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Dendrochronological reconstruction reveals a mixed-intensity fire regime in *Pinus sylvestris*-dominated stands of Białowieża Forest, Belarus and Poland

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Keywords
Central Europe; Fire scar; Forest dynamics; Natural disturbance; Post-fire tree growth; Scots pine; Temperate lowland mixed forest; Tree recruitment; Tree ring

Abbreviation
BF = Białowieża Forest.

Nomenclature
Mirek et al. (2002) for vascular plants ; Ochyra et al. (2003) for bryophytes

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Abstract

Questions: What were the features of the historical forest fire regime, fire intensity in particular, in *Pinus sylvestris*-dominated stands of Białowieża Forest? Did tree recruitment patterns relate to the fire history?

Location: Białowieża Forest, western Belarus and northeast Poland.

Methods: We used dendrochronological methods to reconstruct the fire regime in a 8.5-ha mixed coniferous (*Pinus sylvestris–Picea abies*) forest stand located in the Belarusian part of Białowieża Forest. We analysed fire frequency at stand and point scale, seasonal distribution of fires and fire intensity. We compared the results to a previous study done in a 13.0-ha site of similar habitat and stand structure, located in the Polish part of Białowieża Forest.

Results: We reconstructed fires back to 1655, the most recent fire dating to 1918. Mean fire interval at stand scale during 1645–2010 was 9 $\pm$ 7.8 yrs ($\pm$SD). Fire frequency gradually declined after 1811, with mean fire interval at stand scale increasing from 5 $\pm$ 2.5 yrs prior to 1811 to 18 $\pm$ 9.3 yrs thereafter. Most fires were likely of low intensity, as suggested by (1) small average tree diameter (5.1 $\pm$ 2.9 cm) at the first scar, (2) absence of strong negative growth reactions after fire, and (3) high fire frequency likely limiting fuel build-up. However, a fire in 1718 was intense and resulted in a wave of *P. sylvestris* regeneration. The reconstructed fire history in the Belarusian part of Białowieża Forest showed many similarities with that done in the Polish section of this forest. Similarities included dominance of low-intensity dormant and early-season fires, sporadic occurrence of high-intensity fires, high fire frequencies between the 1650s and the early 1800s, and cessation of fires since the early 20th century. Six out of 50 fire dates reconstructed in both sites were common and represented a level of synchrony that was significantly higher than expected under a random pattern of fire occurrence.

Conclusions: Low-intensity surface fires dominated the historical fire regime of Białowieża Forest. However, occasional high-intensity stand-replacing fires led to successional changes at the stand scale.

Introduction

Pinus sylvestris L. (Scots pine) forest is one of the main forest communities in the temperate part of Central Europe (Timbal et al. 2005). As most in *Pinus* species, *P. sylvestris* has many of the typical traits of fire adaptation, including thick bark and self-pruning of dead branches (Agee 1998; Keeley 2012). Since Scots pine lacks traits that make it adapted to high-severity fires, such as cone serotiny or capacity to resprout (Agee 1998), fire regime in *P. sylvestris* forests is likely to be dominated by low-intensity fires (Agee 1998; Keeley 2012). Throughout the boreal part of *P. sylvestris* distribution low-severity surface fires prevail over stand-replacing high-intensity fire events (Sannikov & Goldammer 1996), as evidenced by common fire-scarred trees and multiple-aged forest stands, both in Europe (e.g. Brūmelis et al. 2005; Blanck et al. 2013) and Asia (e.g. McRae et al. 2006). Also in the southern fringe of the

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geographic range of Scots pine ecosystems, low-intensity surface fires have been suggested to be the dominant fire regime (Marozas et al. 2007; Parro et al. 2009).

There are few data on fire and its impact on Scots pine population dynamics under natural conditions in Central Europe (Timbal et al. 2005; Niklasson et al. 2010). Palaeoecological data have proven that fire was an essential part of forest dynamics in this region during the Holocene (e.g. Tinner et al. 2005), similar to the European boreal (Storaunet et al. 2013; Drobyshev et al. 2014) and Mediterranean (Christopoulou et al. 2013; Fournier et al. 2013) zones. Such data however give limited insight into characteristics of the fire regime and its impact on forest dynamics (Higuera et al. 2005; Ali et al. 2012). Given the anticipated changes in future climate and their potential impact on Scots pine-dominated forests in Europe (Szczygieł et al. 2009), quantitative information on *P. sylvestris* fire regimes, especially in relation to forest dynamics, land use and climate variability is valuable.

In this study we described the historical fire regime of a *P. sylvestris*-dominated stand in the Belarusian part of Białowieża Forest (BF), focusing specifically on the range of historical fire intensities. We used tree diameter at the first fire scar and post-fire growth response as proxies for fire intensity. To evaluate the degree of generality in the results obtained within a single site, and to address the question of climate influence on the historical fire regime in BF, we employed results from a previous study conducted in a structurally similar stand in the Polish section of BF (Niklasson et al. 2010).

