



# Succession patterns and the role of fire in long-term dynamics of a mixed deciduous stand in Białowieża Forest, Poland

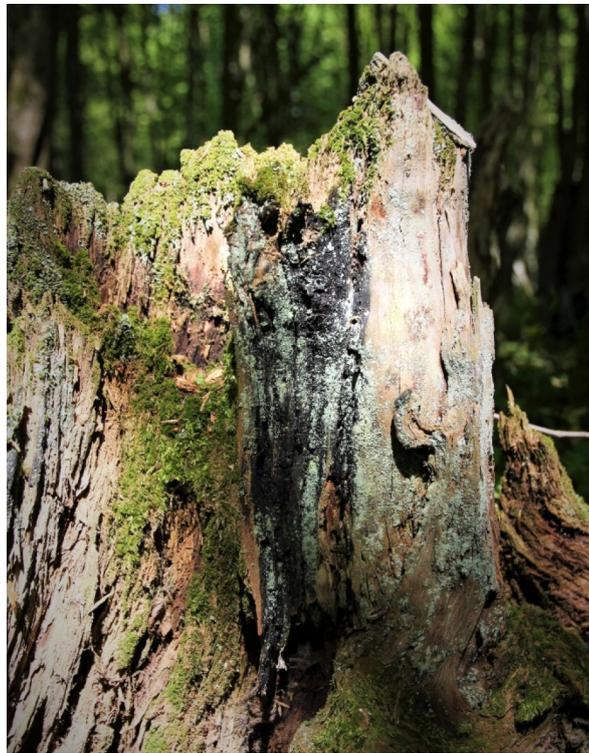


Photo: Marcel Becker

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Ewa Zin, Forest Research Institute (IBL) Białowieża

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Swedish University of Agricultural Sciences

Master Thesis no. 294

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## Abstract

In temperate Europe, the ecological importance of fire is poorly understood, especially in the dynamics of forests with high share of broadleaved tree species. The aim of this thesis was to explore the role of fire in a 43-ha mixed-deciduous forest stand in Białowieża Forest, NE Poland. The changes in the tree species composition were investigated using dendrochronological data obtained from three circular 5000 m<sup>2</sup> sample plots and one 25m-long transect. In addition, to reconstruct the local fire history, all fire-scarred trees from the whole stand were cored and cross-sections from pine and oak stumps were collected. From 288 cores and one pine stump, tree establishment back to the end of the 1500s and 19 fire events between 1720 and 1908 were reconstructed. The stand's age structure revealed a shift from light-demanding fire-adapted species (oak and pine) to shade-tolerant fire-sensitive species (hornbeam and lime) undergoing a transitional phase with codominance of a plastic species (spruce). Up to the end of the 18<sup>th</sup> century, oak and pine regenerated sporadically under frequent fires. The change gradually began with relaxation in the fire regime in the first half of the 19<sup>th</sup> century. This permitted more seedlings to survive and initiated cohorts of both oak and pine, followed by spruce encroachment. The canopy became denser, likely leading to more humid and less flammable fuel conditions after mid-1800s. Thus, the fires propagated less, permitting recruitment of more shade-tolerant species up to date. The data suggests that fire exclusion played an important role in the cessation of oak and pine regeneration in the studied stand. To my knowledge, this study is one of the first in temperate Europe highlighting the role of fire in shaping the long-term vegetation dynamics of mixed-deciduous forest ecosystems.

**Keywords:** dendroecology, disturbance regime, forest history, fire history, regeneration of *Pinus sylvestris* L., regeneration of *Quercus robur* L., temperate lowland *Tilio-Carpinetum* forest, mesophication, fire cessation;

**Abbreviations:** yrs (years); A.D. (Anno Domini); lw (latewood); m a.s.l. (metres above sea level); BF (Białowieża Forest); approx. (approximately); TC (*Tilio-Carpinetum*);

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## 1. Introduction

The composition and spatial structure of a forest stand or landscape are a result of various temporal and spatial processes (Oliver & Larson, 1996). Forests are living ecosystems and thus their development was for a long time discussed under the classical ecological theory of succession (Clements, 1916). Consequently, the forest succession was presented as a sequence of recruitment patterns which results in a self-perpetuating, climax community (Clements, 1916; Kimmins, 1997). Any events (disturbances) disrupting the “steady-state” of the system were stressed as “exceptions” (White & Pickett, 1985; Oliver & Larson, 1996). This view led to unidirectional and cyclical ecological models based on a predictable forest development, e.g. phytosociological approaches based on forest typologies (Ellenberg, 1996). Such deterministic approaches have been challenged though by an increasing number of ecological studies and disturbances (natural or man-made) are now acknowledged as important drivers of forest successional dynamics in Europe (Sidoroff et al., 2007; Niklasson et al., 2010; Trotsiuk et al., 2012; Svoboda et al., 2013; Zin et al., 2015; Kuuluvainen, 2016).

In temperate Europe, the ecological role of fire as a disturbance is yet to be explored. The effect and importance of fire is undoubted in fire-prone landscapes such as boreal conifer forest, Mediterranean forests, eucalypt woodlands, grasslands and savannas (Drobyshev et al., 2004; Bond & Keeley, 2005; Carcaillet et al., 2009). Temperate Europe is generally considered a no-fire zone due to its more humid climate, predominantly broadleaved flora and less flammable conditions (Ellenberg, 1996; Zin, 2016). However, several recent studies have investigated the effect of fire on stand structure and species competition and have thus proven the role of fire in successional dynamics of temperate forest stands (Niklasson et al., 2010; Zin et al., 2015; Zin, 2016). These studies have shown that changes in fire regime and fire cessation in particular (strong decrease in fire frequency) lead to contrasting compositional vegetational changes by the recruitment of fire-sensitive, shade-tolerant species and simultaneous deterioration of conditions that are suitable for the recruitment of species that benefit from fire (Niklasson et al., 2010; Zin et al., 2015; Zin, 2016). However, these findings are limited to coniferous habitats. So far, the knowledge of the role of fire in forests with broadleaved species are basically unknown in temperate Europe (Niklasson et al., 2010; Zin et al., 2015).

Recently, however, a similar pattern of shifts in species composition was stressed in deciduous temperate forests of North America (Varner et al., 2016). The changeover from shade-intolerant to more mesophytic species adapted to closed-canopy conditions (Brose et al., 2014) is known as the

*mesophication* phenomenon (Nowacki & Abrams, 2008b) which has been linked to the absence of stand disturbances (Varner et al., 2016). Changes in the fire regime have a recoiling causal effect on the ecosystem processes. The relationship between tree mortality and survival and, thus, the canopy-opening in the post-disturbance stand, determines the abiotic conditions for regeneration (light, water, nutrients) (Keeley & Fotheringham, 2000; Pausas & Verdú, 2005) and the following tree recruitment patterns (sporadic or cohort regeneration) (Flatley et al., 2013; Storaunet et al., 2013). Mortality is a direct driver of species' compositional changes. Survival of trees is dependent on species specific fire sensitivity that is determined by bark type, thickness and/or other fire-adaptation traits (Stambaugh et al., 2015). Fire changes the ecosystem species' composition on spatial and temporal scales, being a major cause of bottlenecks (Bond & Keeley, 2005). For example, the exclusion of stands' disturbances through fire cessation in North America resulted in poor recruitment of oak species and encroachment of shade-tolerant species such as maple (Nowacki & Abrams, 2008b; Varner et al., 2016). Different fire parameters as well as ecosystem conditions and species composition result in different post-fire succession pathways (Mason & Alía, 2000; Bond & Keeley, 2005). Studies should focus not only on species' persistence traits in a fire regime, but also on the succession dynamics and species competition for resources (Bond & Keeley, 2005). Outside of boreal and Mediterranean regions of Europe, knowledge about the role of fire on long-term population dynamics of different tree species is yet to be improved (Behrens, 2011; Bobiec et al., 2011a; Zin, 2016).

The rareness of natural forests which were affected by recurrent fires in temperate Europe, makes Białowieża Forest (BF) a valuable research area due to its special protection status and well-preserved stand structure (Faliński, 1986; Jedrzejewska & Jedrzejewski, 1998). Here, the presence of fire was mentioned in historical writings and confirmed by empirical data (Niklasson et al., 2010; Latałowa et al., 2015; Zin et al., 2015; Zin, 2016). Fire was probably connected to forest utilization in BF from the early 14<sup>th</sup> century on: beekeeping (14<sup>th</sup> – 19<sup>th</sup> century), tar and potash burning (17<sup>th</sup>-20<sup>th</sup> century), charcoal production (18<sup>th</sup> to early 20<sup>th</sup> century), cattle pasturing (18<sup>th</sup> century to 1970 with local restrictions) and commercial logging (18<sup>th</sup> century – 19<sup>th</sup> century, with high intensities in the first half of the 20<sup>th</sup> century) (Jedrzejewska et al., 1997; Bernadzki et al., 1998; Samojlik, 2005). Lightning strikes occur in BF as well and are known to ignite forest at times (Faliński, 1986), but no quantification of their influence has been done so far. Presence of fire-scarred trees, stumps and snags of *Pinus sylvestris* L. (Scots pine) have been noted from the early 20<sup>th</sup> century (Karpiński, 1948; Faliński, 1986). Karpiński (1948) considered that those trees (Scots pines) were deliberately injured with bonfires to produce more resinous wood, a valuable kindling or smoking fuel used in beekeepers' activities. Such structures (fire-scarred and chipped pines) exist not only in coniferous

habitats, but also in mixed-deciduous stands, connecting these habitats to fire occurrence (Behrens, 2011; Zin, 2016).

BF encloses some of the best preserved mixed-deciduous forest stands with presence of old trees where abundant ecological data from old trees, snags and stumps with long-tree ring sequences can be extracted (Zin, 2016). The most widespread forest association in BF is the *Tilio-Carpinetum* (TC), accounting approx. 47% for the Polish section of BF and approx. 28.5% for the whole BF area (Jedrzejewska & Jedrzejewski, 1998). Interestingly, in this forest association, the canopy is dominated by *Quercus robur* L. (pedunculate oaks), *Picea abies* (L.) Karst. (Norway spruces) and sometimes in the driest form of TC, *Melitti-Carpinetum*, *Pinus sylvestris* L. (Scots pines) (Faliński, 1986; Pawlaczyk, 2009).

Long-term inventories of tree population dynamics of BF revealed a disparity in species composition between the oldest tree populations and the younger generations of mixed-deciduous forests (Bernadzki et al., 1998). The general pattern is a decrease in the share of early-successional species such as oak and pine to the expense of more shade-tolerant hardwoods like hornbeam and linden (Brzeziecki et al., 2016). The shift can be partially explained by investigations on browsing pressure (Kuijper et al., 2010b; Bobiec et al., 2011b). In addition to ungulate pressure, fire has also been stressed to have been a potential successional driver in these forest associations (Kuijper et al., 2010b; Bobiec et al., 2011b). The constant presence of single pines in the meso-eutrophic oak-linden-hornbeam forest and the poor recruitment of this species has been investigated and explained by past fire events (Behrens, 2011). Fire appears to be linked to more forest associations in BF, not only to coniferous habitats (Zin, 2016). However, no studies were carried out to investigate the active role of this disturbance agent on the succession of all species present in deciduous forest stands with post-fire traces, as well as the effect of fire cessation on stand forest dynamics.

