Published in final edited form as:

Rev Palaeobot Palynol. 2013 August 16; 195: 26–36. doi:10.1016/j.revpalbo.2013.03.006.

Pollen percentage thresholds of *Abies alba* based on 13-year annual records of pollen deposition in modified Tauber traps: perspectives of application to fossil situations

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Abstract

Abies alba (fir), a submontane tree from Central European mountains and uplands, is of special interest for palaeoecological and palaeoclimate interpretations due to its sensitivity to air and soil humidity. Its present distribution limit in the uplands of SE Poland is still a matter of debate. In the Holocene fir expanded to Poland very late, but early fir populations are supposed to occur in the Šumava Mts (Czech Republic). The study aims: to estimate pollen thresholds for fir presence/absence in Bohemia (Czech Republic) and Poland on the basis of modified Tauber pollen traps; to use these thresholds for tracing fir presence in two pollen diagrams from Poland (Słone and Bezedna lakes) in the border zone between the Roztocze region (with fir forest stands today) and Polesie (where fir has never played an important role); and to investigate how the percentage presence/absence threshold can be used to trace the occurrence and abundance of fir trees in the Šumava Mts based on the pollen diagrams of Rokytecká slat' and Mrtvý luh.

The fir pollen thresholds estimated in terms of PAR (pollen accumulation rates or pollen influx) range from 843 (grains cm⁻² year⁻¹) (Roztocze) to 61 (Krkonosze) and 49 (Šumava). Percentage thresholds range from 0.3% in Krkonosze where fir trees are not present within 4 km to 22% in fir-dominated woodland of the Roztocze, providing evidence of strong underrepresentation of fir in the pollen deposition. Application of these percentage thresholds to the Słone and Bezedna pollen diagrams indicates that occurrence of fir in the region is possible from 3.5 ky cal BP onwards, though the evidence is not decisive. In the Šumava, a low representation of fir pollen (1–2%) reflecting presence of scattered fir trees was detected as early as ca. 7.0 ky cal BP.

Keywords

Abies alba; pollen accumulation rates; modified Tauber traps; pollen threshold values; Central-Eastern Europe

1 Introduction

Abies alba (fir) is an important European forest-forming tree of great interest for palaeoclimate and palaeoecological reconstructions because it is both sensitive to climate change and to human impact (Finsinger and Tinner, 2006; Kozaková et al., 2011; Rybníček and Rybníková, 1978, 2009; Šamonil and Vrška, 2007; Tanu et al., 2011; Tinner and Lotter, 2006; Tomanek, 1994; Tzedakis et al., 2002; Zagwijn, 1996). North of the European Alps, fir prefers an oceanic cool and wet climate. Limiting factors for its optimum development are mean July temperature of 15 °C and mean January temperature of -4.5°C (Jaworski and Zarzycki, 1983). Northern limit of fir range is associated with annual precipitation of 600 mm, but optimum conditions in the Carpathians are associated with 700 mm of annual totals (Obidowicz et al. 2004). Its ecological requirements are between those of spruce (*Picea abies*) and beech (*Fagus sylvatica*). Fir tolerates low temperatures well in the areas with considerable air humidity. Drought during the growing season may result in the death of *Abies alba* trees (Jaworski and Zarzycki, 1983; Obidowicz et al., 2004; Tomanek, 1994).

At present, fir in Central Europe (Fig. 1A) is mainly distributed in the submontane zone, at altitudes above 400–800 m, and only in the Carpathian foreland of southern Poland does its distribution range extend down into the colline belt (Fig. 2A). In its northern distribution range in Poland, in the Holy Cross Mts (= Góry Świętokrzyskie) and in the Roztocze region of south-eastern Poland (Zajac and Zajac, 2001), fir tree stands are widespread. Together with beech, fir forms also forest stands in the mountains at elevations of 500–1100 m a.s.l., frequently admixed with spruce. In the Tatra Mountains (part of the Carpathian Mts in southern Poland) it occurs very locally up to very high elevations of 1450 m a.s.l. (Tomanek, 1994). North of the Middle Polish Uplands only few and small stands of fir have been recorded. It is, however, still a matter of debate whether the limit of continuous fir distribution was previously more to the north, since suitable habitats seem to exist in the Lublin Upland (Matuszkiewicz, 1991). For example, a suitable location might be the Chełm Hills at the northern edge of the Lublin Upland where Zajac and Zajac (2001) reported isolated fir stands, 50–70 km north of the present continuous fir limit in the Roztocze region. The landscape is hilly with Cretaceous rocks and has abundant beech in forests on dry ground, in which one would also expect fir. However, no pollen-bearing deposits have been found up to now to test the possible former presence of fir.

In the Czech Republic, fir is at present mostly distributed in the lower montane zone. In the Šumava Mts. fir ascends to 1300 m a.s.l. (Hejný and Slavík, 1997) and in the Krkonoše Mts up to 1000 m a.s.l. (Musíl and Hamerník, 2007). The proportion of fir in the Šumava forests is small (only 0.7%). The highest representation (1.1%) is observed between 950 and 1150 m a.s.l. Below 950 m a.s.l., where the best conditions for fir may be expected, it occupies merely 0.3% according to the Forest inventory 1999–2002 (Zatloukal et al., 2005).

In the Holocene, fir often entered as one of the last components into spruce–beech forest. In Poland the first pollen records of fir are from the mountains of the south at ca. 5 cal ky BP (Szczepanek, 2001; Obidowicz et al., 2004). Fir spread from SE Poland into the

neighbouring Roztocze region and the Holy Cross Mts (Fig. 2A), where it reached its maximum ca. 2.5 cal ky BP (Bałaga, 1998; Obidowicz et al., 2004; Szczepanek, 1982). Bałaga (1998) studied sites in the Wieprz river valley in the Roztocze region and found about 1% fir pollen for the Subatlantic period. Korze (2011) found 10% fir pollen in a Subatlantic Roztocze pollen diagram, which testifies to the on-site presence of fir trees. At present, fir trees occupy about 8.5% of Central Roztocze (Izdebski et al., 1992). In the Polesie Lubelskie region, ca. 50 km north-east of the Chełm Hills, on the other hand, Bałaga (2003, 2007) found only 0.2% fir pollen, which might either be long-distance transported from the south or reflecting rare single trees near the sites. Long-distance transport is more likely, as this region has numerous lakes and a prevalence of mires, which is little suitable for fir.