Methods

Study area

Białowieża Forest (BF) is one of the best preserved lowland forests in temperate Europe, situated at the border between Belarus and Poland (52°30′–53° N, 23°30′–24°15′ E). The climate is transitional between Atlantic and continental types (Faliński 1986). Mean annual temperature in 1955–2001 was 6.8 °C, with a mean July temperature of 17.7 °C and a mean January temperature of −4.2 °C. The mean annual precipitation in that period was 633 mm (Pierzgalski et al. 2002). The area of BF is an old-morainic plateau built from gravels, clays and glaciofluvial sands (Kwiatkowski 1994). BF contains a mosaic of forest communities, with the following main tree species: *Quercus robur* L. – pedunculate oak, *Tilia cordata* Mill. – small-leaved lime, *Carpinus betulus* L. – hornbeam, *Acer platanoides* L. – Norway maple, *P. sylvestris*, *Picea abies* (L.) H. Karst. – Norway spruce, *Alnus glutinosa* (L.) Gaertn. – black alder, *Fraxinus excelsior* L. – ash, and *Betula pubescens* Ehrh. – downy birch (Faliński 1986). BF covers ca. 1500 km^2, of which ca. 600 km^2 is located on Polish territory and ca. 900 km^2 in Belarus. Detailed description of forest communities, current nature conservation and forest management activities, and land use history of BF can be found in e.g. Faliński (1986) and Niklasson et al. (2010).

The study site (further referred to as 'Comp. 782') was located in the Belarusian section of BF, in forest compartment number 782 (Fig. 1). The following criteria were used for site selection: (1) presence of fire-scarred *P. sylvestris* trees and stumps; (2) stand structure reflecting relatively low human impact, evidenced by naturally regenerated uneven-aged Scots pine population, numerous old-growth individuals and deadwood continuity providing for long tree ring sequences; and (3) good isolation, by both distance and potential fire borders, from a previous fire history study site, located in the Polish part of BF (Niklasson et al. 2010) and used for comparison.

The study site Comp. 782 was a 8.5-ha mixed coniferous forest stand (*P. sylvestris*–*P. abies*). The stand was dominated by 280- to 290-yr-old *P. sylvestris* trees mixed with younger individuals of both *P. sylvestris* (80–170 yrs old) and *P. abies* (20–140 yrs old). Several scattered *Betula pendula* and a few younger, small-diameter *Q. robur* trees were also present in the canopy. The stand density was ca. 800 stems·ha^{-1}. Advanced regeneration of *P. abies* was abundant in the understorey. The study site lacked *P. sylvestris* regeneration. Ground vegetation comprised *Vaccinium myrtillus* L., *V. vitis-idaea* L., *Trientalis europaea* L., *Dryopteris carthusiana* (Vill.) H.P. Fuchs and *Calamagrostis arundinacea* (L.) Roth. The ground layer was dominated by mosses: *Pleurozium schreberi* (Willd. ex Brid.) Mitt., *Ptilium crista-castrensis* (Hedw.) De Not., *Hylocomium splendens* (Hedw.) Schimp. and *Dicranum undulatum* Schrad. ex Brid. Neighbouring stands were mainly coniferous forests of similar habitat type. The site had no streams, bogs or swampy areas that could have acted as fire breaks.

The site used for comparison (further referred to as: 'Comp. 494') is located in the Polish section of BF, ca. 17 km to the northwest, in forest compartment number 494. It is a 13.0-ha mixed coniferous forest stand (*P. sylvestris*–*P. abies*), similar to Comp. 782 in terms of topography and vegetation (Niklasson et al. 2010). Both sites are separated by several potential fire borders: rivers Przewłoka and Leśna and humid and wet forest sites.

Field methods

We collected *P. sylvestris* wood samples over the 8.5-ha area with a sampling effort similar to that in Niklasson et al. (2010). We collected increment cores from living Scots pines and full or partial cross-sections from all available stumps, snags and logs with fire scars. While sampling living trees, we did subjective sampling of all old individuals with visible fire scars and of trees with

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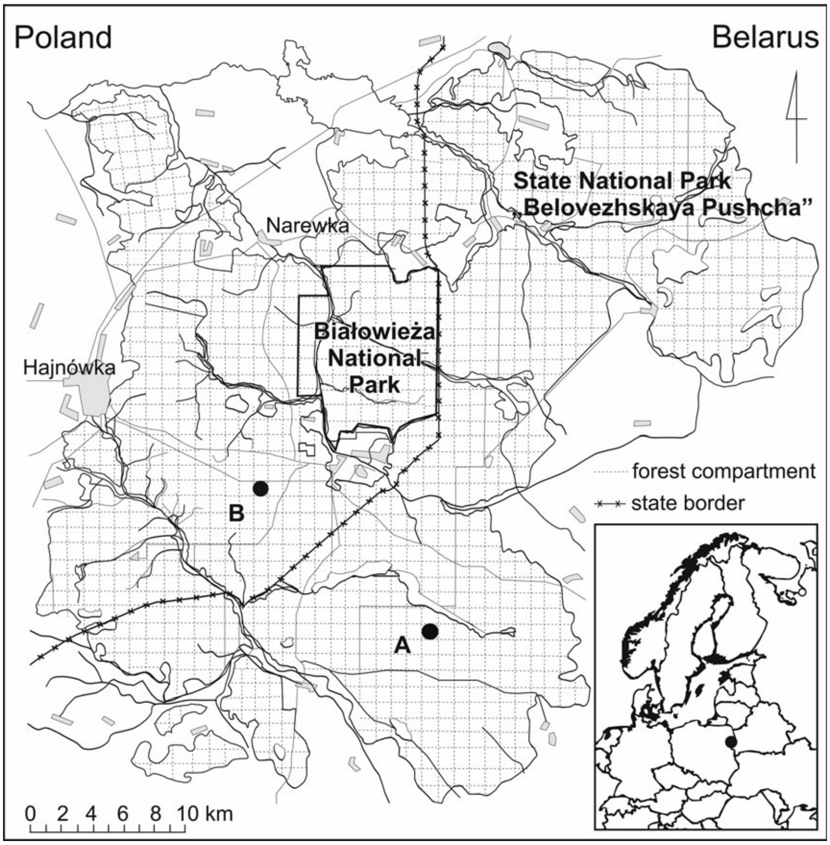

