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REVIEW ARTICLE

From early pollen trapping experiments to the Pollen Monitoring Programme

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Abstract Pollen monitoring has become a standard investigation method for researchers in several disciplines; among them are Quaternary palynologists, who conduct experiments in order to gain insights that will help to interpret the content of pollen in sediments. A review of the literature shows how these experiments diversified during the 1920s and 1930s with an array of different research questions, ranging from pollination biology to hay fever studies. Quaternary palynologists gained renewed interest with the possibility of radiocarbon dating late Quaternary sediments and obtaining accumulation rates. Also, the comprehensive model of pollen deposition and the pollen budget studies by H. Tauber encouraged researchers to conduct similar experiments using the same type of pollen trap, which became the main trapping device for Quaternary palynologists. The high precipitation in the tropics inspired the development of alternative designs. The

equipment used to assess the pollen content in the air has evolved from simple gravity devices to different types of apparatus using a vacuum pump or revolving rods that collect the pollen on impact. Silicone impregnated filters exposed perpendicularly to the wind can also yield a volumetric assessment and have proven useful in areas with a low content of pollen in the air. The literature review is followed by a brief account of the developments which established the basis for the formation of a group of scientists monitoring the pollen deposition at a network of sites using standard pollen traps, the Pollen Monitoring Programme (PMP). Over the last 15 years the network has collected a large dataset, which is now available to answer a number of research questions. A summary of selected regions and environments, for which pollen monitoring results are available, is provided to serve as a complement to the investigations mentioned above and to provide an overview that may stimulate new research.

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Introduction

Investigations that aim to assist in the interpretation of fossil pollen diagrams are of major importance, as they provide the tools to reconstruct past environments. In this respect, much information has been gained from the collection of surface samples of lake sediments, mosses and soil. Studies monitoring the pollen content of air and deposition of airborne pollen have also given enormous insights. Early results of diverse trapping experiments and surface sample studies are summarized by Erdtman (1943).

Since the 1950s, the related research objectives of determining the quantity of pollen in the air, the amount being deposited on the ground, and the proportions of pollen types on the ground have developed independently, but have often inspired each other. The prospect of using modern pollen deposition rates as analogues for past situations (Welten 1944; Davis et al. 1973; Hicks 1994) spurred the formation of the Pollen Monitoring Programme (PMP), which is a network of researchers who have agreed to monitor the pollen deposition using standardised traps.

The aim of this contribution is to provide an account of the history of pollen trapping experiments, highlighting a selection of devices that have been and are being used to trap pollen. This review is by no means comprehensive, but intends to provide an overview of past developments. A further intention is to introduce a selection of natural environments where pollen monitoring experiments are conducted as part of the PMP and which are included in several of the contributions in this volume.

The beginnings of pollen trapping

It is difficult to set a starting date for investigations on the quantity of pollen released by a plant, present in a volume of air, or deposited at a distance from the parent plant. Early aerobiologists like Miquel (1883), who reported on the amount of pollen in the air among other things, probably provided the first information. However, if the lecture by von Post at the 16th convention of Scandinavian naturalists in 1916 is taken as the birth hour of the quantitative study of pollen in late Quaternary deposits, then we must look to Hesselman as the pioneer of pollen trapping experiments. Following von Post's (1918) presentation, Hesselman raised the question of how to separate locally produced pollen from long distance transported pollen (Hesselman 1916; Davis 2000). While von Post pointed out the good match between the occurrence of a pollen type in surface samples and the regional presence of the parent tree, Hesselman (1919a) conducted a pollen trapping experiment designed to quantify long distance pollen deposition. Petri dishes were exposed for consecutive 24-h periods from mid May until the end of June 1918, on two light ships. The Petri dishes contained filter paper soaked in glycerine and were sheltered from the rain. The two light ships were situated in the Baltic Sea 30 and 55 km from the nearest shore and Hesselman reported a total of 16.2 and 8.82 pollen grains per mm² over the period from mid May to the end of June. He argued that it is important to take account of this long distance component when reconstructing the spread of species. Moreover, he suggested that the expression of palynological results as absolute counts per sample, as was commonly done before von Post

described the advantage of percentages, may be better suited to adjust for the long distance component. The idea was to devise threshold values for pollen accumulation rates (PAR) of different taxa that would indicate their local presence. Such threshold values were finally devised by Hicks (2001) for the distribution limits of *Betula*, *Pinus* and *Picea* in northern Finland and were applied to Holocene pollen diagrams by Seppä and Hicks (2006).

In 1919, under Hesselman's supervision, Malmström (1923) conducted similar pollen trapping experiments in a large mire complex in northern Sweden. Malmström placed his pollen trapping Petri dishes in different vegetation types and observed that most *Pinus* pollen was trapped in the pine woodland, although, due to the large amount of *Betula* pollen, this trap had the lowest percentage of *Pinus* pollen. On the other hand, absolute catches of *Picea* pollen were similar for all traps, while its percentage values varied between 8 and 27%.

