reflecting the highly heterogeneous nature of the vegetation canopy at a fine scale as well as seasonal differences in flowering times. In the heathland assemblages, lower similarities appear to be largely due to seasonal effects as well as interannual variations in pollen production. Measuring the surface area of collected mosses would be a useful addition to the methodology as it would enable calculation of pollen concentrations.

Further study of the use of moss polsters as pollen traps is clearly needed, since many questions remain open. Investigation of micro-scale patterns of variation in pollen assemblages across moss polsters and alternative traps, and the relationship of any such patterns with local vegetation, would be a useful place to start. Taking multiple samples within a small area of known radius (e.g. Broström et al., 2004; Mazier et al., 2008) to mitigate against micro-scale variations in pollen influx has been shown to be effective for both moss polsters (Pardoe, 1996) and surface soil samples (Adam and Mehringer, 1975).

This may be especially important for grasslands due to the greater likelihood of fine-scale heterogeneity in the vegetation canopy in both space and time at such sites than in woodlands or heathlands. Collecting mosses at the end of the flowering season to ensure that the full season is sampled and amalgamation of multiple samples may both be desirable, but must be balanced against costs and practicalities. It might be possible to remove the potentially distorting effect of very local vegetation by collecting mosses from locations which naturally lack overhanging vegetation, for example rocks or tree stumps.

Alternative pollen traps could be considered. Tauber traps allow the time period covered by the pollen assemblages to be defined accurately, although the requirement for a long-term continuous series of annually collected data to avoid problems of interannual variations in pollen production (Hicks, 2003) means that this approach is not feasible within the lifespan of many research projects. Bunting et al. (2015) show that there may be a significant degree of local heterogeneity between closely spaced Tauber traps, indicating that micro-scale variation between pollen assemblages is not peculiar to those contained within moss polsters. Lake surface sediment samples are another option (e.g. Soepboer et al., 2007; Poska et al., 2011; Hjelle and Sugita, 2012; Matthias et al., 2012). However, pollen taphonomy in lake sediments is not fully understood, and because lakes have larger pollen source areas than moss polsters (e.g. Sugita, 1994), the area of vegetation to be surveyed is considerably larger, potentially requiring more fieldwork effort.

5. Conclusions

Although only a small pilot study, our findings highlight multiple areas of uncertainty and potential problems with current practice. Methodological studies are difficult to resource,

but given the investment in time and effort required to estimate RPPs, and the significance of the quantitative reconstructions now being developed from pollen data on the basis of RPP estimates, this is an area overdue for attention. Consistency in methodology within a single study, and clear reporting of the methodology to facilitate comparison between studies and allow later modification of data analysis as our understanding of moss pollen assemblage formation improves, are clearly important.

The input data for RPP estimation are inherently imprecise. This is true of much ecological data, and is not a reason to stop making these estimates, but better quantification of errors and uncertainties is needed. RPPs are generally cited to two or three decimal places, and accompanied by error estimates based only on the iterative process of estimation. This level of precision is, we consider, misleading; the data acquisition process also includes many potential sources of errors, and the underlying assumption of a single taphonomic mechanism brings its own uncertainties. With this in mind, perhaps it is worth considering a return to Andersen's (1970; 1973) categorical geometric scale for RPP values.

Acknowledgements

This is paper number 2 from the Crackles Bequest Project, funded by the University of Hull via a bequest from the will of Dr F. Eva Crackles. The authors thank the Yorkshire Wildlife Trust, Natural England and the Ministry of Defence for access to the study sites. Katy Anderson, Sarah Garlick, Gabrielle Jarvis, Simon Kitcher, Francis Rowney and Helen Symons are gratefully acknowledged for their assistance in the field. We also thank the two anonymous reviewers for their useful and constructive comments which helped to improve an earlier version of this manuscript.

References

- Abraham, V., Kozáková, R., 2012. Relative pollen productivity estimates in the modern agricultural landscape of Central Bohemia (Czech Republic). *Rev. Palaeobot. Palynol.* 179, 1-12.
- Adam, D.P., Mehringer, P.J., 1975. Modern pollen surface samples – an analysis of subsamples. *J. Res. U.S. Geol. Surv.* 3, 733-736.
- Andersen, S.T., 1970. The relative pollen productivity and pollen representation of North European trees, and correction factors for tree pollen spectra. *Dan. Geol. Unders.* 96, 1–99.
- Andersen, S.T., 1973. The differential pollen productivity of trees and its significance for the interpretation of a pollen diagram from a forested region. In: Birks, H.J.B., West, R.G. (Eds.), *Quaternary Plant Ecology*. Blackwell, Oxford, pp. 109-116.
- Andersen, S.T., 1974. Wind conditions and pollen deposition in a mixed deciduous forest. II. Seasonal and annual pollen deposition 1967-1972. *Grana* 14, 64-77.
- Autio, J., Hicks, S., 2004. Annual variations in pollen deposition and meteorological conditions on the fell Aakenustunturi in northern Finland: potential for using fossil pollen as a climate proxy. *Grana* 43, 31-47.
- Bennett, K.D., 1995. Pollen Catalogue of the British Isles. <http://chrono.qub.ac.uk/pollen/pc-intro.html>. Accessed 8 May 2015.
- Beug, H.-J., 2004. *Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete*. Verlag Friedrich Pfeil, Munich.
- Bonny, A., 1980. Seasonal and annual variation over 5 years in contemporary airborne pollen trapped at a Cumbrian lake. *J. Ecol.* 68, 421-441.