Fig. 1. Location of the fire history reconstruction sites in Białowieża Forest. A: Comp. 782, a 8.5-ha study site in the Belarusian section (this study), B: Comp. 494, a 13-ha study site in the Polish section (Niklasson et al. 2010). Map re-drawn after figure in Niklasson et al. (2010), modified.

the lowest DBH (diameter at 1.3 m above the ground), assuming that they likely represented the youngest Scots pine generation. In total, we acquired 44 cross-sections and 24 increment cores from 36 dead and 19 living pine trees.

Cross-dating

Wood samples were mounted on boards and slats, and sanded to a fine polish. Ring counts and cross-dating by identifying local pointer years were done under a dissecting microscope with 6–40× magnification (Yamaguchi 1991). For increment cores that slightly missed the pith, the pith date was estimated with a pith locator (Applequist 1958). As positive fire indicators we used fully developed fire scars and – in cases when there was no fire scar, but the particular fire date was confirmed by at least one fire scar in neighbouring sample trees – also sudden short-term (1–5 yrs) growth depressions, that were in many cases accompanied by fire-induced disturbances in tree ring morphology (Niklasson & Granström 2000). Cross-dating allowed identification of exact fire years. Fire season was determined for 90% of fires, using the following categories: early earlywood (EE), middle earlywood (ME), late earlywood (LE), latewood (LW) and dormant (D) (Baisan & Swetnam 1990).

Analyses of fire return intervals

We calculated fire intervals at stand and point (single tree) scales (cf. Niklasson et al. 2010). We analysed temporal dynamics of the fire regime by dividing the period of our reconstruction into two sub-periods, 1731–1811 and 1811–2010, that were selected *post hoc* based on sample depth and known land use history, with 1811 documented as a start of active fire suppression in BF (Niklasson et al. 2010). The null hypothesis that the fire frequency (as revealed by fire intervals at both scales) did not differ between the period before 1811 and thereafter was verified with a Mann–Whitney test, using *STATISTICA* software (v 8; StatSoft, Tulsa, OK, US).

Fire intensity proxies

We used two proxies of fire intensity: tree diameter at the first fire scar and post-fire growth response.

We regarded tree diameter at the first fire scar as a measure of tree susceptibility to fire. Tree diameter is directly related to bark thickness, and the bark insulating efficiency (the time required to raise cambium temperature to lethal levels) is a power function of bark thickness (Dickinson & Johnson 2001). Tree diameter also determines the formation of and residence time of the standing leeward flame at the tree bole, which is responsible for fire scarring (Gutsell & Johnson 1996). Furthermore, tree diameter can also be viewed as a proxy for tree height (Anonymous 2001) and crown length (Przybylski 1970). Capitalizing on the relationship between the height of lethal crown scorch and the fireline intensity (Van Wagner 1973), one can reconstruct the maximum intensity of a particular fire event from the minimum height of surviving trees (Bergeron & Brisson 1990). In our study, we recorded tree diameters at the first fire scar in 32 trees, representing 11 fires.

We assumed that an abrupt decrease in radial growth following a fire reflected a significant loss of crown biomass due to crown scorch (Pearson et al. 1972). Crown scorch is related to flame length, which is an indicator of fireline intensity (Byram 1959; Van Wagner 1973). Therefore, lack of negative growth reactions in surviving trees may be interpreted as flame length and fire intensity not conducive to crown damage. We analysed the post-fire growth data only from trees that, in a given fire year, exhibited a fire scar or a sudden short-term growth depression. We examined changes in tree diameter growth with a conservative approach (Cook & Kairiukstis 1990) and used raw tree ring widths to calculate a post-fire growth index (I_r) as a ratio between radial growth over 10 yrs prior and following a fire:

$$I_r = \frac{\mathrm{TRW}_{10}\,\mathrm{post}\text{-}r}{\mathrm{TRW}_{10}\,\mathrm{pre}\text{-}r}, \quad (1)$$

where: r = fire year, I_r = post-fire growth index defined for the fire in year r, $\mathrm{TRW}_{10\ \mathrm{post}\text{-}r}$ = tree ring width 10 yrs following the fire year r (mm), $\mathrm{TRW}_{10\ \mathrm{pre}\text{-}r}$ = tree ring width 10 yrs preceding the fire year r (mm). We excluded from the calculations growth in the year of the fire itself. To minimize the influence of callus tissue on tree ring width values, we took the measurements as far away from the fire scar as possible, preferring the position directly opposite to a fire scar. We assumed 20% as a possible natural growth/tree ring width variation (Black & Abrams 2003) and defined the following classes of post-fire growth response: (1) negative reaction, $I_r < 0.8$; (2) no response, $I_r = 0.8–1.2$; (3) positive reaction, $I_r > 1.2$.

