



Past and present Scots pine (*Pinus sylvestris* L.) regeneration along site type gradients in Białowieża Forest, Poland



Lina Behrens

Supervisors: Mats Niklasson (SLU) and Ewa Zin (IBL)

Swedish University of Agricultural Sciences

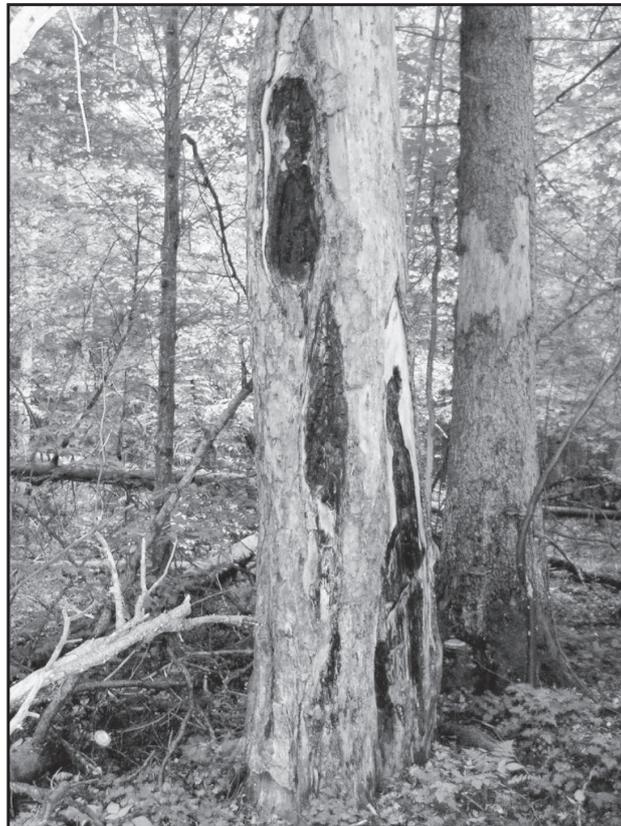
Master Thesis no. 169

Southern Swedish Forest Research Centre

Alnarp 2011



Past and present Scots pine (*Pinus sylvestris* L.) regeneration along site type gradients in Białowieża Forest, Poland



Lina Behrens

Supervisors: Mats Niklasson (SLU) and Ewa Zin (IBL)

Examiner: Jörg Brunet

Swedish University of Agricultural Sciences

Master Thesis no. 169

Southern Swedish Forest Research Centre

Alnarp 2011

Master thesis in Biology,
Advanced level, 30ects(hp), SLU course code EX0503

ABSTRACT

Since 1921 the Białowieża National Park (BNP)/Poland strictly protects one of the best preserved ancient lowland forests of the European temperate zone, with many stands close to natural character. Within the reserve, old *Pinus sylvestris* trees grow on fertile soils in a mixed deciduous forest (oak-lime-hornbeam forest *Tilio-Carpinetum*) with a very rich and dense field layer. This study will explore the features of *P. sylvestris* trees and if this early-successional species is able to regenerate and establish under such habitat conditions as present today. On three such *Tilio-Carpinetum typicum* study areas (in total 230 ha) 723 *P. sylvestris* trees were inventoried and mapped during transect walks over site type gradients. Mean tree density for all sites was low with 3,1/ha. 70% of alive trees had a DBH of 46-89 cm ($\mu= 64,5$) and 50% of alive trees were ≥ 30 m in height. 85% of all trees were estimated to be ≥ 100 -250 years old, none alive tree younger than 50 years. Fire scarred were 18,4% of all Scots pines recorded, half of those additionally modified by chipping for wood splints, beehive caves or axe cutting by people (CMTs). These marks are undoubtedly signs of past anthropogenic utilization impact on appearance and history of the studied forest stands. At least 52 pine trees were multiple fire-scarred, with a range of 2-10 fire events counted. Maximum height for open fire scars was 320 cm. There was no single *P. sylvestris* seedling or sapling found during the regeneration inventories in June 2010. Not even where better light conditions or soil disturbances with a reduced field layer coverage occurred. Due to similarities to Scots pine in its ecology Pedunculate oak (*Quercus robur* L.) was included in the macro-scale regeneration inventory: seedling/sapling density ranged between sites from 1 to 89,1 oak individuals/ha. In the micro-scale regeneration inventory, *Acer platanoides*, followed by *Tilia cordata*, *Fraxinus excelsior* and *Carpinus betulus* seedlings was the tree species with the highest frequency. In the sapling stage instead, the dominant abundance of Norway maple was followed by hornbeam and *Ulmus spp.* In sum 28 dead Scots pines were cored for age determination: the oldest tree on the study sites germinated in 1637, 1642 and 1728 respectively. Overall about 15 irregular regeneration pulses could be detected from the samples for the time period 1637-1852. A share of 33% of all estimated germination dates falls within a 15-year interval, stretching from 1767 to 1782. Longer fire-free periods, e.g. after a likely fire in 1777, allowed Scots pine to recruit and to be resistant enough to survive following fires, as those dated from scars during the 19th century, namely in 1822, 1833, 1851 and 1861. Fire could serve as one hypothetic explanation (besides eutrophication) for the appearance of *P. sylvestris* in richer habitats in BNP, formerly promoted by people in the region due to traditional forest utilization. The diminishing influence of man in BNP may cause the depression in regeneration of short lived pioneers and climax, light demanding tree species like Pedunculate oak and Scots pine.

Keywords: *Pinus sylvestris* regeneration, oak-lime-hornbeam forest *Tilio-Carpinetum*, regeneration pulses, forest and fire history, traditional forest utilization, dendroecology

CONTENTS

Abstract	
CONTENTS.....	2
LIST OF FIGURES	3
LIST OF TABLES	3
LIST OF MAPS.....	3
ABBREVIATIONS.....	4
ACKNOWLEDGEMENTS.....	4
1. INTRODUCTION.....	5
2. MATERIAL AND METHODS.....	6
2.1 STUDY AREA	6
2.1.1 Białowieża Forest (BF).....	6
2.1.2 History of utilization in Białowieża Forest	7
2.1.3 Protection and science.....	7
2.1.4 Climate and weather.....	9
2.1.5 Geomorphology and tree species occurrence.....	9
2.1.6 Forest characteristics.....	9
2.1.7 Oak-Lime-Hornbeam forest type.....	10
2.1.8 Forest type Melitti-Carpinetum	11
2.1.9 Impact of herbivores on vegetation structure and dynamics.....	11
2.1.10 Cattle Pasturing in Forests.....	12
2.2 STUDY SITES	12
2.2.1 Selection of study sites	12
2.2.2 Description site 1: “Dziedzinka”	12
2.2.3 Description site 2: “Orłowska”.....	13
2.2.4 Description site 3: “Uroczysko Paharelec”.....	13
2.3 INVENTORY OF PINE AND OAK SEEDLINGS AND TREES	16
2.3.1 Survey of <i>Pinus sylvestris</i> trees	16
2.3.2 Growing conditions for <i>Pinus sylvestris</i> trees.....	17
2.3.3 Pine and oak regeneration on macro-scale	17
2.3.4 Tree regeneration on micro-scale	17
2.3.5 Tree ring samples of <i>P. sylvestris</i>	18
2.3.6 Laboratory analysis and calculations	18
2.3.7 Mapping	19
2.3.8 Calculation programmes and statistical analysis	19
3. RESULTS	19
3.1 PINUS SYLVESTRIS TREES.....	20
3.1.1 Maps.....	20
3.1.2 Height.....	20
3.1.3 DBH	25
3.1.4 Age.....	26
3.1.5 Crown conditions.....	28
3.1.6 Stem conditions.....	28
3.1.7 Stem modifications.....	28
3.2 RECENT PINE REGENERATION AROUND PINUS SYLVESTRIS TREES (MICRO-SCALE) .	30
3.3 PINE AND OAK REGENERATION ON MACRO-SCALE	30
3.3.1 Maps.....	30
3.4 REGENERATION OF ALL TREE SPECIES ON MICRO-SCALE.....	33
3.4.1 Growing conditions for non-woody plants and tree regeneration.....	36

3.5 FIRE HISTORY	36
3.5.1 <i>Maps</i>	36
3.5.2 <i>Dated fire scars</i>	37
3.5.3 <i>Regeneration pulses of Scots Pine</i>	41
4. DISCUSSION	42
5. CONCLUSIONS	49
REFERENCES	51
APPENDIX I	57

LIST OF FIGURES

<i>Fire-scarred/chipped Scots pine in comp. 317 D with five fire events counted... Front cover page</i>	
2.1.1 <i>Area of Białowieża Forest on the Polish side</i>	6
2.1.3 <i>Land-use history and its impact on forest ecosystems in BF</i>	8
3.1.2 <i>Height of Scots pines</i>	21
3.1.3 <i>Diameter distribution</i>	25-26
3.1.4 <i>Age estimations</i>	27
3.4. <i>Tree species diversity in seedling stage</i>	34-35
<i>Tree species diversity in sapling stage</i>	35
3.4.1 <i>Coverage of field layer species in sample plots</i>	36
3.5.3 <i>Renewal periods</i>	41
<i>Germination dates</i>	42

LIST OF TABLES

3.3.1 <i>Area and Scots pine density for study sites</i>	20
3.1.3 <i>Diameter features</i>	25
3.1.5 <i>Crown conditions</i>	28
3.1.6 <i>Stem conditions</i>	28
3.1.7 <i>Stem modifications</i>	29
<i>Characteristics of fire scarred trees</i>	29
3.3.1 <i>Density of oak regeneration</i>	30
3.4 <i>Density of regenerating trees in sample plots</i>	33-34
3.5.2 <i>Dates of fire scars</i>	37

LIST OF MAPS

2.2.1 <i>Location of study sites</i>	15
3.1.1 <i>Pinus sylvestris trees in site 1 Dziejzinka</i>	22
<i>Pinus sylvestris trees in site 2 Orłowska</i>	23
<i>Pinus sylvestris trees in site 3 Paharelec</i>	24
3.3.1 <i>Oak regeneration in site 2 Orłowska</i>	31
<i>Oak regeneration in site 3 Paharelec</i>	32
3.5.1 <i>Germination and fire-scar year dates in site 1 Dziejzinka</i>	38
<i>Germination and fire-scar year dates in site 2 Orłowska</i>	39
<i>Germination and fire-scar year dates in site 3 Paharelec</i>	40

ABBREVIATIONS

Abbreviation	Full term
A.D.	Anno Domini
approx.	Approximately
a.s.l.	Above sea level
BF	Białowieża Forest
BNP	Białowieża National Park
cm	centimeter
CMT	Culturally Modified Tree
comp.	compartment
CWD	Coarse-Wooded Debris
DBH	Diameter in Breast Height, 130 cm
ha	Hectare
p.a.	Per annum/per year
<i>T-C</i>	<i>Tilio-Carpinetum</i>
<i>M-C</i>	<i>Melitti-Carpinetum</i>
WWI	Word War I

ACKNOWLEDGEMENTS

I am grateful to the supervisors of this Master Thesis, Ewa Zin and Mats Niklasson for academic assistance as well as reading and commenting on earlier drafts. Together with me Ewa Zin collected wood samples in the field, did ring counts and cross-dating of the tree cores in the laboratory. Thanks are also due to the following people: Adam Kudlewski for help with field equipment, Krzysztof Súcaro for GIS advice, Marian L. Mayr for company during the stay in Białowieża and Gabriele Behrens for personal support.

Lina Behrens

Wiershausen, 18th March 2011

1. INTRODUCTION

The influence of fire enriches biodiversity on the landscape, habitat and species level. But this once important ecological process lacks nowadays in many European ecosystems. As up to date research reveals, fire has played a decisive role in determining the structure and dynamics in temperate lowland mixed woodlands, as known for the boreal and Mediterranean region (Zin 2007; Niklasson et al. 2010). In Central Europe, empirical studies of current fire dynamics are limited due to active fire suppression activities (Pyne 1997; Szczygieł et al. 2009). Due to intensive forest management practices in the last centuries, the areas of old-growth forests with a high amount of old trees and dead wood has constantly decreased. This hampers the detailed exploration of past fire regimes. Recording trees are missing to determine fire extension, frequency, intensity, seasonality etc. However, in some remote and protected areas, like the ancient forests of Białowieża in East-Poland, such old trees are still present. Scots pine, as most important tree species in BF today, dominates with a share of 43,2% out of all forest stands. In the strictly protected part, the Białowieża National Park (BNP) currently holds a share of 11%, mainly in mixed and coniferous forest habitats (Samojlik 2006). Surprisingly, in the strict reserve of BNP, pines also occur in rich deciduous forest types such as oak-lime-hornbeam forests (*Tilio-Carpinetum* or *T-C*). Naturally, dependent on edaphic factors, areas with broadleaved trees on ground morainic plains and pine forests on the ablation moraine are often believed to exclude each other (Kwiatkowski 1994). *P. sylvestris* shows characteristics of an early-successional species when it comes to demands for a successful regeneration, first of all requiring light and open conditions (Svenning 2002). Factors like the occurrence of bare soil, former fire influence and/or animal grazing would foster pine regeneration. The species is therefore not expected to be able to establish seedlings under the habitat conditions of a closed deciduous forest with the dominance of shade-giving and shade-bearing tree species as prevailing in the today's *T-C* associations. Inside BNP, pines are found mainly in the age classes from 100-120 years and older, while younger age classes could not show any dominance in forest stands. The number of *P. sylvestris* trees and natural regeneration are on decline in BNP, as a long-term study on compositional dynamics of natural forests has shown during the 20th century (Bernadzki et al. 1998). Fire could serve as one hypothetic explanation for the occurrence of *P. sylvestris* in richer habitats- as the most fire resistant tree species and therefore the one promoted by this disturbance agent.

This Master-Thesis project aims to investigate past and present Scots pine regeneration in richer habitats of the *T-C* forest type in the strict reserve of BNP, a topic which has not been analyzed previously (Bernadzki et al. 1998; Kopyrk et al. 2004; Samojlik 2006; Zin 2007). Pedunculate oak (*Quercus robur* L.) is included in the regeneration study due to similarities in its ecology to pine trees. It requires open forest structures for sapling growth and it is able to survive periodic surface fires even in young age (Brose & Van Lear 1998; Brose et al. 2001).