When Hesselman obtained his pollen trapping results, he realised that this information was also relevant to forestry research, and he also published the results in the communications of the State Institute of Experimental Forestry (Hesselman 1919b). In central Europe, much interest in pollen dispersal stemmed from questions on pollination and reproduction biology. Knoll (1932) conducted experiments to estimate the settling velocity of pollen grains and Pohl (1933) investigated the quantity of airborne pollen around a parent tree. Rempe (1937) repeated and extended Pohl's experiments, exposing cylinders mounted with film and coated with vaseline to measure the amount of impacting pollen, thus simulating the fertilisation of the stigma. Experiments with such impact traps showed that the pollen content of the air dropped away exponentially with increasing distance from the emitting *Corylus* shrub. However, sticky glass plates on the ground indicated that maximum pollen deposition only occurred at some distance away from the plant. A different pattern was observed with increasing distance from a dense stand. The highest pollen counts in impact traps were found 70 to 150 m away from the stand, while there was little decline in pollen deposition on the ground over the first 300 m. To estimate long distance transport, pollen impact cylinders were set up on the island of Helgoland (Germany), situated 51 km from the mainland and 44 km from the nearest island. The most noteworthy result was the impact of 9.5 *Quercus* pollen grains per mm² during a 3.5 day period, which should be sufficient for the fertilisation of an oak tree (Rempe 1937).

Scamoni (1955) started in 1933 to monitor airborne pollen at a forestry station in Eberswalde (Germany) using a microscope slide with an area of 4 cm² coated with glycerine-gelatine. The slide was mounted vertically, under a roof, on a wind vane, 1.6 m above the ground, so that it would be always exposed in the direction of the wind.

During the flowering seasons of the years 1933–1936 and in 1949, the microscope slides were changed daily. Comparison of the results with daily meteorological conditions showed that warmth generally initiated the flowering whereas precipitation and moisture reduced pollen emission or removed the emitted pollen from the air. In 1938 Scamoni set up the same type of pollen trap to study the pollination of *Pinus* and *Picea* along a height gradient in the Krkonoše/Karkonosze mountains along the border between the Czech Republic and Poland (Scamoni 1949). He observed that pollen was transported up and down the mountain, but due to the different times of flowering, pollination may only have been possible within an altitudinal belt of 200 m. Pollen from distant sources was also frequently observed, so pollination from distant trees could not be excluded. He even recorded a pollen grain of *Tilia* on top of the highest peak at 1,600 m.

The impact of pollen on vertical cylinders or horizontal plates is not only related to the pollen content of the air, but also to the wind speed at the sampling location. Erdtman (1937) experimented with vacuum cleaners to obtain a quantitative measure of the pollen content of the air. In 1937, he sampled the pollen content of the air with a vacuum cleaner on a voyage from Göteborg to New York and back. The vacuum cleaner contained a bag of filter paper that could be chemically dissolved and the pollen analysed. He found that the pollen content of the air was lowest in mid ocean and that the overall average of 6.6 pollen grains per 100 m³ during the journey was dwarfed by the approximately 18,000 pollen grains per 100 m³ measured from April to June at the top of the water tower in the city of Västerås, Sweden.

Bertsch (1935) monitored the daily pollen deposition during the years 1932, 1933 and 1934, to facilitate the interpretation of pollen diagrams. He used microscope slides with a 1 cm² area covered with glycerine. By comparing pollen deposition with the local and regional flowering of trees, he was able to separate pollen transported from regional and long distance sources. Regional forest inventory data allowed him to compare average pollen proportions with the proportional abundance of forest trees. As the regional forest was dominated by *Picea* with some *Abies* and *Fagus*, Bertsch observed a rather good agreement between pollen percentages and proportional tree abundance, but found *Abies* to be under-represented.

During 1934 and 1935, Lüdi monitored the pollen deposition in the Davos valley in Switzerland, with the primary aim to collect information with regard to the observation that hay fever was reduced in this high altitude alpine valley (Lüdi and Vareschi 1936; Lüdi 1937a). For pollen traps, he used low rimmed glass cups with glycerine at the bottom. These were placed in the open and thus also collected the pollen in rain water. Lüdi was also interested

in interpreting fossil pollen spectra and therefore also published the results with this focus (Lüdi 1937b). This publication, together with the results obtained by Bertsch (1935), was used for comparison in the interpretation of the first pollen accumulation reconstruction of the laminated sediments of Faulenseemoos by Welten (1944). Welten directed his attention towards the Late-glacial part of the sequence and directly related tree abundance to pollen abundance. However, when considering short term climate fluctuations during the Late-glacial, he proposed that climate change could directly control the amount of pollen produced, but a reaction through a change in population density would be too slow. Welten emphasised that the absolute pollen diagram offered new insights into vegetation history. He concluded that volumetric sampling is important for obtaining absolute pollen deposition values for comparison with modern pollen deposition, but in the absence of pollen deposition values for the tundra he had to turn to Aario's (1940) pollen counts per weight from samples in the Finnish tundra and the tree line.

In most of the pollen trapping experiments described above, the authors clearly stated that the exposed glass dishes or microscope slides were protected from rain. In contrast, Firbas and Sagromsky (1947) reported on a pollen trapping experiment from February to August 1945, when unsheltered cans were exposed in the field for 2–3 consecutive weeks, so that they would also collect rain water. They found that the values obtained compared best with those of Welten (1944) from sub-fossil material and suggested that monitoring should ideally be conducted over several years. However, their primary intention of pollen trapping was not to aid in the interpretation of fossil material, but to estimate the production of proteins and fats by trees.