In the Šumava Mts (Bohemian Forest, Fig. 2B), very early occurrence of fir pollen is dated to ca. 8.2 cal ky BP, whereas the first maximum at ca. 4.5 cal ky BP is synchronous with the results of southern Poland. In the Krkonoše Mts, fir only arrived in the Older Subboreal period, and had its major expansion much later – at ca. 2.5 cal ky BP (Hütteman and Bortenschläger, 1987; Svobodová, 2004a,b; Jankovská, 2007). A decline of fir is registered in the 19th century both historically and palynologically (Kozaková et al., 2011).

Fir begins to produce pollen at a relatively old age, at forest edges at 30–40 years and in dense forests at 60–70 years (Suszka, 1983). Thus only mature fir forests are able to produce pollen in large quantities. Abundant pollen production occurs commonly every 3–5 years in lowlands, every 5–8 years in mountains (Suszka, 1983; Tomanek, 1994). The flowering phenology of fir has not been well studied so far. Fir starts to flower in April and continues in May (Tomanek, 1994). Flower-bud formation takes place in the year before the flowering and is highly influenced by climate factors, mostly temperature (van der Knaap et al. 2010). Data on the driving forces for flower-bud formation are, however, quite scarce and provide a miscellaneous pattern of correlations (Suszka, 1983). The ripening of the pollen of fir takes about 28 days and takes place in spring, during which sudden, short periods of low temperatures (0° C) have no negative impact.

Fir is anemophilous, so its pollen is abundantly produced. The pollen grains are large and heavy, so they are relatively poorly distributed. So far the published record on fir pollen deposition rates is very scarce (Tonkov et al., 2001; Gerasimidis et al., 2006). An essential question for the reconstruction of distribution ranges from fossil pollen percentage data is “What pollen values delimit the presence or absence of a tree species?” (Latałowa and van der Knaap, 2006; van der Knaap et al., 2005). The results can contribute to the discussion on the defining the criteria of first local presence of the tree taxon as exactly as possible based on pollen data (cf. Watts, 1973; Bennett, 1985; Birks, 1989). Modified Tauber traps for monitoring annual pollen deposition (Pollen Monitoring Programme; Hicks et al., 1996) provide the most valuable record for the calculation of such pollen presence/absence thresholds (Hicks, 2001; Hicks and Sunnari 2005), both in terms of pollen deposition (PAR = pollen accumulation rates; pollen influx) and of percentages. Long annual pollen-deposition data series of modified annual Tauber traps are now available from a few areas where silver fir is present (Table 1; Fig. 1B): the Krkonoše Mts and the Šumava Mts in the Czech Republic and the Roztocze region in Poland. The traps are located in different

vegetation units ranging from forest to open land, which enables tracing fir pollen deposition in a variety of situations. Other uses of these data are presented in Pardoe et al. (2010), Pidek et al. (2010a), and van der Knaap et al. (2010).

The aims of this study are:

- 1) to estimate pollen threshold values for the presence of fir (*Abies alba*) for the study regions in the Czech Republic and Poland on the basis of modified Tauber pollen traps, both in terms of pollen deposition (PAR = pollen accumulation rates; pollen influx) and of percentages;
- 2) to use the pollen percentage thresholds in the interpretation of fir presence in two pollen diagrams of the lakes Słone and Bezedna (Table 2; Fig 2A) in the border zone between the Roztocze region (with fir forest stands today) and Polesie (where fir has never played an important role);
- 3) to investigate how the percentage presence/absence threshold values of fir can be used to trace the occurrence of fir trees in the Šumava Mts based on pollen diagrams from Rokytická slat' and Mrtvý luh (Table 2; Fig 2B). Fir pollen was in the period ca. 5.0 cal ky BP so abundant in the Šumava Mts that it has no modern analogue in Central Europe (Svobodová et al., 2002).

2 Material and methods

2.1 Pollen traps

Nine modified annual Tauber pollen traps are placed in the Roztocze region in Poland, and 18 in the Šumava Mts and 19 in the Krkonoše Mts in the Czech Republic. The traps are those used in the Pollen Monitoring Programme (Hicks and Hyvärinen, 1986; Hicks et al., 1996). Each trap is collected and replaced in the field every autumn after the flowering season. Site and laboratory details are in Pidek et al. (2010a). Many traps have missing years (online Fig. A) for different reasons, but this is well compensated by the large number of traps in each study region. The common record of the three regions covers 1998–2010 (13 years). Fir pollen percentages are calculated on the basis of AP = 100% (arboreal pollen, including trees and shrubs). The commonly used basic sum of AP+NAP=100% (arboreal + non-arboreal pollen) was not applied here because of frequent overrepresentation of Poaceae in pollen traps (Pidek et al., 2010b). Averages, both for pollen deposition and percentages, were calculated on the basis of all values in each region (online Table A). Percentages of *Abies* trees in the surroundings were estimated individually at a distance differing in relation to the size of forest opening in which a trap is situated. In case of small openings the radius of ca. 1 km is suggested by Sugita et al. (1999) as a relevant source area of pollen. In case of big openings, the percentage share of fir trees was estimated in ca. 4 km radius.

In order to trace trends in the pollen deposition of fir, three classes are distinguished: high (more than 130% of the mathematical average PAR of the same pollen trap, average (70–130%)), and low (<70%). Additionally, the percentage of pollen traps without any fir pollen is provided (Fig. 3).