In the pollen records, Scots pine is present in BF from early pre-boreal periods (8250-6750 BC) (Faliński, 1986). At present, it is a part of many forest associations: from coniferous stands on poor sandy-soils to admixture with broadleaves on richer sites (Faliński, 1986). On rich soils, pine is a weak competitor on a long-term when compared to other species (Faliński, 1986; Ellenberg, 1996). Fire could be one explanation for the presence of pine in rich habitats in BF under the condition that fires eliminated other species and that fuels then were conducive to fires since today, fuels in rich habitats of BF are rather fire unconducive (Zin & Niklasson, personal observations). Scots pine is a fire-adapted species by its life history and evolutionary traits (thick insulating bark, self-pruning of dead branches, crown base height) and capacity to regenerate quickly (Agee, 1998; Lagueard et al.,

2000; Stephens et al., 2013). Low- to moderate-intensity fires stimulate pine recruitment (Lageard et al., 2000) and the ability to survive fires increases with age (Fernandes et al., 2008). The recruitment strategy of Scots pine implies sporadic regeneration under canopy of old, surviving trees (Zin, 2016) and/or cohort regeneration pulses (Mason & Alía, 2000; Wallenius et al., 2002; Niklasson et al., 2010; Zin et al., 2015) resulting in either park-like (Angelstam & Kuuluvainen, 2004) or multi-aged forest structure (Wallenius et al., 2010; Blanck et al., 2013). The cessation of fire could be one explanation of poor pine regeneration in BF (Niklasson et al., 2010; Behrens, 2011; Zin, 2016).

Pedunculate oak appeared in BF about 9000 yrs ago, replacing the pine-birch forests of the boreal period and increasing in abundance since the end of the 18<sup>th</sup> century (Faliński, 1986; Mitchell & Cole, 1998). At present, oak regeneration appears to be almost inexistent in the forest stands of BF (Bobiec, 2007; Brzeziecki & Bernadzki, 2008; Miścicki, 2016). Oak species' colonisation is tightly connected to disturbances (Vera, 2000; Bobiec, 2007) including the disturbances caused by humans (Bradshaw et al., 2003; Kramer et al., 2003; Bobiec et al., 2011b). The tree recruitment benefits from canopy openness, being prolific especially in larger gaps (Packham et al., 1992; Bobiec, 2007). However, even though seedlings can adapt to shade in the early stages (Feijen, 2003), oak gets easily outcompeted on high quality sites in the absence of canopy disturbances and openness (Johnson et al., 2009). Thus, it is expected that oak is not able to establish seedlings under the habitat conditions of a closed-canopy deciduous forest. Regarding fire, oak individuals can survive surface fires, even in young stages (Brose et al., 2001; Ziobro et al., 2016). Pedunculate oak seeds are resistant to thermal shocks and high temperatures. This is thanks to the size and hard coat protecting the embryo (Reyes & Casal, 2006). Moreover, seedlings of oak species have been shown to be able to regrow if the top of the stem is killed (Brose & Lear, 2004). Hence, past fire events might have played an important role in assuring the dominating position of pedunculate oak in the canopy of mixed-deciduous stands in BF, in a similar way as it has been described for Scots pine in this area (Zin, 2016). However, the knowledge about the relationship between temperate species of oak and fire across more habitats comes from North America and it is limited (Varner et al., 2016). Investigations are needed to understand the relationship between fire and pedunculate oak in BF and Europe.

Norway spruce is a component of BF since the subboreal period (2500-500 BC) and due to its large ecological niche it can be found throughout almost all BF habitats (Faliński, 1986). Spruce is not a fire-adapted species, but can survive low intensity fires as shown in prescribed fire experiments (Linder et al., 1998) and empirical studies (Niklasson et al., 2010; Zin et al., 2015; Zin, 2016). Even more, recent studies have proved that the low-intensity surface fires in BF and the following absence of fires enabled spruce to outcompete pine in coniferous stands (Zin, 2007, 2016; Niklasson et al.,

2010; Zin et al., 2015). Interestingly, spruce presence has been noted in mixed-deciduous stands since early 1800s (Brincken, 1826). Here, it is currently an important component of the canopy (Faliński, 1986), but regenerates weakly (Brzeziecki & Bernadzki, 2008; Brzeziecki et al., 2016). So far, it is not known if changes in the fire regime or other factors have contributed to spruce encroachment in richer habitats of BF (Brzeziecki et al., 2016).

## **Aim of the thesis**

The general objective of this thesis was to explore the influence of fire in long-term dynamics of a mixed stand in BF, where signs of past fire in form of fire-scarred trees and stumps were found. The specific sub-objectives of the thesis were to describe the current structural characteristics, to reconstruct the recruitment pulses and to describe the fire history with highest detail possible. The hypotheses were: (1) the past species composition of present *Tilio-Carpinetum* habitat was dominated by pines and oaks; (2) the changes in the compositional structure up to present can be attributed to modifications of the fire regime.

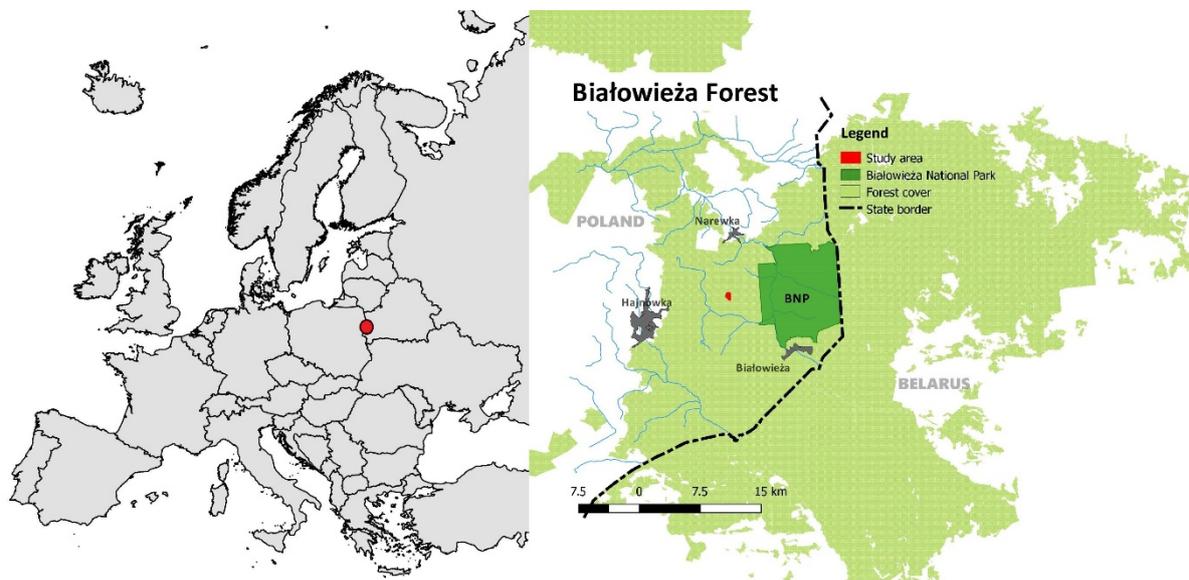
## **2. Materials and methods**

### **2.1. Research area**

Białowieża Forest (52°30′-53° N, 23°30′-24°15′ E, Poland/Belarus) is often regarded as the best-preserved complex of lowland deciduous and mixed forest of temperate Europe (Bobiec, 2002; Jaroszewicz, 2004). Due to its huge potential for provisioning ecological data about natural dynamics of such forest types, BF is regarded as a model ecosystem (Angelstam & Kuuluvainen, 2004) for exploring the role of disturbances in shaping the forest structure and understanding the natural succession patterns of mixed-deciduous forests.

The climate of BF is transitional continental-atlantic, with a mean temperature of 7 °C (-4.2°C in January – 17.7 °C in July) (Faliński, 1986; Jedrzejewska et al., 1997). The mean annual precipitation for the last 5 decades was 633 mm (Pierzgalski et al., 2002) and the average annual snow cover is 92 days (Faliński, 1986). The vegetation season starts in April and lasts for 180 days according to the synphytophenological criterion (the vegetation period in *Tilio-Carpinetum* communities), respectively 206 days according to the temperature criterion (days with temperature over 5 °C). The landform is rather uniform, as BF is situated on an old-morainic plateau that originated from a glaciofluvial relief (135-190 m.a.s.l.) (Faliński, 1986). The soils range from podzols over mesotrophic and eutrophic

brown and lessive soils to gley and organic soil types in the peatbogs and semibog areas (Kwiatkowski, 1994).



**Figure 1.** Location of Białowieża Forest (BF) in eastern Poland/ western Belarus and location of the study area within BF.

The variation in soil typology, hydrology and relief results in a mosaic of different forest communities (Faliński, 1986; Jędrzejewska & Jędrzejewski, 1998). Most common forest type is the rich deciduous forest (*Tilio-Carpinetum*) with *Quercus robur* L. – pedunculate oak, *Tilia cordata* Mill. – small-leaved lime, *Carpinus betulus* L. – hornbeam and *Acer platanooides* L. – Norway maple. Other forest communities are mixed coniferous forest (*Pino-Quercetum*), coniferous forest (*Peucedano-Pinetum*) and small patches of bog alderwoods (*Carici elongatae-Alnetum*), streamside alder-ash forests (*Circaeo-Alnetum*, *Ficario-Ulmetum*) and wet peat forests (*Vaccinio uliginosi-Pinetum* or *Sphagno girgensohnii-Piceetum*) (Faliński, 1986).

Besides the environmental factors, the present structural characteristics come as a result of a long-term history of protection efforts and low-intensity forest utilization. BF bypassed the intense colonization and implicit deforestation which occurred in nearly all European lowlands. Anthropogenic changes occurred in the past, as the area was inhabited by people since early ancient times (Samojlik, 2006), without modifying the intact character of the forest and its unique structure (Samojlik et al., 2013). Starting with the early 15<sup>th</sup> century, BF received a protection status under the Polish-Lithuanian Commonwealth. Later, the Polish kings and the Russian tsars kept the special management, mainly for exclusive royal hunting privilege - the European bison (*Bison bonasus*) was and remains the flagship species of BF. Until the end of the 18<sup>th</sup> century, forest utilization was limited to scything, cattle pasturing, beekeeping and production of potash, tar and charcoal. Timber

harvesting was permitted in the late 17<sup>th</sup> century, (Samojlik & Jedrzejewska, 2004) and in the 1760s; reaching higher intensities in the first decades of the Russian forest administration (1795-1803). The following period was marked by two important actions, restricting the timber exploitation: the 1803's decree restoring the special protection status to BF and the 1860's decision to designate the area as an imperial hunting ground. During the first world war, intense selective and clear-cut logging was operated throughout the whole area. However, patches of not clear-felled stands remained in the future core area of the Białowieża National Park (1921) and several surrounding stands (to become forest reserves at the end of the 20<sup>th</sup>, respectively beginning of the 21<sup>th</sup> century) (Samojlik, 2005). Such forest stands, located in smaller reserves (of approximately 120 km<sup>2</sup> in total) outside of the Białowieża National Park, enclose valuable research sites for understanding long-term forest dynamics through dendrochronology methods (otherwise prohibited in the core area). Presence of fire-scarred trees, stumps and snags have been noted in both coniferous and mixed deciduous stands (Faliński, 1986; Niklasson et al., 2010; Behrens, 2011; Zin, 2016) enhancing the value of these stands also for fire history reconstruction. The management of the forest reserves of BF in the Polish part is under the authority of the State Forest Administration (Jaroszewicz, 2004).