- Boyd, W.E., 1986. The role of mosses in modern pollen analysis: the influence of moss morphology on pollen entrapment. *Pollen Spores* 28, 243-256.
- Bradshaw, R.H.W., 1981. Modern pollen representation factors for woods in South-West England. *J. Ecol.* 69, 45-70.
- Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecol. Monogr.* 27, 325-349.
- 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.
- Broström, A., Nielsen, A.B., Gaillard, M.J., Hjelle, K., Mazier, F., Binney, H., Bunting, J., Fyfe, R., Meltsov, V., Poska, A., Räsänen, S., Soepboer, W., von Stedingk, H., Suutari, H., Sugita, S., 2008. Pollen productivity estimates of key European plant taxa for quantitative reconstruction of past vegetation: a review. *Veg. Hist. Archaeobot.* 17, 461-468.
- Bunting, M.J., Middleton, R., 2009. The Multiple Scenario Approach – a pragmatic method for past vegetation mosaic reconstruction. *Holocene* 19, 799-803.
- Bunting, M.J., Hjelle, K.L., 2010. Effect of vegetation data collection strategies on estimates of Relevant Source Area of Pollen (RSAP) and Relative Pollen Productivity (RPP) for non-arboreal taxa. *Veg. Hist. Archaeobot.* 19, 365-374.
- Bunting, M.J., Armitage, R., Binney, H.A., Waller, M., 2005. Estimates of Relative Pollen Productivity and Relevant Source Area of Pollen for major tree taxa in two Norfolk (UK) woodlands. *Holocene* 15, 459-465.
- Bunting, M.J., Farrell, M., Broström, A., Hjelle, K.L., Mazier, F., Middleton, R., Nielsen, A.B., Rushton, E., Shaw, H., Twiddle, C.L., 2013. Palynological perspectives on vegetation

- survey: a critical step for model-based reconstruction of Quaternary land cover. *Quat. Sci. Rev.* 82, 41-55.
- Bunting, M.J., Grant, M.J., Waller, M., 2015. Pollen signals of ground flora in managed woodlands. *Rev. Palaeobot. Palynol.* doi: 10.1016/j.revpalbo.2015.10.001
- Caseldine, C.J., 1981. Surface pollen studies across Bankhead Moss, Fife, Scotland. *J. Biogeogr.* 8, 7-25.
- Clarke, K.R., Somerfield, P.J., Chapman, M.G., 2006. On resemblance measures for ecological studies including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. *J. Exp. Mar. Biol. Ecol.* 330, 55-80.
- Clymo, R.S., Mackay, D., 1987. Upwash and downwash of pollen and spores in the unsaturated surface layer of *Sphagnum*-dominated peat. *New Phytol.* 105, 175-183.
- Cundill, P.R., 1985. The use of mosses in modern pollen studies at Morton Lochs, Fife. *Trans. Bot. Soc. Edinb.* 44, 375-383.
- Donders, T.H., Hagemans, K., Dekker, S.C., de Weger, L.A., de Klerk, P., Wagner-Cremer, F., 2014. Region-specific sensitivity of anemophilous pollen deposition to temperature and precipitation. *PLoS ONE* 9, 1-15.
- Fagerlind, F., 1952. The real signification of pollen diagrams. *Bot. Not.* 1952, 185-224.
- Gimingham, C.H., Birse, E.M., 1957. Ecological studies on growth-form in bryophytes: I. Correlations between growth-form and habitat. *J. Ecol.* 45, 533-545.
- Goldstein, S., 1960. Degradation of pollen by phycomycetes. *Ecology* 41, 543-545.
- Havinga, A. 1984. A 20-year experimental investigation into the differential corrosion susceptibility of pollen and spores in various soil types. *Pollen Spores* 26, 541-557.
- Hicks, S., 1985. Modern pollen deposition records from Kuusamo, Finland. *Grana* 24, 167-184.

