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A 350-year tree-ring fire record from Białowieża Primeval Forest, Poland: implications for Central European lowland fire history

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Summary

1. Fires are nowadays small, yet frequent, in temperate Central European conifer forests, but little is known about the fire history in this region. This is likely due to the lack of intact forests that contain old trees and dead wood from which fire history may be reconstructed. An exception is the Białowieża Primeval Forest (BPF) in Poland for which we were able to reconstruct the fire history in detail.

2. From 886 tree ring samples collected in a 13-ha conifer-dominated area, we reconstructed fire events and tree establishment back to the mid 1600s. From 1653 to the late 1700s fires were very frequent, with mean point (single tree) fire intervals of 18 years and mean stand scale fire intervals of 6 years. After 1781, the intervals between the fires increased dramatically, and since 1874 no major fire was recorded.

3. Tree establishment underwent substantial changes, closely tracking shifts in fire frequency. When fires were frequent, *Pinus sylvestris* establishment occurred only sporadically. Later, less frequent fires promoted massive establishment of both *P. sylvestris* and *Picea abies*. At present, only *P. abies* and a few deciduous trees regenerate.

4. *Synthesis*. We present the first high-resolution fire history in the Central European temperate lowland forest area. The discovery of old *P. sylvestris* trees and stumps with fire scars in many conifer-dominated parts of BPF show that fire was a major component in the past dynamics of this forest. We also show that historically, fires were recurring at very close intervals, supporting an open, *Pinus*-dominated forest. These result contrasts with the written history of BPF, which focus on a few, large fires from the past. Human influence on the fire regime was probably substantial, although the disentangling of climatic and human impacts needs further studies. We propose that fire should be increasingly taken into consideration in models of disturbance, vegetation development and forest openness in the whole Central European lowland forest region.

Key-words: dendroecology, disturbance history, disturbance regime, forest dynamics, forest history, paleoecology and land-use history, *Picea abies, Pinus sylvestris,* regeneration dynamics, temperate lowland mixed forest

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Introduction

Fires and their history are well studied in Boreal and Mediterranean Europe (e.g. Richardson 2000; Angelstam & Kuuluvainen 2004; Carcaillet *et al.* 2009). In these regions, fire is recognized as a major disturbance agent and driver of ecosystem processes. It influences succession and species composition by eliminating fire sensitive species and promoting fire resistant ones (Sannikov & Goldammer 1996; Willis, Rudner & Sümegi 2000; Kuuluvainen 2002; Pausas *et al.* 2004; Wardle, Walker & Bardgett 2004; Shugart, Leemans & Bonan 2005), and by creating important substrates for many species (Granström 2001).

In present-day Central European lowland forests, fires are frequent in numbers but usually very small (e.g. Pyne 1997; Anonymous 2008). They are almost exclusively ignited by humans and most of them are effectively suppressed and thereby disturb relatively small areas (e.g. Szczygieł, Ubysz & Zawiła-Niedźwiecki 2009). On rare occasions, fires may attain large sizes and thus pose a serious threat to humans or human properties. In contrast to northern and southern Europe, however, much less is known about the natural role of forest fire in Central Europe (e.g. Bradshaw, Tolonen & Tolonen 1997; Tinner *et al.* 2005). Apart from effective fire suppression, the reason for this is likely the significant lack of intact natural forests (e.g. Hannah, Carr & Lankerani 1995) containing old trees and old dead wood, from which fire history and fire influence on succession and forest structure may be studied and reconstructed through time.

Until now, the fire history of Central Europe's forests has been inferred mainly from studies of charcoal influx in peat and lake sediments (e.g. Ralska-Jasiewiczowa & Van Geel 1992; Bradshaw 1993; Mitchell & Cole 1998; Hannon, Bradshaw & Emborg 2000; Rösch 2000; Tinner *et al.* 2005; Carcaillet *et al.* 2007). These studies all show that fires have been a part of Central European forest ecosystems, but they usually give little information on key parameters of fire regime (such as fire frequency, size, seasonality etc.) since charcoal in sediments provides information mainly on fire presence or absence (Higuera, Brubaker & Sprugel 2005; Ohlson, Korbøl & Økland 2006; Higuera *et al.* 2007). Tree ring reconstructions of fire histories on the other hand, cover considerably shorter time periods (c. 300–800 years), but may carry detailed information on fire years, season, frequencies and location (Zackrisson 1977; Niklasson & Granström 2000; Groven & Niklasson 2005; Wallenius, Lilja & Kuuluvainen 2007; Fulé *et al.* 2008). Large data sets of tree ring fire history may provide additional information on the question of climatic vs. human influence on the fire regime (Niklasson & Granström 2000; Drobyshev *et al.* 2004; Kitzberger *et al.* 2007; Granström & Niklasson 2008). Central Europe is densely populated and most of its forests are dominated by flammable conifers, so studies of their fire history and fire ecology should be a high priority. In addition, knowledge about past reference conditions is often stated to be an important basis for sustainable management of natural resources and forest restoration (e.g. Heyerdahl & Card 2000).