## 2.2. Study site

The study was conducted in a 43-ha forest stand, located in the managed part of Białowieża Forest (Figure 1). The criteria for choosing the study site were the following: (1) low anthropogenic impact (naturally regenerated stand, uneven-aged structure, presence of old, large tree individuals, deadwood diversity in amounts and quality: snags, stumps with potential long tree-ring sequences); (2) occurrence of direct fire-evidence: scarred stumps or scarred trees and/or (3) presence of culturally modified trees that were altered by locals as part of the traditional forest utilization linked to fire: chipping, bee hive carving (Behrens, 2011). [see Appendix 4a].

According to the classification of the vegetation, the forest stand represents the *Tilio-Carpinetum* type, subtype *calamagrostietosum* (grąd, grond, grud in Polish), a mesophilous deciduous forest community found on rich soils (Sokołowski 1993). Ground vegetation was characterised by a dense herb layer, dominated by spring geophytes (*Anemone nemorosa*, *Anemone ranunculoides*, *Isopyrum thalictroides*, *Gagea lutea*, *Corydalis solida*) and a continual layer of flora such as *Lamium galeobdolon*, *Stellaria holostea*, *Galium odoratum*, *Hepatica nobilis*, *Carex pilosa*, *Pulmonaria obscura*, *Asarum europeum*, *Oxalis acetosella*, *Viola reichenbachiana*, *Milium effusum*, *Cardamine bulbifera*, *Lathyrus vernus*.

The stand density is approximately 580 N ha<sup>-1</sup> and the mean volume is 395 m<sup>3</sup> ha<sup>-1</sup>. The uppermost tree canopy was dominated by old Scots pines (*Pinus sylvestris* L.), pedunculate oaks (*Quercus robur* L.) and younger generation of Norway spruces (*Picea abies* L. Karst). Old, large individuals of lime and maple were scattered in the site. Admixture of early-successional species (birch, *Betula pendula* Roth) with high diameters was noted in the canopy. The second tree layer consisted of lime and hornbeam and the understorey was abundant with shrubs as hazelnut (*Corylus avellana* L.), Spindle-tree (*Euonymus europaeus* L. and *Euonymus verrucosus* Scop), daphne (*Daphne mezereum* L.) and dense regeneration of hornbeam (*Carpinus betulus* L.), lime (*Tilia cordata* Mill.), especially in gaps. No young individuals of pine, nor oak with a height over 50 cm (lowest browsing-height limit) (Kuijper *et al.*, 2010a) were spotted.

### 2.3. Fieldwork

#### **Inventory of *Pinus sylvestris* L. (Scots pine) and *Quercus robur* L. (pedunculate oak) trees**

To describe the current structure of the pine and oak population, a grid of parallel transects (N-S direction) was established in the stand. The width of each transect was 50 m (25 m on each side of the walking line). The transect length was delimited by the pine presence (the inventory stopped at the last pine tree if no individuals were visible in the further 50 m). This threshold was convenient since pine trees were easy to spot within other deciduous trees due to their particular stem and crown features.

By walking along the transects, a precise inventory of all pine and oak trees (standing, living and dead trees and stumps) was carried out. Orientation in the field was done using a field compass. The satellite position of each tree, snag and stump was recorded with a GPS (Garmin GPSMap 62st). Furthermore, the following measurements were done: the diameter at breast height (DBH) - 130 cm above the ground - by using a diameter tape; tree height (H) and crown base height (CBH) with a VERTEX IV. Any stem modifications suggesting past fire evidence were registered: fire scars, charcoal presence.

Since the inventory was meant to reflect the natural dynamics of pine/oak tree population, a patch of 113 oak trees (S-E of study area) was excluded from the analysis. These trees were distributed in lines next to a road, with equal distances in-between and an even-aged structure (~ 60yrs) and therefore considered to be a plantation resulting from modern forest management activities and hence not representative for the investigated stand.

### **Age structure and long-term population dynamics**

Data describing the long-term succession patterns were gathered from three 5000m<sup>2</sup> sample plots following a circular grid (radius of 39.90 m). All trees with DBH equal and higher than 5 cm were inventoried up to a radius of 12.62 m, all present species were recorded, whereas outside the inner 500 m<sup>2</sup>, only pine, oak and spruce individuals were inventoried. DBH (diameter at breast height,) and H (height, with an accuracy of 5 cm) of all standing trees, both living and dead, were measured. From all recorded trees, cores were extracted with borers of different sizes ( $\emptyset$  12 mm for pine and spruce,  $\emptyset$  5.15 mm for broadleaved species) as close as possible to the mineral soil and to the tree pith. In case of rot presence, the diameter at the coring level was used to estimate the missing core part.

Outside the circular plots, old-growth trees of pine, oak, birch were sampled subjectively for an accurate representation of stand history. To investigate the early growth of pine, oak and spruce on rich soils of BF and to estimate the real germination ages, 42 trees were randomly selected from the trees cored at the ground level and then cored again at the second level (DBH).

To explore the local fire history, all potentially scarred trees from the whole study area were cored. Cross-sections from pine and oak stumps were collected with the chainsaw following the procedure of Arno & Sneek, 1977 and McBride, 1983. In total, we collected 388 cores from living and dead trees and 36 cross-sections.

### **Current tree regeneration**

The survey of all Scots pine saplings and seedlings was carried out together with the mature tree inventory on transects. For the inventory of other tree regeneration on macro-scale, a additional transect of 25 m length and 2 m width was randomly established in the stand (orientated E-W). All tree regeneration up to 50 mm stem diameter was recorded by species and height. Stem sections (48) were collected for age estimation.

To get an indication of the early growth dynamics of the old Scots pine and pedunculate oak individuals on rich soils, seedlings were searched for destructive sampling and analysis. No seedlings of pine were found in the forest stand. Only one pine seedling was found in a large-open gap, which could replicate the same open canopy conditions as resulted after fire events. One oak and two spruce seedlings found near the pine sample were collected as well.

## **2.4. Laboratory work**

### **Dendrochronological procedure on increment cores and cross-sections**

288 increment cores were dried, glued on wooden mounts and sanded (down to 600 grid) for an easy reading of tree ring sequences. Under 6-40x magnification, the cores were visually cross-dated following the standard dendrochronological methodology (Yamaguchi, 1991; Stokes, 1996). Examples of local pointer years, helpful for assigning calendar years to tree rings were: 1821/1822 [narrow sequence]; 1846/1847 [narrow sequence]; 1857 [narrow lw]/1858[narrow]; 1902/1904 [pale in pine cores, narrow in spruce cores]; 1908 [narrow lw]/1909 [narrow]; 1917 [narrow lw]; 1928 [narrow lw or narrow]; 1940 [narrow in pine cores]; 1941 [narrow in spruce cores]; 1964 [narrow]; 1978 [wide]; 1979 [narrow or missing]; 1996 [narrow]; 2006 [narrow]. Ages of trees at coring height were estimated according to the last year (pith). If the pith was missing, a pith locator was used to estimate the pith date (Applequist, 1958).

All developed fire scars found in increment cores and cross-sections were noted (with seasonality, if the position in wood was visible: early, middle, earlywood, latewood, dormant) (Niklasson & Granström, 2000). After a fire wound, a tree can overheat the scar in the cambium, making it difficult to observe (Zin, 2016). Therefore, to reconstruct the fire history (fire events and fire intervals), the disturbances in tree ring morphology or in the growth patterns were noted.

### **Dendrochronological procedure on seedlings and saplings**

Forty-two hornbeam, one maple and one lime seedlings, with heights between 4 and 52 cm (four seedlings were damaged by rot) were investigated. Samples were crossed-cut at root collar and the surface was sanded with fine sand paper (2000 grains/cm<sup>2</sup>) and if needed, smoothed with a clear scalped cut to obtain the clearest possible view of the annual rings. The whole surface was examined under high magnification and rings were followed and counted around the circumference. Most samples were broadleaves (hornbeam and lime) with low contrast between cells and high occurrence of wedging, narrow or even double rings. Thus, several laboratory procedures and methods were explored for as high ring visibility as possible (zinc paste on dry/wet cut-surface, black-pigmented marker on dry wood). The most successful method involved the following procedure: sufficient soaking of the samples in water (2-8h, depending on their size); smooth scalpel cut; clean wetting of the surface; zinc paste application; clean water drop. The rings were counted under the water drop. [see Appendix 3]. To determine the oldest pith date, the small-sized samples were sectioned according to the root collar position (below, at and above root collar).

### Estimation of germination year

Germination years for pines, oaks, spruces and hornbeams were calculated from the age at height corrected by local height growth models obtained from the sample of trees which were cored at two levels and from the ageing of tree saplings [see Appendix 2].

The regression equations (height x age) revealed a growth model for oaks, pine and hornbeam, as following:

Oak: ~ 9 yrs to reach 20 cm; followed by 16 cm/yr [N:17 core pairs and 1 seedling];

Pine: ~7 yrs to reach 25 cm; with a following growth of 27 cm/yr [N:12 core pairs; 1 seedling]

Hornbeam: A simple linear regression model was used to predict age based on height:

$$\ln Age \times 1.58 + 0.04 \times Height, (R^2 = 0.123) [N: 42 seedlings]$$

Spruce samples illustrated inconsistent early growth (min.-max.: 4 cm/yr – 21.4 cm/yr) [N: 13 core pairs; 2 seedlings].

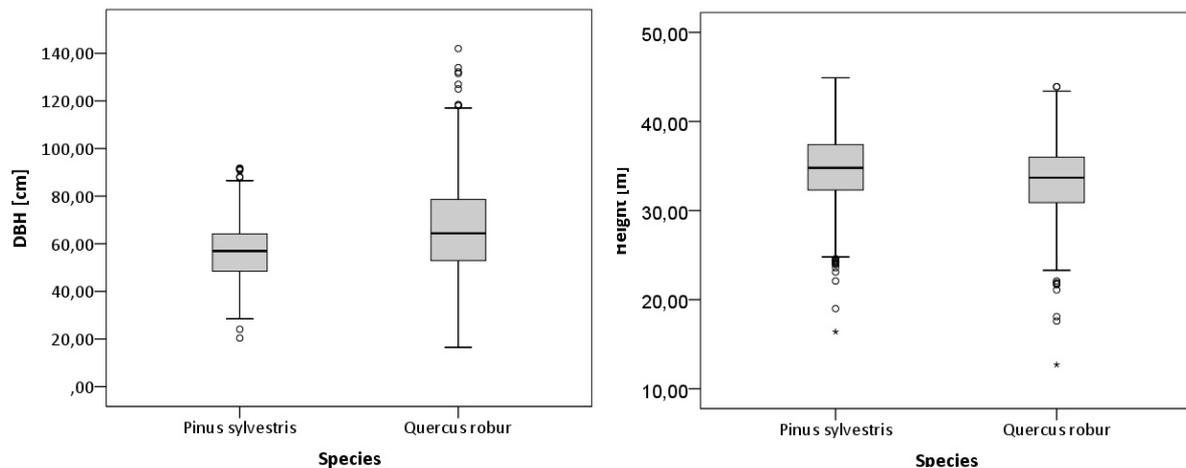
To test group difference and trend analysis, non-parametric tests were carried out (Mann-Whitney U Test, Spearman r correlation), since the data did not comply with the requirements of parametric test methods. All data analyses were performed using SPSS Statistics 24 (IBM Corp. 2016).