In this study we refer to fire intensity and not to fire severity since our focus was on the physical force of the reconstructed fire events in BF (cf. White & Pickett 1985).

Comparison with the Polish site

We analysed temporal pattern in fire occurrence in two study sites in BF using logistic regression, with fire occurrence as binary dependent variable and site and time (calendar year) as explanatory variables. The effect of site was also assessed with a Chi-squared test using a significance level of 5%. Predicted fire occurrence was calculated for the common time period only (362 yrs, 1645–2007). The analyses were performed using the *stats* package in R (v. 2.15.2; R Foundation for Statistical Computing, Vienna, AT; http://www.R-project.org).

Differences in fire frequency between the two sites were tested by the Mann–Whitney test on the stand scale fire intervals and for the whole time period covered by respective reconstruction, using *STATISTICA* software (v 8; StatSoft).

We applied contingency analysis to analyse fire synchrony between the Belarusian and the Polish sites over the common time period (1645–2007). The expected number of co-occurring fire dates was estimated from joint probability of fire (or no fire) occurring within the two sites (Swetnam 1993; Drobyshev et al. 2014). The joint probability was the product of the individual probabilities of fire occurrence within each site, estimated from the observed fire frequency over the respective time period. We used Monte Carlo simulations (n = 1000) to estimate the theoretical probability of empirically observed number of joint fire years, assuming binominal distribution of fire events.

Results

Fire history

We identified 29 fires through dating of a total of 138 fire scars from 34 dead and 16 living sample trees. The oldest fire occurred in 1655 and the most recent in 1918 (Fig. 2). The mean fire return interval at stand scale for the whole period (1645–2010) was 9 ± 7.8 yrs. Between 1731 and 1811 the stand scale fire interval averaged 5 ± 2.5 yrs and ranged from 1 to 9 yrs. During 1811–2010, mean stand-scale fire interval increased up to 18 ± 9.3 yrs, ranging from 8 to 33 yrs (Table 1).

The mean point-scale fire interval for the whole period (1645–2010) was 35 ± 50.0 yrs. In the period 1731–1811 it averaged 8 ± 5.0 yrs, with values ranging from 2 to 28 yrs. After 1811 mean point-scale fire interval increased to 50 ± 28.7 yrs and ranged from 8 to 93 yrs (Table 1, Fig. 3). Half (47%) of all single-tree fire intervals were ≤10 yrs. The shortest point-scale fire interval was 2 yrs. That value was recorded in two sample trees (5.71% of the trees covering the respective period) between the 1753 and 1755 fires and the 1809 and 1811 fires, respectively (Fig. 2).

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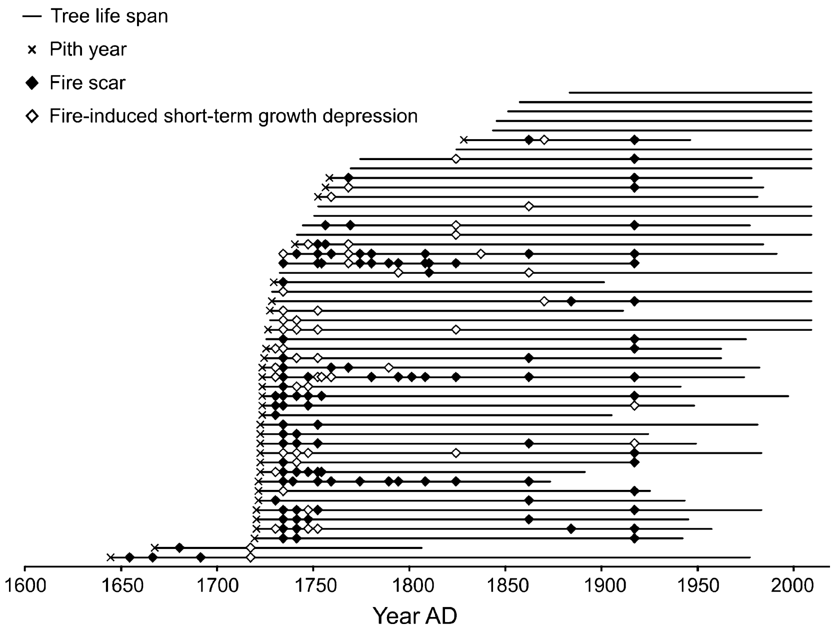

Fig. 2. Fire history of a 8.5-ha mixed coniferous (*P. sylvestris*–*P. abies*) forest stand located in the Belarusian part of Białowieża Forest, over the period 1645–2010, reconstructed by cross-dating of *P. sylvestris* tree ring samples (n = 50, 34 dead/16 live).

The two sub-periods differed significantly in fire frequency, as shown by both the stand-scale (Mann–Whitney test, $P = 0.0006$) and the point-scale fire intervals (Mann–Whitney test, $P = 0.0000$).