The Białowieża Primeval Forest (BPF) (eastern Poland and western Belarus), is one of the largest and best-preserved lowland deciduous and mixed forests in temperate Europe (Faliński 1986; Peterken 1996; Jędrzejewska & Jędrzejewski 1998). In as early as the 14th century this forest was protected as a hunting ground for the Polish kings. This protection enabled the forest to escape destruction and conversion to farmland, unlike most of the surrounding land. Ever since the forest was protected, local peasants were allowed to use the forest, e.g. for cattle grazing, bee-keeping and hay-making. However, all activities (including small-scale logging) were regulated and well controlled so that the forest never lost its unique, intact character. Organized commercial forestry was introduced comparatively late (in 1915) but has never been applied to the whole BPF due to strict protection of substantial areas (Samojlik 2007). A large part of the BPF is covered by conifer forest, dominated by both *Pinus sylvestris* L. (Scots pine) and *Picea abies* (L.) Karst. (Norway spruce). In these parts, and sometimes in mixed forests, fire-scarred trees, snags and stumps have been noted (e.g. Faliński 1986) but have never been the focus of further investigations. The aim of this study was to reconstruct the fire history in detail from ancient trees and old dead wood on the ground found in one such stand. We intended to reconstruct fire timing (year and season) and frequency with a high resolution by applying tree ring methods. As far as we know, this has not been attempted earlier in BPF or in the whole Central European lowland forest area.

Materials and methods

STUDY AREA

Białowieża Primeval Forest is located on the border area between Poland and Belarus (52°30′–53° N, 23°30′–24°15′ E). It covers about 1500 km^2, of which 600 km^2 are in Poland. From the 14th until the early part of the 20th century, this forest escaped the widespread colonization and commercial timber extraction that occurred in most European forests of similar climate and topography (Samojlik 2007). At present, the Polish part of BPF includes managed forest stands (yet with numerous smaller reserves) under the State Forest Administration (about 500 km^2) and Białowieża National Park (105 km^2).

Białowieża Primeval Forest is situated on a flat, undulating plain ranging between 135 and 190 m a.s.l., built from glaciofluvial sands, gravels and clays (Kwiatkowski 1994). The climate has features of both Continental and Atlantic character (Faliński 1986; Jędrzejewska *et al.* 1997). During the last 50 years, mean annual temperature was 6.8 °C, with mean January temperature of −4.2 °C and mean temperature in July of 17.7 °C. Over the same period average annual precipitation was 633 mm (Pierzgalski, Boczoń & Tyszka 2002) and snow cover lasted 92 days on average (Faliński 1986).

Białowieża Primeval Forest consists of a mosaic of various forest communities, either dominated by deciduous (*Alnus glutinosa* (L.) Gaertn. – black alder, *Quercus robur* L. – pedunculate oak, *Betula pendula* Roth. – silver birch, *B. pubescens* Ehrh. – downy birch, and *Carpinus betulus* L. – hornbeam) or coniferous tree species (*P. sylvestris* and *P. abies*) (Faliński 1986). The mosaic of forest types is largely determined by slight variations in topography, soil and hydrology. In the Polish part of BPF, coniferous and mixed coniferous stands dominated by *P. sylvestris* and *P. abies* cover 52% of the forest area, wet deciduous forests dominated by *A. glutinosa* and *Fraxinus excelsior* L. (ash) cover 20%, rich mesic deciduous stands dominated by *Q. robur*, *C. betulus* with admixtures of *Tilia cordata* Mill. (small-leaved lime) and *Acer platanoides* L. (Norway maple) cover 15%, and early successional stands with *B. pendula, B. pubescens* and *Populus tremula* L. (aspen) cover 13% (Jędrzejewska & Jędrzejewski 1998).

The study was conducted in a 13-ha mixed coniferous (*P. sylvestris–P. abies*) forest stand situated in the managed part of BPF (Białowieża Forest District, Fig. 1). According to the vegetation classification by Faliński (1986), this forest stand has attributes of both *Peucedano-Pinetum* and *Pino-Quercetum* types. Due to its semi-natural character, this stand has been partly protected (informally) since 1992 as a permanent research plot of the Forest Research Institute, Department of Natural Forests, Białowieża. The canopy is co-dominated by several 250–350-year-old, large-diameter *P. sylvestris* trees mixed with younger (50–170 years) *P. sylvestris* and *P. abies* trees, where some *P. abies* individuals belong to the lower layer. *Betula pendula* constitutes < 5% of canopy-forming trees and, until recently, sporadic *Q. robur* individuals were also present (documentation from the Białowieża Forest District 1948–1968, unpubl.), although *Q. robur* seedlings may be found throughout the whole stand. Many *P. sylvestris* individuals, both dead and alive, have open fire scars near the ground (Fig. 2). Tree density is c. 300 stems ha^{-1} and a few gaps in the canopy have recently been formed by wind fall. Ground vegetation is dominated by *Vaccinium myrtillus* L., *V. vitis-idaea* L., *Pteridium aquilinum* (L.) Kuhn, *Dryopteris carthusiana* (Vill.) H.P. Fuchs and *Calamagrostis arundinacea* (L.) Roth. The bottom layer is dominated by typical boreal feather mosses: *Pleurozium schreberi* (Brid.) Mitt., *Ptilium crista-castrensis* (Hedw.) De Not. and *Hylocomium splendens* (Hedw.) Br. Eur. The surrounding stands are largely dominated by conifers, but deciduous trees (*B. pendula*, *P. tremula* and scattered *Q. robur*) may also be found.