## 3. Results

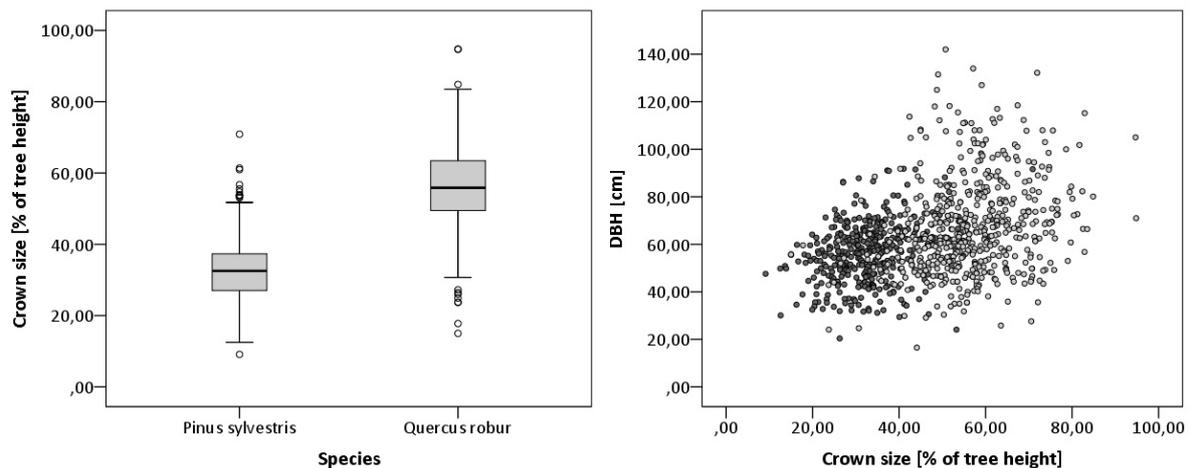
### 3.1. Structural characteristics of oak and pine population

The total surveyed area was 43 ha. The area delimited by pine population was 27 ha. The total number of inventoried trees for stand structure was 1615 (1058 living trees, 77 snags, 519 stumps). The total number of oaks and pines (living/dead standing trees) inventoried was 1066 (933/68). Two old individuals of maple and lime were noted in the studied area.

The mean number of pine trees was 15 ha<sup>-1</sup>. Oak density was 24 trees ha<sup>-1</sup>. The basal area and volume of living trees were dominated by oaks, with 70 % share of the total mean values (131.7 m<sup>3</sup>ha<sup>-1</sup> from a total growing stock of 185.8 m<sup>3</sup>ha<sup>-1</sup>) [see Appendix 1].

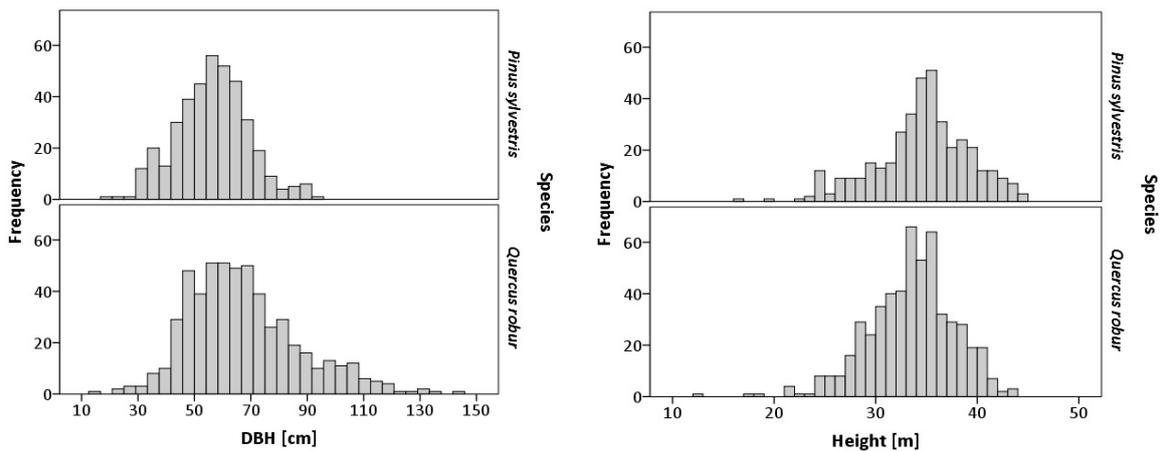


**Figure 2. (a)** Mean diameter and **(b)** height per species. N = 390 (*P. sylvestris*), N = 540 (*Q. robur*). Individuals over 10 cm DBH. Diameter/ height values per species [mean  $\pm$  SE, min.-max. ]:  
*P. sylvestris*: 56.5 cm  $\pm$  0.65, 20.4 - 91.8 cm / 34.5 m  $\pm$  0.23 m, 19.0 – 44.9 m  
*Q. robur*: 67.5 cm  $\pm$  0.86, 16.5 – 142.0 cm / 33.5 m  $\pm$  0.18, 12.7 – 43.9 m.

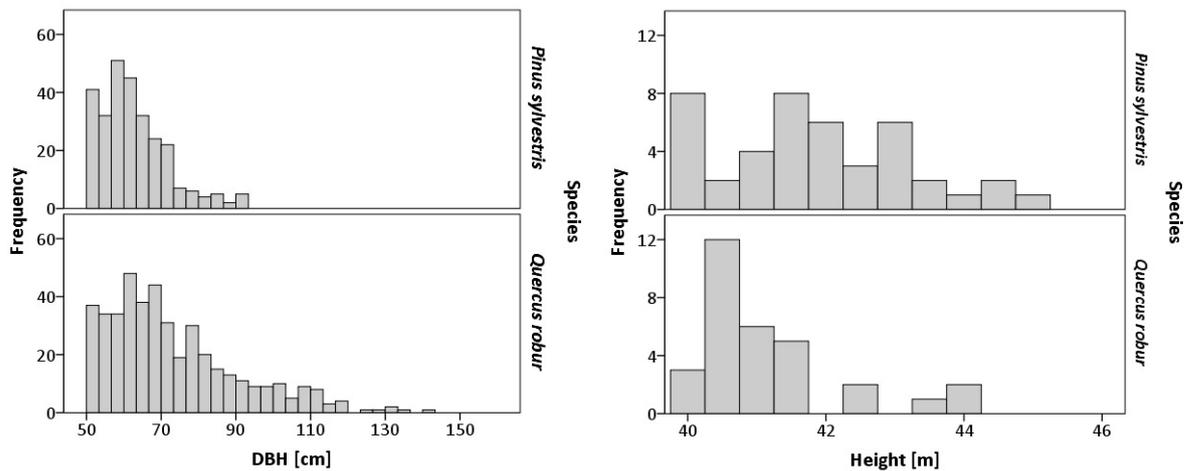


**Figure 3. (a)** Mean crown size [percentage of the total tree height] per species.  
**(b)** Variability of crown size in relationship with DBH per species.  
N = 387 (*P.sylvestris*, dark grey); N = 539 (*Q. robur*, light grey).

Oaks accounted for 20 % more stems and had significantly bigger diameters (Mann Whitney U, Z=-8.446, p<0.001, N=931) (Figure 2 a), while pines dominated the canopy layer with significantly higher heights (Mann Whitney U, Z=-3.972, p<0.001, N=930) (Figure 2 b). Values for diameter (mean  $\pm$  SE; min. - max.) for pine were 56.5 cm  $\pm$  0.65; 20.4 - 91.8 cm; and for oak 67.5 cm  $\pm$  0.86; 16.5 – 142.0 cm. Mean height per species (mean  $\pm$  SE; min. - max.) were 34.53 m  $\pm$  0.23 m; 19.0 – 44.9 m (pine); respectively 33.5 m  $\pm$  0.18; 12.7 – 43.9 m (oak). Pine crowns were smaller than oaks' (Mann Whitney U, Z=-23.237, p<0.001) and situated higher on the stem (Mann-Whitney U, Z=-22.833, p<0.001, N=926) (Figure 3). Average values for crown base height were: pine, 23.1 m ( $\pm$  0.2 SE; min. - max.: 9.9 - 32.7 m) and oak, 14.5 m ( $\pm$  0.17 SE; min.-max.: 4.9 - 28.9 m).



**Figure 4. (a)** Diameter and **(b)** height distribution per species. Individuals over 10 cm DBH. N = 390 (*P.sylvestris*); N = 540 (*Q. robur*).



**Figure 5. (a)** Diameter and **(b)** height distribution of large trees per species. Individuals with **(a)** DBH larger than 50 cm. N = 276 (*P.sylvestris*); N = 437 (*Q. robur*) and **(b)** height over 40 m. N = 43 (*P.sylvestris*); N = 31 (*Q. robur*).

The frequencies peaked in the 50 to 70 cm diameter classes and in 33 - 36 m interval of heights (Figure 4). Approximately 10 % of the trees (N=92) reached over 80 cm in diameter and 8 % over 40 m in height (N=74) (Figure 5).