The share of fir trees differs between the trapping sites and so does the size of forest opening and the distance of the nearest fir tree to the trap (Fig. 4). Thus fir pollen deposition can be traced in different situations. The pollen-trap sites show interesting differences between the Czech and Polish study regions. In Poland, some traps are located in fir-dominated forest (trap G-1) or close to it (traps G-2–G-4), whereas in the Czech mountains the traps are placed along altitudinal transects across different vegetation units and biotopes. In Poland the traps are placed at ca. 300 m a.s.l. or lower, in the Czech Šumava Mts between 750 and 1350 m a.s.l. and in the Krkonoše Mts between 759 and 1555 m a.s.l. In Poland and in the Šumava Mts, most traps are located in forested areas, however with different admixtures of fir, and in the Krkonoše Mts mainly in open arcto-alpine tundra. Marked differences can therefore be expected in the amounts of fir pollen.

2.2 Fossil pollen records

Samples for pollen analysis were analyzed in Słone and Bezedna lakes deposits every 5–10 cm, in the Rokytecká slat' and Mrtvý luh profiles every 4–5 cm or in smaller intervals in places with significant changes of tree pollen curves. The samples (1 cm³ sediment) were macerated by Erdtman's acetolysis after removal of carbonates by means of 10% HCl and of the mineral fraction by means of 40% HF (Berglund and Ralska-Jasiewiczowa, 1986). Each pollen sample was counted on microscope slides 18x18 mm in surface. Percentages of individual types of tree and shrub pollen (AP) are calculated based on the sum of AP = 100%. The results are presented in Figs. 5 and 6.

Age–depth model was made for the sediment sequence from the Słone lake (online Figure B) in psimpoll v. 4.263 (Bennett, 2008) using loess smoothing. No radiocarbon dating is available for Bezedna lake, so age indications depend on pollen-stratigraphic correlation with Słone lake. The radiocarbon dates were calibrated (1 σ age ranges) using OxCal, version 3.10 (Bronk-Ramsey, 1995, 2001, 2005) and IntCal09 (Reimer et al., 2009).

Four Holocene pollen diagrams from SE Poland, available in the European Pollen Database, (EPD) were selected for comparison with the Słone and Bezedna diagrams: Tarnawa Wy na (Ralska-Jasiewiczowa, 1980), Pu cizna R kowia ska (Obidowicz, 1989), Tarnowiec (Harmata, 1987) and Słopiec (Szczepanek, 1982). Geographical coordinates are presented in online Table A. Together they form a S–N transect in SE Poland from the Carpathians mountain forests with abundant presence of fir via the Carpathian foreland to the Holy Cross Mts at the same latitude as Roztocze. Robust time scales could be made for these diagrams by calibration and linear interpolation of the radiocarbon dates available in the EPD (Fig. 7).

3 Results

3.1 Estimating percentage and PAR threshold values

3.1.1 Variation in annual fir PAR values—The fir pollen record of the traps shows large year-to-year variation (Fig. A online). Most pollen traps have for most years a fir pollen deposition value below 70% of the average of all annual values for individual trap. The average fir pollen deposition for the Roztocze region (PAR: 843 fir pollen grains cm⁻² year⁻¹) is much higher than for the Krkonoše Mts (61) and the Šumava Mts (49).

Figure 3 presents temporal trends in regional fir in the traps. In three years (2003, 2007, 2009), fir pollen deposition is generally low in all the three regions. The tendencies of low, average or high pollen deposition agree fairly well between the two mountain regions (Šumava and Krkonoše) in spite of the large distance between them (260 km), whereas in three years (2001, 2004, and 2010) the tendencies are opposite between the lower-lying Roztocze region and the two mountain regions. The largest contrast was in 2001, when fir pollen deposition was in Roztocze at its lowest but in the two Czech mountain regions at its highest in almost all pollen traps. In both Czech regions, the peak year of 2001 was preceded by three years of generally low to average fir pollen deposition and followed by nine years of nearly consistently low fir pollen deposition. This implies that long time series are needed for obtaining realistic long-term averages of fir pollen deposition. 2004 and 2010 were peak years in Roztocze, with more than twice the average fir pollen deposition. In Roztocze, years of very low fir pollen deposition were 1998, 1999, 2001, 2003, 2007, and 2009, whereas 2000, 2002, 2005, 2006 and 2008 showed no clear tendency: About 30–70% of the pollen traps showed low values while the rest recorded average or even high values.

3.1.2 Fir pollen deposition (PAR) and pollen percentages in relation to tree abundance

Poska and Pidek (2010) showed in simulation experiments of fir pollen dispersal in the Roztocze region that a study site records changes in fir population size by pollen only when the population is no more than 300 m away. A fir pollen grain is heavier than one of *Picea abies* or *Pinus sylvestris*. Eisenhut (1961, after Suszka, 1983) showed experimentally that fir pollen has the highest fall-speed (12.0 cm s^{-1}) of ten studied fir species, twice as high as *Picea* (6 cm s^{-1}) and three to four times as high as *Pinus* ($3.1\text{--}4.5 \text{ cm s}^{-1}$). Most fir pollen is therefore not transported far. According to Eisenhut (1961), most pollen of *Abies concolor* (native to North America) is deposited within 0.5 km of the pollinating tree, where it has an average annual deposition of $2\text{--}35 \text{ grains cm}^{-2}$, and the deposition at 2 km from the source is only $0.13 \text{ grains cm}^{-2}$. The about twelve times higher long-term average fir pollen deposition in Roztocze compared with the Šumava and Krkonoše Mts reflects the contrast between close proximity and abundance of fir trees in the former with scarcity and larger distances in the latter (Fig. 4).