SAMPLE COLLECTION

The method for sampling of wood from living and dead trees was designed to cover the area as well as possible and to acquire a sufficient number of old trees for the construction of a chronology of pointer years. The chainsaw fire scar sampling procedure followed the procedure described by e.g. Arno & Sneck (1977) and McBride (1983).

In 2007, data were collected in 29 square plots of two sizes with the same centre points (20 × 20 m = 0.04 ha and 65 × 65 m = 0.42 ha), placed in a 65 × 65 m grid that sampled the entire stand. In the 0.04-ha plots, stand regeneration (species and numbers of saplings up to 1.3 m) was surveyed. In each 0.42-ha plot, wood samples (cross-sections) from *P. sylvestris* stumps or fallen trees, preferably with visible fire scars, were collected with a chain saw, usually three samples per plot. In addition, cores from two living *P. sylvestris* trees were taken: one from an old tree to allow the chronology to be built and one from the *P. sylvestris* tree closest to the plot centre, irrespective of age. In total 58 *P. sylvestris* trees were sampled. One core from the living *P. abies* tree (d.b.h. ≥ 20 cm) closest to the plot centre was also sampled. The cores were extracted with an increment borer (Ø 12 mm), as close to the ground as possible (20–80 cm). From half of the *P. sylvestris* trees, cores were taken at two levels (at 130 cm above ground and close to the mineral soil, usually at about 45 cm), to obtain information about early height increment.

In addition to samples collected in 2007, we also analysed data obtained from 724 cores, all from *P. sylvestris* trees, that were collected from the same stand in 1994 for a study of age structure (Korczyk 1994). All 58 *P. sylvestris* individuals cored in 2007 had already been sampled in 1994. This allowed us to establish a long pointer year chronology for later cross-dating of dead wood samples.

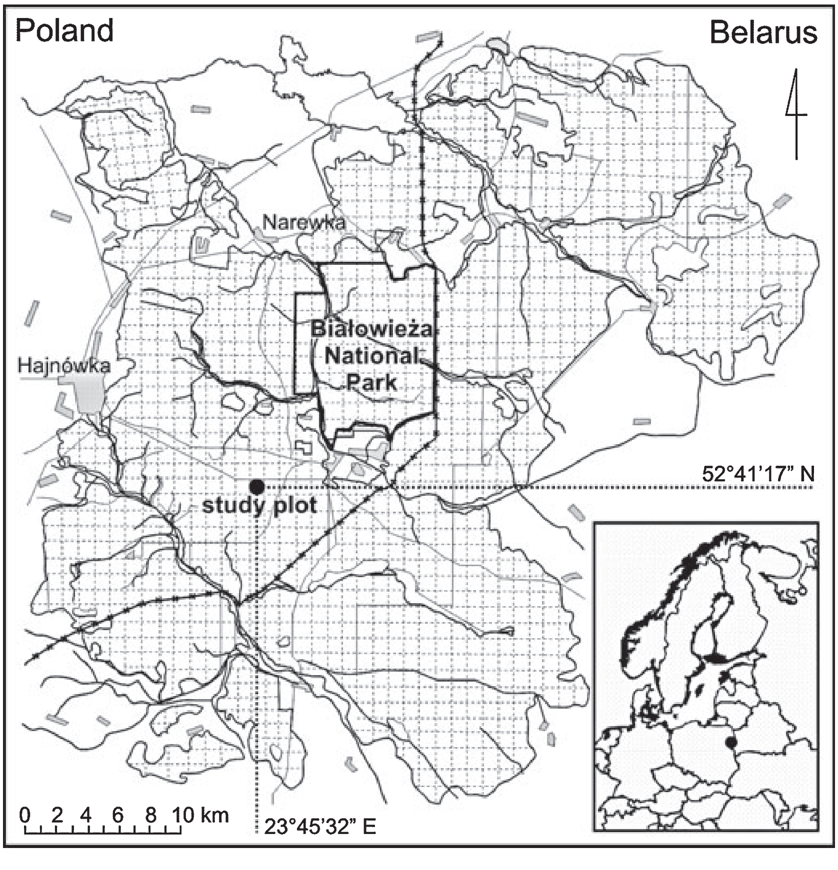

Fig. 1. Location of the 13-ha study area in the Polish part of Białowieża Primeval Forest.