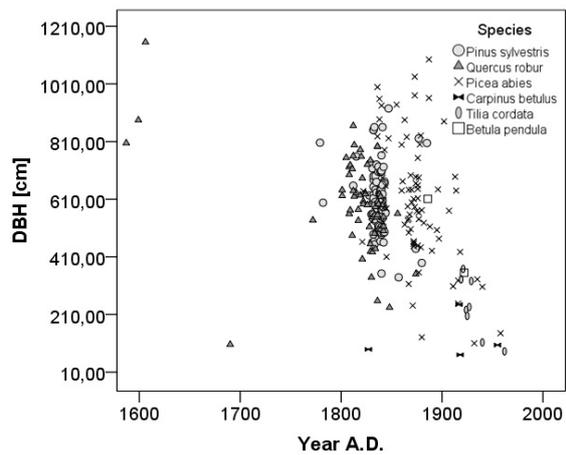
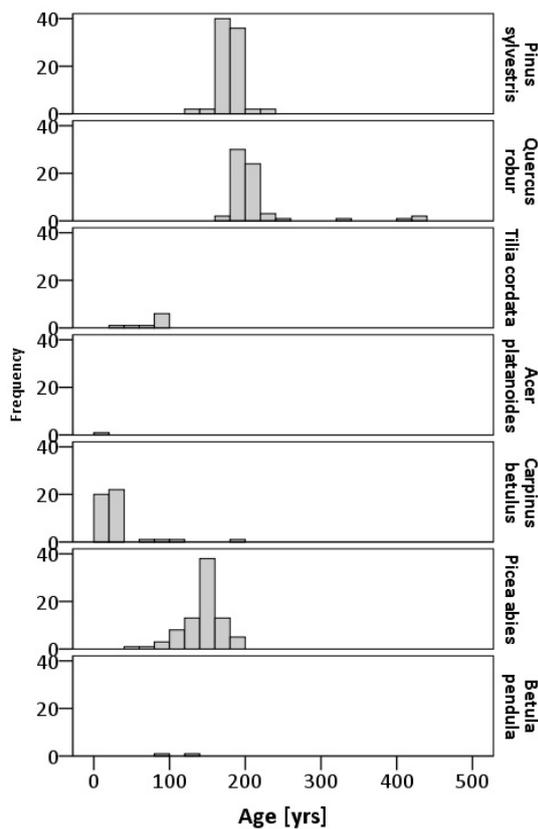
### 3.2. Present age structure

The upper canopy layer consisted of old cohorts of pines and oaks and a population of spruce with higher age variation. The lower layer was characterised by younger hornbeam, lime and birch trees (Figure 6). The oldest trees in the canopy were oaks, whereas the spruces belonged to younger generations (Kruskal-Wallis,  $df=2$ ,  $p<0.001^*$ ,  $N=230$ ). The population of Scots pine was characterised by trees with ages from 171 to 190 yrs, occurring in highest frequencies between 171 and 180 yrs.

Age structure of spruce displayed a peak in the 141 - 160 yrs' class and a variation from 60 to 190 yrs. Most oak individuals belonged to age classes from 181 to 220 yrs, but they displayed the features of a cohort recruitment. 32 oak individuals were dated to be over 200 yrs and 3 individuals over 400 yrs old. Maximum values for ages were 430 yrs (oak), 238 yrs (pine) and 203 yrs (spruce). Neither oaks, nor pines younger than 140 yrs, respectively 132 yrs were found.

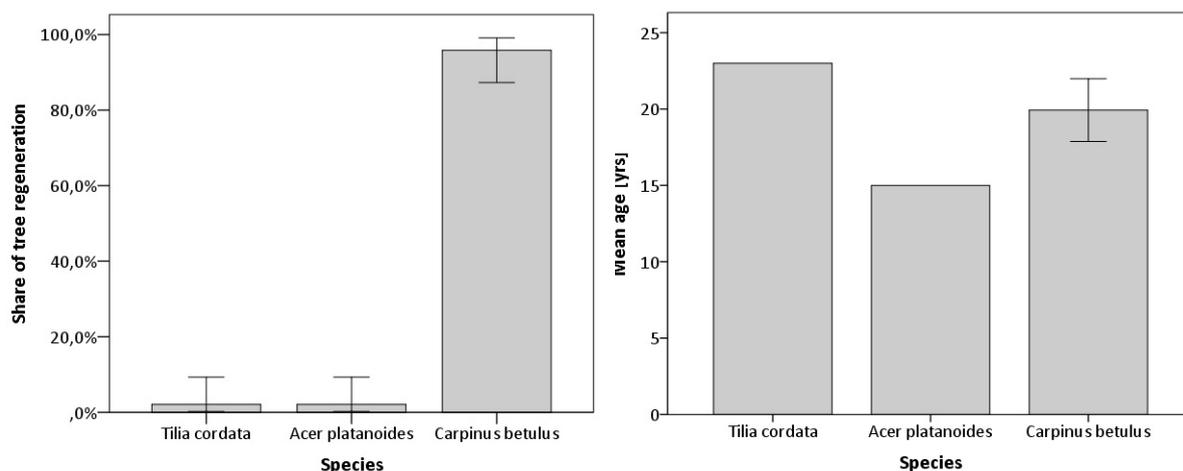
Cored individuals of other tree species belonged to younger age classes: lime and hornbeam (61-100 yrs) and birch (95, respectively 131 yrs).

The regeneration was highly dominated by hornbeam (more than 90 % share) (Figure 7 a.). The mean age of the saplings from the transect in the stand was 20 yrs ( $\pm 1.02$ , min. - max.: 7 - 32 yrs) (Figure 7 b.). Other species found in the transect were lime and maple. In the whole studied area (43 ha), no oak or pine sapling of more than 50 cm in height was found.



**Figure 6. (a)** Age structure and **(b)** diameter variation in relationship with germination year per species.

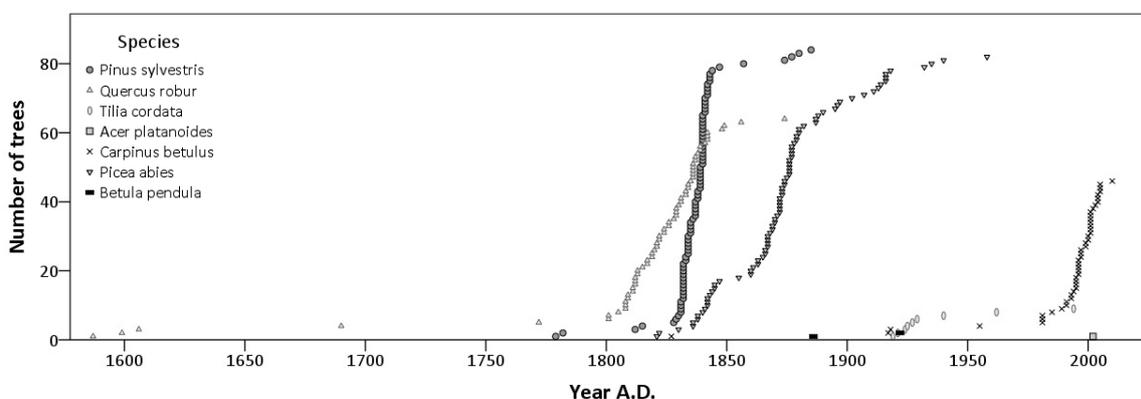
N = 84 (*P. sylvestris*); N = 64 (*Q. robur*);  
 N = 9 (*T. cordata*); N = 1 (*A. platanoides*);  
 N = 46 (*C. betulus*); N = 82 (*P. abies*); N = 2 (*B. pendula*)



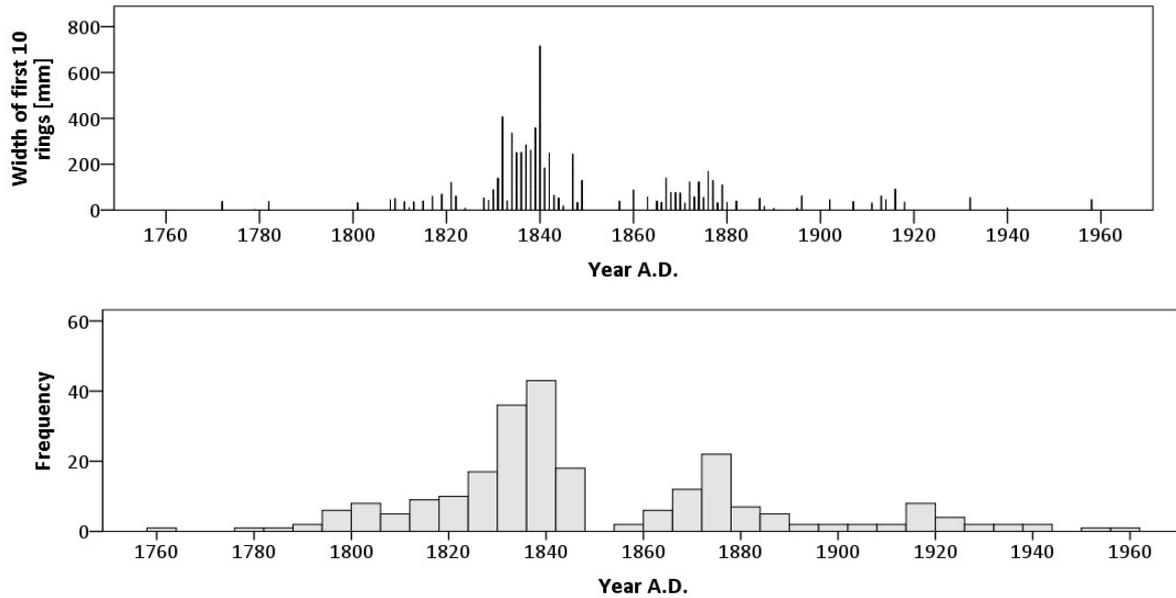
**Figure 7. (a)** Composition (N=48) and **(b)** mean age (N=44) of the tree regeneration per species. Individuals over 50 cm height and under 5 cm diameter. Error bars : +/- 2SE.

### 3.3. Succession patterns

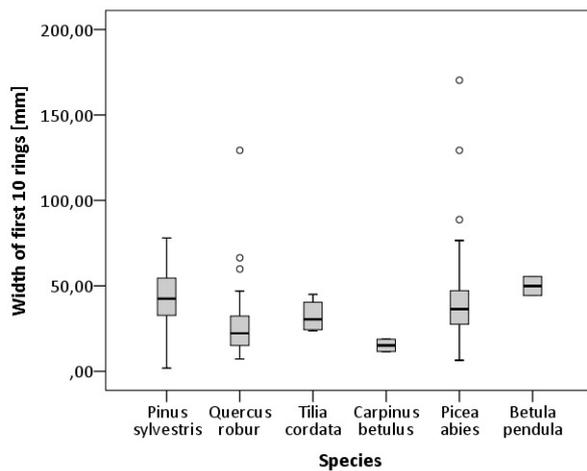
The cumulative curve of estimated germination years shows sporadic regeneration of oak prior to 1800s, followed by a rapid oak and pine regeneration with gradual spruce encroachment (Figure 8). Cohort regeneration characterises the pines and the oaks in the studied stand, with recruitment starting in 1815; 1830 and 1859 for oak and 1837 and 1884 for pine. Approximately 85 % of the pines and 80 % of the oaks originated from the 1830-40s. Generally, both oak and pine present similar steep recruitment patterns, followed by a relaxation in regeneration around the 1870s. The last recruitment of pine was in 1888 and in 1874 for oak. Spruce regeneration started in the 1820s as a more gradual process. Overall, periods noted to show sporadic tree recruitment were in the late 1840s' and 1850s' decades. Hornbeam, lime and birch occurred around 1920s, simultaneously with a decrease in germination rates of spruce.



**Figure 8.** Cumulative tree germination diagram per species. N = 288.



**Figure 9. (a)** Distribution of growth rates in early stages (growth of the first 10 yrs). Data from cores with distance to pith less than 15 mm. **(b)** Tree establishment distribution. Data from trees with reliable real age estimation. N = 75 (*P. sylvestris*); N = 40 (*Q. robur*); N = 72 (*P. abies*).