It was possible to determine the pith date in 64% ($n = 32$) of sampled trees. Most of the cross-dated samples came from trees that regenerated in the 1720s ($n = 25$), especially in the period 1720–1724 ($n = 19$). Sporadic tree establishment occurred in the 1750s and the 1820–1840s. Only two samples (representing 4% of the total material and 6.3% of the material with identified pith year) went substantially further back in time, with pith years 1645 and 1668. These two trees had evidence of a fire in 1718, which preceded the majority of the sampled trees (Fig. 2).

Fire seasonality was successfully identified for 90% of the fires. Dormant season fires accounted for 73.1% and early-season fires (ME and LE) for 23.1% of all the dated fire events in the study site. There was only one late-season fire in 1681 (Appendix S1).

Tree diameter at the first fire scar and post-fire growth response

Tree age at the first fire scar ranged from 5 to 34 yrs (mean 11.9 ± 5.8 yrs, median 11.9 yrs), with corresponding

Table 1. Summary of fire history reconstructions from two sites in mixed coniferous (*P. sylvestris*–*P. abies*) stands in Białowieża Forest.

	Comp. 782 (this study)			Comp. 494 (Niklasson et al. 2010)
		Sub-periods*		
Length of tree ring record	1645–2010	1731–1811	1811–2010	1642–2007
Number of dated fires	29	18	6	27
% co-occurring fires (n = 6)	20.69			22.22
Fire interval, stand scale (yrs)				
Mean (±SE)	9.4 (±1.5)	4.7 (±0.6)	17.8 (±3.8)	10.3 (±2.3)
n	28	17	6	26
Range (min–max)	1–33	1–9	8–33	1–49
Fire interval, single tree scale (yrs)				
Mean (±SE)	34.8 (±4.6)	8.4 (±0.6)	49.8 (±8.0)	36.3 (±4.4)
n	120	73	13	78
Range (min–max)	2–183	2–28	8–93	5–185

*For details see the sub-section Analyses of fire return intervals in Methods.

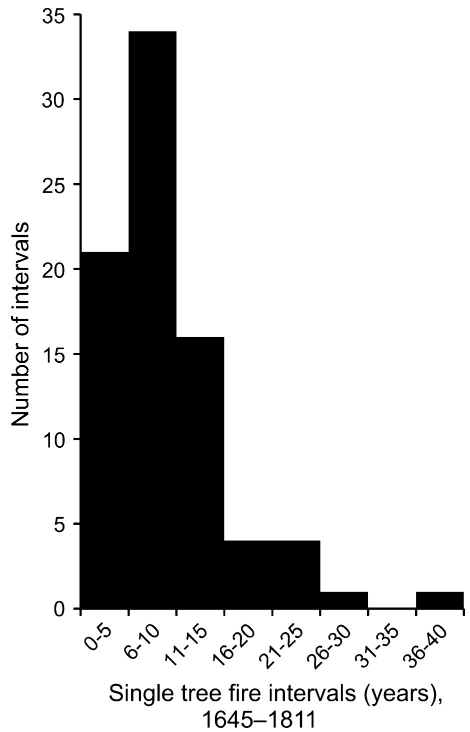

Fig. 3. Fire intervals in single trees in the studied site (Comp. 782) for the period 1645–1811.

diameters ranging from 1.4 to 16.4 cm (mean 5.1 ± 2.9 cm, median 4.9 cm). Over half (63%) of the trees evidenced diameter at the first fire scar below 6.0 cm (Fig. 4).

Fires hardly affected the growth of surviving trees, with a mean post-fire growth response index (I_r) of 1.08 (Table 2). Post-fire growth response was mainly positive or absent (Appendix S1). An exception to this pattern was the 1718 fire, which was recorded in two older samples as clear and strong growth depressions, accounting for the two lowest I_r values, 0.1 and 0.31 (Table 2, Fig. 5, Appendices S1 and S2). At the time of the fire, these two trees were 73 and 50 yrs old and 24.3 and 16.6 cm in diameter, respectively. Immediately after 1718 massive Scots pine regeneration took place (Fig. 2). There was no correlation between the tree diameter and the post-fire growth response ($r = -0.1777$, $P > 0.05$; Fig. 5).

Comparison with the Polish fire history record from BF

The fire histories developed on the two sites in BF reveal similarities in seasonal and temporal distribution of historical fires. The majority of fires occurred in the dormant (73.1%; Appendix S1; 63%, Niklasson et al. 2010) and early season of cambium activity (23.1%; Appendix S1; 26%, Niklasson et al. 2010). Both sites showed the same (difference statistically not significant, $P = 0.58$) pattern in fire presence over the last 360+ yrs (1645–2007), being a decreasing trend ($P < 0.0001$; negative slope-value: −0.013033). There was no difference in stand-scale fire intervals between the two sites (Mann–Whitney test, $P = 0.8830$), evidencing similar fire frequencies between the 1650s and the onset of fire decline (early 1800s in the Belarusian site and late 1700s in the Polish site). In both sites the cessation of fires began in the early 20th century (Figs 2 and 6; cf. Niklasson et al. 2010).