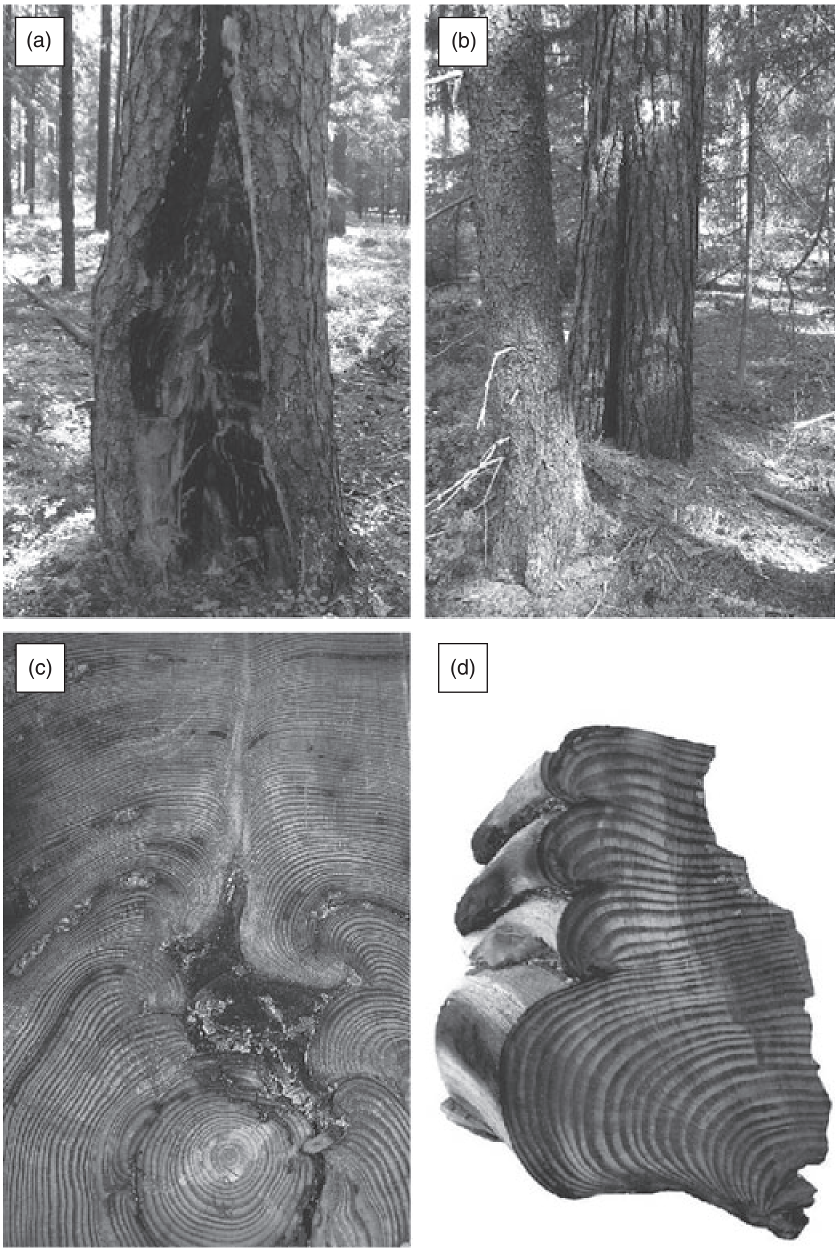

Fig. 2. (a) and (b): fire-scarred living *Pinus sylvestris* in the study plot. The tree shown in (a) was the oldest dated *P. sylvestris* in the stand with germination around 1635. (c) and (d): samples from *P. sylvestris* stumps with fire scars. Photos by M. Feijen (a, b) and E. Zin (c, d).

After discarding samples from stumps too degraded for analysis, 43 partial or full *P. sylvestris* cross-sections and 843 cores from 756 living trees (724 from *P. sylvestris* and 32 from *P. abies*) were used in the analysis.

LABORATORY ANALYSIS AND CALCULATIONS

All wood samples were glued and mounted on slats and boards, dried and finally sanded with a belt sander (down to grit 600) to get a clear picture of tree ring sequences. Zinc paste and a scalpel were used when needed to assure better visibility of the ring pattern. Ring counts (*P. sylvestris* trees cored in 1994) and cross-dating were done under a dissecting microscope with 6 × 40 magnification, according to standard dendrochronological methods (Stokes & Smiley 1968; Yamaguchi 1991). Examples of local pointer years used for cross-dating were: 1695 (narrow), 1702/03 (wide/wide), 1760 (narrow), 1762 (narrow), 1779/80/81 (wide/narrow/narrow), 1811 (narrow), 1848 (wide), 1900 (narrow), 1902 (narrow and/or pale), 1940 (narrow/pale), 1976 (narrow), 1980 (narrow). In cores where the pith was slightly missed, the pith date was estimated after defining the distance to the pith (Brown & Wu 2005; Brown 2006) and mean annual radial growth in the youngest age (after measuring the width of the oldest three rings visible).

Each cross-section was carefully searched for fire scars and sudden strong growth depressions (typically lasting 2–10 years) often caused by fires (M. Niklasson, pers. obs.). Where possible, fire season was determined based on the cambial development at the time of fire (e.g. Baisan & Swetnam 1990). When such growth depressions occurred simultaneously with fire events dated in scars in other trees in the stand, the growth depression was recorded as a fire event occurring in the same year as the scar. When at least one fire scar was found, this was recorded as a fire event.

In order to estimate the year of germination of *P. sylvestris* and *P. abies* trees, height increment of the early part was estimated from the literature (Kowalski 1972; Hawryś *et al.* 2004; Zielonka 2006) and, in the case of *P. sylvestris*, also by additional coring at two heights above ground.

Fire statistics were calculated in two ways: point intervals and stand-scale intervals. Point intervals refer to the mean interval between fire events that have scarred one tree, thus having the potential to reflect the minimum interval possible due to fuel build-up time. Stand-scale fire intervals reflect the intervals between any fire that has occurred in the stand, irrespective of fire size or location. To analyse changes of fire frequency in time, both point and stand scale intervals were plotted against calendar years. Scatterplots were smoothed by the Lowess method (locally weighted regression; Cleveland 1979) to detect temporal patterns. Lowess smoothing suggested three periods with varying fire frequencies. The differences in fire intervals among these periods were tested with nonparametric Kruskal–Wallis ANOVA (as frequency distributions of intervals at both scales were not normal).