**Figure 10.** Early growth rates [growth in the first 10 yrs]. N; mean $\pm$ SE; min.-max.:  
*P. sylvestris*: N = 73; 43.73 mm  $\pm$  1.85 (1.86 - 77.04);  
*Q. robur*: N = 37; 27.50 mm  $\pm$  3.64 (7.24 - 129.3);  
*T. cordata*: N = 4; 32.39 mm  $\pm$  5.01 (23.67 - 45.04);  
*C. betulus*: N = 2; 15.18 mm  $\pm$  3.58 (11.6 - 18.7);  
*P. abies*: N = 69; 63.69 mm  $\pm$  2.75 (6.46 - 170.30);  
*B. pendula*: N = 2; 49.90 mm  $\pm$  5.535 (44.37 - 55.44).

The highest values for early growth investigated in the first 10 yrs were in the 1830s' (up to 30mm) (Figure 9 a), in the same time interval when pine recruitment reached the highest frequency (44 % relative frequency of the whole pine population) (Figure 9 b). The fastest growth rate in the first 10 yrs was recorded by birch and pine, followed by spruce, lime and oak. Hornbeam had the lowest value of early growth of 15 mm (Kruskal Wallis, df=5, p<0.0001\*, N= 187) (Figure 10).

### **3.4. Fire evidence**

From the 518 stumps inventoried, 42 presented evidence of past fire occurrence (charcoal presence and/or fire scars). Nine pine and four oak stumps presented visible multiple fire scars in the outer part [see Appendix 4]. Due to time limitation, only one pine sample was crossdated. The fire history in this pine stump (~75 cm diameter and the oldest ring in 1675) evidenced fires in the years: 1720; 1754; 1763; 1769; 1797; 1808; 1809; 1817; 1826; 1847/1848; 1858.

One culturally-modified tree, with a beehive, was noted [see Appendix 4].

Fire scars were found in the cores of oak, pine and spruce. In total, eight fires were dated from scars in the increment cores of pine, oak and spruce: 1797 [one sample]; 1826 [one]; 1830 [one], 1837 [two], 1845 [six], 1857 [three], 1882 (lw) [one], 1888 [two], 1894 (lw) [four], 1908 [two]. The fires in 1797 and 1826 corresponded to the fires in the stump material. Except 1845 and 1894, which are represented the best, the fires were found in only one or two tree cores, most of the times situated in the vicinity of each other. Sudden growth depressions, narrow rings (mainly very narrow lw with a narrow following year) were noted in many cores in: 1764-1773; 1826-1828, 1837, 1845-1847, 1872-1881, 1888-1889, 1908-1909, 1939-1941, 1961-1964. Oak cores illustrate the best the 1845 fire as a scar or narrow ring and the 1830 fire as disturbances in the cell morphology. Releases in the growth exhibited by obvious wider rings in spruce cores were between the periods 1896-1898, 1911-1914 and 1918-1919.

Other scars have been identified in 1917 and 1924, but due to little evidence and lack of clear disturbances in ring morphology specific to fire wounds, it is not sure whether they were fire-caused.

## **4. Discussion**

The present study revealed that the species composition in the deciduous-dominated forest stand in BF changed from dominance of light-demanding fire-adapted trees (pine, oak) to a higher share of shade-tolerant fire sensitive species (lime, hornbeam) undergoing a transitional phase with a plastic species (spruce). We can divide the tree succession pathways into three main periods: (a) 1600-1800 with sporadic recruitment of oak; (b) 1800-1900 dominated by regenerating and fast-growing cohorts of oak, pine with later spruce encroachment and (c) 1900s to-date with the gradual recession of oak and pine in favour of hornbeam and lime. We found synchronicities between the regeneration shifts and modifications in the fire regime: the highest number of scars in the increment cores were in the 19<sup>th</sup> century (b), while in the latter period (c), we recorded fire events only at the beginning of the 20<sup>th</sup> century (1908 last fire record). The focus was to investigate if fire was present as disturbance agent in the rich habitats of BF, so the underlying causes of fire were not considered, neither were

the fire parameters (such as calculating the fire intensity). The degree to which fire drives the dynamics of the mixed-deciduous habitats is shaped not only by the fire parameters, but also by the structure of the ecosystem subjected to this agent (Bond & Keeley, 2005). By looking at the successional pathways and discussing the species' ecological niches, we can deduce the characteristics of the fire regime and their direct or indirect effect on the regeneration changes.

#### **4.1. Stand structure until the 19<sup>th</sup> century**

The oldest three trees in the studied stand are oaks originating from the late 16<sup>th</sup> century, probably among the oldest published ages of oak and trees in general from BF (Keczyński, 2017). These oak individuals were dispersed over an area of 27 ha (data not shown) suggesting sporadic and spatially sparse oak regeneration prior to 1800s. There is no pine recorded from the cores originating during this 200 yrs period. This is congruent with other studies from BF that found oak to originate prior to 1750 (Bobiec, 2012) or discussed that cohorts of pine might have appeared only after fire relaxation, in the 18<sup>th</sup> century (Niklasson et al., 2010; Zin et al., 2015). This age values are valuable empirical data and it appears that oaks were part of the canopy in the studied stand for more than 400 yrs.

The fast early-growth of pine in the 1830s cohort indicates that soil fertility is not an impediment of the pine recruitment in this stand. The stand was most likely open and sparse due to frequent burning and thus the light conditions were not a limiting factor for recruitment prior to 1810s (the first cohorts). The fire records from the stump indicate frequent burning in the 18<sup>th</sup> century (even one-year interval between 1808 and 1809 fires). Both oak and pine benefit from disturbances that keep the canopy open (Mason & Alía, 2000; Reyes & Casal, 2006; Varner et al., 2016). Brincken (1826) noted the presence of pioneer species in the deciduous stands of BF that indicate a more open environment. The structure of the stand between the 16<sup>th</sup> and the 19<sup>th</sup> century appeared to have been more open than nowadays and grass-dominated similarly to previous findings (Zin, 2016). The stand was thus also more flammable than at present times and the lack of oak and pine recruitment before 1800s can be attributed to mortality in the low level caused by frequent fires.

#### **4.2. Regeneration structure at the beginning of the 19<sup>th</sup> century**

The first abrupt change in the regeneration patterns in the study area is in the 19<sup>th</sup> century, a rapid recruitment of oak and pines. Oak and pine originated at the beginning of the 1800s (peaking in frequency in 1830s) forming cohort structures. Oak regeneration pulse appeared in 1815 and then in 1831, while pine in 1837; however no clear data of forest history that could explain the origin of these first cohorts was found. One explanation might be due to changes in the fire regime (Zin,

2016). This cohort structure is most likely the result of a similar situation. Since most of the BF area was subjected to fires at the beginning of 1800s, followed by restricting fire regulations, especially after the historical fire of 1811 (Brincken, 1826; Niklasson et al., 2010; Zin et al., 2015), changes in the stand can be attributed to modification of the fire regime. Relaxation in the fire promoted firstly oak and pine and later on, spruce, which was before insignificant in this stand. Oak and pine were shown to prevail the regeneration fields after higher-intensity fires followed by a no-fire relaxation period that could explain the cohort initiation (Niklasson, 1998; Ziobro et al., 2016). The oak and pine cohorts resulted most likely from the relaxation in the fire regime between 1826 and 1845. The stand conditions for recruitment were probably suitable for pine and oak due the effect of the previous fires in 1808; 1809; 1817; 1826.

#### **4.3. The spruce encroachment and following succession changes in the 19<sup>th</sup> century**

The spruce regeneration started in the 1820s in the studied stand, consistent with the general observations of Genko (1902 - 1903) and Krüdener (1909, see Appendix 5). Brincken describes that spruce appeared in the deciduous forest communities and more humid forest communities. The timing of the spruce encroachment in the studied stand is indeed earlier than in the coniferous stands as evidenced by recent tree ring studies (Zin, 2007; Niklasson et al., 2010). The spruce regeneration seems to occur at the expense of oak and pine recruitment. The germination waves occurred simultaneously with the fires in 1830, 1837 and 1845 and these fires did not change the species composition immediately, encouraging oak and pine recruitment, as expected. This is probably due to the characteristics of those fires, which we assume to have been frequent but of very low intensity and patchy. Spruce encroachment is a strong indicator of relaxation in the fire intensity: low intensity fires do not kill the seedlings, neither provoke the mortality in the overstorey. Spruce has a strong competitive advantage in the overshadowing conditions of the stand (Niklasson, 1998; Niklasson et al., 2010; Zin, 2016). We assume that the fires of 1830, 1837, 1857 were patchy, as they were recorded only by one or two cores from neighbouring trees. Therefore, a big percentage of seedlings have escaped the disturbance. According to literature, fires in BF occurred indeed almost at annual basis (Brincken, 1826), confirmed to some extent by the recent fire history studies (Zin, 2016). Due to more humid and therefore less flammable conditions the fires were probably milder, especially since the fuel is a limiting factor under frequent fires (Granström & Niklasson, 2008). Litter of deciduous trees is also less flammable than many other fuels, under coniferous stands for example. This can also explain the earlier spruce encroachment in this stand compared to coniferous habitats where some fires were of higher intensity (Zin et al., 2015).

#### **4.4. The recession of oak and pine**

The last cohorts of oak and pine from 1884-1887 fit to the 1882 fire event which might have created more open light conditions and eliminated some competitive species (relaxation in spruce recruitment occurs synchronic to these cohorts). The 1882 fire could thus have been of somewhat higher intensity than the previous events, however, still many seedlings survived. The following fire events (1888, 1894 and 1908) were most likely again too mild to kill the competing spruce seedlings and to create appropriate germination conditions for pine and oak by opening the closed-canopy layer, which is formed by the old oak trees, new cohorts of oak and pine and the multi-aged spruces. Pine and oak can be outcompeted in conditions of low-intensity fires. These do not eliminate the competitive species from the understory, much less do they kill any individuals from the overstorey that would open the canopy and provide suitable growth conditions for these light-demanding species (Niklasson, 1998; Bobiec, 2007; Niklasson et al., 2010). The regeneration of these two species ceases after 1880s and the conditions in the stand become most likely increasingly overshadowing.

#### **4.5. 20<sup>th</sup> century species recruitment and the present stand structure**

The last period (20<sup>th</sup> century) is best described as a period of recruitment of shade-tolerant species such as hornbeam and lime. Such species are indicators for low light conditions in the stand (Ellenberg, 1996). The complete recession of the fire events in this period is parallel in time with the germination of these fire-sensitive species. Last abrupt regeneration pulse of spruces follows the 1908 fire.

#### **4.6. Other disturbances**

Other agents such as browsing or intensive timber exploitation shape the dynamics of mixed-deciduous stands of BF and can explain the contrasting changes in the vegetation composition (Kuijper et al., 2010a; b; Bobiec et al., 2011a; Bobiec, 2012).