The results from the Roztocze region yield an average fir pollen deposition of ca. $2600 \text{ grains cm}^{-2} \text{ year}^{-1}$ when fir dominates the forest at the sites, ca. $900\text{--}1100$ when fir stands are very close, and ca. 200 when fir trees are absent (Table 3). Trap G-9 has the lowest average fir pollen deposition. This is amazing because the small distance of 40 m to the nearest adult fir tree contrasts with a larger distance (500–1000 m) in three pollen traps that have a larger average fir pollen deposition (204–292). The low deposition in trap G-9 is probably related to the position of this trap almost under the canopy of beech woodland, whereas the other three traps are placed in large forest openings of at least 100 m across. It seems that more fir pollen from longer distances enters a trap when the forest opening is larger. These relations are similar for fir pollen percentages: 22% for a trap inside a fir stand, 5–6% in traps close to fir forest, 1–1.2% in traps away from fir trees but placed in large forest openings, and 0.5% in trap G-9 situated almost under the canopy of beech.

In the Šumava Mts, five groups of pollen traps are distinguished on the basis of position in the landscape:

- (1) Traps SA1 to SA4 are placed in small forest clearings on the highest, spruce-covered mountain tops, apart from trap SA2 that is directly under the canopy. The long-term average of fir pollen deposition is 34 grains cm⁻² year⁻¹, or 1.5%.
- (2) Traps SA5 to SA7 are on lower, also spruce-covered mountain tops. Average fir pollen deposition is 86 (2.8%).
- (3) Traps SA9 and SA10 are in spruce forest on slopes between mountain tops and in mires. Average fir pollen deposition is 65 (2.1%).
- (4) Traps SA11 to SA15 are located in large openings formed by montane ombro-oligotrophic peat-bogs. Average fir pollen deposition is 63 (3.2%).
- (5) Traps SA16 to SA18 are located in the sub-continental valley bogs of the Vltavský luh upper valley. Average fir pollen deposition is 30 (1.4%).

Summarizing, fir pollen deposition in the Šumava Mts is low and of the same order of magnitude in different parts of the landscape, which indicates that the scale of deposition is regional. The only exception are traps SA13 and SA9 where fir trees locally are abundant (up to 20-30%).

Average fir pollen deposition in traps without fir trees around them up to 500–1000 m distance is much lower in the Šumava Mts (11–41) than in Roztocze (200–300). In terms of percentages, however, the range of values is very similar, namely 0.5–2.3% in Šumava and 1.0–1.3% in Roztocze. The difference in fir pollen deposition between the two regions results both from presence of pure fir stands in Roztocze and from more frequent occurrence of high pollen production years in upland areas than in the mountains. Pollen deposition is therefore in this case a more sensitive indicator of regional fir tree abundance than pollen percentages.

In the Krkonoše Mts, three groups of pollen traps are distinguished according to their position in relation to the anemo-orographic systems of deep valleys and plateaus:

- (1) Six pollen traps are located in the western Krkonoše Mts, under the influence of the anemo-orographic system of the Labský d l and Dlouhý d l valleys (Jeník, 1961). A group of fir trees is growing at lower altitudes of 1000 m a.s.l. approximately 3.5 km from the traps. Trap KR2 and KR4 are located in the cryo-eolian zone of mountain tops, KR9 and KR12 in glacial valleys, and KR6 and KR7 in arctic raised bogs of mountain tops. The long-term average of fir pollen deposition is 129 grains cm⁻² year⁻¹, or 3.8%.
- (2) Seven pollen traps are located in the eastern Krkonoše Mts under the influence of the two anemo-orographic systems of the Modrý d l and Ob í d l valleys (Jeník, 1961). Trap KR1 is located in the cryo-eolian zone of mountain tops, KR3 and KR5 in complexes of mountain arctic raised bogs with *Pinus mugo*, KR10 and KR11 in glacial valleys, and KR8 and KR13 in a mosaic of alpine vegetation and *Pinus mugo* communities. Average fir pollen deposition is 17 (0.8%).

- (3) Six pollen traps are located in alpine mountain meadows of the eastern Krkonoše Mts (KR14, KR15, KR16, KR17, and KR19) or in forested mire (KR18). Average fir pollen deposition is 43 (1.6%).

Fir pollen deposition was on average higher in the western than in the eastern Krkonoše Mts (Table 3). However, two extremely high values from the highest pollen deposition year 2001 in the western Krkonoše Mts (1648 in KR4, 5179 in KR9) considerably influence the average, both as deposition and as percentages. In spite of the large distance of these two traps to the nearest *Abies* tree (2.5–3 km), their position above timberline made them available for pollen deposition by strong winds that can transport huge amounts of pollen from lower elevations. Such a wind effect is, however, difficult to quantify. Average fir pollen deposition ranged in 2001 from 3 to 527 (0.2 to 12.8%), which indicates a very uneven distribution of the fir pollen masses. The low and the high extremes concern traps positioned at similar distance to timberline (175–240 m) and at similar distance to the nearest *Abies* trees (2–3 km). In traps above timberline in the eastern Krkonoše Mts, average fir pollen deposition and percentages are lower for traps closer to timberline than for traps further away from the timberline (Table 3). For example KR1, located 640m above timberline, has much lower values (10 in terms of PAR and 0.4%) than KR3 (52 and 2.7%). This points again to the importance of strong winds for the transport of pollen above the tree crowns. In case of the KR3 site, it was 1999 year when PAR as high as 338 was recorded that contributed most to the average PAR value. PAR from traps positioned below timberline in eastern Krkonoše Mts seem to reflect the distance from *Abies* trees much better. Two traps (KR16, KR17), located about 1 km from *Abies* trees, recorded higher values (31–202 and 1.5–5.5%) than other traps (KR14, KR15, KR18, KR19) at a distance of ca. 2 km from fir trees (4–10 and 0.2–1.5%).

3.1.3 Fir pollen threshold values for regional and local tree presence/absence and abundance—

The lowest limits of the values of *Abies* PAR and percentages collected in Table 3 have been treated here as the pollen presence/absence thresholds (Table 4). These values are confirmed in several trapping sites thus their reliability increases. Traps from Roztocze showed the most clear pattern (Fig. 4). PAR around 2500 (=22%) marks the on-site presence of fir forest, local presence of fir forest is reflected by PAR 900–1100 (=5–6%) and regional – by ca. 200 (=1%).