Results

FIRE HISTORY

We were able to date 27 fire events between 1653 and 1920 (Table 1 and Fig. 3). Fires that scarred or affected more than five trees occurred in the years 1671, 1677, 1689, 1718, 1738 and 1874. In the whole period with recorded fires (1653–1920), the average fire interval at stand scale (for definition see Materials and methods) was 10 years with a variation from 1 to 49 years (Table 2). At point scale, the average interval between fires was 36 years, with a range of 5–185 years (Table 2).

Over the whole tree ring recording period (1650–2007) the fire regime underwent significant changes and three periods with significantly different fire intervals were distinguished (Kruskal–Wallis ANOVA, $H = 12.7$, d.f. = 1, $P = 0.002$ for tree stand scale; $H = 46.6$, d.f. = 1, $P < 0.0005$ for point scale). Stand-scale fire intervals were short (mean: 9 years) and declined through the period 1653–1706. In the period 1706–1781, fire intervals were even shorter (mean: 5 years) (Table 2). After 1781 until 1920, the intervals between fire events greatly increased (mean: 28 years, maximum 49). Throughout the 19th and 20th centuries, only four fires were recorded, with that in 1874 affecting most of the sampled trees (Fig. 3). In 2007, 135 years had elapsed since the last significant fire had passed through the stand. Fire intervals at point scale increased over the whole period from an average of 11 years in 1653–1706, to 23 years in 1706–1781, and 82 years in 1781–1920 (Table 2).

Seasonal dating of fire scars showed highly skewed distributions (Table 1). Nearly two-thirds of the recorded fires (63%) took place in the dormant period of cambium activity, and the

Table 1. Cross-dated fires in the 13-ha coniferous (*Pinus sylvestris-Picea abies*) forest stand in the Białowieża Primeval Forest, Poland

Fire date	Fire season (%)	Number of trees with fire scar/reaction	Total number of analysed trees (trees present to record the fire)	Fire index (%)	Number of years since last fire
1653	18	2	8	25	
1671	D	7	15	47	18
1677	86	8	17	47	6
1683	96	3	17	18	6
1689	D	9	18	50	6
1696	D	5	18	28	7
1706	D	2	19	11	10
1708	D	1	20	5	2
1712	14	4	20	20	4
1718	7	13	20	65	6
1724	D	1	21	5	6
1726	D	1	22	5	2
1738	D	7	22	32	12
1746	57	3	23	13	8
1749	D	2	23	9	3
1758	D	1	23	4	9
1760	D	1	23	4	2
1768	D	2	23	9	8
1776	D	3	27	11	8
1777	D	1	28	4	1
1779	D	1	28	4	2
1781	57	2	28	7	2
1795	D	3	29	10	14
1811	7	5	28	18	16
1825	D	5	29	17	14
1874	57	26	39	67	49
1920	93	2	23	9	46

Fire season is mean percentage cambial development of scarred tree ring in the year of fire; Fire index is the percentage of scarred trees of the total number of analysed trees; D, dormant season scars (no cambial division recorded).

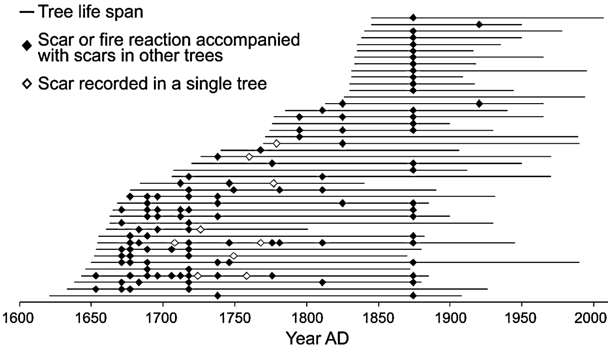

Fig. 3. Fire history of coniferous (*Pinus sylvestris-Picea abies*) tree stand in Białowieża Primeval Forest, Poland, in 1650–2007, reconstructed by cross-dating of *P. sylvestris* tree rings.

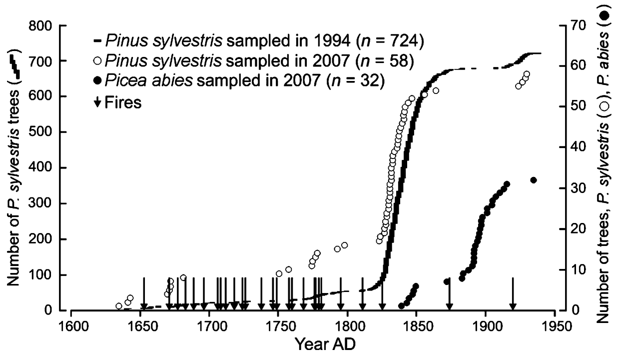

Fig. 4. Cumulative germination diagram of *Pinus sylvestris* and *Picea abies* trees (reconstructed by dating tree rings in cores) in relation to fire events (marked by arrows) in the study plot.