The pollen content of air

Monitoring the pollen content of the air has become standard practice, and during the flowering season, daily results and forecasts are often part of weather reports to inform those with hay fever. The research on airborne allergenic pollen is part of the field of aerobiology, which as a research topic has a long history, including Pouchet (1860) and Pasteur (1862). However, a specific focus on airborne pollen started only with the discovery of the cause of “summer catarrh”, as hay fever used to be called, by the English doctor Charles Blackley (1873). He constructed a roofed impact pollen trap with the microscope slide exposed vertically and a wind vane to orientate the sticky surface against the wind. Thus he was probably the first person to record the occurrence of atmospheric pollen during the flowering season.

Microscope slides coated with a sticky substance were hence already exposed to the atmosphere before Quaternary palynologists took an interest. However, when European Quaternary palynology took off, there seems to have been an enormous exchange of ideas and results. In contrast, in North America, the research on the pollen content of the air developed before an increased interest in Quaternary palynology and quickly became important (Wodehouse 1935). Durham (1928) published the design of a simple sampler consisting of a coated microscope slide placed between two horizontal metal discs, and suggested a standardised sampling and counting procedure to obtain comparable results (Durham 1946). This sampler was widely used in the USA and similar designs were employed in Europe.

A similar setup was employed by Hyde (1950) in 1943 to sample the atmospheric pollen content at a number of stations throughout England and Wales. In 1952 the English phytopathologist Hirst (1952) published the design of a volumetric sampler, which, with modifications, was produced by Burkard Manufacturing Ltd. and is therefore known as Burkard trap or Hirst sampler. This device is equipped with a vacuum pump that reduces pressure within the sampling chamber. The air is accelerated through a narrow orifice onto a sticky tape covering a drum and the tape is moved forward by clockwork. This type of volumetric air sampler has become the most commonly used sampler in aeropalynology in Europe. In North America the Durham device is only rarely used today, whereas the Rotorod sampler manufactured by Multidata Sampling Technologies has become the most widely used device there (Frenz and Lince 1997). In the Rotorod sampler, small rods coated with a silicone based medium are rotated through the air and the particles impacting on the rods are analysed (Di-Giovanni 1998).

In 1974, Cour published the description of an impact sampler consisting of five layers of cellulose gauzes set in a 20 × 20 cm frame and mounted on a wind vane, so that the filter would always be perpendicular to the wind (Cour 1974). The gauze is impregnated with silicone oil, creating an adhesive surface for pollen grains, and with the installation of an anemometer at the level of the frame, the amount of pollen in the air can be calculated. The Cour trap is relatively easy to construct and its comparably large surface increases the amount of pollen that is caught. For this reason it is often chosen in regions with thin vegetation cover and therefore little pollen production, such as in the Sahara where it was first applied (Cour and Duzer 1973) or the Tibetan plateau (Cour et al. 1999). The trap may also be effective for studies of the long distance transport of pollen (Rousseau et al. 2006).

Pollen influx versus pollen accumulation rates

Absolute pollen analytical results are usually referred to as pollen influx or PAR, and there is often confusion over the difference between the two terms. The early history of the two terms provides some insights. With the invention of radiocarbon dating it became possible to estimate sediment accumulation rates of deposits other than varved lake sediments. Consequently Davis and Deevey (1964) carefully sampled and dated the Late-glacial sediments from Rogers Lake, Connecticut USA, established an age-depth model, and estimated absolute pollen deposition. The title of this publication was “Pollen accumulation rates: estimates from Late-Glacial sediment of Rogers Lake”, and thus the term pollen accumulation rate (PAR) was coined. In her second publication on the Late-glacial and Holocene sediments from Rogers Lake, Davis (1967) also used the terms “total pollen deposition” and “accumulation rate”. However, the term “influx” emerged in the third publication on Rogers Lake (Davis 1969), where Davis stated that E. J. Cushing suggested this term to her. For some reason this term stuck in the heads of Quaternary palynologists and became generally used to describe the amount of pollen in volumes of sediment with known deposition time, as well as that deposited in gravity pollen samplers. The term was criticised as early as 1980 by Thompson (1980) in a letter to the editor of *Quaternary Research*, where he pointed out that the term was imprecisely used by palynologists. His main argument was that the dimensions of the term are not consistent with those of related properties used in physics. Thompson suggested that the term “influx” should be used as the time integral of flux density (accumulation rate) and expressed in units of volume, mass, or numbers of grains. The term flux may be used in the same way as in physics ($\text{grains} \times \text{year}^{-1}$), but applying it to pollen in lake sediments would require knowledge on the lake surface area, the average sediment accumulation rate and the average pollen concentration in the sediment. Following his argument, the term “flux” as well as his suggested use of the term “influx” could easily be used to describe the amount of pollen caught in a pollen trap, while it would prove difficult to quantify for a lake. He argued that the quantity: “pollen grains \times unit surface⁻¹ \times unit time⁻¹” is comparable to the physical quantity of “flux density” and therefore the use of the term “pollen accumulation rate” is preferable, as it had been used in the pioneering article by Davis and Deevey (1964). While palynologists adopted the term “influx” within a few years, they have not fully managed to return to the original term in 30 years, although no arguments defending the term against Thompson’s (1980) criticism were found in the available literature. Related to this discussion are studies showing the differential deposition of pollen and sediment

in lake basins which have recently been summarized by Giesecke and Fontana (2008).