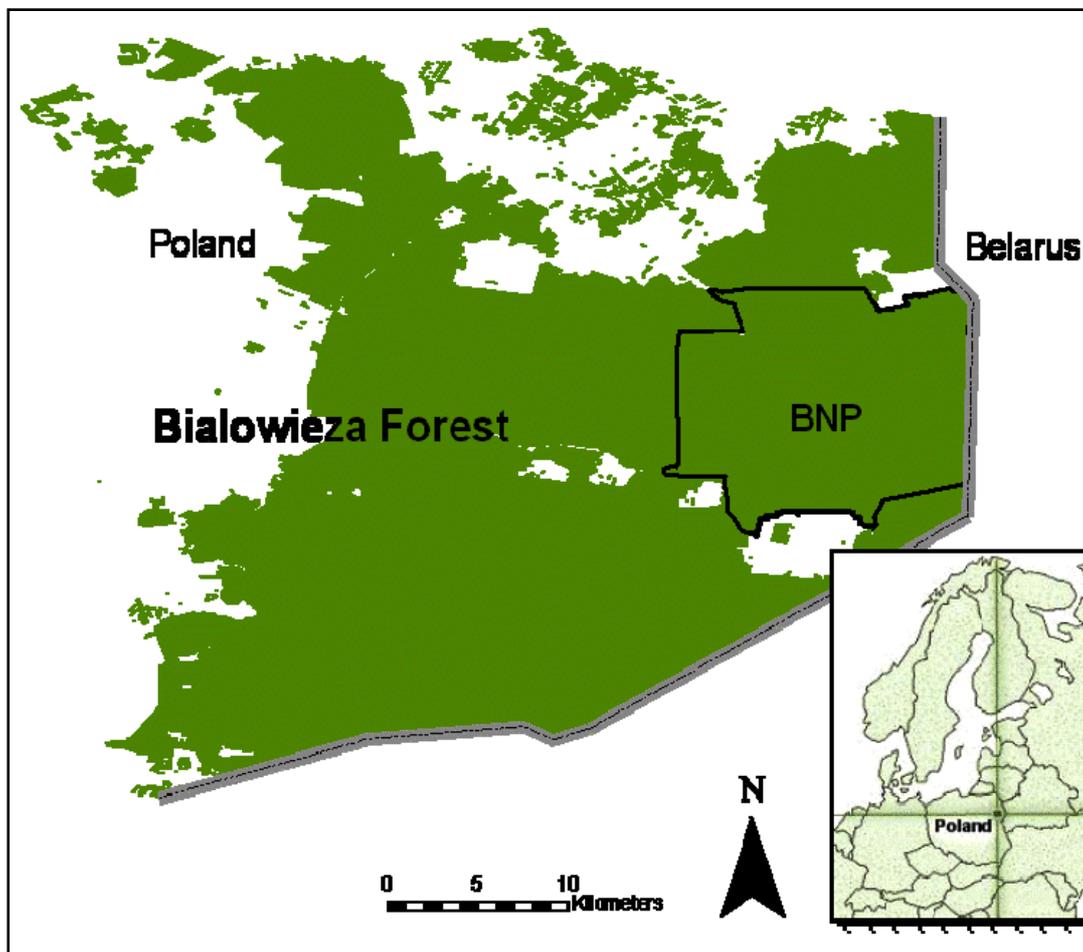
2. MATERIAL AND METHODS

2.1 STUDY AREA

2.1.1 Białowieża Forest (BF)

BF is the best preserved old-growth forest complex of the temperate zone in the European lowlands. It has a surface area of 1450 km². About 600 km² of BF is situated in Poland's north-eastern region Podlasie; approx. 850 km² lie behind the eastern state border in Belarus (Figure 1). Associated with smaller neighboring forest areas (Puszcza Swislocka, Szereszewska and Ladzka) the core complex stretches from 52°29' to 52°57' N latitude and 23°30' to 24°21' E longitude (Faliński 1986). BF is a territory with large, only slightly fragmented, natural vegetation complexes, including communities of primary origin. Anthropogenic elements are rare and even semi-natural and synanthropic vegetation show primitive traits. The degree of neophytism and invasive species is low (Faliński 1986, 1994).

Figure 1: Area of Białowieża Forest on the Polish side, with boundaries of Białowieża National Park (BNP) marked in black.



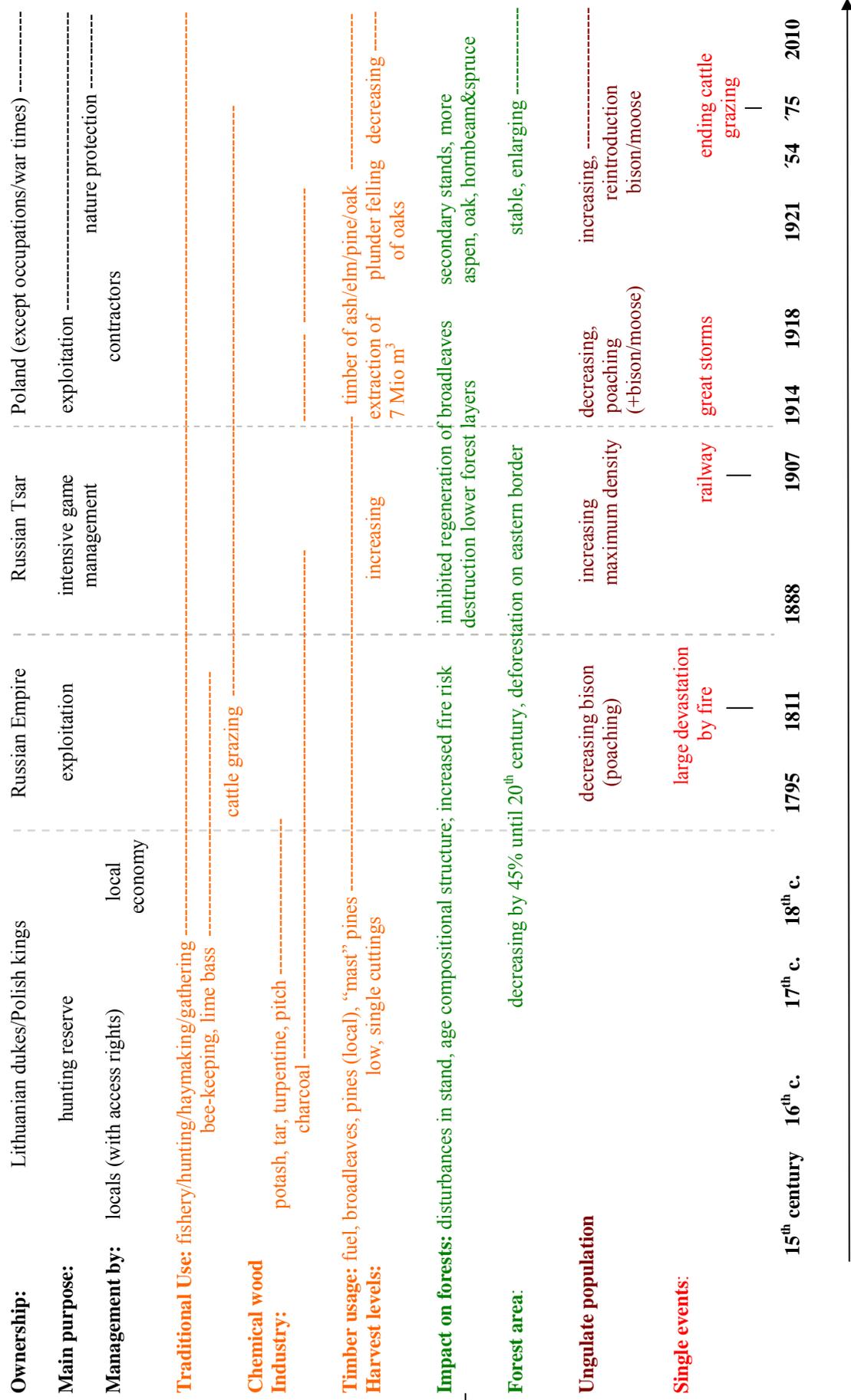
2.1.2 History of utilization in Białowieża Forest

The BF complex is present today due to its enduring state of protection during the last centuries. Nevertheless human influences halved its size since the Middle Ages. Since the 15th century BF was a separate administrative and independent management unit. Until 1914 the area was used as a hunting reserve; first of Polish and Lithuanian Kings as well as nobility and later of the Russian Tsar. They were especially attracted by the unique richness of royal game such as bison (*Bison bonasus* L.), moose (*Alces alces* L.) and red deer (*Cervus elaphus* L.) A combination of different factors conserved BF: limited game hunting and tree cuttings as well as local forest guards and restricted access-rights concerning traditional forest uses. For a short period after World War I (WWI), industrial exploitation of timber resources took place. Until nowadays the State Forest Administration manages actively the major part of the Polish BF, including silvicultural measures. The land use history of BF is summarized in Figure 2.

2.1.3 Protection and science

Due to BF's exceptional state of conservation, Poland's first national park was established here in 1921, the Białowieża National Park (BNP) or Białowieski Park Narodowy (BPN). Initially, 47 km² of the present Orłówka District was set under protection. After enlargement in 1996, the so called *strict reserve* of the BNP, covers nowadays 57 km². This most natural part of BNP constitutes approx. 10% of the Polish part of BF. The present BNP, also includes a part with active nature conservation management (Hwoźna District), giving it a total size of 105 km² (see Figure 1). Together with other reserves in BF the protected polish zones are 225 km² in total (Bobic et al. 2005). BF has become a unique valuable territory for scientists from around the world to study how a forest restrictively used by man in the past is developing back to a true primeval forest (Szafer 1922 in Faliński 1986). Numerous long term research programmes have been launched by several research institutions like European Centre for Natural Forests of the Forest Research Institute (IBL), Mammal Research Institute of the Polish Academy of Sciences (MRI PAS), Białowieża Geobotanical Station of Warsaw University and the Scientific Laboratory of the Białowieża National Park. The park also serves for educational purposes and is rather restrictively used for tourism. In 1979 BF was inscribed into the list of UNESCO World Heritage Sites (Unesco 2010).

Figure 2: Land-use history and its impact on forest ecosystems in BF, with dates important for the study. Dashed vertical lines: duration of process; c.: century, +: die out of species. Own diagram based on the sources: Faliński 1986; Jędrzejewska et al. 1997; Bernadzki et al. 1998; Bobiec et al. 2005; Samolik 2005; 2007; Zin 2007.



Time in years

2.1.4 Climate and weather

BF has a sub continental climate of the cool temperate zone. The forest obtains both nemoral and boreal features due to its boundary location between the transitions from an Atlantic to a continental climate (Faliński 1986). The mild and moist western European conditions acquire eastern, more continental features. These are shorter vegetation season, average length of 206 days with air temperature >5 °C, and longer snow cover subsistence, on average 92 days. Absolute minimum air temperature recorded was - 38,7 °C and maximum + 34,5 °C. Mean air temperature of January is - 4,7 °C and of July 17,8 °C. Mean annual precipitation is 641 mm, with amplitude ranging from 426 to 940 mm. Precipitations fall to 85% as rain, mainly during summer months (Faliński 1986). During the last 60 years the climate has become more oceanic. Temperature is increasing and its amplitude decreasing. Mean annual air temperature has risen from 6,8 to 7,4 °C. The snow melts earlier in spring and earlier runoff affects growing season and water conditions in forest habitats. Extremely dry years with low precipitation occurred in 1991, 1997, 2000 and 2005. Prevailing winds come from south-western and south-eastern directions. These ones reach highest velocities. Northern winds are rare and blow with lower speed (Malzahn 2009).

2.1.5 Geomorphology and tree species occurrence

Ecosystems of BF developed on an old-morainic plateau with glacial sediments deposited in the Warta sub stage of Middle Poland glaciations. It is a flat undulating plane on which elevation ranges from 134 to 202 m a.s.l. This uniform relief is little differentiated by river valleys. The complex pattern of parent rocks is responsible for the mosaic of soils. Depending on edaphic factors, biotic components are highly variable like e.g. forest types and tree species (Kwiatkowski 1994; Prusinkiewicz & Michalczuk 1998). Naturally the extent of forests with predominantly Scots pine (*Pinus sylvestris* L.) covers precisely the boundaries of ablation plateaus and dune lands with an elevation of 160 to 190 m a.s.l. Trees grow on leached brown soils, lessivé soils or poorer podzolized brown soils. The occurrence of deciduous forests with hornbeam (*Carpinus betulus* L.), small-leaved lime (*Tilia cordata* Mill.) and Norway maple (*Acer platanoides* L.) correspond to the boulder clays which are associated with ground moraines in an elevation of 145 to 165 m a.s.l. and eutrophic/mesotrophic brown or lessivé soils (Kwiatkowski 1994).

2.1.6 Forest characteristics

A simultaneous occurrence and mix of deciduous forest elements of Central Europe and evergreen coniferous forests of the Taiga is characteristic for BF. Mainly mesotrophic oak-lime-hornbeam forest (*Tilio-Carpinetum*), meso-oligotrophic mixed oak-spruce-pine forest (*Pino-Quercetum*) and oligotrophic/fresh pine forest (*Peucedano-Pinetum*) grow on the postglacial North European Lowland plains. All 19 forest types typical for the region are present. In the core area of BNP, forest stands are characterized by multi-species, multi-

layered and different-aged structures of trees (Faliński 1994). Single trees reach immense sizes and have long life-spans of up to 400 years. Dead wood reaches volumes of 120 m³/ha (Bobic et al. 2005).

2.1.7 Oak-Lime-Hornbeam forest type

The most common type of forest ecosystems is the association of *Tilio-Carpinetum typicum* (*T-C*) in which Norway spruce (*Picea abies* L. Karst.) is constantly present (for classification system see Appendix A). *T-C* forests cover 44% of the area of BNP. They are very differentiated and mainly interspersed with the wetter form of *Tilio-Carpinetum stachyetosum*, in which elms (*Ulmus spp.* L.), European ash (*Fraxinus excelsior* L.) and Black alder (*Alnus glutinosa* Mill.) participate. Here, maximum tree dimensions of the whole BF are reached. All tree species participate in the uppermost tree layer and usually build a compact forest canopy. Hornbeam could exclusively form the second and third tree layer (Prusinkiewicz & Michalczyk 1998). Adjacent forest types of *T-C* are *Circaeo-Alnetum* (streamside alder-ash forest), *Ficario-Ulmetum* (deciduous floodplain forest), *Pino-Quercetum* (mesotrophic oak-pine mixed forest) and *Potentillo albae-Quercetum* (thermophilous oak forest) (Faliński 1986).

The shrub and moss layer is poorly developed while the herb layer is rich in species and coverage. It consists of two to three layers of numerous spring geophytes (*Anemone nemorosa*, *Ranunculus ficaria*, *Gagea spp.*, *Allium ursinum*), partly evergreen plants (*Lamium galeobdolon*, *Stellaria holostea*, *Galium odoratum*, *Oxalis acetosella*, *Milium effusum*) and other deciduous plants (*Aegopodium podagraria*, *Dentaria bulbifera*, *Lathyrus vernus*, *Equisetum pratense*) (Faliński 1986).

A large amount of litter is produced annually in *T-C* forests. High biological activity and consequently quick decomposition processes in soils hinder formation of a thick organic horizon (Prusinkiewicz & Michalczyk 1998).

In the past BF's *T-C* forests were subjected to heavy human transformation. As early as with the establishment of *tumulus* burying grounds in the 10th century, forest land was converted to settlement and agricultural land. *T-C* forests were preferentially chosen to graze farm animals and processing of potash and charcoal was common. Felled trees served as building material for houses in the surrounding villages; smaller assortments as fuel for locals. Also pines which grew in this forest type could have been served for the usage as ship masts due to their dimensions in length and width, as well as durability and low weight of the wood. Heavy timber extraction of broadleaves (pedunculate oak, Norway maple, elms and ash trees) and Norway spruce at the beginning of the 20th century deprived the stand richness in some areas. Often only a hornbeam thicket remained. After local plunder fellings in BF via the clear-cut system after WWI, mainly trees with wind-carried seeds as aspen (*Populus tremula* L.) and birch (*Betula spp.* L.) regenerated. At the same time the groundwater level rose which led to increased bogginess of *T-C* areas (Faliński 1986, 1994).

2.1.8 Forest type *Melitti-Carpinetum*

The *Melitti-Carpinetum* (*M-C*) community is described as dry thermophilous oak-hornbeam forest with admixture of pine, spruce, birch and aspen trees. In the field layer the presence of *Melittis melissophyllum* gives the name for this association. *M-C* occurs on ablation-moraine undulated plains and tops of kame hillocks on higher elevations. The connected soil types are leached and podsollic brown soils as well as lessivé soils, formed on glacial sands, ablation loams and occasionally sand-dunes. The ground water level lies at a depth of 5-15 m.

The proportion in which tree species and especially pines are present in *M-C* forests reflects earlier forest management practices. Strong human utilization pressure was focused in the past on this habitat (Kwiatkowski 1994; Kwiatkowski et al. 2009).

2.1.9 Impact of herbivores on vegetation structure and dynamics

In BF all Europe's large herbivorous ungulates are present, like roe deer (*Capreolus capreolus* L.), elk, red deer and European bison plus the revived carnivorous predators: wolf (*Canis lupus* L.) and lynx (*Lynx lynx* L.). Beside those, the omnivore wild boar (*Sus scrofa* L.) is important in affecting lower plant layers and soil conditions in BF (Jedrzejewska et al. 1997). Bison, red deer and wild boar live in larger groups and preferentially stay and feed in *T-C* forest ecosystems, which is followed by a limitation of plant biomass increase (Faliński 1986; Kuijper et al. 2009, 2010a).