Six out of 50 fires recorded in both sites were common (1718, 1760, 1781, 1795, 1811, 1825), which represented a higher synchrony in fire occurrence than expected: the Monte Carlo experiment suggested 2.2 ± 2.1 joint fire events over the common time period and a significant difference ($P = 0.023$) to the observed value.

Discussion

Our results showed that the historical fire regime in *P. sylvestris* forests of Białowieża was likely dominated by frequent low-intensity fires. However, tree recruitment data and reconstruction of fire intensity also evidenced the occurrence of stand-replacing high-intensity fires. These events initiated cohort regeneration in the midst of long periods with only sporadic tree establishment.

Frequent low-intensity fires and their impact on forest vegetation – ground fuels, tree regeneration and post-fire tree growth

Fire intervals reported from Eurasian *P. sylvestris* forests range between 5 and 300 yrs (Niklasson & Granström 2000; Hellberg et al. 2004; McRae et al. 2006; Niklasson et al. 2010). The lowest limit of fire intervals is partly controlled by fuel build-up, which varies along a gradient of climate and soil fertility (Schimmel & Granström 1997; Marozas et al. 2007, 2011). The point-scale fire intervals recorded in our study were considerably shorter than those in northern boreal *P. sylvestris* forests (10–20 yrs; Niklasson & Granström 2000; McRae et al. 2006). This is in line with earlier results from the temperate zone, where fire history records suggest a minimum fire return interval of ca. 5 yrs (Niklasson et al. 2010; Niklasson 2011). A point-scale fire interval of 2 yrs in two of our samples (Fig. 2) is, to our knowledge, the shortest interval documented in a *P. sylvestris* tree, with values of 3, 4 and 5 yrs being the lowest record until now (Ivanova et al. 2010; Niklasson et al. 2010; Niklasson 2011).

Under frequent fires, fuels may have been a limiting factor for fire spread (Schimmel & Granström 1997). Differences in minimum fire return intervals between the boreal and temperate zones may indicate different patterns of fuel

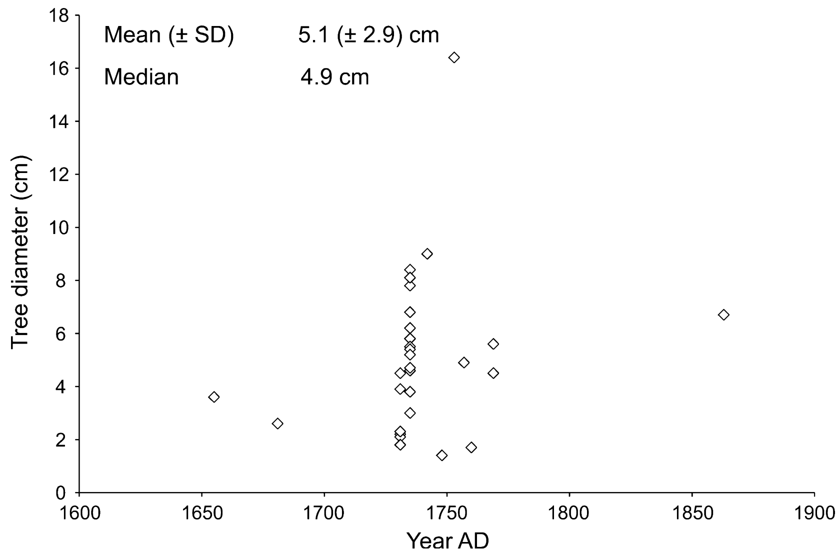

Fig. 4. Tree diameter at the time of the first fire scar (data for 32 trees and 11 different fire events) in the studied site (Comp. 782) over the period 1645–2010.

Table 2. Statistics on post-fire growth response index (I_r) recorded in *P. sylvestris* trees after fires in the studied site (Comp. 782) over the period 1645–2010.

	Range (min–max)	Mean (±SD)	Median	*n**
All fires	0.10–3.39	1.08 (±0.50)	1.01	141
1718 fire	0.10–0.31	0.21 (±0.15)	0.21	2
Fires before 1718	0.46–1.70	0.93 (±0.60)	0.78	4
All fires other than 1718	0.42–3.39	1.09 (±0.49)	1.01	139

*Number of observations of the post-fire growth response index (I_r), calculated for each fire event recorded in each tree ring sample, where it was possible to measure tree ring width of 10 yrs before and 10 yrs after the recorded fire. Because of different fire recording ability of trees, *n* reflects neither the total number of fires nor the complete number of analysed sample trees.

build-up, with shorter ground vegetation recovery and hence a shorter period of non-flammability in the Central European Scots pine forests. Based on our own field observations and other studies from the region (A. Matuszkiewicz, unpubl. data – in Faliński 1986, p. 215–217; Skre et al. 1998; Marozas et al. 2007; Parro et al. 2009), we propose that fuel composition under frequent fires in BF was dominated by grasses, e.g. *Agrostis* spp., *Calamagrostis* spp., *Deschampsia* spp. or *Molinia* spp. Grasses are promoted by fires (Bond et al. 2005) and have a shorter regeneration time than feathermosses and ericaceous *Vaccinium* shrubs (Marozas et al. 2007; Parro et al. 2009), which are common fuel types in *P. sylvestris* ecosystems nowadays, both in temperate and boreal Europe (Faliński 1986; Schimmel & Granström 1997). Also, *Calluna vulgaris* (L.) Hull (heather) may have been common, since it is known to recover faster than *Vaccinium* species in burned areas (Skre et al. 1998; Marozas et al. 2007).