- Hicks, S., 2001. The use of annual arboreal pollen deposition values for delimiting tree-lines in the landscape and exploring models of pollen dispersal. *Rev. Palaeobot. Palynol.* 117, 1–29.
- Hicks, S. 2003. Towards better temporal, spatial and ecological resolution in palaeoecological reconstructions: the role of pollen monitoring. In: Tonkov, S. (Ed.), *Aspects of Palynology and Palaeoecology. Festschrift in honour of Elissaveta Bozilova.* Pensoft, Sofia, pp. 43-60.
- Hill, T.R., 1996. Statistical determination of sample size and contemporary pollen counts, Natal Drakensberg, South Africa. *Grana* 35, 119-124.
- Hjelle, K.L., 1998. Herb pollen representation in surface moss samples from mown meadows and pastures in western Norway. *Veg. Hist. Archaeobot.* 7, 79–96.
- Hjelle, K.L., Sugita, S., 2012. Estimating pollen productivity and relevant source area of pollen using lake sediments in Norway: how does lake size variation affect the estimates? *Holocene* 22, 313-324.
- Hope-Simpson, J.F., 1940. On the errors in the ordinary use of subjective frequency estimations in grassland. *J. Ecol.* 28, 193-209.
- Huusko, A., Hicks, S., 2009. Conifer pollen abundance provides a proxy for summer temperature: evidence from the latitudinal forest limit in Finland. *J. Quat. Sci.* 4, 522–528.
- Kindt, R., Coe, R., 2006. *Tree diversity analysis: a manual and software for common statistical methods for ecological and biodiversity studies.* World Agroforestry Centre, Nairobi.

- Kirby, K.J., Bines, T., Burn, A., Mackintosh, J., Pitkin, P., Smith, I., 1986. Seasonal and observer differences in vascular plant records from British woodlands. *J. Ecol.* 74, 123-131.
- Kitcher, S.J., 2014. Reconstructing palaeoenvironments of the White Peak region of Derbyshire, northern England. Ph.D. Thesis, University of Hull, UK.
- Kuoppamaa, M., Huusko, A., Hicks, S., 2009. *Pinus* and *Betula* pollen accumulation rates from the northern boreal forest as a record of interannual variation in July temperature. *J. Quat. Sci.* 24, 513-521.
- Lisitsyna, O.V., Hicks, S., Huusko, A., 2012. Do moss samples, pollen traps and modern lake samples all collect pollen in the same way? A comparison from the forest limit area of northernmost Europe. *Veg. Hist. Archaeobot.* 21, 187-199.
- Losvik, M.H., 1991. A hay meadow in western Norway – changes in the course of a growing season. *Nord. J. Bot.* 11, 577–586.
- Markgraf, V., 1980. Pollen dispersal in a mountain area. *Grana* 19, 127-146.
- Martínková, J., Šmilauer, P., Mihulka, S., 2002. Phenological pattern of grassland species: relation to the ecological and morphological traits. *Flora* 197, 290-302.
- Matthias, I., Nielsen, A.B., Giesecke, T., 2012. Evaluating the effect of flowering age and forest structure on pollen productivity estimates. *Veg. Hist. Archaeobot.* 21, 471–484.
- Mazier, F., Broström, A., Gaillard, M.J., Sugita, S., Vittoz, P., Buttler, A., 2008. Pollen productivity estimates and relevant source area for major taxa in a pasture woodland (Jura Mountains, Switzerland). *Veg. Hist. Archaeobot.* 17, 479–496.

- Mazier F., Nielsen A.B., Broström A., Sugita S., Hicks S., 2012. Signals of tree volume and temperature in a high-resolution record of pollen accumulation rates in northern Finland. *J. Quat. Sci.* 27, 564–574.
- Moore, P.D., Webb, J.A., Collinson, M.E., 1991. *Pollen Analysis*. Blackwell Scientific, Oxford.
- Mulder, C., Janssen, C.R., 1998. Application of Chernobyl Caesium-137 fallout and naturally occurring lead-210 for standardization of time in moss samples: recent pollen-flora relationships in the Allgäuer Alpen, Germany. *Rev. Palaeobot. Palynol.* 103, 23–40.
- Mulder, C., Janssen, C.R., 1999. Occurrence of pollen and spores in relation to present-day vegetation in a Dutch heathland area. *J. Veg. Sci.* 10, 87–100.
- Nielsen, A.B., Møller, P.F., Giesecke, T., Stavngaard, B., Fontana, S.L., Bradshaw, R.H.W., 2010. The effect of climate conditions on inter-annual flowering variability monitored by pollen traps below the canopy in Draved Forest, Denmark. *Veg. Hist. Archaeobot.* 19, 309–323.
- Pardoe, H.S., 1996. Micro-scale patterns of modern pollen deposition within three alpine plant communities. *New Phytol.* 132, 327–341.
- Pardoe, H.S., Giesecke, T., van der Knaap, W.O., Svitavská-Svobodová, H., Kvavadze, E.V., Panajiotidis, S., Gerasimidis, A., Pidek, I.A., Zimny, M., Święta-Musznicka, J., Latalowa, M., Noryśkiewicz, A.M., Bozilova, E., Tonkov, S., Filipova-Marinova, M.V., van Leeuwen, J.F.N., Kalnina, L., 2010. Comparing pollen spectra from modified Tauber traps and moss samples: examples from a selection of woodlands across Europe. *Veg. Hist. Archaeobot.* 19, 271–283.
- Poska, A., Meltsov, V., Sugita, S., Vassiljev, J., 2011. Relative pollen productivity estimates of major anemophilous taxa and relevant source area of pollen in a cultural landscape of the hemi-boreal forest zone (Estonia). *Rev. Palaeobot. Palynol.* 167, 30–39.