During the time of intensive Russian game management, population sizes of ungulates grew artificially by about 400% in the time from 1894-1902, from ca. 3000 to ca. 11 000 animals. This policy, especially the temporarily introduction of the foreign fallow deer (*Dama dama* L.) increased zoogenic pressure and coincidences with changes in structure and dynamics of deciduous and mixed forest ecosystems. Large forest regions remained without tree regeneration, therefore a depression in age structure of now 90-110 year old trees (mainly broadleaves such as ash, hornbeam, lime, maple, lime) is observed in BF. Norway spruce could expand and is responsible for the so called *boreal aspect* in BF (Bernadzki et al. 1998; Bobiec et al. 2005). Furthermore the game is supplementary fed in winter since centuries (Faliński 1986; Jedrzejewska et al. 1997). It can be hypothesized that most likely game densities in BNP today cannot be seen as close to natural conditions, also because one large predator, the endemic brown bear (*Ursus arctos arctos* L.) still is missing. Whether game densities, e.g. of red deer, are higher in protected areas than outside those is discussed controversially (Bobiec et al. 2005; Kuijper et al. 2010a). It's already high mean population density rose during the period from 1995 to 2008 from 42 to 60 red deer per 1000 ha (Dzięciołowski 1996; Borowik et al. 2008). In BNP it preferentially browses saplings of elm, birch, lime, rowan (*Sorbus aucuparia* L.) and ash; 90% of all young trees species are browsed in a height of 60–90 cm (Kamler et al. 2004). Generally it is stated that forest regeneration in BNP is overexploited as a feeding resource of ungulates (Miścicki 1996).

2.1.10 Cattle Pasturing in Forests

Since the 15th century traditional pasture of livestock by local people was common on meadows and in the forest. After the 1850s cattle grazing intensified with an increase of animal heads and used area for pasture. From 1880 to 1914 grazing impact on forest ecosystems was heaviest. A number of 6000-8300 stationary cattle plus 3000-4000 yearly driven oxen in comparison to about 11 000 game heads should have been present (Jędrzejewska et al. 1997).

2.2 STUDY SITES

2.2.1 Selection of study sites

In the strict reserve of the BNP three study sites were selected for the inventory (Map 1) based on the following criteria:

1. Classification as forest type “*Tilio-Carpinetum typicum*” (Lsw) according to the map “Forest habitat types” published in Michalczyk (2001). This source diagnoses the ecological forest landscapes of Białowieża on the basis of the site’s ground vegetation, soil and stand characteristics.
2. Occurrence of the tree species *Pinus sylvestris*, as observed during transect walks in winter and spring 2010 before leaf-flush, assuring good stem visibility up to 200 m inside tree stands

2.2.2 Description site 1: “Dziedzinka”

Study site 1 is about 72 ha in size. It spreads over the compartments 373 C/D and 402 A/B/C, in the neighborhood of the old “Dziedzinka” yard (former forester’s house) (Map 2). These squares are situated in the drainage basins of the Orlówka River (Malzahn et al. 2009). Adjacent forest types are the moister and richer form of *T-C*, so called *T-C caricetosum remotae* (Lw) and *M-C*.

The dominant forest type of the site is *T-C*, growing on flat plains and undulating elevations of basal moraine (Kwiatkowski et al. 2009). Partly, the site is classified as semi-natural *M-C* (LMsw) forest community. Along the Browska road and on the western border of the compartment 402 *P. sylvestris* trees occur (Kwiatkowski 1994).

The dominant tree species are oak and hornbeam with an age of over 100 years. The former dominance of old spruces along the road Poprzeczny Tryb is diminished because of storm-felling, fungi and insect diseases. Instead old pine and oak trees dominate nowadays in two larger gaps, opened during the last 20 years. Along the Browska road aspen trees (*Populus tremula* L.) younger than 100 years in age dominate (Kwiatkowski et al. 2009). Together with birch, this secondary stand probably self-sowed after cuttings of noble species and pines at the beginning of the 20th century. It regenerated naturally also due to decreasing zoogenic

pressure during that time. Since then, spontaneous secondary succession led to a slow die off of the pioneer tree species and to regeneration into an oak-lime-hornbeam forest (Prusinkiewicz & Michalczyk 1998; Faliński 1986).

In parts cattle grazing were common in the site until the year 1902 (Faliński 1986).

2.2.3 Description site 2: “Orłowska”

Study site 2 is 105 ha in size. It stretches over the compartments 317 B/C/D, 318 A/C/D and 344 A/B/C/D, at the Orłowska road (or: Orłowski Tryb) (Map 3). These squares are situated between the boundaries of the drainage basins of the Narewka, Hwoźna and Orłówka rivers respectively (Malzahn et al. 2009). The site is surrounded by the forest types of *M-C* (LMsw), *Quercus-Piceetum* (BMw) and *T-C caricetosum remotae* (Lw) as well as *Sphagno girgensohnii Piceetum* (LMw) a type which describes moist coniferous forest with pine and spruce and admixture of birch and aspen.

The site is dominated by *T-C typicum* forest type growing on flat plains and undulating elevations of basal moraine and here as well on the undulating plains and heights of ablation moraine. Elevation ranges between 160 and 165 m a.s.l. (Kwiatkowski et al. 2009).

Oak and hornbeam with an age over 100 years dominate the site; to a lesser extent also maple along the Orłowska road. Younger lime tree dominated stands occur in square 317. A 200 m wide belt of an old *P. sylvestris* dominated stand is found in compartment 344, there forming the main compositional tree element (Kwiatkowski et al. 2009). In the ascending hills in the northern part of the site, a subassociation of *T-C*, *T-C calamagrostietosum* occurs. There spruce, pine, aspen and birch participate in the tree stands. Abundance of lime is less and maple is totally absent. The field layer is characterized by the occurrence of *Carex spp.*, *Anemone nemorosa* and *Vaccinium myrtillus* (Faliński 1986). Single fallen spruce and oak logs pose mainly the coarse-woody debris (CWD).

In compartment 317 D a rich field layer and recruiting saplings of elm, maple and hornbeam were present. In square 318 D hornbeam forms as a second tree layer an open forest with few bushes and woody plants over 30 cm in height in the understorey. A covering layer of leaf litter results in a species poor field layer.

Small areas in square 318 were clear-cut and then regenerated naturally through self-seeding. Earlier, during the Tsars intensive game management period, small glades were present in the same square, where feeding was put for animals (Prusinkiewicz & Michalczyk 1998, Michalczyk 2001). On the border between compartment 345 and 344 there was a charcoal burning mound situated (Samojlik 2007). In 1921 the compartments 318, 319 and 344 became a strict Nature Reserve within the Browsk Forest District (Okołów 2009).

2.2.4 Description site 3: “Uroczysko Paharelec”

Study site 3 had an area of 53 ha. It lays within the squares 340 E/F, 369 B/E/F and 398 B at the Objazdowa road (Map 4). The squares are situated in the drainage basins of the Narewka

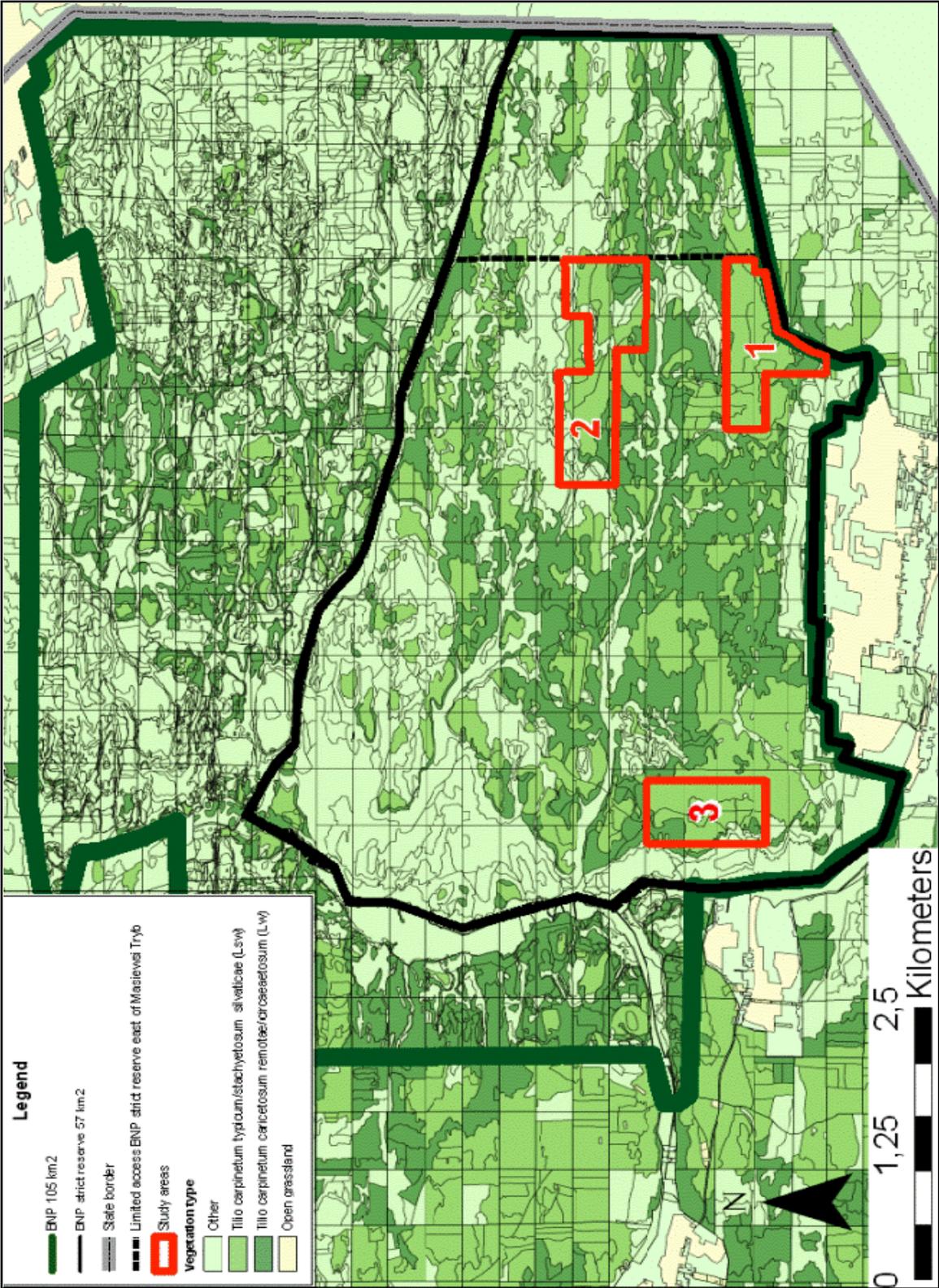
River (Malzahn et al. 2009). Adjacent are the forest types of *T-C caricetosum remotae* (oak-hornbeam forest with remote sedge) and *Sphagno girgensohnii-Piceetum* (lowland sub boreal spruce forest) situated.

The *T-C typicum* forest type occurs here on flat plains and undulating elevations of basal moraine and on undulating plains and heights of the ablation moraine. The elevation ranges between 150 m and 160 m a.s.l. Dominant tree species are hornbeam and maple over 100 years old. Along both sides of the Objazdowa road, old oaks and younger lime stands are present (Kwiatkowski et al. 2009).

The forest stand west to the Objazdowa road in compartment 369 is in a stand development phase of secondary succession (Faliński 1986). This area was anthropogenically destructed at the end of the 18th century after which spruce appeared but again disappeared in the middle of the 20th century (Keczyński 2007). Small hornbeams and limes, to a lower extent spruce, grow densely as a second layer under the canopy of older oaks and pines. This stand will probably develop into a state and type of a late-successional forest similar to the one which lies east of the road (Faliński 1986).

Traces of human utilization in this site are present in various forms. From *tumuli* (cemeteries) dating back to the 10-12th century to numerous presumable potash burning places, which were especially associated with mixed *T-C* forests and stands where pines today grow close to river courses (Samojlik 2005, 2007; Kwiatkowski et al. 2009). In compartment 398 there are found remnants of old settlements; in 369, according to a legend the village of charcoal-burning people, called Pogorzelce, was situated (Keczyński 2007). At the border between compartments 398 and 369 existed in the past a water storage for timber in a water body, probably a pond (Michalczuk 2001). Until 1902 cattle grazing was common in parts of compartment 369 and 398 (Faliński 1986).

Map 1: study sites 1 “Dziedzinka”, 2 “Orłowska”, 3 “Paharelec in the strict reserve of BNP. The study sites lie in larger continuous forests of *Tilio-Carpinetum typicum/stachyetosum silvaticae* (Lsw: fresh deciduous forest).



2.3 INVENTORY OF PINE AND OAK SEEDLINGS AND TREES

For *P. sylvestris* trees the current state and growing conditions were registered. Detailed regeneration inventories were carried out at two spatial scales, one for young pine and oak trees and one for all tree species regenerating in the study sites.

2.3.1 Survey of *Pinus sylvestris* trees

The aim was to inventory all *P. sylvestris* trees > 5 cm in DBH in each study site. After testing different transect widths in field after leaf-flush in spring 2010, a transect width of 50 m (25 m to each side of the transect walker) was chosen. Due to the clear stem features of pines, their detection was easy among other trees. The belt transects ran parallel to each other, in east-western or north-southern direction dependent on the study sites' shape. Satellite positions of the location of their starting and end points were taken with a Garmin 60CSx GPS receiver as well as for the location of each pine tree. For orientation in the field a SILVA compass was used. Extent and length of transects was first of all determined by the limit of the forest type or when the border of BNP was reached.

The following features of the trees were also recorded:

1. Height to the nearest meter (German "Blume-Leiss" hypsometer)
2. DBH with a diameter tape
3. A rough age estimation in field based on habitus and bark features
4. Crown conditions in four classes:

Living trees	Vital crown (1)	Dying crown (2)
Dead trees	With intact crown, without fine branches (3)	Snag or stump without crown (4)

5. Stem conditions in four classes:

Living trees	Stem healthy, bark/texture intact (1)	Stem damaged or bark fragmented (2)
Dead trees	Stem dead, bark intact (3)	Stem dead, bark absent (4)

6. Stem modifications, e.g. from burning and lightning, anthropogenic chipping and bee-hive carving. Those trees are defined as culturally modified trees (CMT) that have been altered by native people as part of their traditional use of the forest (Stryd 1997). When a fire scarred tree was found, the number of scars (consecutive over healing), their width and height, number of events, and orientation in North, South, West or East direction were noted. Pictures of all fire scarred trees were taken with a digital photo camera.

2.3.2 Growing conditions for *Pinus sylvestris* trees

The growing condition for each inventoried pine trees was assessed in the following way:

Canopy density in five classes:

1	2	3	4	5
Several tree crowns would fit in gap	One tree crown would fit in gap	Less than the size of one tree crown would fit in gap	Twigs of neighbouring tree crowns are touching each other	Twigs of neighbouring tree crowns grow interconnected

Under the crown of pine trees, the ground was carefully searched for recently established pine regeneration (seedlings up to ≤ 30 cm in height), especially when soil disturbances as uprooting caused by wind-throw or game occurred.

2.3.3 Pine and oak regeneration on macro-scale

Within each 50 m transect, oak and pine regeneration was registered in a 3 m wide, parallel belt transect which ran 1,5 m at each side of transect's middle. Established saplings of at least ≥ 30 cm height up to 4 m height of young trees were registered. GPS positions of each recorded sapling were taken with a Garmin 60CSx GPS receiver. Height was measured with a centimeter tape. Age was estimated by the intercept method, counting bud scars on oak stems (Dyer & Bailey 1987). Health conditions were noted as "healthy" or "damaged" and if the cause of damage was clearly visible, this was noted, e.g. browsing, fungi, insect etc.

2.3.4 Tree regeneration on micro-scale

For each of the sites a detailed study of natural regeneration of all tree species was conducted. In each site 30 to 32 circular sample plots were placed in a regular grid to cover the whole study area walked during the inventory of pine trees. The width between the parallel running regeneration transects ranged from 200 to 300 m. The sample plots for detailed regeneration inventory on transects were placed in a distance of 100 m to each other. No sample plot was laid closer than 50 m to roads to avoid edge effects like higher light penetration through opened canopy or trampling.