Tauber's pollen trap

Working in the radiocarbon laboratory of the National Museum in Copenhagen, Denmark, Tauber came in contact with palaeoecologists and took an interest in the transport and deposition of pollen. In 1965 he published his model of pollen dispersion, which built on published concepts of particle transport in the atmosphere and a few results from pollen trapping experiments, among which he made most use of those published by Rempe (1937). In order to test his theory with measurements, he devised a gravity pollen trap, which differs from earlier designs in having an aerodynamic collar (Fig. 1), and installed it both with and without a roof on a raft floating in a small lake within a wood on Sjælland, Denmark (Tauber 1967). The trap, thenceforth named a Tauber trap, quickly became popular among palaeoecologists, who set out to conduct new experiments with it (Berglund 1973; Andersen 1974; Hicks 1974; Bonny 1976), although Tauber only published the detailed description of the design in 1974. Peck (1972) even tested it in a turbulent water flow and conducted a trapping experiment where the trap was used above as well as below the water surface (Peck 1973). In a comparison of Tauber traps with open glass cups without lids, Krzywinski (1977) noted that the Tauber trap lid was at times covered by pollen, and he speculated that this pollen could be washed into the trap by rain drops. He conducted an experiment with coal dust and *Corylus* pollen, and showed that large quantities of dust and pollen can be transported into the trap by raindrop splash. Bonny and

Allen (1983) conducted a field experiment to investigate this problem further, but could not find conclusive evidence for the suggested transport of pollen from the lid through splashing rain drops. However, they did find that the average pollen catch was consistently higher in the Tauber trap, but attributed this to a discrepancy in performance between the traps in moving air.

Tauber himself continued pollen trapping experiments over a period of 5 years to test his theoretical model of pollen transport and deposition (Tauber 1977). Andersen (1967, 1970), who at the time worked at the Geological Survey of Denmark, investigated the relationship between pollen proportions in surface samples and the tree composition of a small forest in southern Jylland, Denmark. So it is no surprise that Andersen had already installed traps of Tauber's design in the forest by 1967 (Andersen 1974). What is astonishing is that this monitoring experiment has been kept going, so that this dataset is the longest continuous pollen monitoring record in existence, much to the credit of Peter Friis Møller at the Geological Survey of Denmark and Greenland (Nielsen et al. 2010). Andersen also played a part in the development of tablets with *Lycopodium* spores (Stockmarr 1971) for 'spiking' samples prior to preparation as a means of estimating pollen concentrations and accumulation rates (Birks 2009). The use of an exotic marker was less time consuming than earlier methods used to establish the absolute pollen content of a sample (Davis 1966) and thus may have helped encourage more trapping experiments. Although Stockmarr's tablets of *Lycopodium* spores are not the only way of spiking a sample (Bonny 1972), they are the most widely used, because they come as a convenient tablet.

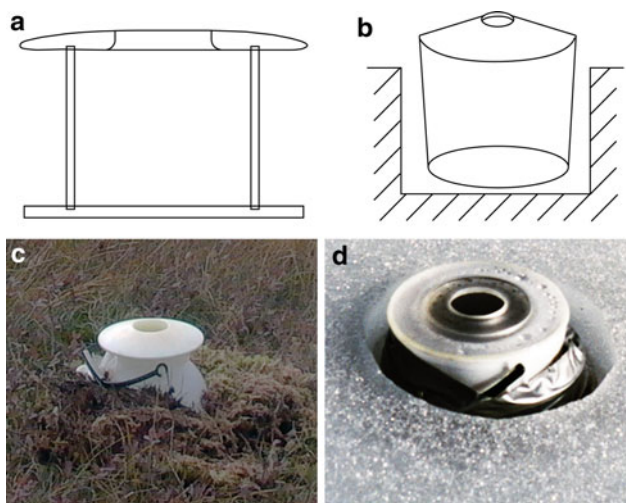


Fig. 1 Comparison of **a** Tauber's original design (Tauber 1974) to **b** one modification commonly used within the Pollen Monitoring Programme (PMP; Hicks et al. 2001), and photos of the two trap designs in the field **c** with Tauber collar and **d** flat sloping lid

Other modern gravity samplers

Pollen traps of Tauber's design have been used in different parts of the world and in different vegetation types, such as the Egyptian desert (Ritchie 1986), the prairie of northern Texas (Hall 1992), the Australian rainforest (Kershaw and Strickland 1990), the pampas grassland of Argentina (Majas and Romero 1992), and in Iceland and Svalbard (Hattestrand et al. 2008). However, what is termed a Tauber trap in recent publications is often missing the typical characteristic of Tauber's (1974) design, the aerodynamic lid (Fig. 1). In this respect it is important to note that the standard traps used in the pollen monitoring network (PMP) generally lack the aerodynamic lid, but retain a collar that gently slopes up to a hole in the centre (Fig. 1; Hicks et al. 2001). The traps in the PMP network are generally installed in such a way that the collar is at or slightly above ground level, where wind speeds are low and the aerodynamic effect of the collar is less important.

With a similar reasoning, Cundill (1986) constructed a pollen trap that was modelled on the pollen collection by a moss surface, so that results from the trap and the moss sample could be compared. He used a flower pot sunk into the ground and with the top covered with acetate wool and a metal mesh. The flower pot drains excess water and the acetate wool imitates a moss surface and traps the pollen. Acetate wool has the advantage that it can be dissolved in acetone to liberate the pollen grains. For this reason acetate fibre had already been used in the pollen trap designed by F. Oldfield and modified and described by Flenley (1973). In this design, the idea was not necessarily to simulate the trapping characteristics of moss, but to cope with the large precipitation in a tropical rainforest. Thus the acetate fibre (de-oiled acetate yarn) was placed on a sintered glass filter sitting in a polythene funnel, which led into a container with an overflow so that water was retained in the container but prevented from rising up into the filter.