Although frequent fires apparently caused high mortality of *P. sylvestris* regeneration, they seemed to be of low intensity in absolute terms, as revealed by small diameters at the first fire scar in surviving trees (Fig. 4). Tree seedlings are generally easily killed by fire, simply because of their small height and thin bark (Sidoroff et al. 2007; Kukavskaya et al. 2014). However, occasionally, seedlings seem to have escaped to 'safer' sizes, resulting in sporadic tree recruitment under the canopy of mature pine trees. Such pattern of Scots pine regeneration under frequent low-intensity surface fires, creating multiple-aged pine stands, has been recorded in numerous studies across Eurasia (McRae et al. 2006; Niklasson et al. 2010; Storaunet et al. 2013). Our data suggest that trees typically needed to reach an age of 5–12 yrs and ca. 5 cm in stem diameter to survive a fire, which is equivalent to a height of 6–8 m (Anonymous 2001). Such height of surviving trees would reflect maximum fire intensities of 250–400 kW·m^{-1} and flame lengths of 0–1 m (Van Wagner 1973; Bergeron & Brisson 1990; Agee 1993; Pyne et al. 1996). This intensity is classified as low-severity surface fire (Van Wagner 1983) or creeping or gentle surface fire (McRae et al. 2006). Comparable data on diameter at the first fire scar in *P. sylvestris* ecosystems are rare (but see: Lehtonen 1998).

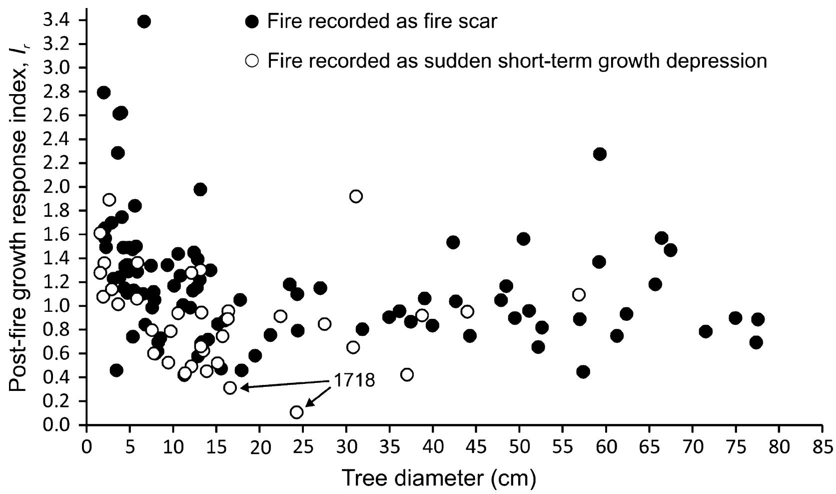

Fig. 5. Post-fire growth response recorded in sampled *P. sylvestris* trees to all fires reconstructed in the study site (Comp. 782) over the period 1645–2010, plotted against tree diameter. Proposed threshold values of the post-fire growth response index (I_r) for: (1) negative reaction = $I_r < 0.8$, (2) no response = I_r of 0.8–1.2, (3) positive reaction = $I_r > 1.2$.

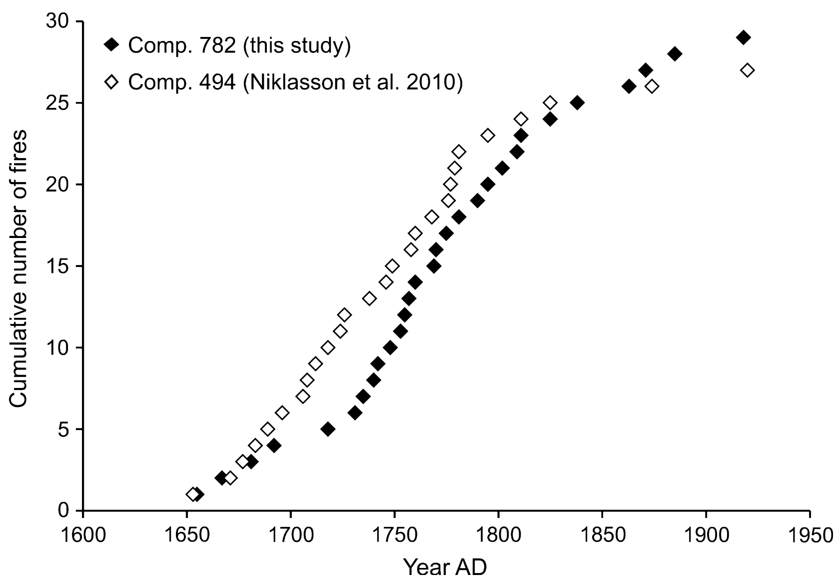

Fig. 6. Cumulative number of fires over time recorded in a 8.5-ha mixed coniferous (*P. sylvestris*–*P. abies*) forest stand located in the Belarusian part of Białowieża Forest (Comp. 782, this study) and in a 13.0-ha coniferous tree stand of the same forest type in the Polish section of that area (Comp. 494; Niklasson et al. 2010).