Each circular plot had an area of 5 m² (radius = 1, 26 m). The total woody plant strata were recorded to a diameter of 5 cm in DBH. Plants younger than 2 years were defined as seedlings and plants of 2 years age or older as saplings. Number of seedlings and saplings respectively was recorded per species. For saplings, height was measured and age estimated. Health conditions were described as "healthy" or "damaged" and if visible, the cause of damage was noted, e.g. browsing, fungi, insect etc. Information about site conditions was collected

including type of soil disturbance, canopy closure in five classes (see 2.3.2) and the occurrence of seed trees within the range of visibility. The field layer within the sample plot was described. The most dominant species and its area coverage (%) in relation to all other field layer species were noted. Furthermore, total cover of all field layer species (%) was estimated.

2.3.5 Tree ring samples of *P. sylvestris*

Tree ring samples (increment cores) were collected in total from 28 recently dead *P. sylvestris* trees, coring of living trees was not permitted by the National Park Administration of BNP within the three study sites of the strict reserve of BNP. These trees were described and mapped earlier during transect walking. The trees were primarily cored for age determination and if possible for detection of past fire year(s). In the latter case the increment core was extracted close to the open fire scar on the stem. The cores were extracted with a “Haglöf” increment borer. On trees cored for age determination the corer was placed as close to the ground as possible (40–130 cm). Coring height was noted to recalculate germination dates in the laboratory analysis (McBride 1983; Niklasson et al. 2010). On trees with open fire scars it was aimed to hit the youngest scar (M. Niklasson pers. inform.).

2.3.6 Laboratory analysis and calculations

Laboratory analysis followed the common practice in dendrochronology of preparing and evaluating wood cores (Zin 2007; Niklasson et al. 2010). The cores were glued on wooden slats and after drying sanded with a belt sander. A sanding paper grid sequence of 40, 100, 150, 240, 320, 400 and 600 was used. Applying scalpel and zinc paste further increased the visibility of even very narrow tree rings. Under a dissecting microscope with a magnification of 6x40 magnification ring counts and cross-dating according to standard dendrochronological methods (Stokes & Smiley 1968; Yamaguchi 1991) were carried out. Examples of local pointer years used for cross-dating are: 1976 (narrow), 1952 (narrow), 1940 (narrow and/or pale), 1848 (wide), 1811 (narrow), 1762 (narrow), 1760 (narrow), 1695 (narrow). When in the sample the pith of the tree was missed, the year of the pith was estimated. After estimating the distance to the pith with a tool called “pith estimator”, then measuring the width of the last three rings present in the sample, it was possible to calculate mean annual growth in millimeter of the young tree. Dividing the width of “missing rings” by this value, the estimated distance to the pith in years could be calculated (Brown & Wu 2005; Brown 2006; Zin 2007). If a tree was rotten inside and it was not possible to calculate the distance to the pith from the sample, the pith year was estimated with help of the following method: The missing radial length in cm (all DBH of pine trees were measured) was compared with a site adapted growth curve. This curve was derived from the mean radial increment in cm reached by trees with complete rings until the pith in the juvenile age from 10 to 80 years. Then the pith years of the rotten samples could be roughly estimated by adding the missing years in

relation to missing cm of the core's length. To correct coring height and then be able to estimate the real age and germination years of cored trees, it was referred to Zin (2007) in which empirical data for height growth increment of young *P. sylvestris* trees in BF was gathered. In addition each tree core was carefully examined for anomalies in growth patterns which could be caused by the influence of fire on the tree. Visible fire scars and suddenly occurring strong growth depressions, which could last for 2–10 years are thereby assumed as indicators (Schweingruber et al. 2006; M. Niklasson, pers. obs. in Niklasson et al. 2010). If growth depressions as described above were seen in the same year as a fire scar recorded in another tree of the same site, this was noted as a fire event.

2.3.7 Mapping

The production of maps and spatial measurements was done with the geographic information systems Quantum GIS Enceladus 4.0 and ArcGIS 9.3.

2.3.8 Calculation programmes and statistical analysis

Calculations and statistical tests were performed in Microsoft Office Excel and Minitab 15.

3. RESULTS

In sum 723 *Pinus sylvestris* individuals were found in the three study areas. Mean number of pine trees over all three sites was 3,1 per hectare (Table 1). Most of the trees were large in diameter and height and assessed to be between 100 to 250 years old. Fire scarred were 18,4% of all pine trees recorded (133 trees) and about half of them also chipped for wood splints by people (culturally modified trees- CMTs). Of those, 52 trees were multiple fire-scarred.

Oak regeneration density was highest in site 3 “Paharelec” with 89,1 trees per hectare. There was no single *Pinus sylvestris* regeneration found on the macro- and micro-scale inventory. Also *Picea abies* regeneration was sparse with low seedling and sapling density in sample plots of site 2 “Orłowska”. The tree species with the highest frequency in the regeneration sample plots of all sites was *Acer platanoides* for both seedling and sapling stage. *Tilia cordata* was found to be the second most frequent tree species in the seedling stage followed by *Fraxinus excelsior* and *Carpinus betulus*. In the sapling stage instead *C. betulus* was the second frequent tree species regenerating followed by *Ulmus spp.*

In sum 28 Scots pine trees were cored: nine in site 1 “Dziedzinka”, 11 in site 2 “Orłowska” and eight in site 3 “Paharelec”. In site 1 “Dziedzinka” the oldest recording tree germinated in 1637, in site 2 “Orłowska” in 1642, in site 3 “Paharelec” in 1728.

3.1 PINUS SYLVESTRIS TREES

3.1.1 Maps

The spatial structure of standing pines and locations of fire scarred trees are depicted for each site (Map 2, 3, 4). The number of inventoried pine trees were different for the three sites were: in Dziejzinka 262, in Orłowska 416 and in Paharelec 45 trees per hectare, and varied from 0,86 to 3,96 trees per hectare (Table 1).

In site 2 “Orłowska” most pines in total numbers and highest densities per hectare were found. Especially the compartment 344 is rather a pine dominated stand, although classified as *T-C* forest type. In squares 318 C and D trees aggregate in smaller groups and/or close to the adjacent forest types, in square 317 D close to the bordering stand of *M-C* (LMsw) type.

In site 1 “Dziejzinka” tree density per hectare is little less than in Orłowska. The pines are concentrated parallel along the road Poprzeczny Tryb.

In site 3 ”Paharelec” trees are scarcer with main occurrence along the road Objazdowa Droga. One third of all trees are located in a group close to the moist *Sphagno girgensohnii-Piceetum* (LMw) forest type in the western part of the site.

Fire scarred trees were distributed evenly in sites 2 and 3 whereas in site 1 “Dziejzinka” fire scarred trees were mainly grouped a little south of the road Poprzeczny Tryb in compartment 402 A, another two in 402 B.

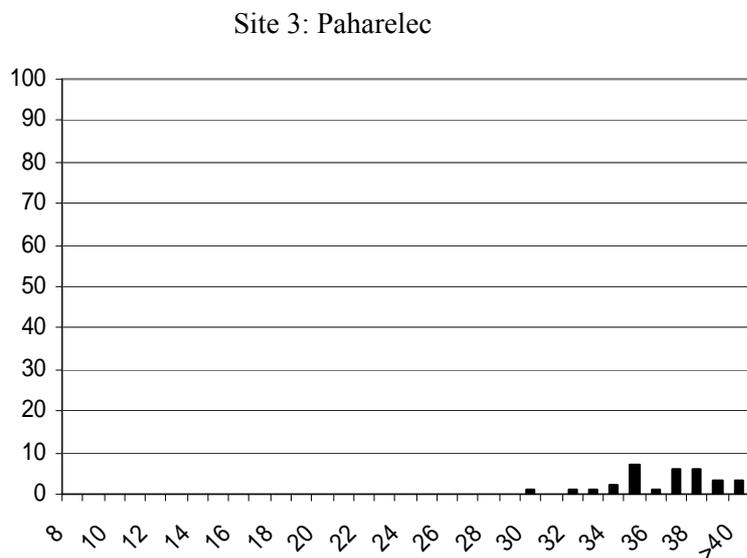
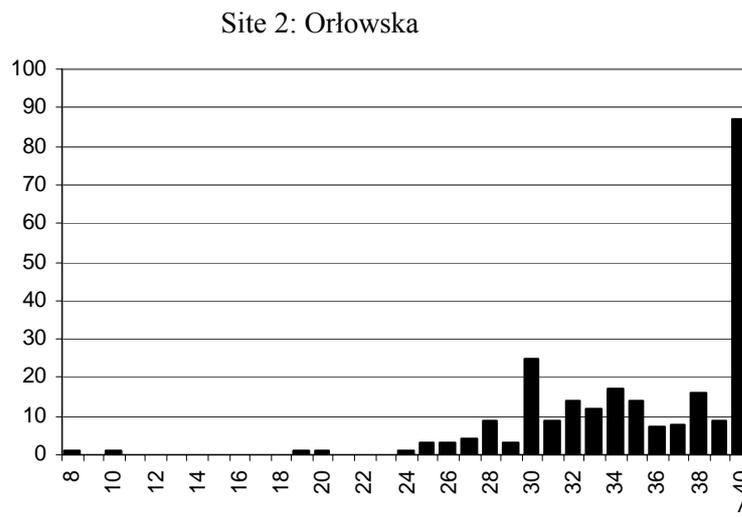
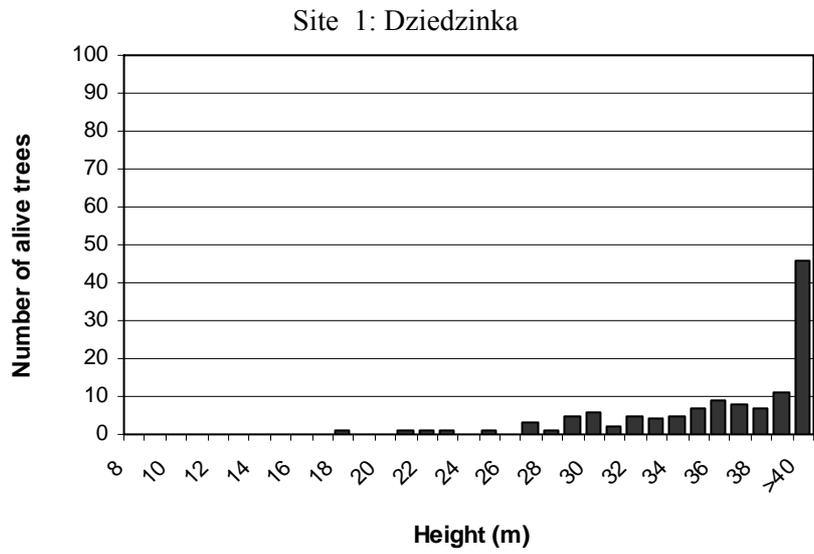
Table 1: Survey area, total number and density of pine trees for study sites.

Site	Survey area [ha]	Pine trees [N]			Density [N/ha]
		alive	dead	total	
1: “Dziejzinka”	71,8	124	138	262	3,6
2: “Orłowska”	105	245	171	416	3,96
3: “Paharelec”	52,5	32	13	45	0,86
All sites	229,3	401	322	723	Area weighted mean 3,1

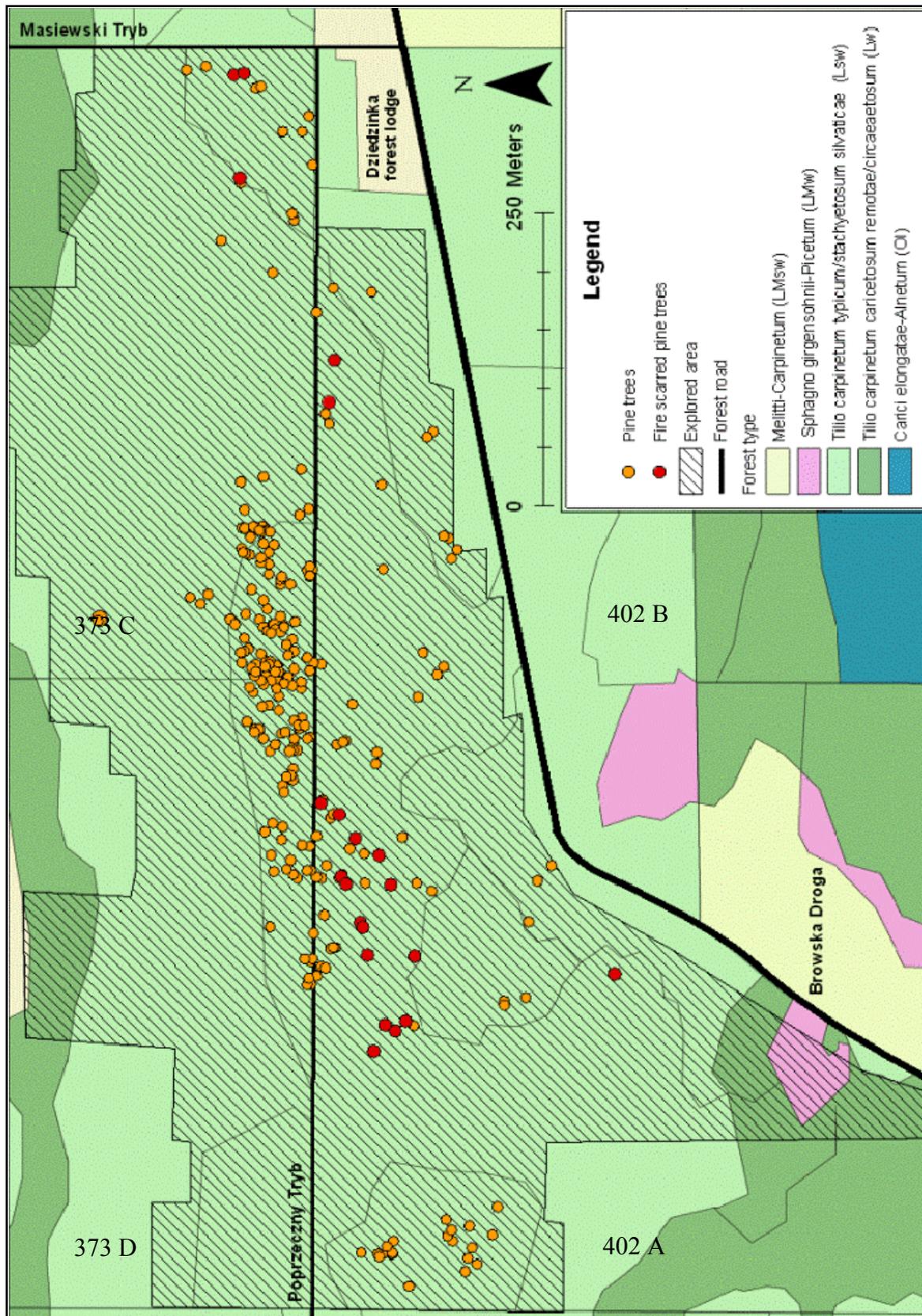
3.1.2 Height

Heights of living trees varied between 8 and 46 m, average tree height ranged between 29 to 32 m for the three study sites. 359 living pine trees ≥ 30 m (50% of all recorded trees) participate in the uppermost crown layer and their crowns reach above the canopy of surrounding trees.