Bush (1992) experimented with this design in different environments, which resulted in a modified version. Due to problems in obtaining acetate fibre, and its behaviour in the field and in the laboratory, he used viscose rayon sitting in a glass-fibre filter. In the laboratory, the rayon is dissolved in acetolysis mixture and the glass-fibre filter can be thoroughly washed. Behling et al. (1997) described how the rayon can be washed and squeezed during standard pollen preparation rather than dissolved, and Gosling et al. (2003) showed that this procedure had little influence on the composition and amount of pollen recovered. Gosling et al. (2003) observed that the rayon in Bush's (1992) trap design remained dry even if the bottle was filled with water, and thus argued that the bottle is not necessary. Also, Behling and co-workers have developed a simplified design, consisting of a large centrifuge tube containing some glycerine in the bottom and with rayon squeezed in the top to retain pollen if the tube overflows (Niemann et al. 2009).

Surface samples that represent one or more years of pollen deposition may be difficult to obtain in the tropics in general, and specifically in situations with seasonal flooding such as in the Amazon basin (Gosling et al. 2003). Here pollen traps are important surface samples, which may explain why the results are often only reported as percentages. Little is known about pollen production and deposition in the tropics (Hamilton and Perrott 1980; Meadows 1984), and pollen traps of various designs will surely help to gain more insight.

The Pollen Monitoring Programme

In contrast to tropical pollen trapping, pollen monitoring in Europe has a long history, the early part of which was reviewed above. Pollen trapping experiments have already

yielded insights on several aspects of average pollen deposition, its inter-annual variability, the relationship between the abundance of trees and PAR, and the influence of climatic variability on annual pollen deposition (Andersen 1974, 1980). In more recent years, trapping experiments and long monitoring series from northern Finland have continued to demonstrate the usefulness of this research (Hicks 1985, 2001). Hicks (1994) showed that various vegetation types could be characterised in terms of PAR, the results from which could be used for the interpretation of sub-fossil pollen profiles. Hyvärinen (1975, 1976) presented PAR from small lakes in northern Finland, showing that they could be compared between lakes despite potential problems of re-deposition and sediment focussing. The successful comparisons between these PAR from lake sediments and those from pollen traps (Hicks and Hyvärinen 1999; see also Giesecke and Fontana 2008) may also have stimulated new interest in pollen trapping experiments. Thus the prospect of using the results of pollen monitoring experiments directly to interpret the estimated PAR in sediment cores led, in 1995, to the formation of an INQUA working group to monitor pollen deposition in Europe. The geographical focus was soon broadened to welcome scientists from outside Europe, and

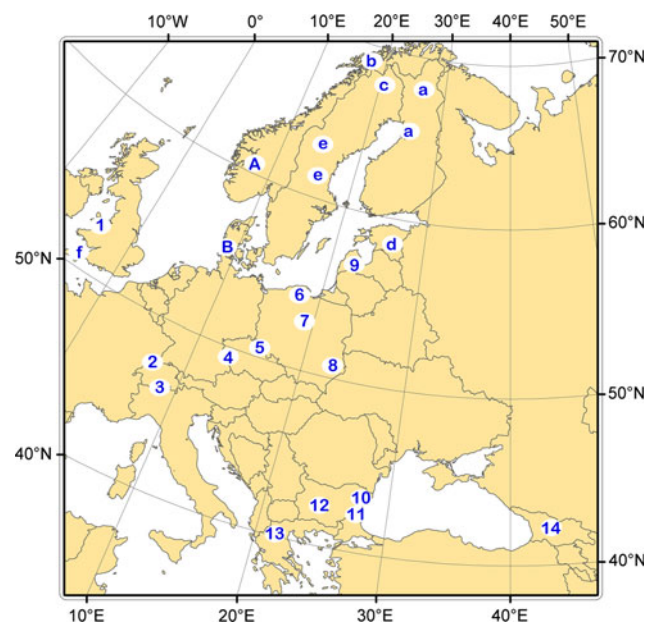


Fig. 2 Distribution of regions with available data on annual pollen deposition as monitored according to the guidelines of the Pollen Monitoring Programme (PMP) in selected parts of Europe and Asia. Numbers mark the regions specified in Table 1. Capital letters indicate the locations of site specific studies A Birks and Bjune (2010) and B Nielsen et al. (2010). Lower case letters mark selected monitoring studies published elsewhere: a Hicks (1985, 1992, 2001); b Jensen et al. (2007); c Hattestrand et al. (2008); d Koff (2001); e Giesecke and Fontana (2008); f Tinsley (2001)

the group has taken the name “Pollen Monitoring Programme” (PMP). Participants in the programme have set up pollen traps in various regions (Fig. 2) and situations using a standard design of modified Tauber trap (Fig. 1). The group’s main activity is the organisation of meetings every 2 or 3 years open to all those interested in pollen trapping experiments. In addition, a website is maintained at <http://pmp oulu.fi> and a database stores the results obtained from the standardised experiments.