In the Šumava Mts. the pollen thresholds for the local presence of fir trees are 50 and 1.8%, which have been determined based on the sites SA3 and SA4. Fir trees are not abundant in the vegetation (ca.1%) around these sites and occur at a distance of 0.2–0.5 km. Much higher values (88–149 and 1.8–7.9%) were recorded in SA13 and SA9 where fir is locally very abundant (up to 30% and 20%, respectively). Regional presence of scattered fir trees, at a distance 0.5–3.4 km, is 11 (=0.5%). However in many traps in the Šumava Mts these values are higher. The very high deposition year of 2001 contributed enormously to the average PAR and percentage values due to upslope pollen transport.

The pollen values (3–10 and 0.2–0.3%) are considered as the lowest limits reflecting the presence of scattered fir trees at a distance of 4 km from pollen traps in the Krkonoše Mts

(Fig. 4, Table 4). Much higher values can be associated with upslope transport of pollen promoted by anemo-orographic system.

3.2 Application of the fir pollen thresholds to fossil pollen data

Here we apply the obtained fir pollen thresholds for fir-tree presence/absence to the fossil pollen datasets from Bezedna and Słone lakes in Poland (Fig. 5). The diagrams show the Holocene pollen succession of the main trees. In both diagrams, the beginning of regular fir pollen occurrence coincides with higher pollen values of beech (*Fagus sylvatica*), which indicates probably the establishment of beech forest. The fir pollen curve is in both diagrams not continuous and the values are generally low (<1%). In Bezedna, fir pollen first appears in the Subboreal and in Słone at the beginning of the Subboreal ca. 5.3 cal ky BP and more regularly about 4.1 cal ky BP. Fir pollen deposition calculated in fossil samples of Słone increases significantly about 3.5 cal ky BP but never exceeds the value of 200 that is supposed to indicate presence of fir tree stands. The values are close to 40, at the most suggesting scattered presence of fir trees at a distance of 0.5–1.0 km. The pollen-trap results from the two Czech mountain regions show, however, that such small amounts of fir pollen as found in Bezedna and Słone lakes can be transported over rather long distances. In the period of interrupted fir pollen curves in the two diagrams, fir was growing abundantly several tens of km to the south in the Roztocze region and also about 100 km away in the Carpathian Mts, especially before human impact on the landscape became stronger 2.5 cal ky BP (Obidowicz, 1996, 2003; Szczepanek, 2001; Margielewski and Zernitskaya, 2003; Margielewski et al., 2003; Obidowicz et al., 2004). The fir pollen in the two lakes could be of long-distance origin, or at least in part. Alternatively, fir may have been growing in the region in very low numbers. This possibility is supported by Watts (1973), Bennett (1985) and Birks (1989) who state that the first arrivals of trees with low pollen representation may be undetected palynologically and suggested that sporadic pollen grains prior to continuous occurrence may reflect local presence of small populations rather than long-distance pollen transport. Summarizing, a former natural occurrence of fir in the Chełm Hills in Poland is possible, but the pollen diagrams are not decisive.

Four Holocene pollen diagrams in a S–N transect in SE Poland show that fir expanded from the south-east and established at different dates (Fig. 7). In the following, the interpretation of fir presence at each site is based here for the first time on presence/absence thresholds calculated for the same region.

In the pollen diagram from Tarnawa Wy na (Ralska-Jasiewiczowa, 1980), 0.1–0.2% fir pollen between 5.75–5.35 cal ky BP indicates the presence of fir trees, ca. 1% around 3.15 cal ky BP indicates major fir expansion and regional fir forests, and 6% around 2.7 cal ky BP indicates that local fir tree stands were present.

The site Pu cizna R kowia ska (Obidowicz, 1989) in the western part of the Western Carpathians at 656 m a.s.l. has the earliest fir pollen of the four sites, in single samples with 0.2–0.7% dated to ca. 10.2 and 9.4 cal ky BP. Fir pollen reaches 1% ca. 7.9 and 6.8 cal ky BP, which indicates presence of fir trees. This lasted up to about 5.8 cal yr BP when fir pollen abruptly increased followed by sudden drop, which however cannot be interpreted as evidence for local fir expansion due to the position of the site in the mountains, where

upslope pollen transport can be significant, as suggested by the Šumava and Krkonoše pollen monitoring results. Low fir pollen values from 5.4 to 4.7 cal yr BP either indicates a decline in fir trees or it is a percentage effect due to the expansion of beech (*Fagus*), or both. Initial fir pollen peak values at 4.6 cal ky BP and a subsequent constant rise from about 4.3 cal ky BP (~ 3%) evidences fir tree expansion. Initially, these might have been scattered fir trees at lower elevation, but the values of 9.5–29% around 3.9 cal ky BP can indicate the establishment of large local fir tree stands, which were in expansion until ca. 3.4 cal ky BP and persisted in the landscape until about 0.3 cal ky BP.

The site Tarnowiec (Harmata, 1987) lies in the Jasło-Sanok depression in the northern foreland of the Carpathian Mts, at an elevation of similar to that of Roztocze (220 m a.s.l.). Fir pollen first appeared ca. 6.0 cal ky BP with 0.2%, but this might have been long-distance transported from the Carpathians where fir trees were present. 1% fir pollen around 4.6 cal ky BP indicates regional presence of fir trees, and 4.5–6% fir pollen around 4.4 cal ky BP indicates local fir-dominated forests.