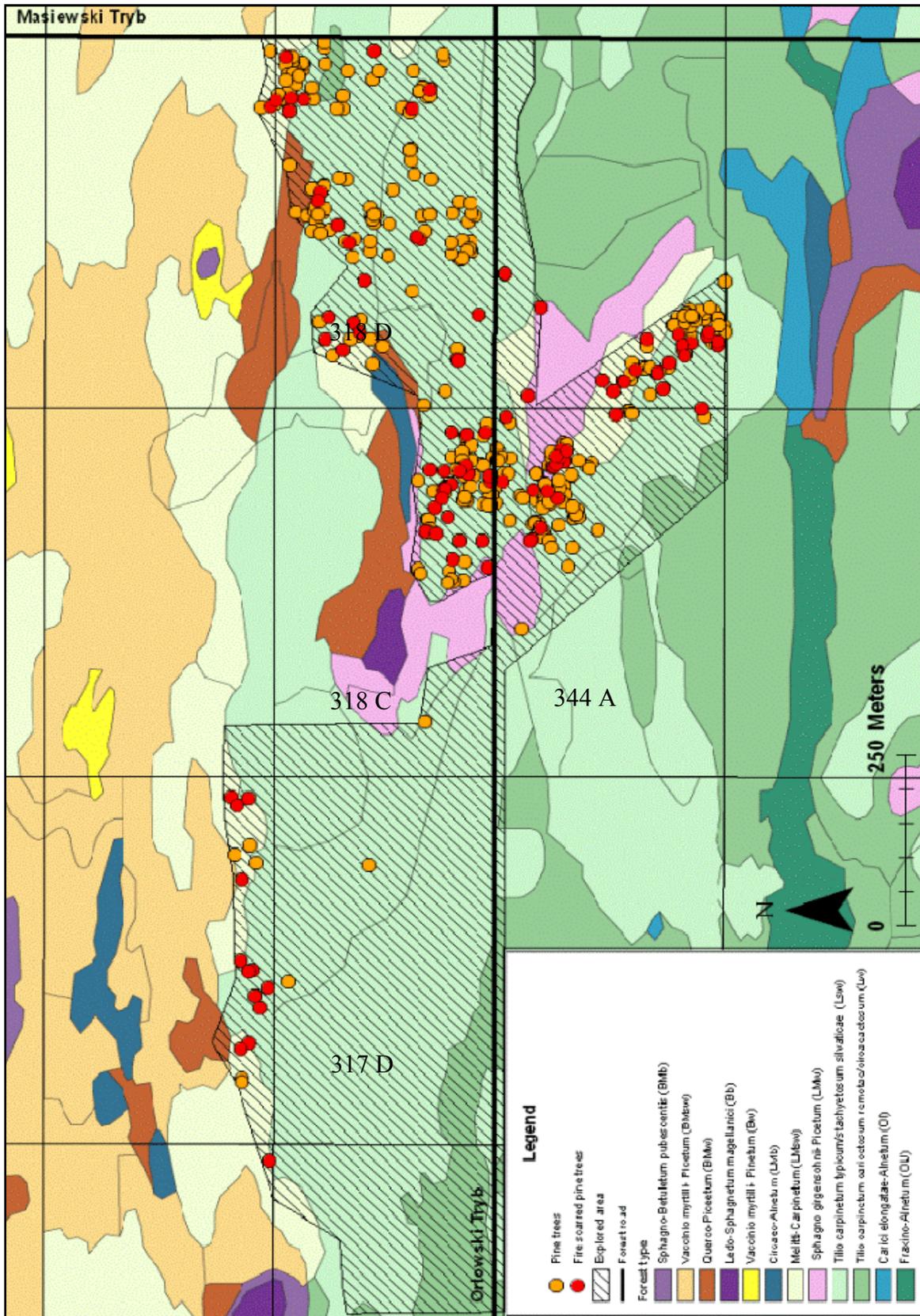
Figure 3: Height distribution of live pine trees.



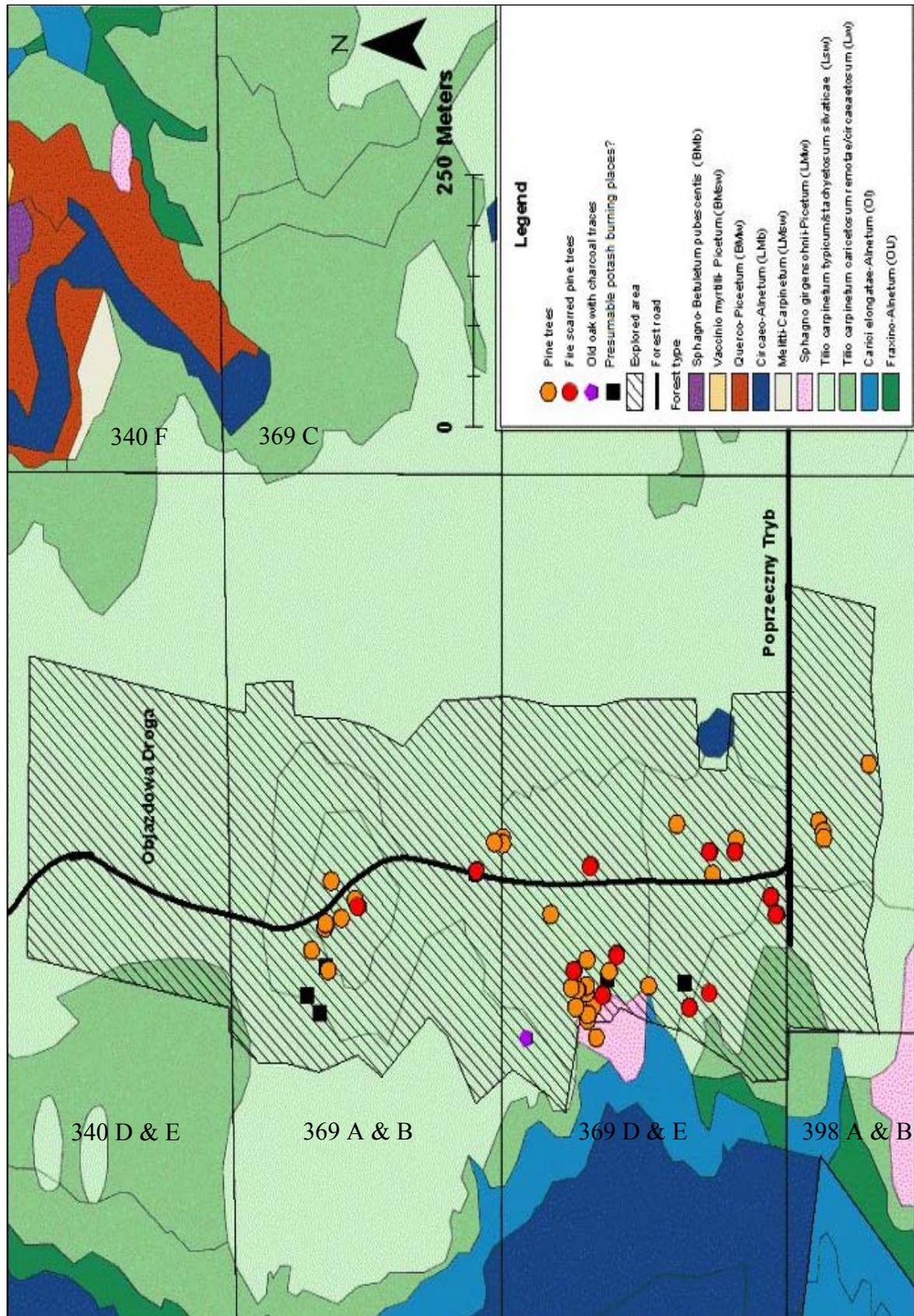
Map 2 : Site 1: "Dziedzinka"



Map 3: Site 2: "Orłowska"



Map 4: Site 3: "Paharelec"



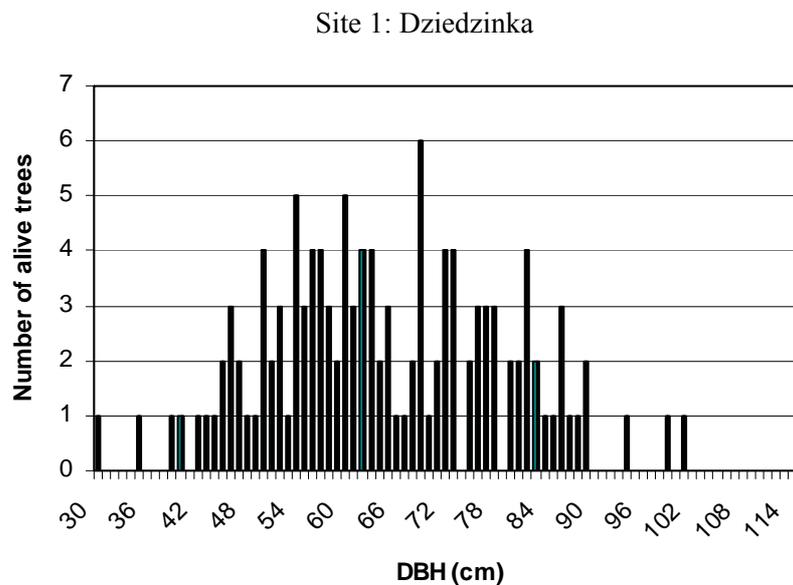
3.1.3 DBH

The pattern of diameter distribution for the sites is similar when comparing means values of DBH generally, standard deviations and ranges (Table 2 and Figure 4). In site 3 Paharelec mean diameter is higher than in the other two sites and the smallest living pine tree has a DBH of 52 cm. More than 70% of all recorded pines had a DBH of 46-89 cm. Only in site 2 “Orłowska” seven *P. sylvestris* trees had a DBH < 30 cm. Only three trees had a DBH < 20 cm: they had 5, 8 and 15 cm respectively and all of them were dead. For all sites and trees a normal distribution is confirmed by using the Kolmogorov-Smirnov (K-S) test, with an approximate P-value of > 0,15.

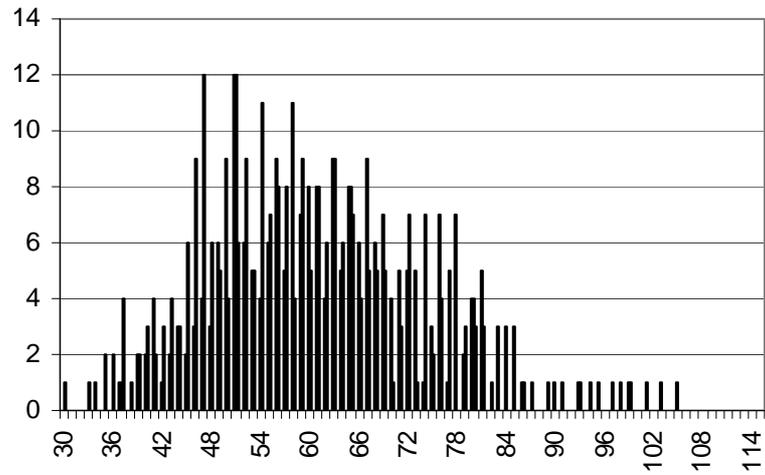
Table 2: Mean diameter and diameter range of live pine trees for study sites and in total.

Site	Arithmetic mean μ	Standard deviation	Range [cm]
1: “Dziedzinka”	65,2	$\pm 14,9$	30 - 115
2: “Orłowska”	62,7	$\pm 13,0$	34 - 105
3: “Paharelec”	76,3	$\pm 12,9$	52 - 105
All	64,5	$\pm 14,1$	30 - 115

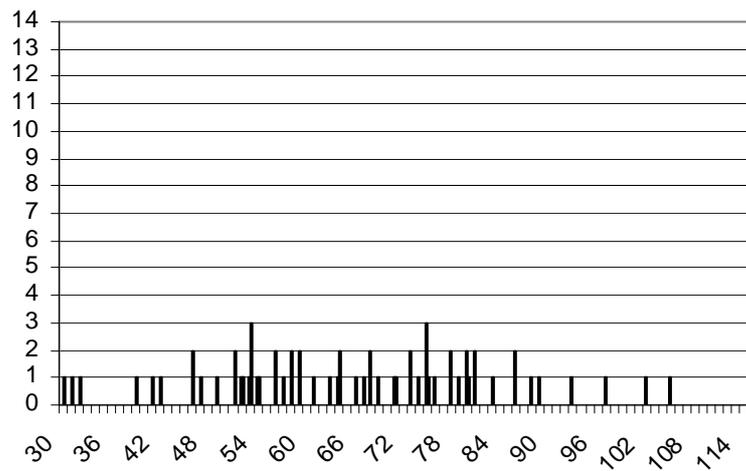
Figure 4: Diameter distribution of live pine trees for study sites.



Site 2: Orłowska



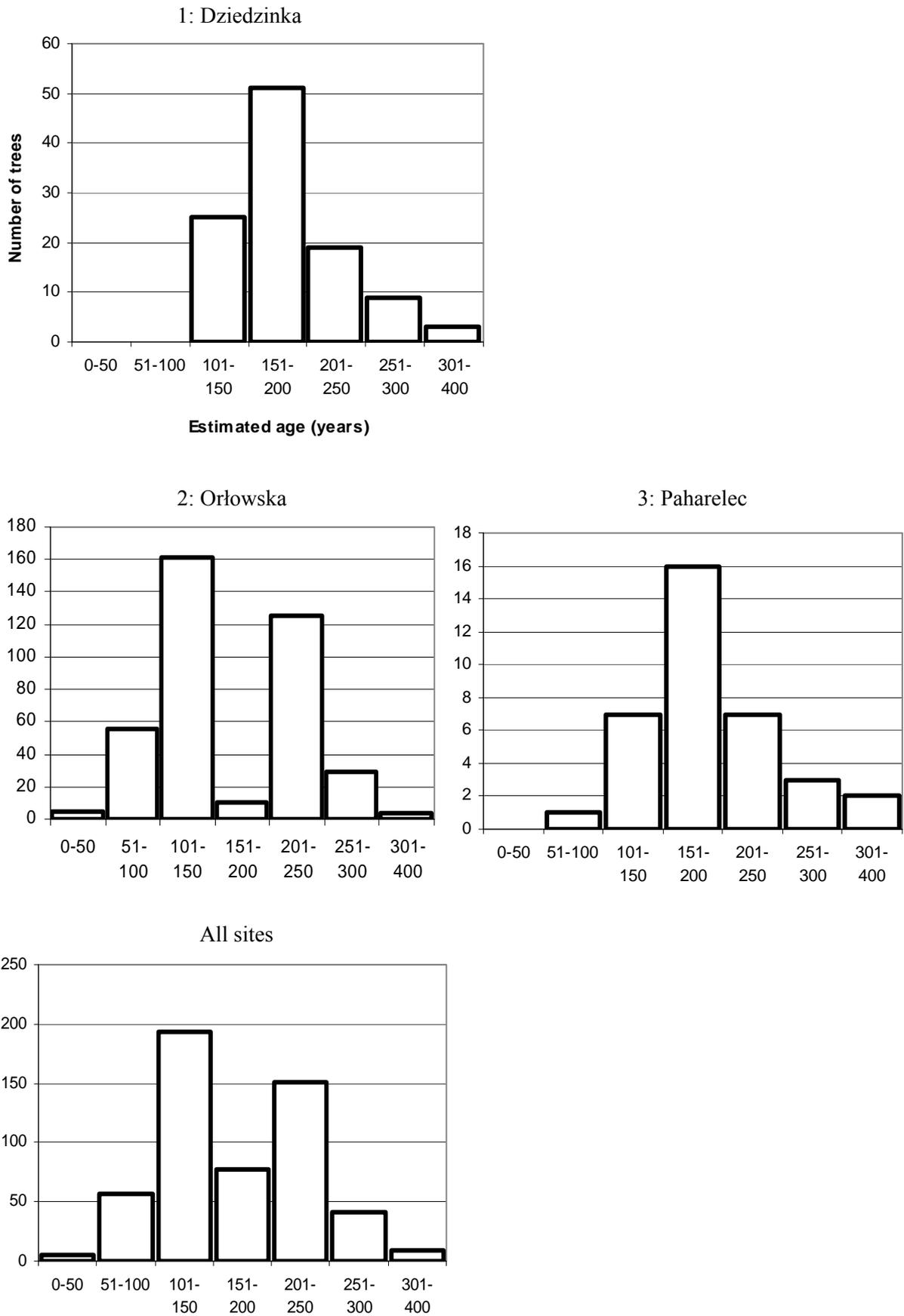
Site 3: Paharelec



3.1.4 Age

Estimated ages of pine trees in height classes can be seen in Figure 5. Of all values for age, 85% of all trees seem to be ≥ 100 to 250 years old. Only eight trees in Orłowska are suspected to be younger than 100 years. In sum nine pines are assumed to be older than 300 years.

Figure 5: Age estimations of pine trees for study sites and in total.



3.1.5 Crown conditions

There is a variation of vitality of living pine trees concerning crown conditions between sites (Table 3).

Table 3: Crown conditions of alive pine trees for study sites in % of all recorded trees.