- Räsänen, S., Hicks, S., Odgaard, B.V., 2004. Pollen deposition in mosses and in a modified 'Tauber trap' from Hailuoto, Finland: what exactly do the mosses record? *Rev. Palaeobot. Palynol.* 129, 103–116.
- Räsänen, S., Suutari, H., Nielsen, A.B., 2007. A step further towards quantitative reconstruction of past vegetation in Fennoscandian boreal forests: Pollen productivity estimates for six dominant taxa. *Rev. Palaeobot. Palynol.* 146, 208–220.
- Ribeiro, H., Abreu, I., 2014. A 10-year survey of airborne allergenic pollen in the city of Porto (Portugal). *Aerobiologica* 30, 333-344.
- Roulston, T.H., Cane, J.H., 2000. Pollen nutritional content and digestibility for animals. *Plant Syst. Evol.* 222, 187-209.
- Soepboer, W., Sugita, S., Lotter, A.F., van Leeuwen, J.F.N., van der Knaap, W.O., 2007. Pollen productivity estimates for quantitative reconstruction of vegetation cover on the Swiss Plateau. *Holocene* 17, 65-77.
- Sugita, S., 1994. Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *J. Ecol.* 82, 881-897.
- Sugita, S., 2007a. Theory of quantitative reconstruction of vegetation. I. Pollen from large sites REVEALS regional vegetation composition. *Holocene* 17, 229–241.
- Sugita, S., 2007b. Theory of quantitative reconstruction of vegetation. II. All you need is LOVE. *Holocene* 17, 243–257.
- Sugita, S., Gaillard, M.-J., Broström, A., 1999. Landscape openness and pollen records: a simulation approach. *Holocene* 9, 409-421.
- Sugita S, Hicks S, Sormunen H., 2010. Absolute pollen productivity and pollen-vegetation relationships in northern Finland. *J. Quat. Sci.* 25, 724-736.

- Tauber, H., 1965. Differential pollen dispersion and the interpretation of pollen diagrams. *Dan. Geol. Unders.* 89, 1–69.
- Tauber, H., 1967. Investigations of the mode of pollen transfer in forested areas. *Rev. Palaeobot. Palynol.* 3, 277–286.
- Tosunoglu, A., Bicacki, A., 2015. Seasonal and intradiurnal variation of airborne pollen concentrations in Bodrum, SW Turkey. *Environ. Monit. Assess.* 187, 167.
- Twiddle, C.L., Jones, R.T., Caseldine, C.J., Sugita, S., 2012. Pollen productivity estimates for a pine woodland in eastern Scotland: the influence of sampling design and vegetation patterning. *Rev. Palaeobot. Palynol.* 174, 67–78.
- Ugolotti, M., Pasquarella, C., Vitali, P., Smith, M., Albertini, R., 2015. Characteristics and trends of selected pollen seasons recorded in Parma (northern Italy) from 1994 to 2011. *Aerobiologica* 31, 341–352.
- Usher, M.B., 1980. An assessment of conservation values within a large Site of Special Scientific Interest. *Field Stud.* 5, 323–348.
- van Vliet, A.J.H., Overeem, A., de Groot, R.S., Jacobs, A.F.G., Spieksma, F.T.M., 2002. The influence of temperature and climate change on the timing of pollen release in the Netherlands. *Int. J. Climatol.* 22, 1757–1767.
- von Stedingk, H., Fyfe, R., Allard, A., 2008. Pollen productivity estimates for the reconstruction of past vegetation at the forest tundra ecotone. *Holocene* 18, 323–332.
- Wilmshurst, J.M., McGlone, M.S., 2005. Origin of pollen and spores in surface lake sediments: Comparison of modern palynomorph assemblages in moss cushions, surface soils and surface lake sediments. *Rev. Palaeobot. Palynol.* 136, 1–15.

Figure captions

Fig. 1 Map showing the location of Yorkshire within the British Isles (right) and of study sites within Yorkshire (left). SC = Strensall Common, WI = Wheldrake Ings, NCW = North Cliffe Wood.

Fig. 2 Frequency plots of I_B values for all possible pairs from each set of ten simulated pollen assemblages. Plot titles indicate the site providing the underlying probability distribution and the simulated count size; see section 2.4.2 for details.