Słowiec (Szczepanek, 1982) is the northernmost of the four EPD sites. It is situated in the Holy Cross Mts at the same altitude as Roztocze. Today *Abies alba* forms forest stands here and belongs to the main tree species. The pollen curve of *Abies* starts at 3.7 ky cal BP which is about 2.2 ky later than in the Carpathians foreland. The population expansion was probably very quick here: around 3.2 ky cal BP the percentages of fir pollen cross the threshold of 1% that indicates presence of fir tree stands. Major expansion took place before 2.5 ky cal BP when the values exceeded 4% fir pollen in the total AP sum.

Two pollen diagrams from the Šumava Mts in the Czech Republic (Fig. 6) were interpreted by means of the fir pollen presence/absence thresholds calculated for Šumava (Table 4). Rokytecká slat' site (Fig. 6A) has the longer pollen record. Single fir pollen grains appear regularly since 7.4 cal ky BP and start forming a continuous curve which about 6.8 cal ky BP reaches 1%. This indicates scattered fir trees at a distance of 0.5–1 km. Then followed a slow expansion up to 4.8 cal ky BP when 6% fir pollen indicates local presence of fir tree stands, followed by a rapid expansion crossing the 22% pollen threshold around 3.8 cal ky BP, indicating local fir-dominated forests. The Mrtvý luh pollen diagram from the Šumava Mts (Fig. 6B) starts at 6.3 ky cal BP with a continuous fir pollen curve. Percentages quickly reach 1–2% at about 6.2 ky cal BP, which indicates presence of fir trees within 1 km distance. The values remain low until 5.5 ky cal BP except for a peak of 14% at ca. 6.0 cal ky BP which could have been a contamination with younger material. A sharp increase of fir pollen around 5.0–4.8 cal ky BP exceeds the 5–6% threshold, which indicates local presence of fir tree stands. The 22% threshold is exceeded around 3.5 cal ky BP, indicating local fir-dominated forests.

4 Discussion

4.1 Pollen–vegetation relationships

The present study of fir pollen based on annual modified Tauber traps helps to shed light in the matter of pollen representation of fir trees. According to Eisenhut (1961) most fir pollen is not transported over great distances. This was for the Roztocze region confirmed by Poska

and Pidek (2010). A constant presence (closed curve) of fir pollen in fossil pollen diagrams therefore strongly suggests that fir trees were present within about a km of the study site. Sugita et al. (1999) considered similar area (800–1000 m radius from the sampling site) as the relevant source area of pollen for small lakes (ca. 3 ha). The surface area of the Słone and Bezedna lakes in Poland (3.5–5 ha) allows us to suggest that low PAR (ca. 40) and percentages (<1%) may reflect scattered fir trees within 1 km from the lakes. Although the evidence is not decisive the hypothesis can be supported additionally by probable underrepresentation of *Abies* in pollen record. The study by Križo (1963) compared the proportion of fir pollen in surface samples with abundance of *Abies* trees on the stands. The author concluded that on stand with majority of *Abies* trees (70%) the proportion of fir pollen was on average 22.5% thus *Abies* was strongly underrepresented.

In the Roztocze region of Poland, 22% of fir pollen inside a forest with at least 75% fir trees confirms Križo's (1963) finding of strong underrepresentation of fir in the pollen rain, and about 1% of fir pollen when large patches fir trees grow at 0.5–1 km distance confirms the short dispersal distance of most fir pollen. In spite of the fact that two *Abies* high pollen deposition years have been recorded in the Roztocze during the period 1998–2010, the observed *Abies* PAR (covering the period of 13 year) are very close to the values obtained by Poska and Pidek (2010) based on eight years data 1998–2005 (high year of 2004 included). Mean PAR with 0.95% confidence limits calculated by Poska and Pidek (2010) revealed that 200 grains cm⁻² year⁻¹ represented regional presence of fir, 1000 – local presence and more than 2000 – on-site presence of fir forest.

In the studied mountain regions in the Czech Republic, the main fir tree occurrences are at considerably lower altitudes than the pollen-trap sites. The fir pollen was therefore transported upslope. The pronounced anemo-orographic systems of the Krkonoše Mts may help explain the high fir pollen deposition of 2001 in three pollen traps (KR4, KR9, and KR16) even though the nearest fir trees grow at 1–3 km distance. The fir pollen deposition was in that year as high as the average deposition in a pollen trap in the Roztocze region where the nearest fir trees grow at a mere 60 m distance. The lower fir pollen deposition of 2001 in the Šumava Mts than in the Krkonoše Mts may be due to the less pronounced anemo-orographic systems in the former mountain area. Pollen traps above timberline in Krkonoše and in large mires (ca. 100 ha) in the Šumava Mts (for example SA15 – 103 ha, SA11 – 142 ha, SA18 – 99 ha) recorded, as a rule, extremely high *Abies* pollen deposition in the high year 2001. This reflected abundant flowering of fir trees in the whole region even if fir trees very sometimes very distant (ca. 3–4 km). This is consistent with the opinion by Sugita (2007) that only pollen data from big lakes (about 100 ha) can provide estimates of regional vegetation.

4.2 Fir migrations reconsidered

In Poland the main fir expansion occurred about 3.5 cal ky BP in the Western Carpathians (Obidowicz et al., 2004). The pollen diagrams of Bezedna and Słone lakes in the Chełm Hills in SE Poland (Fig. 5) indicate that 2.5 cal ky BP most of the landscape was occupied by a colline vicariant with beech of sub-continental oak–hornbeam forests with lime, which Matuszkiewicz (1991) considers as the present-day dominant potential natural vegetation.

According to pollen, fir trees were either absent or scarce in the region. Fir became with certainty present at the moment that also beech expanded markedly. The appearance of fir is in this region quite late compared to the Carpathians and their forelands. The earliest record from the four analysed EPD sites has the Pu cizna R kowia ska site (Obidowicz, 1989). The application of our fir pollen presence/absence threshold (1%) to this diagram suggests 6.8 cal ka BP as the arrival time of fir trees, whereas Obidowicz et al. (2004) had the opinion that fir appeared in Western Carpathians around 5 cal ky BP. They may, however, not have belonged to the same fir population that expanded later. According to Obidowicz et al. (2004), fir first appeared 4.5 cal ky BP fir in the northern forelands of the Carpathians. Fir increased slightly earlier according to the diagram of Tarnowiec (Harmata, 1987), about 4.8 cal ky BP. The late appearance of fir in the Holy Cross Mountains agrees well with the data from Roztocze.