At the 15th INQUA Congress in 1999, the first *Symposium on Modern Pollen Deposition* was conducted and a collection of papers from the symposium, together with additional results from the PMP, were collected in a special volume of *Review of Palaeobotany and Palynology* published in 2001. Within this volume, Hicks et al. (2001) introduced the PMP and its short history and drew together the first tentative observations based on results from the network of standardized pollen traps. Since its beginnings, regular PMP meetings have inspired participants and colleagues to conduct and publish individual pollen trapping experiments or to interrogate individual datasets in new ways (Kvavadze 2001; Räsänen et al. 2004; Fontana 2003; Hicks and Sunnari 2005; Gerasimidis et al. 2006; Pidek 2007; Sjögren et al. 2008; Giesecke and Fontana 2008; Bennett and Hicks 2005; Huusko and Hicks 2009; Sugita et al. 2009; Pidek et al. 2009; Poska and Pidek 2010). The present volume brings together three investigations that combine most of the local and regional pollen trapping experiments to investigate the variation in PAR of *Fagus* (Pidek et al. 2010), differences in the representation of pollen in moss samples versus pollen traps (Pardoe et al. 2010), and the interaction between inter-annual climate variability and annual pollen deposition (van der Knaap et al. 2010). Filipova-Marinova et al. (2010) estimate pollen productivity based on Bulgarian and Georgian pollen monitoring results, Sjögren et al. (2010) further develop the method of estimating absolute pollen productivity based on Swiss results, Birks and Bjune (2010) compare the trapping of pollen to that of macroscopic plant remains, and Nielsen et al. (2010) present the continuation of Andersen’s (1974) trapping experiments. As many of the questions asked in these investigations have already been addressed by Sheila Hicks (Hicks 1999), her long monitoring series from northern Finland were not included in the analyses above. However, more investigations should follow that make use of this large dataset and, of course, include the Finnish results.

PMP trapping regions

The investigations by Pidek et al. (2010), van der Knaap et al. (2010), Pardoe et al. (2010), Filipova-Marinova et al. (2010), and Sjögren et al. (2010) make use of pollen

monitoring results from a number of regions, which are briefly presented below. A summary with details of the different regions is presented in Table 1.

Poland

Gdańsk region. Four traps are located in the Oliwa forest, part of Trójmiejski landscape park. The forest consists of different associations of *Fagus* with *Pinus*, *Quercus*, *Picea*, *Carpinus* and *Larix*. Communities dominated by *Alnus* and *Ulmus* surrounded by patches of *Carpinus* woodland occur along watercourses.

The Kashubian lake district has a great variety of surface relief, soil and local climate. This is reflected by the diversity of plant communities including *Fagus* dominated forest, *Fagus-Quercus* forest with *Pinus*, *Pinus-Betula* forest on poor sands, patches of *Picea* forest, and open areas. Six pollen traps are located in these communities. *Pinus* and *Picea* plantations are also widely distributed in the region.

The Tuchola forests include woodlands on the Brda and Wda river outwash plains as well as on moraine islands. *Pinus* forests dominate vast areas. Three traps are located in Wierzchlas reserve (southeastern Tuchola forests), in *Carpinus-Tilia* woodland with *Taxus* and nearby stands of *Alnus* and *Ulmus*. In the *Taxus* Reserve, yew forms the lower tree layer, representing the remains of the Tuchola primeval forest. Six traps are situated in the Zaborski landscape park (western Tuchola forests), in *Pinus* forest, dry ground forest, mixed forest with *Pinus* dominance and open landscapes.

Brodnica lakeland. Three traps are located in forest openings and in an open area close to the lake Strażym. Mixed forests and pine woods occupy over 40% of the area. Subcontinental dry ground forest, composed of *Quercus*, *Tilia*, *Carpinus* and *Alnus* woods, and riverine forest, is less abundant.

Toruń basin. Las Piwnicki reserve lies in the northern part of an isolated dry ground forest patch with *Carpinus*, *Quercus*, *Tilia* and *Pinus*. The forest is surrounded on one side by *Pinus* forests and on the other side by the almost treeless open land in the suburbs of Toruń. *Alnus* dominates a nearby wetland and riverine forest. Two traps are located inside the dry ground forest and on its edge, and a third trap is situated in an open area.

The Roztocze region in south eastern Poland belongs to the middle Polish upland belt. Roztocze national park protects the most natural parts of the forests. Nine pollen traps are located in the national park near the village of Guciów. Here there is a mosaic of plant communities including *Abies* wood, mixed forest dominated by *Fagus*, *Abies* and *Pinus*, cultivated fields and pure *Fagus* forest (Pidek 2004).

Table 1 Summary of particularities for regions with pollen traps that were considered in the analysis of Pidek et al. (2010), van der Knaap et al. (2010), Pardoe et al. (2010), Filipova-Marinova et al. (2010), and Sjögren et al. (2010)