Fig. 3a Proportions of pollen count (diagonally striped bars) and distance-weighted plant abundance cumulated to 10 m (plain bars) and 100 m (dotted bars) in moss samples and vegetation survey data collected from North Cliffe Wood (for dates see Table 1a). Grey shading shows where x10 exaggeration has been used to improve the legibility of a less abundant taxon. AP/NAP_POL shows the proportion of arboreal/non-arboreal palynological equivalent (pe) types recorded in the pollen assemblages which originate from plants not recorded within 100 m of the sampling point. NAP_PLA shows the proportion of non-arboreal plants recorded within 100 m of the sampling point which were not recorded in any of the pollen assemblages from that point.

Fig. 3b Proportions of pollen count (diagonally striped bars) and distance-weighted plant abundance cumulated to 10 m (plain bars) and 100 m (dotted bars) in moss samples and vegetation survey data collected from Wheldrake Ings (for dates see Table 1b). Grey shading shows where x10 exaggeration has been used to improve the legibility of a less abundant taxon. AP/NAP_POL shows the proportion of arboreal/non-arboreal palynological equivalent

(pe) types recorded in the pollen assemblages which originate from plants not recorded within 100 m of the sampling point. NAP_PLA shows the proportion of non-arboreal plants recorded within 100 m of the sampling point which were not recorded in any of the pollen assemblages from that point.

Fig. 3c Proportions of pollen count (diagonally striped bars) and distance-weighted plant abundance cumulated to 10 m (plain bars) and 100 m (dotted bars) in moss samples and vegetation survey data collected from Strensall Common (for dates see Table 1c). Grey shading shows where x10 exaggeration has been used to improve the legibility of a less abundant taxon. AP/NAP_POL shows the proportion of arboreal/non-arboreal palynological equivalent (pe) types recorded in the pollen assemblages which originate from plants not recorded within 100 m of the sampling point. NAP_PLA shows the proportion of non-arboreal plants recorded within 100 m of the sampling point which were not recorded in any of the pollen assemblages from that point.

Table captions

Table 1a Summary plant survey and pollen assemblage data for North Cliffe Wood. X indicates presence of plant in plant list or pollen type in pollen assemblage. S indicates presence of non-pollen-producing seedling in the plant survey. Palynological equivalent (pe) types are given for the first listed plant species included in that type only; thus for example *Cirsium*-type pollen is produced by both *Cirsium arvense* and *Cirsium vulgare*.

Table 1b Summary plant survey and pollen assemblage data for Wheldrake Ings. X indicates presence of plant in plant list or pollen type in pollen assemblage. S indicates presence of non-pollen-producing seedling in the plant survey. Palynological equivalent (pe) types are given for the first listed plant species included in that type only; thus for example Apiaceae pollen is produced by both *Oenanthe fistulosa* and *Silaum silaus*.

Table 1c Summary plant survey and pollen assemblage data for Strensall Common. X indicates presence of plant in plant list or pollen type in pollen assemblage. S indicates presence of non-pollen-producing seedling in the plant survey. Palynological equivalent (pe) types are given for the first listed plant species included in that type only; thus for example Cyperaceae pollen is produced by both Cyperaceae and *Trichophorum germanicum*.

Table 2a Bray-Curtis Indices for pair-wise comparison of samples from North Cliffe Wood; “shared taxa” analyses only consider taxa found in both the pollen assemblages and the plant lists at this site.

Table 2b Bray-Curtis Indices for pair-wise comparison of samples from Wheldrake Ings; “shared taxa” analyses only consider taxa found in both the pollen assemblages and the plant lists at this site.

Table 2c Bray-Curtis Indices for pair-wise comparison of samples from Strensall Common; “shared taxa” analyses only consider taxa found in both the pollen assemblages and the plant lists at this site.

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Table 1a. Summary plant survey and pollen assemblage data for North Cliffe Wood. X indicates presence of plant in plant list or pollen type in pollen assemblage. S indicates presence of non-pollen-producing seedling in the plant survey. Palynological equivalent (pe) types are given for the first listed plant species included in that type only; thus for example *Cirsium*-type pollen is produced by both *Cirsium arvense* and *Cirsium vulgare*.