Table 2. Intervals between consecutive fires recorded in the study area, based on dendrochronological dating of fire scars in 43 *Pinus sylvestris* stumps (shown in Fig. 3)

	Intervals between fires (years)			
Period (years AD)	*N*	Mean (±SE)	Minimum–maximum	Temporal trend of change
Tree stand scale				
1653–1706	6	8.8 (±1.9)	6–18	↓
> 1706–1781	15	5.0 (±0.9)	1–12	__
> 1781–1920	5	27.8 (±8.1)	14–49	↑
Whole period	26	10.3 (±2.3)	1–49	↓__↑
Individual tree scale (point scale)				
1653–1706	21	11.0 (±1.1)	6–24	↑
> 1706–1781	35	22.7 (±2.2)	5–49	↑
> 1781–1920	22	82.1 (±9.5)	30–185	↑
Whole period	78	36.3 (±4.4)	5–185	↑

N, number of intervals.

remaining ones (37%) occurred in the growing season (7–96% cambial development). The seasonal pattern of fires did not differ among the three periods listed in Table 2 ($H = 2.4$, d.f. $= 1, P = 0.305$).

TREE ESTABLISHMENT

Before 1781, during the period when fires were very frequent, establishment rates of *P. sylvestris* were low (Fig. 4). After the 1825 fire, the 49-year long fire-free period was characterized by a burst of *P. sylvestris* regeneration and establishment in the stand, with a 10–60-fold increase compared to the previous period. However, in the period 1850–1875, establishment rates of *P. sylvestris* decreased to a low level again. Both samples of cores (collected in 1994 and 2007) gave very similar patterns of *P. sylvestris* establishment in the stand (Fig. 4). The oldest sampled *P. abies* tree appeared in the stand between 1825 and 1850, yet the massive establishment of *P. abies* in the studied tree stand occurred after 1875. At present, the whole stand is dominated by the 1825–1875 cohort of *P. sylvestris* and post-1875 cohort of *P. abies*. The oldest living *P. sylvestris* tree was 372 years and the oldest living *P. abies* tree 156 years. In recent years, *P. abies* has heavily dominated sub-canopy regeneration. In 2007, among 764 saplings, 61% were *P. abies*, 39% were deciduous trees (mainly *Q. robur*, *Sorbus aucuparia* L. – European rowan and *B. pendula*), and only 0.25% (2 individuals) were *P. sylvestris*.

Discussion

FIRE REGIME IN BPF

To our knowledge, this is the first detailed reconstruction of forest fire history in the temperate forest zone of lowland Europe. One reason for the lack of such studies in the region could be the scarcity of old trees and old dead wood with long records of fire events. In Central Europe, most oldgrowth or semi-natural conifer forests were cleared during the last millennium (e.g. for Poland see Maruszczak 1999) or have been transformed into younger, even-aged, managed forests during the last 200 years (Farrell *et al.* 2000). Another reason for the lack of research in Central European fire history may be the common presumption that fire was less important as disturbance agent in the temperate zone in the past (e.g. Ellenberg 1988; Bennett, Simonson & Peglar 1990; Vera 2000; Timbal *et al.* 2005).

Due to the unusual preservation state of BPF (even taking into account recent forest management activity), we have been able to reconstruct a disturbance regime of frequent fires during the 17th and 18th centuries and after that a prolonged relaxation in fire frequency. We believe that fires during this period were of low intensity because there is no evidence of subsequent tree mortality in any of the 27 recorded fires (Fig. 4) or of stand replacement and massive regeneration that often follows high-intensity fires elsewhere in conifer forests in other continents (see e.g. Brown & Wu 2005; Savage & Mast 2005). Tree recruitment was sporadic under a sparse canopy of multi-age, fire-scarred *P. sylvestris*, which is also an indication of low-intensity fires (Lehtonen, Huttunen & Zetterberg 1996).

Compared with Fennoscandian or western Russian tree ring fire histories, fire intervals in BPF were twice as short as the shortest mean intervals reported so far, and about eight to ten times shorter than in fire histories from the northern part of the boreal zone (Zackrisson 1977; Engelmark 1984; Niklasson & Drakenberg 2001; Drobyshev *et al.* 2004; Hellberg, Niklasson & Granström 2004; Wallenius, Lilja & Kuuluvainen 2007). The difference between the fire history of BPF and that of eastern Siberian *P. sylvestris* forests, with return intervals as short as 15 years (Sannikov & Goldammer 1996), is much less. To conclude, the fire intervals found in BPF are among the shortest reported from a *P. sylvestris*-dominated ecosystem so far, but there are no other studies for comparison from this region. However, the shorter intervals found in BPF, compared to tree-ring fire histories to the north, are in line with the natural gradient of shorter fire intervals associated with a warmer climate (Sannikov & Goldammer 1996).

TREE SPECIES COMPOSITION

Fluctuations in tree establishment seem to correspond well with changes in fire regime. Establishment rates of *P. sylvestris* were low during the period when fires were frequent. We propose that the intervals were too short for trees to grow a bark thick enough to allow survival of subsequent fires (Linder, Jonsson & Niklasson 1998; Brown & Wu 2005). Germination of *P. sylvestris* after fires can be prolific (Schimmel & Granström 1996), but a new fire too soon afterwards will kill most of the seedlings that have germinated. This type of fire regime is common in other *Pinus*-dominated ecosystems, such as *Pinus ponderosa* Douglas ex Lawson & C. Lawson (ponderosa pine) forests in the western United States (Brown & Wu 2005; Kitzberger *et al.* 2007; Iniguez, Swetnam & Baisan 2009). High-frequency, low-intensity fire regimes that promote *P. sylvestris* dominance have also been reported from southern Scandinavia (Niklasson & Drakenberg 2001; Groven & Niklasson 2005) and the southern taiga in eastern Siberia (Sannikov & Goldammer 1996). This fire regime in BPF changed abruptly after 1781, when fire intervals lengthened. After the 1825 fire, fires were absent for 49 years and massive *P. sylvestris* regeneration occurred during that period. Around 1850, establishment rates of *P. sylvestris* levelled out, most probably due to lack of space and competition from previously established seedlings (Brown & Wu 2005). It is interesting to note that some young *P. abies* trees survived the fire in 1874. This may be an indication of mild fires, but it could also be that some areas or patches did not burn. *Picea abies* trees are capable of surviving very mild fires, a phenomenon described from the boreal zone (Zackrisson 1977; Esseen *et al.* 1992; Niklasson 1998, 2002).