Study area	Number on map	Contributors	Number of traps	Starting year	Latitude	Longitude	Elevation (m a.s.l.)	Dominant vegetation	Habitat	Dominant trees
Wales UK: Capel Curig	1	Heather Pardoe	5	1996	53°05'02" to 53°06'00" N	03°53'04" to 03°55'00" W	145–500	Oak wood	Mountains	<i>Quercus</i>
Switzerland: Swiss Jura	2	Pim van der Knaap, Jacqueline van Leeuwen	5	2002	46°32'14" to 46°32'47" N	06°13'14" to 06°14'24" E	1,315–1,410	Conifer-dominated forest and pasture	Mountains	<i>Picea</i> , <i>Abies</i> , <i>Fagus</i>
Switzerland: Swiss Alps	3	Pim van der Knaap, Jacqueline van Leeuwen	28	1991	45°59'10" to 46°43'10" N	07°46'40" to 08°04'00" E	1,525–3,000	Subalpine conifer forest and alpine pasture	Mountains	<i>Picea</i> , <i>Pinus cembra</i> , <i>Larix</i> , <i>Alnus viridis</i>
Czech Republic: Šumava mountains	4	Helena Svitavská-Svobodová	17	1997	48°46'16" to 49°10'26" N	13°10'56" to 13°51'27" E	735–1,378	<i>Picea</i> forest and raised bogs with <i>Picea</i>	Mountains	<i>Pinus × pseudopumilio</i>
Czech Republic: Krkonoše mountains	5	Helena Svitavská-Svobodová	19	1998	50°39'36" to 50°47'20" N	15°31'49" to 15°51'12" E	759–1,554	Raised bogs with <i>Pinus mugo</i>	Mountain valleys	<i>Picea</i>
Poland: Gdańsk region	6	Marcelina Żimny, Joanna Święta-Musznicka	4	2002	54°26'53" to 54°26'70" N	18°29'40" to 18°29'56" E	140	Mixed forest	Lowlands	<i>Fagus</i>
Poland: Kashubian lake district	6	Marcelina Żimny, Joanna Święta-Musznicka	6	2002	54°15'47" to 54°23'13" N	17°42'53" to 18°01'85" E	185–220	Mixed forest	Bogs and lakeland	<i>Fagus</i> , <i>Quercus</i> , <i>Pinus</i> , <i>Picea</i>
Poland: Tuchola forests	6	Agnieszka Noryskiewicz, Anna Filbrandt-Czaja	6	1998	53°31'10" to 53°56'23" N	17°31'21" to 18°07'26" E	104–105	<i>Pinus</i> forest with patches of dry-ground forest	Lowlands	<i>Pinus</i> , <i>Taxus</i> , <i>Carpinus</i> , <i>Tilia</i>
Poland: Brodnica lakeland	7	Bożena Noryskiewicz	3	1998	53°19'25" to 53°21'15" N	19°25'32" to 19°28'26" E	85–114	Mixed forest	Lakeland	<i>Quercus</i> , <i>Carpinus</i> , <i>Tilia</i>
Poland: Toruń basin	7	Anna Filbrandt-Czaja	3	1998	53°05'23" to 53°04'27" N	18°32'02" to 18°33'31" E	64–66	<i>Pinus</i> forest with patches of dry-ground forest	Lowlands	<i>Pinus</i> , <i>Carpinus</i> , <i>Quercus</i> , <i>Tilia</i>
Poland: Roztocze National Park	8	Irena Pidek	9	1998	50°34'20" to 50°35'41" N	23°04'25" to 23°03'14" E	243–355	Mixed forest	Valleys and low hills	<i>Fagus</i> , <i>Abies</i> , <i>Pinus</i>
Latvia	9	Laimdota Kalnīpa	12	1997	56°12'00" to 57°10'20" N	21°05'09" to 26°28'11" E	5–190	Mires, <i>Pinus</i> , <i>Picea</i> forest, mixed forest	Lowlands	<i>Pinus</i> , <i>Picea</i>
Bulgaria: Black Sea coast	10	Mariana Filipova-Marinova	4	2002	42°09'56" to 43°09'15" N	26°45'33" to 27°53'21" E	9–297	Mixed deciduous forest	Coastal area and mountains	<i>Fraxinus</i> , <i>Ulmus</i> , <i>Carpinus</i>
Bulgaria: Strandzha mountains	11	Mariana Filipova-Marinova	3	2002	42°04'11" to 42°06'40" N	27°50'17" to 27°51'39" E	130–140	Mixed deciduous forest	Mountains	<i>Fagus orientalis</i> , <i>Quercus</i> spp.
Bulgaria: Rila mountains	12	Elissaveta Bozilova, Spassimir Tonkov	2	1993	42°09'26" to 42°12'38" N	23°24'23" to 23°24'29" E	1,800–1,840	Mixed forest	Mountains	<i>Pinus peuce</i> , <i>P. sylvestris</i> , <i>Picea</i> , <i>Fagus</i>
Greece: Pieria mountains	13	Achilles Gerasimidis, Sampson Panajiotidis	6	1996	40°14'19" to 40°18'20" N	22°09'15" to 22°10'15" E	1,260–1,990	<i>Pinus</i> -dominated forest	Mountains	<i>Pinus sylvestris</i> , <i>P. nigra</i>
Georgia: Lagodekhi reserve	14	Eliso Kvavadze	8	1996	41°50'52" to 41°52'30" N	46°16'44" to 46°22'27" E	450–2,250	Mixed forest	Mountains	<i>Carpinus</i> , <i>Fagus</i> , <i>Betula</i>

The order of regions and their numbers correspond to the numbers in Fig. 2

Latvia

Traps are placed in various landscapes across Latvia ranging from coastal lowlands to semi-continental uplands stretching over a strong gradient in continentality. Due to vandalism, the number of working traps for any given year varies greatly. In 2007 a total of 24 traps were set out in nine regions, while 12 traps in five regions are currently in operation and have yielded results. The traps are often placed in large raised bog complexes (Seda, Teici and Kēmeri), and also in small openings and under the tree canopy. Three traps are positioned at the western boundary of the city of Riga in different environments: agricultural land, woodland and raised bog. The most abundant tree near all traps is *Pinus sylvestris* and *Picea abies* is common or abundant near most of the traps. Pollen traps near Riga also collect the pollen from several exotic tree species planted in the suburbs of the city.