Plant species	Presence in plant survey			palynological equivalent	Presence in pollen samples		
	06-May	21-Jun	20-Sep		06-May	21-Jun	20-Sep
<i>Alnus glutinosa</i>			X	<i>Alnus glutinosa</i>	X	X	X
<i>Angelica sylvestris</i>	X			Apiaceae		X	X
<i>Moehringia trinervia</i>		X		<i>Arenaria</i> -type			
<i>Betula</i> sp.	X	X S	X	<i>Betula</i>	X	X	X
<i>Cardamine pratensis</i>		X		Brassicaceae undiff.	X	X	X
<i>Caltha palustris</i>	X			<i>Caltha palustris</i> -type			
<i>Cerastium fontanum</i>	X			<i>Cerastium</i> -type			
<i>Ceratocapnos claviculata</i>	X	X	X	<i>Ceratocapnos claviculata</i>			
<i>Circaea lutetiana</i>	X	X	X	<i>Circaea</i>			
<i>Cirsium arvense</i>		X	X	<i>Cirsium</i> -type			
<i>Cirsium vulgare</i>	X						
<i>Corylus avellana</i>	X	X S	X	<i>Corylus avellana</i> -type	X	X	X
<i>Carex remota</i>		X		Cyperaceae	X	X	X
<i>Dryopteris dilatata</i>	X	X	X	<i>Dryopteris</i> -type	X	X	X
<i>Chamerion angustifolium</i>		X	X	<i>Epilobium</i> -type			
<i>Epilobium</i> sp.	X						
<i>Filipendula ulmaria</i>	X			<i>Filipendula</i>	X	X	X
<i>Iris pseudacorus</i>	X	X	X	<i>Iris</i>			
<i>Juncus</i> sp.	X	X	X	Juncaceae			
<i>Lonicera periclymenum</i>	X	X	X	<i>Lonicera periclymenum</i>			
<i>Lythrum salicaria</i>		X		<i>Lythrum salicaria</i> -type			
<i>Lycopus europaeus</i>	X			<i>Mentha</i> -type			
<i>Mentha aquatica</i>	X		X				
<i>Mercurialis perennis</i>	X	X	X	<i>Mercurialis perennis</i>		X	X

<i>Myosotis sylvatica</i>		X		<i>Myosotis arvensis</i> -type				
<i>Oxalis acetosella</i>	X	X	X	<i>Oxalis acetosella</i>				
<i>Brachypodium sylvaticum</i>	X			Poaceae		X	X	X
<i>Deschampsia flexuosa</i>		X						
<i>Poa nemoralis</i>	X	X						
Poaceae		X	X					
<i>Primula vulgaris</i>	X	X	X	<i>Primula veris</i> -type				
<i>Glechoma hederacea</i>			X	<i>Prunella vulgaris</i> -type				
<i>Pteridium aquilinum</i>	X	X	X	<i>Pteridium aquilinum</i>		X		
<i>Quercus robur</i>	X		X	<i>Quercus</i>		X	X	X
<i>Quercus</i> sp.	S	X S	X					
<i>Ranunculus acris</i>	X	X		<i>Ranunculus acris</i> -type				
<i>Ranunculus repens</i>	X	X	X					
<i>Galium aparine</i>		X		Rubiaceae				
<i>Galium palustre</i>	X	X						
<i>Galium</i> sp.			X					
<i>Rubus fruticosus</i> agg.	X	X	X	<i>Rubus</i> undifferentiated				
<i>Rubus idaeus</i>			X					
<i>Rumex acetosa</i>	X			<i>Rumex acetosa</i>				X
<i>Rumex obtusifolius</i>	X	X	X	<i>Rumex obtusifolius</i>				
<i>Salix caprea</i>	X	X		<i>Salix</i>		X	X	X
<i>Salix</i> sp.			X					
<i>Hyacinthoides non-scripta</i>	X	X		<i>Scilla</i> -type				
<i>Scrophularia nodosa</i>	X			<i>Scrophularia</i> -type				
<i>Ajuga reptans</i>	X	X	X	<i>Scutellaria</i> -type				
<i>Scutellaria galericulata</i>		X	X					
<i>Crataegus</i> sp.		S	S	<i>Sorbus</i> -type		X	X	X
<i>Prunus spinosa</i>	X		X					
<i>Sorbus aucuparia</i>	X S	X S	X S					
<i>Lamium</i> sp.	X			<i>Stachys</i> -type				
<i>Stachys officinalis</i>		X						
<i>Stellaria holostea</i>	X	X	X	<i>Stellaria holostea</i>				
<i>Urtica dioica</i>	X	X	X	<i>Urtica dioica</i>				
<i>Viola</i> sp.	X			<i>Viola palustris</i> -type			X	

Other pollen types recorded*Acer campestre*-type

Asteraceae (Asteroideae)
Asteraceae (Lactuceae)
Calluna vulgaris
Cereal-type
Chenopodiaceae
Fagus sylvatica
Fraxinus excelsior
Lysimachia vulgaris-type
Phragmites-type
Picea
Pinus sylvestris
Plantago major
Polygala
Polypodium
Populus
Potentilla-type
Pteropsida (monoete) undiff.
Rhododendron ponticum
Rosaceae undiff.
Ulmus
Viola arvensis-type

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Table 1b. Summary plant survey and pollen assemblage data for Wheldrake Ings. X indicates presence of plant in plant list or pollen type in pollen assemblage. S indicates presence of non-pollen-producing seedling in the plant survey. Palynological equivalent (pe) types are given for the first listed plant species included in that type only; thus for example Apiaceae pollen is produced by both *Oenanthe fistulosa* and *Silaum silaus*.