After the last major fire in 1874, tree establishment patterns were reversed compared to those after the 1825 fire. Since 1874, seedling establishment has been almost exclusively of *P. abies* (Fig. 4). We interpret this shift to be the result of the combined effects of the absence of a major fire since 1874 (permitting continued survival of post-fire regeneration) and of too much shade (due to a high survival rate of high-canopy trees), permitting post-fire *P. sylvestris* establishment. Similar fire-induced regeneration of the more shade-tolerant *P. abies* has been described from boreal Europe (Niklasson 1998, 2002; Wallenius 2002; Wallenius, Kuuluvainen & Vanha-Majamaa 2004). In summary, we believe the relaxation in fire frequency promoted massive regeneration of first *P. sylvestris* and later *P. abies*. It is well established that in the absence of fire or in a fire regime with long intervals, shade-tolerant, fire-sensitive species eventually dominate (Esseen *et al.* 1992; Sannikov & Goldammer 1996; Angelstam & Kuuluvainen 2004). Without fires in the future, the stand in our study area will continue its transition into a *P. abies*-dominated stand. This transition has in fact been observed previously in BPF; Genko (1902-1903) and Paczoski (1925) described a widespread encroachment of *P. abies* into *P. sylvestris* stands in the 19th and early 20th centuries, but they did not link this phenomenon to changes in fire regime.

A similar process has been observed in North American *P. ponderosa* forests in the recent centuries (Fulé, Covington & Moore 1997). When an earlier fire regime of frequent fires (up until the late 19th century) changed to fire exclusion in the 20th century, species composition shifted from a dominance of *P. ponderosa* to a greater dominance of conifers less adapted to frequent fires, e.g. *Abies concolor* (Gordon et Glend.) Lindl. ex Hildebr. (white fir), *Pseudotsuga menziesii* (Mirb.) Franco (Douglas fir) and deciduous trees like *Quercus gambelii* Nutt. (Gambel oak).

CAUSES OF FIRES: HUMANS *VERSUS* NATURE

Every fire history reconstruction must face the difficult issue of fire cause. Historical sources from BPF repeatedly mention only three large fires: in 1811, 1819 and 1834 (Brincken 1826; Jarocki 1830; Ronke 1830; Bobrovskii 1863; Genko 1902-1903). In our material, we dated a fire to 1811 but in a different location from the fire reported in the literature. According to contemporary sources, the 1811 fire affected the south-eastern (at present Belarussian) part of BPF (Genko 1902-1903). We found no evidence of the 1819 and 1834 fires at our study site. Of the 27 fires we dated, only one coincided in time, but not in space, with fires known from written documents. Thus, historical sources, possibly biased towards large and spectacular fire events, seem to be less useful for the *quantification* of the fire regime in the area. On the other hand, several sources do have important *qualitative* information, especially on the human use of fire in the BPF area in the past.

In BPF, the main human activities in coniferous, *Pinus*-dominated forests were: (i) Bee-keeping in tree cavities, an important part of the economy, first documented in the 16th century, but probably present since the 14th century. Tree bee-keeping declined after 1800 and was officially banned by the late 19th century. (ii) Tar and potash burning, taking place from the late 17th up till the early 20th century. (iii) Charcoal production, documented from the second half of 18th century until the early 20th century. (iv) Pasturing of cattle, practiced from the 18th century up until the 1970s, but restricted to forests around villages. (v) Commercial logging sporadically occurred in the second half of the 18th century up to the mid 19th century. From 1915 until the present, commercial logging has been the main human activity in BPF outside strictly protected areas (Hedemann 1939; Samojlik & Jędrzejewska 2004; Samojlik 2006, 2007). These activities required the use of fire or – as in the case of logging and cattle pasturing – were accompanied by human use of fire. Moreover, tracts of dry and clear *Pinus*-forests were the most convenient routes for pathways and roads (Samojlik 2007), which increased human presence. Due to these activities, forest fires were often started unintentionally (Brincken 1826; Genko 1902-1903; Krüdener 1909; Paczoski 1930; Hedemann 1939; Karpiński 1948; Samojlik & Jędrzejewska 2004; Samojlik 2006, 2007). For example, G. Harnak (1764, translated from Polish) wrote: "Frequent fires happen in the forest because of beekeepers' carelessness, when they – passing from place to place after their beehives with lit torches – start, even unwillingly, a fire" (*Summariusz z Podatków Łowieckich 1764;* National Historic Archive, Vilnius, inventory no. SA 11575). A similar observation was given by Brincken (1826) who also mention bee-keepers' and shepherds' camp fires as sources of forest fires. However, it is still difficult to determine to what degree human fires were intentional or unintentional, although the positive effects of fire for grazing conditions must have been a good argument for intentional ignition. Actually, controlling wildfires by intentional back-burning was a well-known practice in Poland and Lithuania in the past (Brincken 1826). This is strong evidence of a tight human–fire relation with a deep practical knowledge about fire behaviour and fire control. This, in turn, suggests that fires in the past may have been intentionally ignited and even controlled to a large degree.