Clear-cuts can result in the initiation of quick establishment of oak and pine, by creating suitable growth conditions for seedlings of these light-demanding species. However, the first cohorts from the study area appeared in 1830 and between 1820-1839. Clear-cuttings were strictly forbidden in BF at that time (Genko 1902-1903; cf. Zin 2007). No obvious releases in the growth were found in the cores synchronic with the establishment of these cohorts and neither for the latter ones in 1880s (data not shown) indicating that intense clear-cut can be excluded as main driver of pine and oak succession in the studied stand. Stumps are though present in the stand and therefore timber

extractions cannot be disregarded, especially in the period prior to the 19<sup>th</sup> century and the oak/pine cohorts. The openness of the stand, characteristic to the oak-pine structure of the stand before 1800s could be attributed to cuttings as well. However, many stumps in the stand are most likely from the 20<sup>th</sup> century since decomposition rates of wood in BF are probably substantially faster than in colder and drier climates (Stokland, 2001). Regulations regarding forest utilization in BF were changing often and it is known that harvesting of trees was carried out. During this period, a railway was constructed in BF and selective logging was carried out during and between the world wars which might have affected the studied stand as well (Jedrzejewska et al., 1997; Samojlik & Jedrzejewska, 2004). Spruce cores present releases or mechanical damages in the 20<sup>th</sup> century (data not shown) suggesting disturbances in the stand. These events resulted most likely in small openings in the canopy, encouraging recruitment of spruce and birches and probably other pioneers like willows, poplars, but the overall regeneration pattern is still dominated by shade-tolerant, fire-sensitive species to-date.

Besides fire, browsing is most likely a complementary determinant of the species composition shift from oak and pine to hornbeam and lime. Oak and pine are palatable and sensitive to browsing by ungulates, while the latter species can tolerate increased levels of browsing due to their adaptive traits (Kuijper et al., 2010a). Most of the oak individuals had suppressed growth in the early ages suggesting slow growth after the top is killed. This can be attributed to competition for light, fire effects and/or browsing pressure. The 1857 fire, most likely low in intensity, altogether with the general allowance of cattle grazing in the 1860s in BF (Faliński, 1986; Jedrzejewska et al., 1997; Samojlik et al., 2016) resulted in inhibiting oak and pine regeneration in the stand.

#### **4.7. Study limitations**

During the field work, individuals with less than 5 cm DBH were not cored. The young age classes might have been underrepresented mostly for spruce and hornbeam, since no oaks or pines were under 10 cm DBH. This, however, does not affect the findings prior to the 20<sup>th</sup> century. In addition, the estimation of the real germination year/ages can be challenging in dendroecological studies. However, the cores were extracted with high accuracy (most of the cores with pith or distance to pith less than 30 mm) and the correction of the coring height was based on trees cored at two different levels. The number of trees cored at two levels which were used to determine the early growth of trees is unreliable for a robust growth model, but seedlings of oak and pines were not present in the stand. The spruce growth dynamics is also very irregular. Spruce is a plastic species, which can show either a very suppressed or a fast early-growth (Niklasson, 2002; Silvertown &

Charlesworth, 2009). The cores of shade-tolerant species presented many wedging rings and it is difficult to get a proper cell contrast for the correct ring counting. The oaks had often a suppressed early growth. This could be due to damages of the terminal buds from repeated grazing or high competition in dense simultaneous regeneration and/or closed canopy of overstorey. Thus, due to the lack of samples in the field and in absence of prior empirical data on growth dynamics of different tree species on such rich sites to compare our data with, the germination ages might have been under- or overestimated. For the fire evidence prior to the 19<sup>th</sup> century, the stumps' investigation is imperative for long-term fire history reconstruction similarly to other studies (Niklasson, 1998; Niklasson & Drakenberg, 2001; Zin, 2016).

#### **4.8. Comparison with other studies and conclusion**

To my knowledge, this study is one of the first in temperate Europe linking changes in the tree composition of a mixed-deciduous forest with the occurrence of frequent fires. Fire evidently occurred in the studied stand and other records of fire scars and observations (Zin & Niklasson, personal observations) and empirical data (Behrens, 2011) confirm the more widespread occurrence of fire in more forest associations of BF. Thus, fire has had a wider impact on BF and has not only been confined to conifer-dominated forest types. Successional dynamics of these habitats are far more complex than previously considered - undergoing contrasting regeneration patterns. A sparse number of studies were exploring the long-term tree population dynamics in these ecosystems (Nowacki & Abrams, 2008a; Behrens, 2011; Stambaugh et al., 2015; Varner et al., 2016). One reason is the lack of potential research areas, possessing high-naturalness forest stands and a high density of old trees (Hannah et al., 1995). Another reason is that fire was usually disregarded in studies of forest dynamics in the temperate region, since those ecosystems – that contain high share of broadleaved species – were often regarded as non-flammable (Ellenberg, 1996; Vera, 2000). So far only the studies in North America have proven the contrary (Abrams, 1992, 2008; Hart et al., 2008; Nowacki & Abrams, 2008a). The stand conditions of mixed-deciduous forests of BF were also most likely different in the past. For instance, pollen and flora studies from BF showed a higher proportion of Gramineae and other species indicating an open environment around 1750 A.D. (Mitchell & Cole, 1998; Zin, 2016). Brincken (1826) notes that before the 19<sup>th</sup> century, the forests of Białowieża in general were dominated by pines, while the deciduous stands represented dispersed enclaves. Changes in the fire regime, the vegetation composition and in the canopy conditions are interrelated (Angelstam & Kuuluvainen, 2004; Bond & Keeley, 2005; Pausas & Keeley, 2009; Zin, 2016).

The changes in the succession pathways of mixed stands of BF from light-demanding, fire-benefiting to shade-tolerant fire-sensitive species, coincide with the general pattern of BF (Niklasson et al., 2010; Zin, 2016). The shift from pine to spruce, and consequently from a more open-habitat to a closer-canopy has been noted in coniferous stands (Zin, 2016). These findings were tightly connected to fire occurrence and to changes in the fire regime: the decline of fire frequency started in mid 1800s, with evidence of last fires in mid 1800s and early 1900s (the period of fire cessation). This pattern fits well to our stand dynamics. Fire impact on rich sites with less flammable conditions might not be as straightforward to understand as in dry coniferous habitats, but it appeared to gradually change the species composition of the stands. An open environment due to canopy disturbance and less competition in the regenerative field, where competitive fire-sensitive species are eliminated by fire, were the prerequisites of oak and pine dominance in BF. The oak and pine ecology has similarities and the establishment rate of these two species in the deciduous forest type continues to recess not only in BF, but also across many oak and pine habitats in North America (Bobiec, 2007; Niklasson et al., 2010; Varner et al., 2016). While the interdependence between fire and pine regeneration has been acknowledged, the oak-fire relationship is still poorly understood. In the absence of this disturbance agent, species composition shifted to dominance of shade-tolerant species to the expense of oak and pine recruitment. The regeneration of pine and oak is dependent on a combination of variables (Mason & Alía, 2000; Hille & den Ouden, 2004; Annighöfer et al., 2015) and has been proven to be inhibited by high levels of browsing in BF (Kuijper et al., 2010b). The present study illustrates the importance of fire in the rich deciduous habitats and thus this agent could be a valuable tool also in forest management practices in temperate Europe.

## 5. Appendices

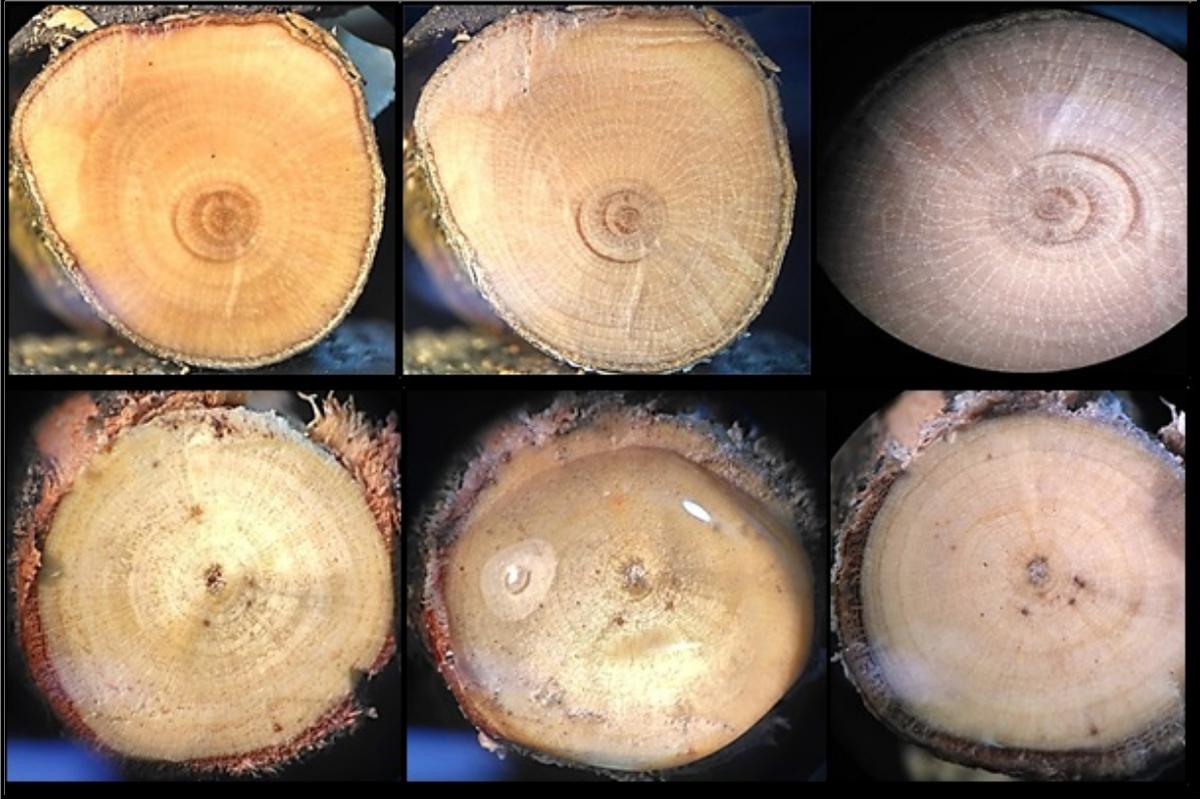
### Appendix 1. Structural characteristics of the study plots.