Plant species	Presence in plant survey			palynological equivalent	Presence in pollen samples		
	12-May-11	23-Jun-11	02-Sep-10		12-May-11	23-Jun-11	02-Sep-10
<i>Achillea ptarmica</i>	X	X	X	<i>Achillea</i> -type			X
<i>Oenanthe fistulosa</i>	X			Apiaceae	X	X	X
<i>Silaum silaus</i>	X	X					
<i>Cardamine pratensis</i>	X	X	X	Brassicaceae undiff.	X	X	X
<i>Caltha palustris</i>			X	<i>Caltha palustris</i> -type			
<i>Cerastium fontanum</i>	X	X	X	<i>Cerastium</i> -type	X	X	
<i>Stellaria graminea</i>	X	X	X	Caryophyllaceae			X
<i>Crepis</i>			X	Asteraceae (Lactuceae)	X	X	X
<i>Hypochaeris radicata</i>	X						
<i>Leontodon autumnalis</i>		X					
<i>Taraxacum officinale</i> agg.	X	X	X				
<i>Carex acuta</i>	X			Cyperaceae	X	X	X
Cyperaceae	X	X	X				
<i>Filipendula ulmaria</i>	X	X	X	<i>Filipendula</i>	X	X	X
<i>Glyceria fluitans</i>		X		<i>Hordeum</i> -type	X	X	
<i>Lotus corniculatus</i>		X		<i>Lotus</i>		X	
<i>Lotus</i> sp.	X		X				
<i>Lychnis flos-cuculi</i>	X	X		<i>Lychnis flos-cuculi</i>			
<i>Lysimachia</i>			X	<i>Lysimachia vulgaris</i> -type			
<i>Myosotis laxa</i>		X		<i>Myosotis arvensis</i> -type			
<i>Myosotis</i> sp.	X						
<i>Persicaria amphibia</i>	X	X	X	<i>Persicaria amphibia</i>			
<i>Plantago lanceolata</i>	X	X	X	<i>Plantago lanceolata</i>	X	X	X
<i>Agrostis</i> sp.		X		Poaceae	X	X	X

<i>Alopecurus geniculatus</i>	X	X					
<i>Alopecurus pratensis</i>	X	X	X				
<i>Anthoxanthum odoratum</i>	X	X					
<i>Bromus sp.</i>		X					
<i>Festuca sp.</i>		X					
<i>Glyceria maxima</i>	X	X	X				
<i>Lolium perenne</i>		X					
<i>Phalaris arundinacea</i>	X	X	X				
<i>Phleum pratense</i> agg.		X					
<i>Poa sp.</i>		X					
Poaceae	X	X	X				
<i>Ranunculus</i>			X	<i>Ranunculus acris</i> -type	X	X	X
<i>Ranunculus acris</i>	X	X					
<i>Ranunculus ficaria</i>	X						
<i>Ranunculus flammula</i>	X	X	X				
<i>Ranunculus repens</i>	X	X					
<i>Galium palustre</i>	X	X	X	Rubiaceae			
<i>Rumex acetosa</i>	X	X	X	<i>Rumex acetosa</i>	X	X	X
<i>Rumex obtusifolius</i>			X	<i>Rumex obtusifolius</i>	X		X
<i>Rumex crispus</i>	X	X		<i>Rumex sanguineus</i> -type			
<i>Sanguisorba officinalis</i>	X	X	X	<i>Sanguisorba officinalis</i>			
<i>Stellaria palustris</i>	X	X		<i>Stellaria holostea</i>			
<i>Trifolium dubium</i>	X			<i>Trifolium</i> -type			
<i>Trifolium pratense</i>	X	X					
<i>Trifolium repens</i>		X					
<i>Veronica catenata</i>	X	X		<i>Veronica</i>			
<i>Veronica serpyllifolia</i>	X	X					
<i>Vicia cracca</i>	X	X	X	<i>Vicia cracca</i>			
<i>Lathyrus pratensis</i>	X	X	X	<i>Vicia sylvatica</i> -type			

Other pollen types recorded

Acer campestre-type
Alnus glutinosa
Artemisia-type
Asteraceae (Asteroideae)
Betula
Calluna vulgaris
Cereal-type
Chenopodiaceae
Corylus avellana-type

Empetrum nigrum
Fagus sylvatica
Fraxinus excelsior
Phragmites-type
Picea
Pinus sylvestris
Potentilla-type
Prunella vulgaris-type
Pteridium aquilinum
Pteropsida (monoete) indet.
Quercus
Ranunculus arvensis
Rosaceae undiff.
Salix
Sorbus-type
Tilia
Ulmus
Vaccinium-type

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Table 1c. Summary plant survey and pollen assemblage data for Strensall Common. X indicates presence of plant in plant list or pollen type in pollen assemblage. S indicates presence of non-pollen-producing seedling in the plant survey. Palynological equivalent (pe) types are given for the first listed plant species included in that type only; thus for example Cyperaceae pollen is produced by both Cyperaceae and *Trichophorum germanicum*.