Czech Republic

The Krkonoše mountains. These, rising to over 1,500 m, are part of the high Sudetes in the northern outlier of the Bohemian massif. The submontane zone (400–800 m) has broadleaved and mixed forests of *Fagus* together with *Picea* and *Abies*, *Acer pseudoplatanus*, *Fraxinus*, *Sorbus* and *Alnus incana*. Above this is a pure *Picea* forest belt. A total of 19 pollen traps are placed within the *Picea* belt and above the tree line.

The Šumava mountains/Böhmerwald rise to over 1,350 m and lie on the border of the Czech Republic with Germany and Austria. They have a mosaic of temperate deciduous broadleaved forest, and at higher elevations coniferous forest, as well as peat bogs and open areas. Lower elevations are dominated by acidophilous *Fagus-Abies* and herb-rich *Fagus* forests. *Picea* woods cover the hilltops above 800 m and mires occur between 600 m and the mountain tops. Most of the 18 traps are placed within these mires. Large areas around the mires are dominated by *Picea* and *Sorbus aucuparia*, while *Pinus rotundata* is prevalent on raised bogs.

Switzerland

The Swiss Jura is part of the large central European Jura mountain range, which stretches from the lower Rhône valley in France along the Swiss-French border into southern Germany. The bedrock is mainly calcareous. The colline zone is dominated by thermophilous deciduous forest with abundant *Carpinus*, *Quercus*, *Ulmus*, *Tilia* and *Fagus*. The vegetation in the montane zone consists mainly of *Fagus* forest. In the sub-alpine zone *Picea* and *Abies*

increase in abundance with altitude. The five traps are located in this zone.

The Swiss Alps have a highly varied forest composition depending on elevation, distance to the lowlands, local climate and other factors. All pollen traps are placed in the sub-alpine or alpine zone, in the following four regions: Grindelwald (8 traps) in the northern, sub-oceanic Alps, with predominantly *Picea* forest and the local presence of *Pinus cembra* and *P. mugo*; Aletsch (9 traps) in the sub-continental central Alps, with a *Pinus cembra*—*Larix* forest belt and a *Picea* belt above it with the occurrence of *Alnus viridis*; Simplon (4 traps) with a similar forest composition but mostly open; and Zermatt (5 traps) lying mostly above the tree line, and forests consisting of *Pinus cembra* and *Larix* (see van der Knaap et al. 2001).

Greece

The six traps in the Pieria mountains, northern Greece, are located in an altitudinal transect from 1,200 to 2,000 m and cover a range of landscapes from forests composed of *Pinus sylvestris* and/or *P. nigra* to open sub-alpine communities with dwarf shrubs, mostly *Juniperus communis* ssp. *nana* (see Gerasimidis et al. 2006, 2008).

Bulgaria

The Bulgarian traps are placed in several different regions. Two traps are located in openings in mixed conifer forest in the central Rila mountains, southwestern Bulgaria (see Tonkov et al. 2001). The altitudinal vegetation belts here range from *Quercus* forests on the lowest slopes, through *Fagus* forest, coniferous forests, to alpine vegetation on the summits. One trap is on a south facing slope with *Pinus peuce*, *P. sylvestris* and *Picea*, the other on a north facing slope with *Pinus peuce*, *Picea* and *Pinus mugo*.

Several traps are situated near the Black Sea coast including one in the vicinity of the Kamchia river estuary, another near Arkutino lake; at both sites *Fraxinus oxycarpa* and *Ulmus minor* are important. Three traps are situated in the Strandzha mountains with mesophytic forests dominated by *Fagus orientalis*, with an understory of *Rhododendron ponticum*, and a higher proportion of *Quercus polycarpa*, *Q. cerris* and *Q. frainetto* in drier areas. In the protected valleys of the Preslavka mountains, one trap is located in *Aesculus* dominated forest with some *Juglans*, *Fraxinus*, *Carpinus orientalis*, *Corylus* and other trees, and another in mesophytic *Cercis* dominated woodland.

Georgia

There are ten pollen traps in the Lagodekhi reserve in the Caucasus mountains, along a 2,000 m altitudinal transect

on a steep ridge line (Kvavadze 1999, 2001). The vegetation grades from wet forest in the valley dominated by *Pterocarya*, *Alnus barbata*, *Carpinus betulus* and *Acer trautvetteri*, through forests dominated by *Carpinus caucasica* and *Tilia*, higher altitude woods dominated by *Fagus orientalis* and *Carpinus caucasica*, subalpine woods of *Acer velutinum* and *Betula litwinowii*, to an alpine belt where the highest trap is located.

Wales, UK

The Welsh sites are on the slopes of Moel Siabod, close to Capel Curig. The lowest three traps are in Bryn Egan, a semi-ancient deciduous wood dominated by *Quercus petraea*, fringed by *Corylus* and *Ilex* and with a ground layer of *Pteridium* and *Rubus*. Above the wood and on surrounding slopes are plantations of conifers. Two traps are located in heathland, on the upper slopes of Moel Siabod, where *Calluna*, *Vaccinium myrtillus*, *Erica cinerea* and grasses dominate.

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