Plot [size in ha]	Species	DBH [cm]	Height [m]	Density [N ha <sup>-1</sup> ]	BA/ha [m <sup>2</sup> ha <sup>-1</sup> ]	Vol/ha [m <sup>3</sup> ha <sup>-1</sup> ]
D1 [27 ha]	Pine	56.46	34.53	15	3.67	54.1
	Oak	67.50	33.45	24	7.68	131.7
EZ.14.X [0.5 ha]	Spruce	59.83	35.00	28	8.69	126.61
	Pine	56.93	36.08	24	6.24	93.81
	Oak	64.70	32.77	6	2.11	28.56
	Average/Total	59.13	35.22	58	17.04	248.98
EZ.15.X [0.5 ha]	Spruce	34.34	21.96	10	1.30	17.91
	Pine	62.63	33.90	6	1.85	25.22
	Oak	54.61	33.07	46	11.14	123.51
	Average/Total	52.12	31.35	62	14.29	166.64
EZ.16.X [0.5 ha]	Spruce	48.31	31.54	16	3.33	40.56
	Pine	59.64	38.73	34	9.97	136.56
	Oak	59.26	34.78	50	14.66	199.59
	Average/Total	57.64	35.60	100	27.96	376.71

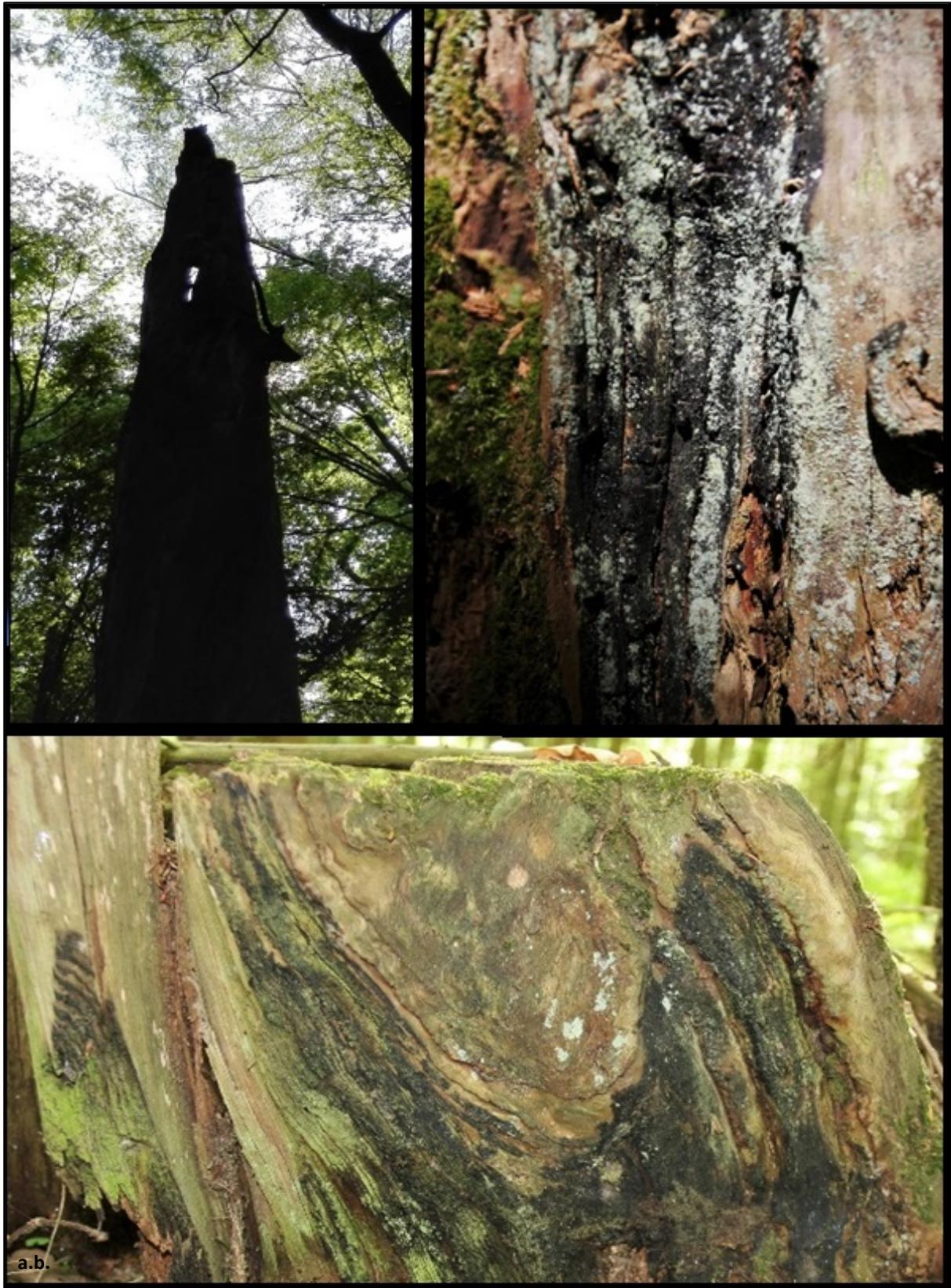
**Appendix 2.** Growth patterns in rich habitats of BF: **(a)** Increment cores extracted at 2 different heights from same tree individual [above the mineral ground (30cm) and at breast height (130 cm)]; **(b)** Variation of growth [width of tree rings] between tree species.



**Appendix 3.** Enhanced cell contrast with zinc paste and water for age determination of 2 tree seedlings. [6–40 × magnification].



**Appendix 4.** Fire evidence: **(a)** Culturally modified tree (pine with a bee-hive); **(b)** multiple-scarred pine stumps in the field; **(c)** fire scars (FS) in pine stump cookies with fire dates or interval between fires [yrs]; **(d)** fire scars in the increment cores.



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**Stump sample** [total number of FS]

Fire event [A.D.]

or

Fire interval [yrs]

(from pith to outerbark)

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c.

**D11-9**  
[11 FS]

1720  
1754  
1763  
1769  
1797  
1808  
1809  
1817  
1826  
1847/1848  
1858



**D11-2**  
[7 FS]

7  
3  
12  
1  
2  
20



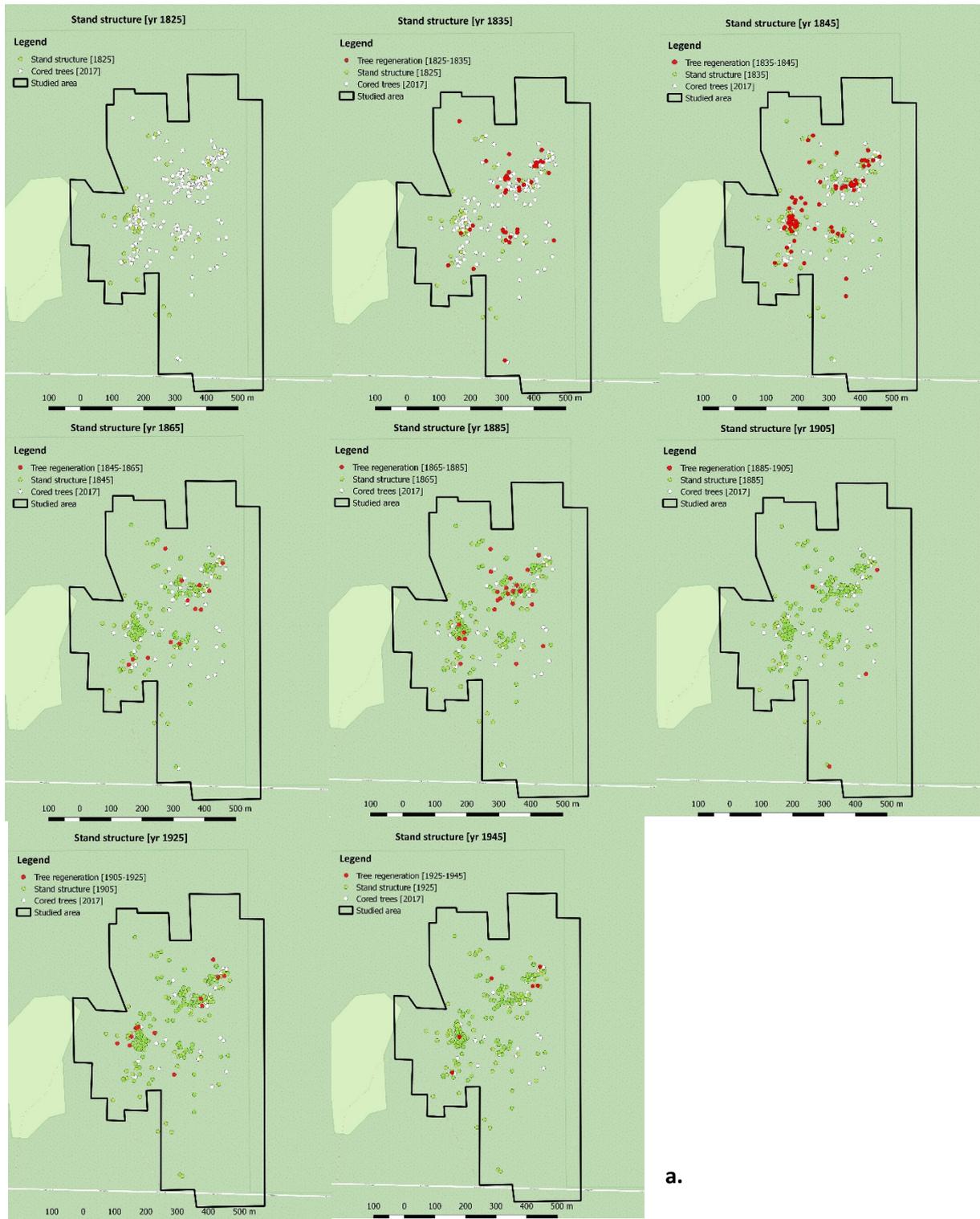


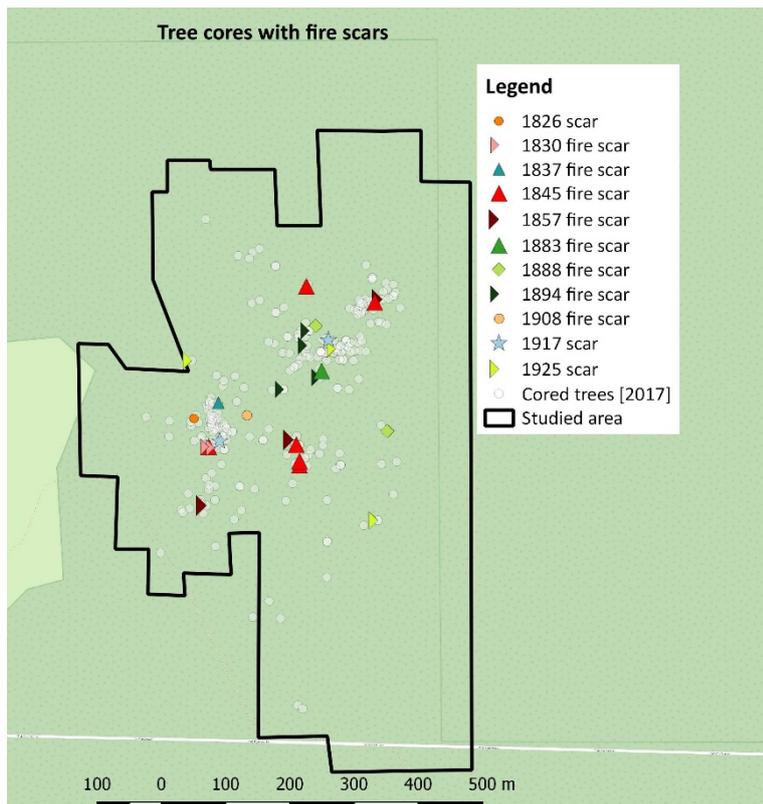
d.

**Appendix 5.** Spruce regeneration in a pine-dominated stand of BF at the beginning of the 20th century  
Source: Kruedener 1909.



**Appendix 6.** Descriptive maps of **(a)** spatial and temporal patterns of tree succession and **(b)** fire scar distribution in the studied stand.





b.

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