Crown condition	Site 1: Dziejzinka	Site 2: Orłowska	Site 3: Paharelec
Healthy	47	58	75
Damaged	2	1	5

3.1.6 Stem conditions

There is a variation of vitality of living pine trees concerning stem health conditions between sites (Table 4), which seem to correspond with the values for crown conditions (Table 3).

Table 4: Stem conditions of alive pine trees for study sites in % of all recorded trees (dead trees included).

Stem condition	Site 1: Dziejzinka	Site 2: Orłowska	Site 3: Paharelec
Healthy	43	58	78
Damaged	4	1	3

3.1.7 Stem modifications

Type and amount of trees with stem modifications are presented in Table 5.

12 living pines were lightning scarred. 18,4 % (133) of all recorded pine trees were fire scarred and about half of them (59) also chipped for wood splints by people (culturally modified trees- CMTs). All seven trees with bee-hives were dead and stand as broken topped snags under a closed canopy layer. They all show similar characteristics as: large diameter, high age with estimations in a range of 250-300 years and smaller fire scars present on stems (on six out of seven trees). Two stumps of pines in site 3 were obviously cut by axe presumably at the beginning of the 20th century. When excluding lightning scarred trees a share of 19% of all pines obtain at least one or more features of a CMT, fire scars included. If lightning and fire scars are excluded, 0,97% (7) of all recorded trees obtain a feature of a CMT. When the index is split up for sites, in Dziejzinka 8%, in Orłowska 25 % and in Paharelec 29% of all recorded trees show at least one feature of a cultural modification. Considering this value without fire scars, 9,5% of all recorded trees were modified by chipping for wood splints, bee-hive caves or axe cutting. These marks are undoubtedly signs of past anthropogenic utilization impact on forest stands in the strict reserve of BNP. Due to the differences in individual stand history, it is difficult to assess the former total number of

pine trees and furthermore the rates of CMT. Especially the probable cuttings of pines, which are documented for site 1 and 3 from the 18th to the early 20th century (Michalczuk 2001; Keczyński 2007) could have influenced either an increase or decrease of the CMT rate, depending on which wood qualities were favored during extraction.

Table 5: Stem modifications of pine trees for study sites.

Tree Modification	Site 1: “Dziedzinka”	Site 2: “Orłowska”	Site 3: “Paharelec”	Total (all sites)	Share of total trees (%)
Lightning scarred	4	7	1	12	1,7
Fire scarred, dead	16	59 (7 closed)	3	78 (7 closed)	10,8
Fire scarred, alive	5	43 (33 closed)	7	55 (33 closed)	7,6
Chipped for wood splints	20	33	6	59	8,2
Bee-hive caves	2	4	1	7	1
Stumps cut by axe	-	-	2	2	0,3

The total number of fire events on multiple fire scarred trees was difficult to count due to the frequent impact of chipping within the fire scar (Table 6). The number of multiple-fire scarred trees is therefore probably underestimated. On some pine trees located in the vicinity of ones with open fire scars, smaller scars on the higher part of the stem were observed, possibly marks from fires too but impossible to examine in detail. The number of counted fire events as scars ranged from two to 10 for all study sites. Maximum height for open fire scars was 320 cm.

Table 6: Characteristics of fire scarred trees in study sites.

	Total [N]	Multiple scarred [N]	Recorded orientation of fire scars	Min/max DBH [cm]	Min/max Age estimation [years]
Dziedzinka	21	6	S, W, SW	56/91	150/400
Orłowska	102	46	N, E, S, W	24/120	50/300
Paharelec	10	-	N, E, W	39/105	100-150/300

3.2 RECENT PINE REGENERATION AROUND PINUS SYLVESTRIS TREES (MICRO-SCALE)

There were no *P. sylvestris* seedlings or saplings (0-30 cm height) in a circular area of 100 m² around all the recorded pine individuals, not even where better light conditions (larger gaps) or soil disturbances (uprooting by game or wind-throw) occurred.

3.3 PINE AND OAK REGENERATION ON MACRO-SCALE

3.3.1 Maps

Regeneration of *P. sylvestris* was neither seen in the seedling nor in the sapling stage during the 3-meter wide transect walks within the three sites.

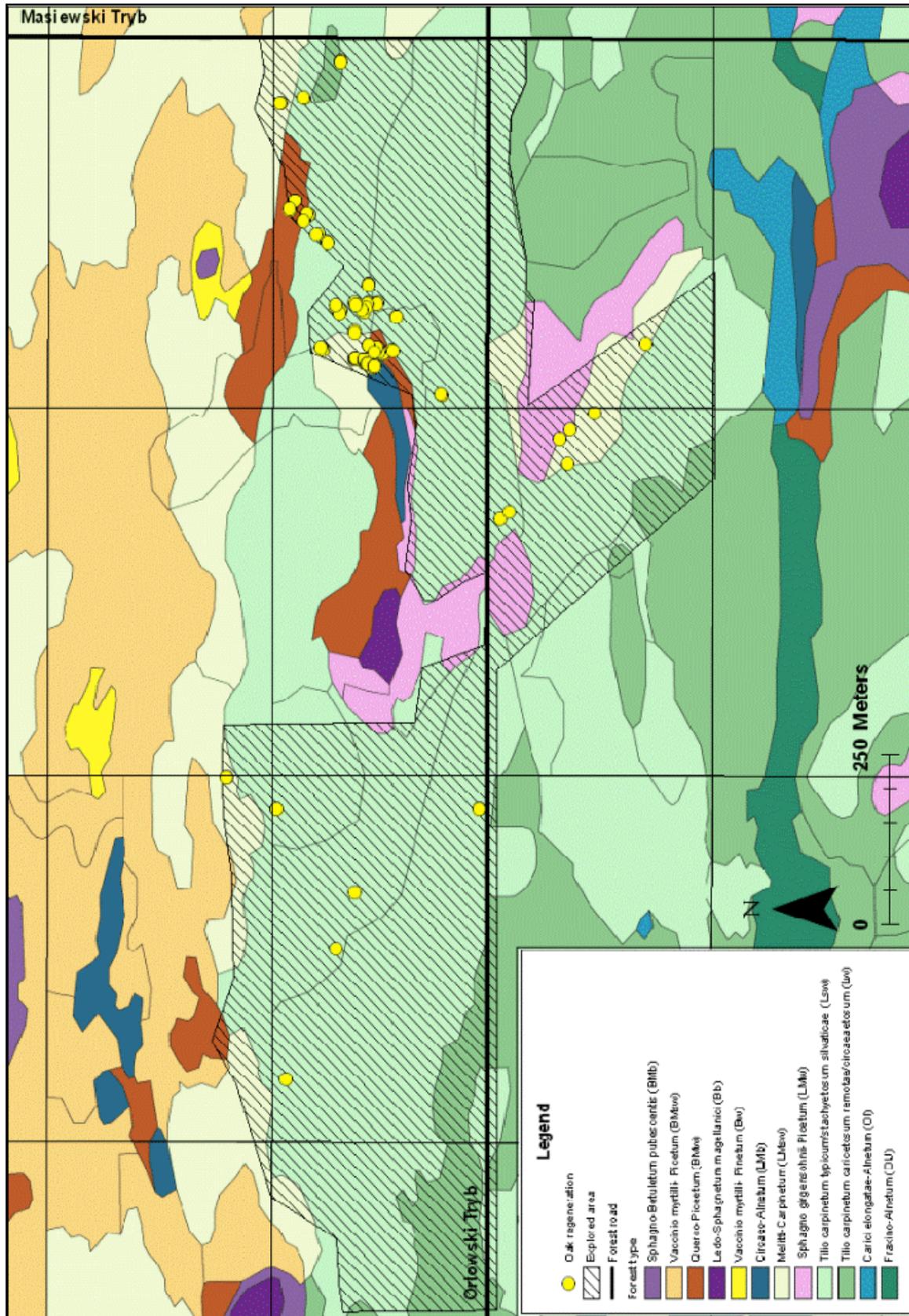
The spatial distribution of oak regeneration is depicted in Maps 5 and 6. In site 1 “Dziedzinka” only two oak individuals in young sapling stage were found and therefore no map has been produced separately. In “Orłowska”, oak regeneration was concentrated on borders between the forest types of *Tilio-Carpinetum* and *Querco-Piceetum*. On 23 spots seed trees were in a visible range. In site 3 “Paharelec” the distribution of oak regeneration seems more evenly spread over the whole site, seed trees were always present in direct view.

Densities of oak regeneration per hectare for the three sites are very different and highest in site 3 “Paharelec” (Table 7). In parts of the forest stands of site 2 and 3 oak is the dominant tree species and obviously can produce seedlings to a higher amount.

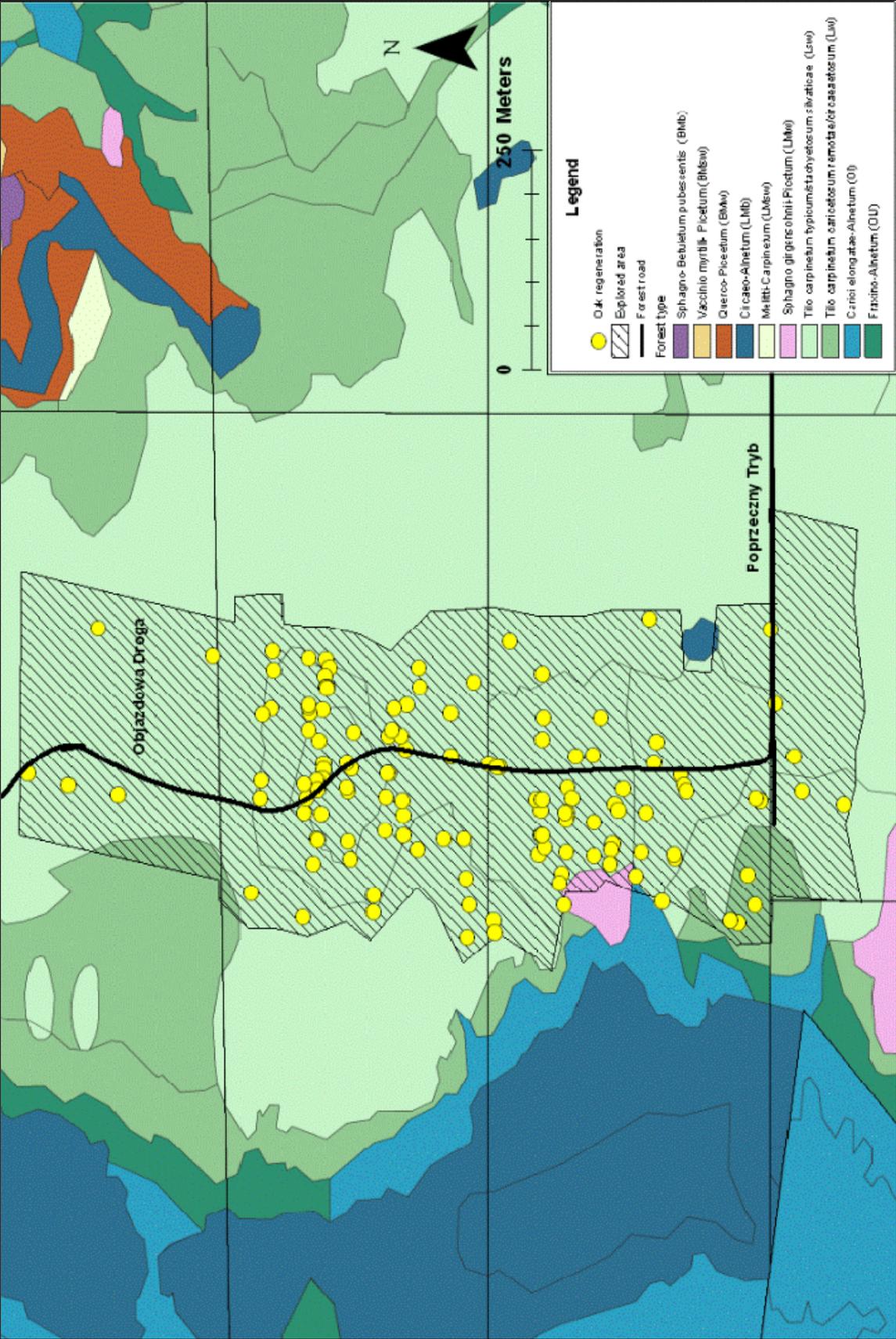
Table 7: Total number and density per hectare of oak regeneration for study sites.

Site	Transects [N]	Covered transect area [ha]	Total oak regeneration [N]	Density [N/ha]
Site 1: “Dziedzinka”	37	2,1	2	1
Site 2: “Orłowska”	41	4,4	68	15,5
Site 3: “Paharelec”	27	2,2	196	89,1

Map 5: Oak regeneration in site 2: "Orłowska"



Map 6: Oak regeneration in site 3: "Paharelec"



3.4 REGENERATION OF ALL TREE SPECIES ON MICRO-SCALE

In none of the 93 analyzed sample plots seedlings or saplings of *P. sylvestris* were found. Also spruce regeneration was rare, only five seedlings and one sapling were recorded in total. The tree species with the highest frequency in all sites was Norway maple for both seedling and sapling stage (Table 8).

In all sites species richness was low in the seedling stage, consisting to a major part of three tree species, namely Norway maple, small-leaved lime and hornbeam. In site 3 “Paharelec” the second frequent tree species was ash (Figure 6).

The species richness in the sapling stage is generally more diverse than in the seedling stage (Figure 7). Besides Norway maple, lime and hornbeam mainly broadleaved species like elm, European ash, aspen, birch, elder (*Sambucus spp.* L.), common hazel (*Corylus avellana* L.), pedunculate oak and rowan were found. A single spruce sapling in the “Orłowska” site appeared. These tree species appeared with higher frequencies compared to their shares in seedling stages, with exception of ash in site 3 whose share decreased in the sapling stage considerably.

Overall, limes in the sapling stage are less frequent than in the seedling stage (2-7% to 4-29%). Vice versa, hornbeam accounts for 15-22% of the saplings in all plots, while its frequency varies from 2 to 20% in the seedling stage.

Between the three sites there was a difference in mean maple seedling and sapling numbers per plot. In the sites “Orłowska” and “Paharelec” and probably as well in “Dziedzinka” (see Discussion: uncertainty of data) more seedlings than saplings were present.

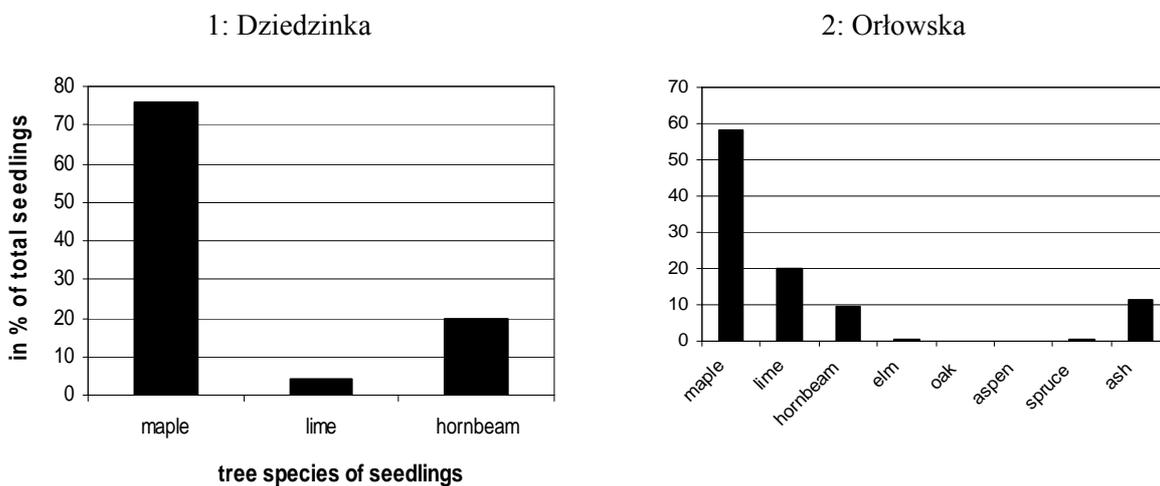
Table 8: Mean and total density of all regenerating trees in the seedling and sapling stage per sample plot and for all study sites.