However, studies on post-fire mortality have revealed an increase in survival rates with larger DBH, with tree survival in low- to moderate-intensity fires greatly increasing as trees reach a threshold of 4–8 cm DBH (Kolström & Kellomäki 1993; Linder et al. 1998; Sidoroff et al. 2007; Kukavskaya et al. 2014).

Our second proxy of fire intensity, the post-fire growth response (Fig. 5, Appendix S1), revealed mainly positive or no influence of fires on radial growth, supporting the notion that these disturbances were of low intensity. This is in line with earlier studies in Europe (Blanck et al. 2013) and Asia (Wirth et al. 2002), all indicating that low- to moderate-severity fires promote growth of Scots pine. The post-fire growth response may also be influenced by e.g. humus consumption (Hille 2006) or general variability in tree growth, related to e.g. climate or tree age (Cook & Kairiukstis 1990). Since our conservative approach disregards the age-related decrease in linear growth increment (Cook & Kairiukstis 1990), our results are likely biased towards a more negative growth response.

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Occasional high-intensity fires and cohort regeneration – evidence of a mixed-intensity fire regime

The period of frequent low-intensity fires in this study was interrupted by a high-intensity fire event in 1718. The only two surviving trees were then 15- to 20-m high, as reflected by their time-of-fire diameter and age (Anonymous 2001). This height would correspond to a maximum fireline intensity of ca. 1000–1600 kW·m^{-1} (Van Wagner 1973; Bergeron & Brisson 1990) and to flame lengths of ca. 1–2 m (Agee 1993; Pyne et al. 1996). Such fires are classified as high-intensity disturbances, with significant or even complete post-fire tree mortality (Van Wagner 1983) and, alternatively, as low to highly vigorous surface fires (McRae et al. 2006).

The 70–90% post-fire growth reduction recorded in the two 1718 surviving individuals (Fig. 5, Appendices S1 and S2) was likely the result of significant crown damage. Since these trees had diameters of 17 and 24 cm at that time, their bark was probably thick enough to prevent cambial injury from elevated temperatures (Dickinson & Johnson 2001). Still, the actual amount of crown scorch in these trees was likely less than reflected in growth, due to the non-linear relationship between crown injury and post-fire tree condition (Pearson et al. 1972; Hood et al. 2010).

The large recruitment wave of Scots pine immediately after 1718 is another indication that fires in BF could be of stand-replacing intensity. Severe forest fires are often followed by regeneration cohorts as a result of high overstorey mortality and increased light levels (Wallenius et al. 2002; McRae et al. 2006). It can be argued that cohort regeneration might occur after other types of large-scale disturbance (Zielonka et al. 2010; Reinikainen et al. 2012), as there was no fully developed fire scar from 1718 in our sample material. However, we suggest that both windthrow and insect outbreak are unlikely. First, there was no compression wood in tree ring samples from the two pre-1718 individuals (E. Zin and M. Niklasson, unpubl. data) that could indicate a possible wind disturbance (Zielonka et al. 2010). Second, *P. sylvestris* has been reported to successfully survive even severe defoliation by insects, with growth losses still lower than the values recorded in the two 1718 surviving trees (e.g. Långström et al. 2001). Finally, the microsites created by wind and/or insect disturbances are less favourable for Scots pine regeneration than the improvement in seedbed conditions caused by fire (Kuuluvainen & Rouvinen 2000; Hille & den Ouden 2004). A regeneration cohort of *P. sylvestris* and an indication of strong growth depressions in the surviving trees were also observed after the 1825 fire in the Polish fire history record from BF (Zin 2007; Niklasson et al. 2010).

The level of fire synchrony between the two locations in BF was higher than could be expected by chance, which suggests climate as a forcing factor (Kitzberger et al. 2007; Drobyshev et al. 2014). Interestingly, both the 1718 fire and the 1825 fire were synchronous between the two sites. There may be a link between high fire intensity and fire synchrony, with more intense fires being associated with stronger droughts representing, in turn, geographically larger climate anomalies (Drobyshev et al. 2012). Further analyses of climate forcing upon fire activity in BF would require larger data sets and should also involve analysis of human land use patterns (Drobyshev et al. 2004; Niklasson et al. 2010).

In summary, our results provide evidence that low-intensity surface fires likely dominated the historical fire regime in *P. sylvestris* ecosystems of Białowieża Forest. The fires of this type probably allowed only sporadic tree recruitment. We suggest this pattern as common over the whole BF area, given the similarities between the two studied sites. However, occasional stand-replacing fires led to the resetting of forest succession and major regeneration waves. Although rare, such events should have been important for the dynamics of these forest ecosystems, with their legacy lasting for several centuries. This is an important result since fire regime and fire intensity variations have received little emphasis in earlier studies of historical fire regimes in Scots pine forests.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Fires reconstructed in the study site (Comp. 782) over the period 1645–2010.

Appendix S2. Tree ring samples from *P. sylvestris* stumps collected in the studied site (Comp. 782).

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