In the Czech-Moravian Uplands in the Holocene, fir often entered as one of the last components into spruce-beech forests. The earliest appearance of fir in the montane areas of Šumava Mts is dated to 8270 ± 70 BP and agrees well with the opinion by Finsinger and Tinner (2007) that after 8200 cal BP the climate shifted to more humid and less continental conditions which promoted the expansion of fir. The early appearance of fir in the Šumava region is associated with the close distance to glacial refugia (Terhürne-Berson et al., 2004; Terhürne-Berson, 2005).

6 Conclusions

13-year time-series of monitoring the annual pollen deposition of fir revealed great inter-annual variability, among which are two years (2004 and 2010) of very high pollen deposition in Roztocze (SE Poland) and one high year (2001) in the Šumava and Krkonoše Mts of the Czech Republic. Average fir pollen deposition is with $843 \text{ grains cm}^{-2} \text{ yr}^{-1}$ in Roztocze, where fir forms forest stands, much higher than in the Šumava Mts (49) and Krkonoše Mts (61). Regional presence of fir forest is reflected by an average fir pollen deposition of 200 or 1% of total tree + shrub pollen.

The following fir pollen presence/absence threshold values were calculated from the monitoring results: scattered fir pollen deposition $<10 \text{ grains cm}^{-2} \text{ yr}^{-1}$ ($<0.5\%$) means either long-distance pollen transport or local presence of few fir trees; >50 ($>1\%$) means local presence of few fir trees; >1000 ($>6\%$) means local presence of fir forest; >2500 ($>22\%$) means local fir-dominated forest.

The percentage thresholds were applied to eight fossil pollen diagrams. The two Czech diagrams from the Šumava Mts (Rokytecká and Mrtvý luh) reflect presence of scattered fir trees about 6.8 and 6.2 cal ky BP, respectively. Fir expansion seemed slow until 4.8 cal ky BP when the values reached 6% and can be interpreted as local presence of fir tree stands. Since then the rapid expansion was evidenced by the quick increase in percentage values which crossed the 22% threshold (on-site presence of fir dominated forests) at about 3.8 and 3.5 cal ky BP, respectively. Application of the fir pollen threshold values to two Polish diagrams (Słone and Bezedna) from the border zone between Roztocze (with fir forest stands today) and Polesie (where fir has never played an important role) indicates that the

presence of scattered fir trees was possible from ca. 3.5 cal yr BP, which coincides with the establishment of beech (*Fagus*). Based on four other, published pollen diagrams from Poland, the spread of fir was traced from the Carpathians and their forelands to the upland belt of Middle Poland, where fir appeared ca. 0.5 cal ky BP later than in the Carpathians.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgements

This paper contributes to the Pollen Monitoring Programme PMP (<http://www.pollentrapping.net>). The research was supported partly by state funds of the Faculty of Earth Sciences and Spatial Management UMCS in Lublin and the project (No. 13) of cooperation between the Hungarian and Polish Academies of Science (2011–2013). The Czech part of this study was supported as a long – term research development project No. RVO 67985939.

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Fig 1.

A- Present-day distribution of *Abies alba* in Central Europe (after Jalas and Suominen, 1972 and Boratyński, 1983); **B-** Regions of pollen monitoring in Poland (Roztocze region) and the Czech Republic (Šumava Mts and Krkonoše Mts) in Europe

Fig 2.

Location of the sites under investigation:

A - in Poland . Explanations: distribution of *Abies alba* in Poland (after Zaj c and Zaj c, 2001). Marked are the Roztocze region (pollen trapping sites), two fossil sites (1 – Słone and Bezedna lakes in the northern part of the Lublin Upland) and four fossil sites from the EPD (2 – Tarnawa Wy na, 3 – Tarnowiec, 4 – Pu cizna R kowia ska and 5 – Słopiec)

B - in the Šumava National Park.

Explanations: fossil pollen sites Rokytecka slat' (A) and Mrtvy luh (B); distance to *Abies* trees between 0.2-0.9km (black circles), more than 1 km (grey circles), *Abies* trees locally abundant - up to 20-30% (big circles).

C - in the Krkonoše National Park.

Explanations: distance to *Abies* trees less than 1 km (big circles), less than 2 km (grey circles), between 2-3.5km (white circles).

Fig 3.
Percentage of pollen traps with high, average low, and no *Abies* pollen deposition.

Fig 4.

Abies pollen percentages according to the sum of trees + shrubs = 100% versus percentages of fir trees in vegetation in three regions under investigation and *Abies* PAR (grains cm⁻² yr⁻¹) and percentages (further explanation in text).

Fig 5.

Simplified pollen diagrams of the main trees in the Słone (A) and Bezedna (C) fossil pollen sites in Poland. Percentages are calculated according to the sum of trees + shrubs = 100%. B – *Abies* pollen percentages and deposition ($\text{grains cm}^{-2} \text{yr}^{-1}$) in Słone Lake deposits against calibrated age

Fig 6.

Abies pollen percentages against the calibrated age in the fossil sites at Rokytecká slat' and Mrtvý luh (Šumava Mts., Czech Republic). Percentages are calculated according to the sum of trees + shrubs = 100%.

Fig 7.

Abies pollen percentages in fossil pollen diagrams from Poland available in the European Pollen Database (EPD): Tarnawa Wy na (Ralska-Jasiewiczowa, 1980), Tarnowiec (Harmata, 1987), Pu cizna R kowia ska (Obidowicz, 1989) and Słopiec (Szczepanek, 1982). Percentages are calculated according to the sum of trees + shrubs = 100%.