Seedlings of the species	Site 1: “Dziedzinka”	Site 2: “Orłowska”	Site 3: ”Paharelec”
<i>Acer platanoides</i>	7,0	17,2	12,6
<i>Tilia cordata</i>	0,4	8,5	3,8
<i>Carpinus betulus</i>	1,8	3,7	0,5
<i>Ulmus spp.</i>	0	0,03	0,2
<i>Populus spp.</i>	0	0,07	0
<i>Picea abies</i>	0	0,17	0
<i>Quercus robur</i>	0	0	0,1
<i>Fraxinus excelsior</i>	0	0	7,1
Total seedling density	9,1	29,8	24,3

Saplings of the species	Site 1: "Dziedzinka"	Site 2: "Orłowska"	Site 3: "Paharelec"
<i>Acer platanoides</i>	14,1	2,2	7,6
<i>Tilia cordata</i>	0,3	0,3	0,2
<i>Carpinus betulus</i>	2,8	0,7	2,6
<i>Ulmus spp.</i>	0,2	0,3	0,9
<i>Corylus avellana</i>	0,1	0,03	0
<i>Sambucus spp.</i>	0,3	0	0
<i>Quercus robur</i>	0,1	0,1	0
<i>Betula spp.</i>	0,1	0	0
<i>Populus spp.</i>	0,1	0,1	0
<i>Sorbus aucuparia</i>	0,3	0	0
<i>Picea abies</i>	0	0,03	0
<i>Fraxinus excelsior</i>	0	0,17	0,3
Total sapling density	18,4	4,0	11,7

Mean total seedling density for all sites	21,1
Mean total sapling density for all sites	11,4

Figure 6: Share of different tree species regeneration in the seedling stage for study sites and in total.



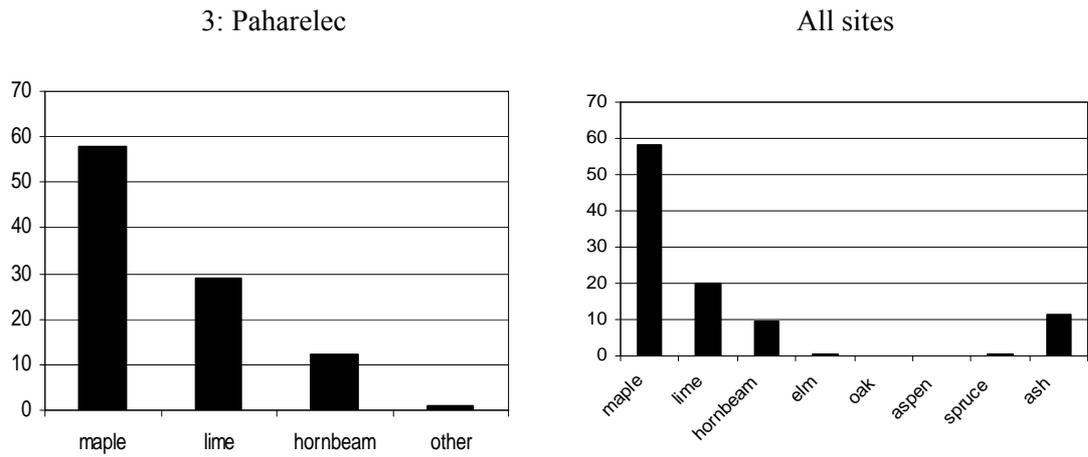
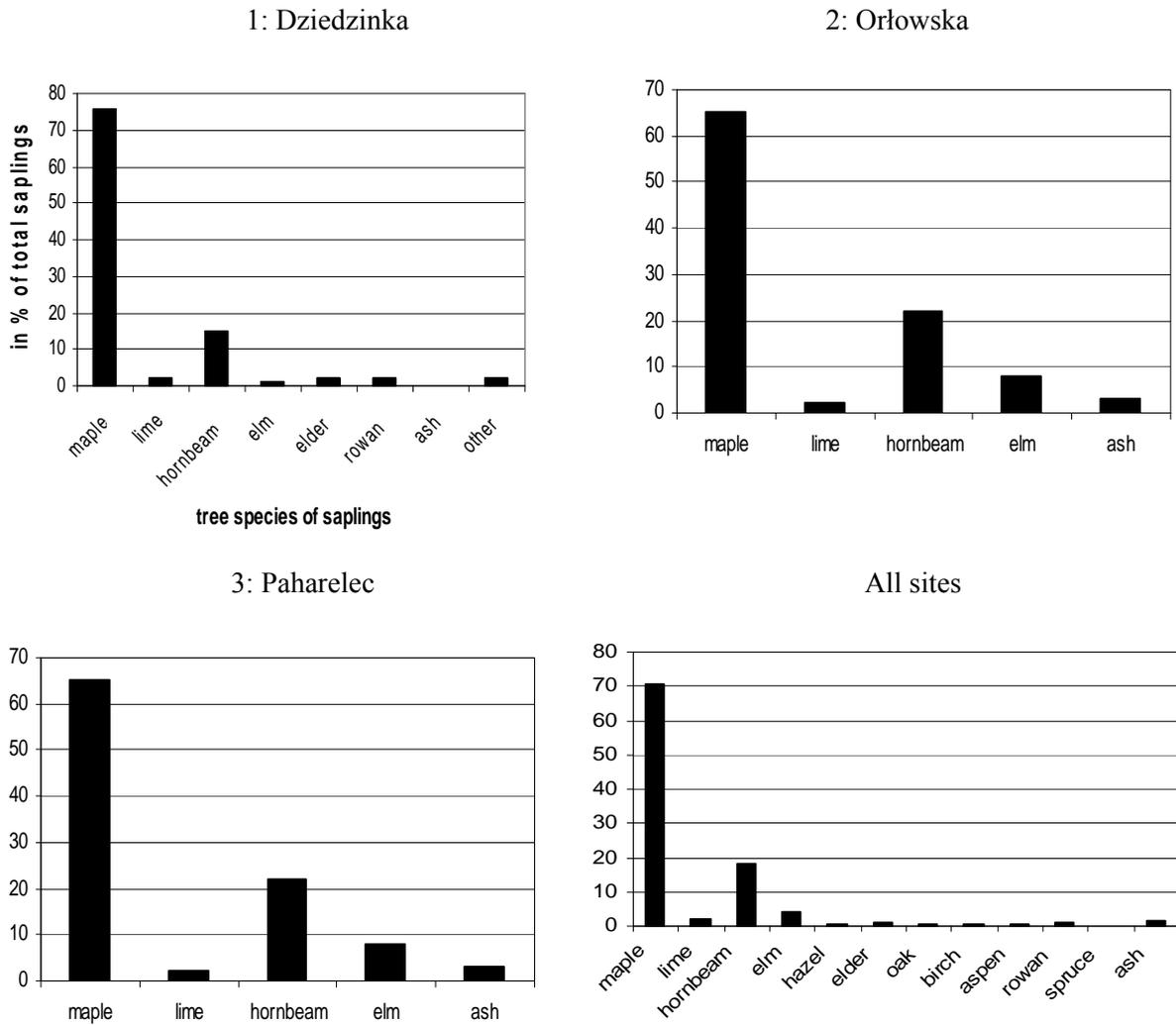


Figure 7: Share of different tree species regeneration in the sapling stage for study sites and in total.

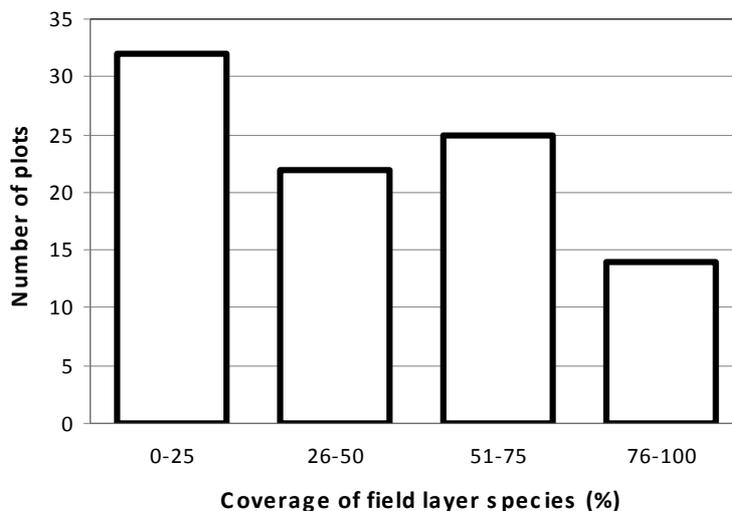


3.4.1 Growing conditions for non-woody plants and tree regeneration

The whole range of possible coverage values was captured within regeneration sample plots: from ones without any field layer vegetation at all (including plots with soil disturbance) to ones with almost total coverage (Figure 8). The value for ground coverage of non-woody plants in all 93 sample plots ranged from 0 to 99%.

Sample plots were laid out from very open conditions with canopy density class 1 (situated in wind-throw gaps) to dense conditions with canopy class 5.

Figure 8: Coverage of field layer species in sample plots pooled for all study sites.



3.5 FIRE HISTORY

In sum 28 Scots pine trees were cored: nine in site 1 “Dziedzinka”, 11 in site 2 “Orłowska” and eight in site 3 “Paharelec”.

The length of the time period for which fire history could be constructed differs between the sites. In site 1 “Dziedzinka” the oldest recording tree germinated in 1637, in site 2 “Orłowska” in 1642, in site 3 “Paharelec” in 1728. For all sites conclusions can be drawn until close present because all of cored pine trees were recently dead.

3.5.1 Maps

The spatial location of cored Scots pines, germination dates and dated open fire scars can be seen in Maps 7, 8 and 9. All three sites are interspersed by forest roads of the reserve and consecutively provide easy access.

Trees, which germinated during the 1770s until the beginning of the 19th century aggregate in larger groups on little higher elevation than the surrounding stands, e.g. in the eastern and north-central part of site 1 “Dziedzinka”, in site 2 “Orłowska” south of the road Orłowski

Tryb. In site 3 “Paharelec” a group of pines with approx. the same age occurs close to the forest type of *Sphagno girgensohnii-Picetum* (LMw). In site 1 “Dziedzinka” the oldest cored trees stand close to each other south of the road Poprzeczny Tryb. Age classes were mixed spatially at one location, which means that the older trees probably served as seed trees for the younger ones, e.g. in site 2 “Orłowska” close to the road Masiewski Tryb and the forest type *M-C*, and in the northern part of site 3 ”Paharelec”.

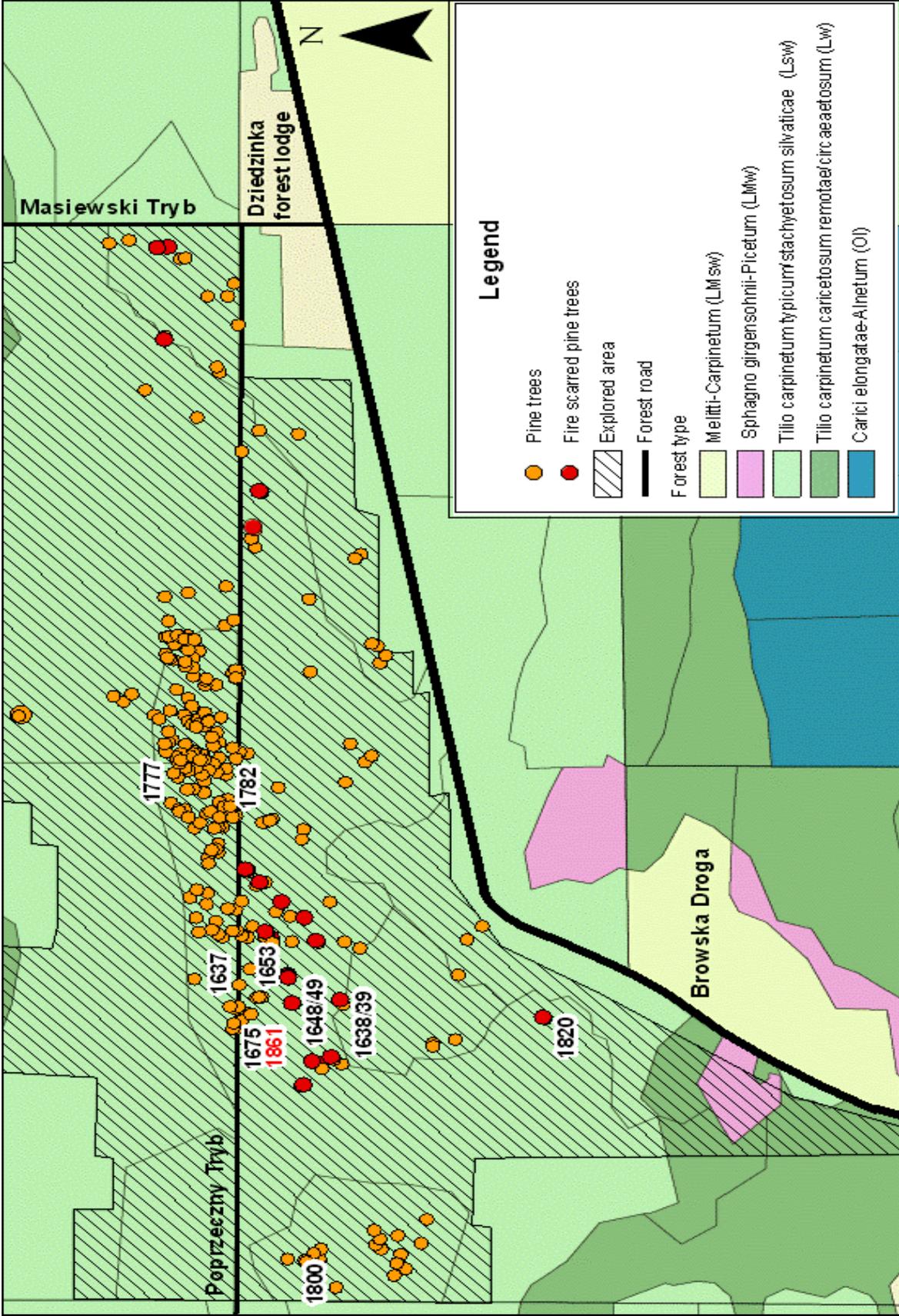
3.5.2 Dated fire scars

In sum, four fire-scars in three pine trees were dated from site 1 “Dziedzinka” and site 2 “Orłowska”. In site 3 “Paharelec” no trees were found with open fire scars. One fire was dated to 1861 in site 1 “Dziedzinka” and in site 2 fires were dated to 1822, 1833 and 1851 (Table 9).