plant species	Presence in plant survey				palynological equivalent	Presence in pollen samples			
	20-Apr	20-May	21-Jun	06-Sep		20-Apr	20-May	21-Jun	06-Sep
<i>Betula</i> sp.		S	S	S	<i>Betula</i>	X	X	X	X
<i>Calluna vulgaris</i>	X	X	X	X	<i>Calluna vulgaris</i>	X	X	X	X
<i>Campanula rotundifolia</i>				X	<i>Campanula</i> -type				
Cyperaceae	X	X			Cyperaceae	X		X	
<i>Trichophorum germanicum</i>			X	X					
<i>Juncus</i> sp.	X	X	X	X	Juncaceae				
<i>Luzula multiflora</i>			X						
<i>Phragmites australis</i>	X	X	X	X	<i>Phragmites australis</i> -type	X	X	X	X
<i>Pinus</i> sp.	S	S	S	S	<i>Pinus sylvestris</i>	X	X	X	X
<i>Molinia caerulea</i>		X	X	X	Poaceae	X	X	X	X
Poaceae	X	X							
<i>Potentilla erecta</i>			X		<i>Potentilla</i> -type	X	X		
<i>Quercus</i> sp.			S	S	<i>Quercus</i>	X	X	X	X
<i>Salix repens</i>			X S	X	<i>Salix</i>	X	X	X	X
<i>Erica tetralix</i>	X	X	X	X	<i>Vaccinium</i> -type	X	X	X	X

Other pollen types recorded

Acer campestre-type
Alnus glutinosa
Artemisia-type
Asteraceae (Lactuceae)
Brassicaceae undiff.
Caryophyllaceae undif.
Cereal-type
Chenopodiaceae

Corylus avellana-type
Fagus sylvatica
Filipendula
Fraxinus excelsior
Ilex aquifolium
Picea
Plantago lanceolata
Pteropsida (monoete) indet.
Ranunculus acris-type
Rosaceae undif.
Rumex obtusifolius
Rumex undiff.
Tilia
Ulmus
Viola palustris-type

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Table 2a. Bray-Curtis Indices for pair-wise comparison of samples from North Cliffe Wood; “shared taxa” analyses only consider taxa found in both the pollen assemblage and the plant lists at this site.

	06/05 v ^s 21/06	06/05 v ^s 20/09	21/06 v ^s 20/09
%dwp(10) (all taxa)	0.872	0.861	0.960
%dwp(10) (shared taxa)	0.872	0.870	0.978
%dwp(10) (all taxa, no trees)	0.630	0.592	0.865
%dwp(100) (all taxa)	0.892	0.828	0.894
%dwp(100) (shared taxa)	0.922	0.847	0.895
pollen proportions (all taxa)	0.819	0.797	0.886
pollen proportions (shared taxa within 10m)	0.854	0.831	0.923
pollen proportions (shared taxa within 100m)	0.846	0.834	0.910

Table 2b. Bray-Curtis Indices for pair-wise comparison of samples from Wheldrake Ings; “shared taxa” analyses only consider taxa found in both the pollen assemblage and the plant lists at this site.

	12/05 v ^s 23/06	12/05 v ^s 02/09	23/06 v ^s 2/09
%dwp(10) (all taxa)	0.737	0.604	0.668
%dwp(10) (shared taxa)	0.652	0.649	0.852
%dwp(100) (all taxa)	0.746	0.661	0.725
%dwp(100) (shared taxa)	0.654	0.679	0.834
pollen proportions (all taxa)	0.629	0.654	0.542
pollen proportions (shared taxa within 10m)	0.638	0.725	0.606
pollen proportions (shared taxa within 100m)	0.638	0.725	0.606

Table 2c. Bray-Curtis Indices for pair-wise comparison of samples from Strensall Common; “shared taxa” analyses only consider taxa found in both the pollen assemblage and the plant lists at this site.

	20/04 v ^s 25/05	20/04 v ^s 21/06	25/05 v ^s 21/06	20/04 v ^s 06/09	25/05 v ^s 06/09	21/06 v ^s 06/09
%dwp(10) (all taxa)	0.874	0.915	0.765	0.931	0.732	0.722
%dwp(10) (shared taxa)	0.926	0.963	0.960	0.911	0.881	0.880
%dwp(100) (all taxa)	0.878	0.908	0.944	0.766	0.764	0.763
%dwp(100) (shared taxa)	0.926	0.956	0.968	0.907	0.896	0.896
pollen proportions (all taxa)	0.859	0.733	0.836	0.520	0.535	0.608
pollen proportions (shared taxa within 10m)	0.900	0.765	0.847	0.376	0.394	0.538
pollen proportions (shared taxa within 100m)	0.896	0.744	0.824	0.369	0.388	0.388

Highlights

- The impact of fieldwork timing on standard methods for estimation of RPP was tested
- Heath vegetation quite stable over season, grasslands and woodland understorey differ
- Phenological timing of vegetation survey in grasslands crucial for RPP estimation
- Pollen assemblages vary across field season in all habitat types
- Both seasonal variation and micro-scale heterogeneity may affect pollen assemblages

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