Table 1Description of distribution of *Abies alba* trees in three pollen monitoring regions

Region	Distribution of fir trees in the regions under pollen monitoring
Roztocze (SE Poland)	Pine communities are most widespread among forests. Fir woodlands (at least 75% of <i>Abies alba</i> trees) occupy ca. 8.3% of the central Roztocze and are protected in the Roztocze National Park. Single <i>Abies alba</i> trees occur as admixture in the Carpathian beech woodlands which occupy 25% of the forests area (Izdebski et al., 1992).
Krkonoše Mts. (N Bohemia; Czech Republic)	At present fir is very rare in the montane forests; it forms only 0.1% of natural forests of the Krkonoše Mts. Forests with significant admixture of fir form only a narrow belt on the lower slopes. Fir reaches not higher than the submontane altitudinal zone in broadleaved and mixed forests together with spruce and beech (Boublík, 2007).
The Šumava Mts. (SW Bohemia, Czech Republic)	Present vegetation is a mosaic of temperate deciduous broad-leaved forest with coniferous forest at higher elevations, and treeless areas in part resulting from past and recent human impacts. Fir occurs within the altitudinal distribution range of beech forests (400–800 m a.s.l.) and climbs to 1300 m a.s.l. in Boubin Mt. in the central part of the Šumava. Six associations of forest with fir admixture have been distinguished floristically, differing in soil chemistry, nutrient status and water regime (Boublík, 2007). Most of these communities have been degraded by spruce plantation dating back to the 19th century.

Table 2

Sites for fossil pollen of fir investigations in Poland and Czech Republic

Name of the site	Geographical coordinates and surface area	Short description of the region
Stone Lake	φ 51°18'15" N; λ 23°21'55" E; elevation 185.6 m a.s.l.; 5 ha lake, maximum depth of 8.1 m	Two small eutrophic lakes surrounded by mires, situated in the northern part of the Lublin Upland (Chełm Hills). The lake basins were formed in Upper Cretaceous carbonate rocks in the Late Glacial (Kulesza et al., 2011, 2012; Pidek et al., 2011).
Bezедna Lake	φ 51°06'08" N; λ 23°30'22" E; elevation 191.0 m a.s.l.; 3.5 ha lake; maximum depth of 9.8 m	
Rokytecká sla mire	φ 49°1'11"N, λ 13°25'8"E elevation 1120 m a.s.l.; area of 200 ha	Mire complex situated in the central part of the Šumava Upland Plateau in mountain taiga with prevalent <i>Picea abies</i> . Peat thickness reaches 7.5 m. (Svobodová et al., 2002).
Mrtvý luh mire	φ 48°52'26"N; λ 13°51'57"E elevation 737 m a.s.l.; area of 630 ha	Mire complex in the upper Vltava river valley at the confluence of Studená Vltava and Teplá Vltava rivers, in the southern part of the Šumava Mts. Sediment core was taken from the south eastern part of the mire (Svobodová et al., 2001)

Table 3

Ranges of PAR values for *Abies alba* and percentages according to the sum of trees and shrubs = 100% based on the results of pollen monitoring in Roztocze, Krkonoše Mts. and Šumava Mts.

	Range of PAR value	Range of % percentage value
ROZTOCZE (2 very high deposition years included)		
Onsite presence of fir stands (G1)	2600	22%
Fir trees not present Within 40 m (G2,G3)	900-1000	5-6%
Fir trees not present Within 100-300 m (G4,G5)	1100	6-6.5%
Fir trees not present Within 500-1000 m (G6, G7,G8)	200-300	1-1.3%
ŠUMAVA MTS (1 very high deposition year included)		
Fir trees not present within 200-500 m (SA3, SA4, SA7, SA9, SA13)	50-149	1.8% - 7.9%
Fir trees not present within 500-1000 m (SA1, SA10, SA11, SA14)	11 – 41	0.5 -2.3%
Fir trees not present within 1100-2000 m (SA2, SA12, SA15-SA18)	12 – 114	0.5-6.0%
Fir trees not present within 3400 m (SA5, SA6)	21-35	1.1-1.9%
KRKONOŠE MTS (1 very high deposition year included)		
Western Krkonoše (all traps above timberline, at a distance of 2-4 km from the nearest pollinating <i>Abies</i> tree)		
---Distance to timberline 80-240 m (KR7, KR9, KR12)	3-527	0.2-12.8%
---Distance to timberline 780-1150 m (KR2, KR4, KR6)	7-181	0.6-6.4 %
Eastern Krkonoše (traps above timberline, at a distance of 2-3.5 km from the nearest pollinating <i>Abies</i> tree)		
---Distance to timberline 220-420 mm (KR10, KR11)	6-19	0.3-0.5%
---Distance to timberline 540-1500 mm (KR1, KR3, KR5, KR8, KR13)	4-52	0.2-2.7%
Eastern Krkonoše (traps below timberline)		
---Distance to nearest pollinating <i>Abies</i> tree >1 km (KR16, KR17)	31-202	1.5-5.5%
----Distance to nearest pollinating <i>Abies</i> tree <2 km (KR14, KR15, KR18, KR19)	4-10	0.2-1.5%

Table 4

Estimated PAR and percentage pollen threshold values of fir in three regions under investigation.

Presence of <i>Abies</i> trees in the landscape	Estimated PAR	Estimated percentage value (in relation to AP sum)
Scattered fir trees at a distance of 4 km	3-10	0.2-0.3% (Krkonosze)
Local presence of fir trees at a distance of 0.2-0.5 km	50	1.8% (Šumava)
Regional presence of fir tree stands	200	1% (Roztocze)
Regional presence of scattered fir trees at a distance of 0.5-3.4 km	11	0.5% (Šumava)
Local presence of fir tree stands	1000	5-6% (Roztocze)
On-site presence of fir dominated forest	2500	22% (Roztocze)