Changes in human use of BPF closely match the three periods of different fire frequency that we report. The ways of human utilization of BPF that were conducive to fires seem to have been steadily increasing from the 15th century onwards, with a peak in the 18th century (Samojlik 2007). Abrupt changes in the political and conservation status of BPF after 1795 (when Poland was divided and BPF fell under the Russian rule) and the subsequent decline of traditional modes of forest utilization were followed by a decline in fire frequency. The beginning of active human-governed fire prevention measures and suppression of fires are documented from the late 18th century (Hedemann 1939) and became rather strict after the disastrous fire in 1811 (Genko 1902-1903). With the exception of the fire in 1874, no more major fires occurred after 1825 in the studied stand. The change in attitude towards fire originated from an increased interest in conservation of timber resources in the same time (Genko 1902–1903; cf. Pyne 1997, p. 185). In boreal Fennoscandia, the beginning of industrial timber exploitation has been proposed as a main reason for shifts in fire regime (Granström & Niklasson 2008).

Although our study period covers substantial climatic fluctuations in the past, e.g. the coldest phase of Little Ice Age (Luterbacher *et al.* 2001), we have too few fire events within the series of available temperature data for the region (temperature data going back to 1780, see Jędrzejewska *et al.* 1997) to perform a robust analysis. Local or regional climate reconstructions (e.g. from tree rings) covering the early part of our reconstructed fire record are still lacking. In addition, our reconstruction of fires has been carried out over too small an area to permit analysis of possible correlation between burned area and climate. The number of fires over time and the indication of small fire sizes do, however, still give reason to believe that the number of fires substantially exceed natural background levels of ignition (e.g. Granström 1993; Sannikov & Goldammer 1996).

However, a deeper analysis of climatic vs. human influence on the fire regime needs, amongst others things, a fairly good estimation of past fire sizes ⁄ or the extent of the fire to be reconstructed (Grissino-Mayer & Swetnam 2000; Niklasson & Granström 2000; Hellberg, Niklasson & Granström 2004; Kitzberger *et al.* 2007). We could not reconstruct the size of individual fires, but we detected a few borders within our 13-ha study area (data not shown), which is an indication that at least some fires were small, possibly at the scale of tens of hectares.

We cannot completely rule out a natural fire regime in the area in the more distant past. Lightning-ignited fires do occur in BPF (e.g. Brincken 1826) and charcoal particles in the local peat profiles are found throughout the last 1500 years (Mitchell & Cole 1998). A pre-supposed change from a more natural fire regime to the anthropogenic one was therefore not necessarily a change from absent to frequent fires. Rather, it may have been a change from fewer, larger fires to many small fires, a situation that has been reported from elsewhere (Minnich 1983, 2001; Page *et al.* 1997; Niklasson & Granström 2000). In addition, periods of high fire frequency are possible even when natural sources of ignition are scarce, if the resulting fires cover large areas (cf. Niklasson & Granström 2000).

THE FUTURE OF *PINUS*

Our studied stand is not exceptional in BPF. Numerous other conifer sites contain fire-scarred trees and stumps. They provide further support for our findings that frequent fires – probably most of them of low intensity – were an integral part of the conifer-dominated parts of this forest in the past. A key question is whether this pattern may also hold for other regions of temperate Europe, as has been postulated by e.g. Svenning (2002). Today, it is forest management, not fires, that maintains the *P. sylvestris* dominance in a substantial part of Central European forests, mostly on poor soils (Timbal *et al.* 2005). Under natural conditions and in the absence of large disturbances, *P. sylvestris* is a weak competitor, especially on mesic and rich soils where both *P. abies* and temperate broad-leaved species easily outcompete it (Faliński 1986; Peterken 1996; Willis, Rudner & Sümegi 2000). In a fire-free landscape, *P. sylvestris* will be confined to the most oligotrophic or xeric soils (Faliński 1986; Esseen *et al.* 1992; Angelstam & Kuuluvainen 2004). Our data on tree establishment dynamics clearly demonstrate this phenomenon, with *P. abies* successfully outcompeting *P. sylvestris* in the absence of fires, just as described from most of its vast distribution range (e.g. Zackrisson 1977; Linder 1998; Wirth *et al.* 1999; Angelstam & Kuuluvainen 2004; Wallenius, Lilja & Kuuluvainen 2007). If the absence of fire continues, *P. sylvestris* is likely to be found only in marginal parts of the BPF, on the most oligotrophic and xeric sites. Projected climate warming (e.g. IPCC 2007) may, however, result in more fires that are difficult to suppress and thus lead to a situation more similar to the past.

Palaeoecological data show a clear connection between *Pinus* abundance and charcoal in many parts of Europe (e.g. Rösch 2000; Bradshaw & Lindbladh 2005; Carcaillet *et al.* 2009). Thus, it cannot be ruled out that fires, similar in frequency and intensity to those described here, have been an important and integral part of most European lowland *Pinus* forests over much of the Holocene until the relatively recent past.

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