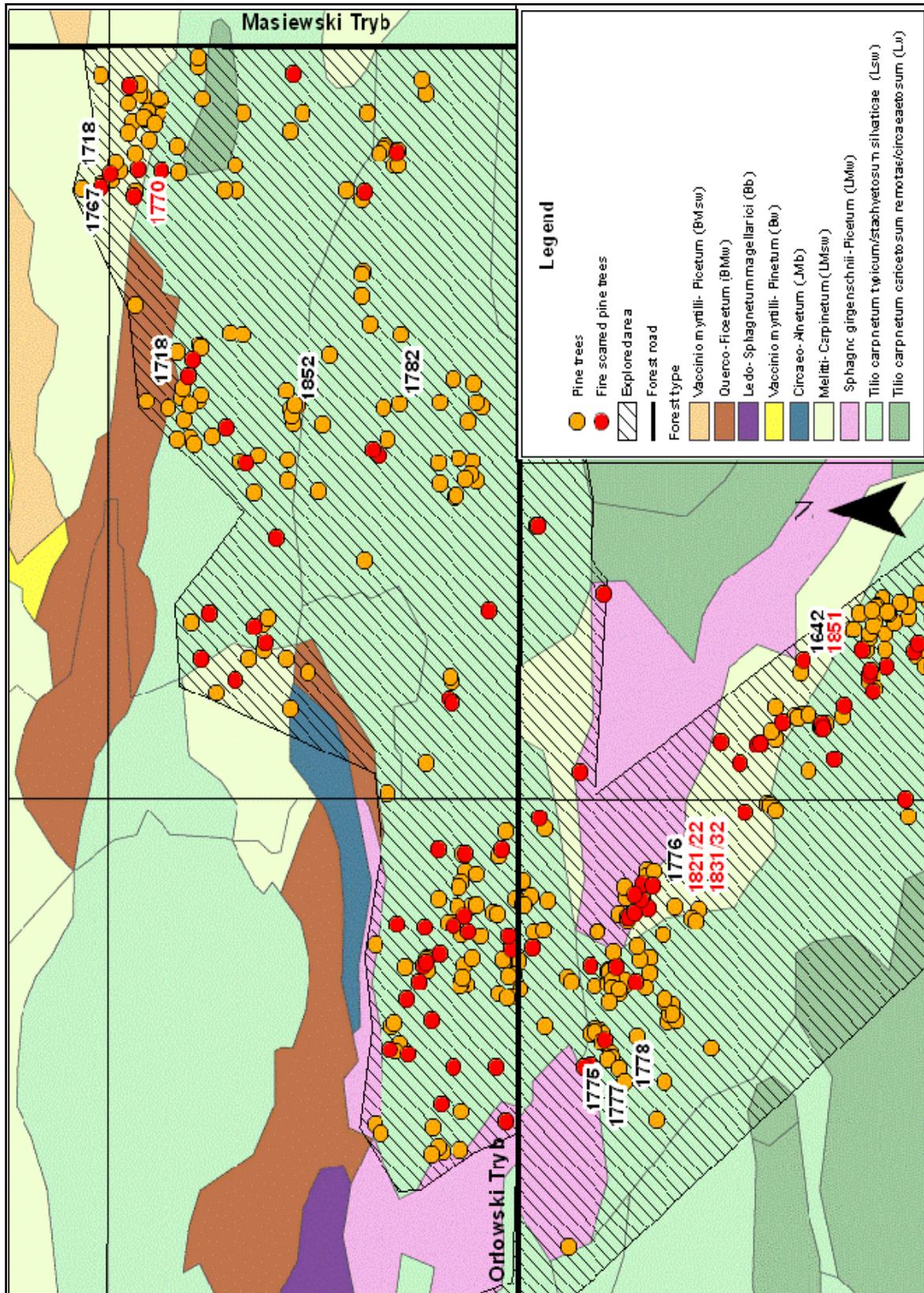
Table 9: Dated fire scars in the study sites, recording trees in the same stand and all analyzed trees from the three study sites recording a fire year as growth depression.

Site	Fire date [years]	Trees with fire scar/ reaction [N]	Trees of all sites with fire scar/reaction in same year [N]
1: “Dziedzinka”	1861	6	6
2: “Orłowska”	1821/22	3	4
	1832/33	1	5
	1851	4	19

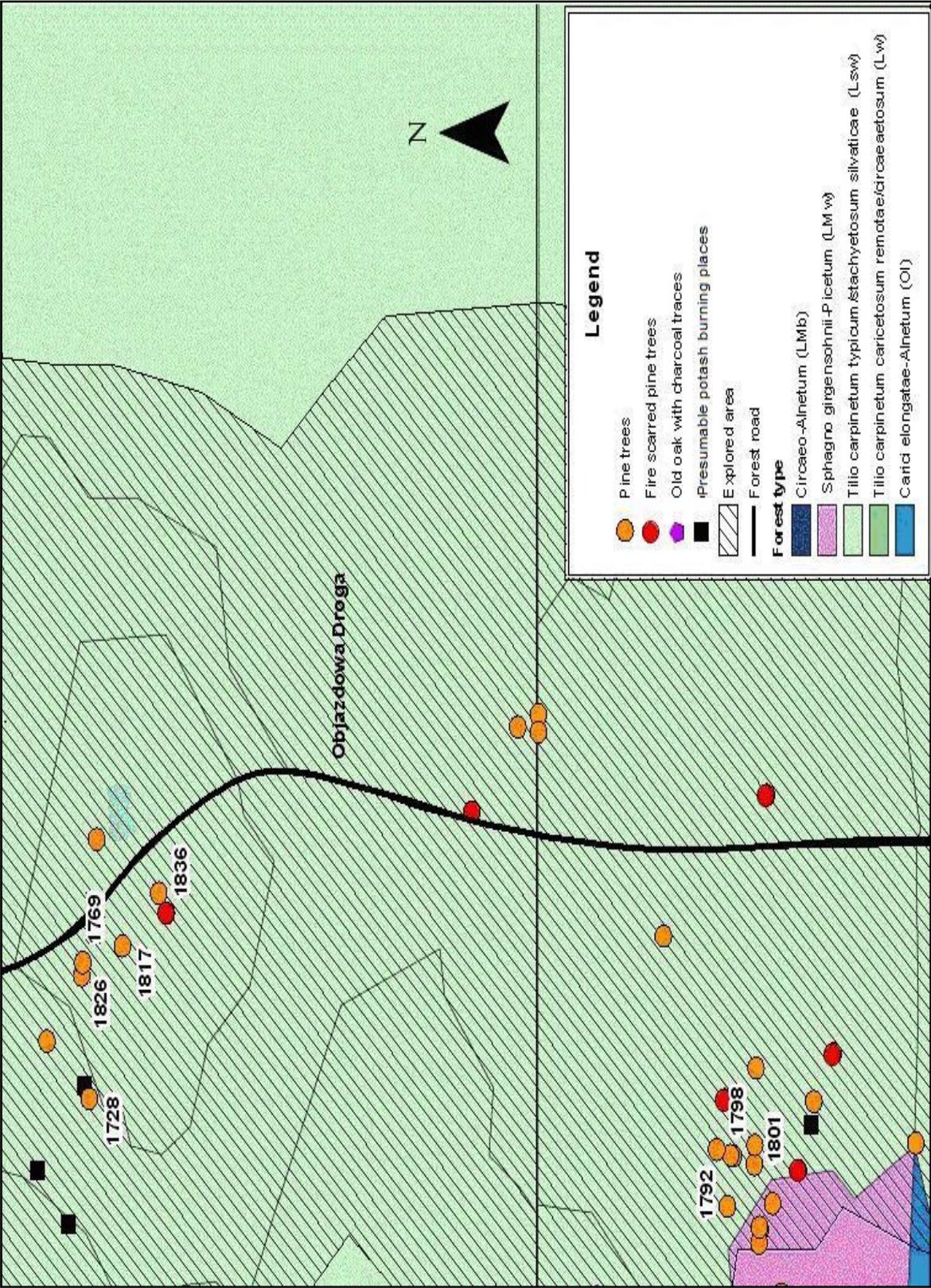
Map 7: Site 1 "Dziedzinka", Germination dates of cored pine trees in black, dated open fire scar years in red.



Map 8: Site 2 “Orłowska”: Germination dates of cored pine trees in black, dated open fire scar years in red.



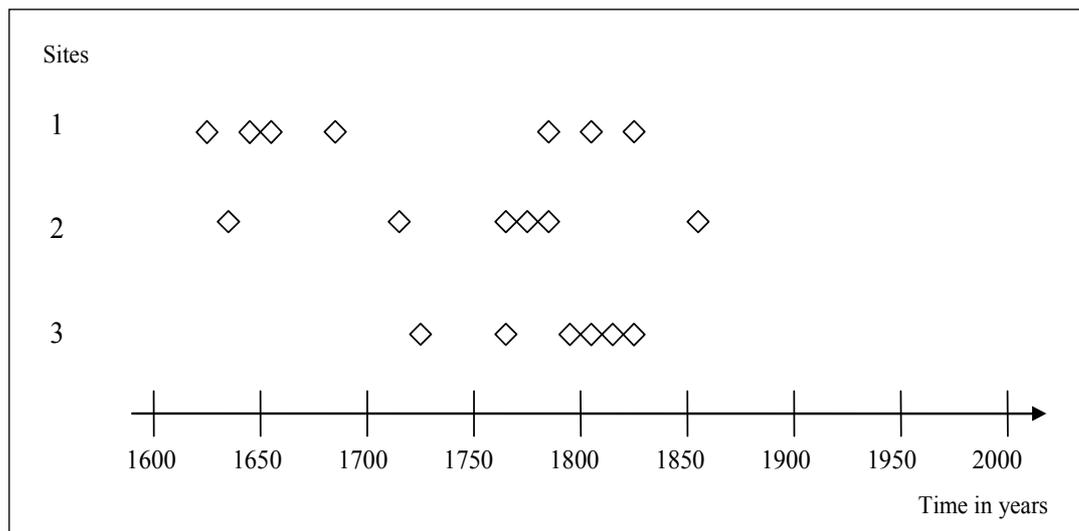
Map 9: Site 3 “Paharelec”: Germination dates of cored pine trees in black, no open fire scars on pine trees.



3.5.3 Regeneration pulses of Scots Pine

Following renewal periods of Scots pines can be distinguished for the three sites in accordance with germination dates (Figure 9).

Figure 12: Renewal periods of Scots pine in the study sites. Dates or periods marked with \diamond



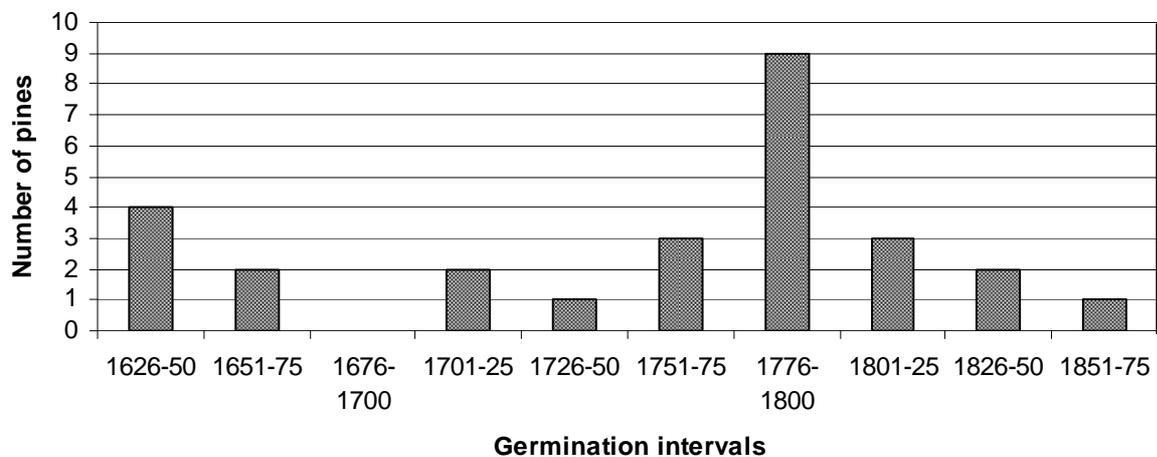
Site 1 "Dziedzinka": 1637/38, 1648-53, 1675, 1777-82, 1800, 1820.

Site 2 "Orłowska": 1642, 1718, 1767, 1775-78, 1782, 1852.

Site 3 "Paharelec": 1728, 1769, 1792, 1798-1801, 1817, 1826, 1836.

Site 1 and 2 showed the same favorable germination period lasting from 1775 to 1782. If compared to estimated age classes and corrections due to laboratory analysis of wood cores, there is a peak in age class of 250 years for the studied pines in BNP. This major part of the trees would in such case have germinated in a period of 20 years, namely 1760-1780. This time period correlates well with germination dates estimated for the cored pines which as well show a peaking curve in the mid 1770s (Figure 10). A share of 33% of all germination dates falls within a 15-year period, stretching from 1767 to 1782. There are two Scots pine trees in site 1 "Dziedzinka" present which record a growth depression in exactly 1777 but not with an open fire scar (of six potential trees older than this fire year available to record with fire scars or growth depressions). The trees were in the year 1777 130 respectively 140 years old and recorded the event with a growth depression.

Figure 10: Germination dates for sampled Scots pines pooled for all sites.



The possible absence of fires for about 45 years after the likely fire in 1777 allowed Scots pine to regenerate, establish and to grow fast in juvenile age. When the next fire occurred in 1822, these trees were already resistant enough to be able to survive this fire and the following ones (1832 and 1851 in Site 2 “Orłowska”; 1861 in site 1 “Dziedzinka”). The same may be true for Scots pine trees in site 1 and 2, which germinated in the period 1637-1718 to resist the fire in 1777 or the next recorded fires in these stands: in 1861 (site 1) and 1822 (site 2).

4. DISCUSSION

Occurrence of *P. sylvestris* in *Tilio-Carpinetum*: Ending of traditional forest utilization and eutrophication?

When soil factors are considered as the underlying cause of occurrence for the tree species *P. sylvestris* is not considered a natural component in the *Tilio-Carpinetum* (*T-C*) forest association (Kwiatkowski 1994; Prusinkiewicz & Michalczyk 1998; Michalczyk 2001). In the literature, several other factors have been presented to explain the presence of Scots pine in richer habitats.

Relicts of past climatic conditions

One of the early suggested explanations for Scots pine presence in *T-C* was that of being relicts of past climatic and water-soil conditions or that they had been planted. Paczoski (1930) based his supposition “on the abundant occurrence of the *Tilio-Carpinetum* in the

neighbourhood of pines and other species (birch, aspen) specific to the forest regeneration phases and on the frequent traces of old field ridges.” Invasion of pine in brushwoods under willow and aspen was common in the 19th century after abandonment of fields. The “*splendid pines in the fragments of oak-linden-hornbeam forests*” could be of secondary but spontaneous origin. He adds that this suggestion needs “*still to be proved*” (Faliński 1986, p.58-59, p.444).

Those causes appear, however, rather unlikely: planting and regeneration on old fields cannot be witnessed by historic sources. Data about past climate and water-soil conditions from other scientific studies, dating back to the time of initial stocking of the studied forest sites of BNP are not available until now.

Abandonment of grazing by domestic cattle

Mitchell & Cole (1998) concluded from their pollen analysis that the today’s forests of *T-C* – type expanded during the last centuries on the expense of wet mixed coniferous *Pino-Quercetum* communities. According to the authors, massive self-thinning of *Picea* during the Middle Ages (which was promoted by anthropogenic activity before) caused high fuel loads and could be the reason for local fires. The expansion of *Pinus* was not promoted, because grazing pressure was moderately low during this period and allowed broadleaved taxa to regenerate continuously. This change in extension of the named forest types is not considered as an effect of the Little Ice Age in Europe with a climate cooling during 1600-1800, because in this time *T-C* expanded, although the *Pino-Quercetum* community should have increased. Instead Mitchell & Cole (1998) suggest that the changes could have resulted from the abandonment of grazing household animals in the forest, which led to a recession of mixed pine and oak forests. As a consequence, these forests became shadier and moister and hence many light demanding species, e.g. regeneration of the tree species *P. sylvestris* and *Quercus robur* disappeared. Simultaneously the use of fire was banned. The succession that followed can thus be seen as a result of the plant cover’s reaction to the release from various forms of human impact. This means that the Scots pines found in the study sites could be a man made assemblage/phenomenon (Kurowski 2004).

In formerly *Pinus* dominated forests, e.g. of the type *Peucedano-Pinetum*, reduced incidences of fires and high browsing pressure caused the increased cover of *Picea* during the late 19th and early 20th century. When grazing of household animals decreased and game heads were controlled since the establishment of the National Park, generally hornbeam and lime, in some parts also aspen (and oak) invaded the forest stands. Again intensive self-thinning of *Picea* was observed in the 1980ies (Faliński 1986) in stands where the tree species expanded in response to the high game densities in the last century (Mitchell & Cole 1998).

Eutrophication

A theory of Sokołowski (1991) gives more weight to the changes in soil properties during the last decades. In BNP fertilization from dead wood is constantly taking place because all

timber is left in the forest habitat (Pawlaczyk 2009). But especially the artificially high deposition of nitrogen is of importance. Nitrogen deposition in BNP ranged between 7-16 kg N/ha p.a. over the years 1986–2007. Currently the value has stabilized at 12 kg N/ha p.a., but exceeds the value being assumed as uncritical for natural forests of 2–5 kg N/ha p.a. As a consequence eutrophication of forest habitats is observed since the last 40 years (Malzahn 2009), playing a decisive role in forest dynamics today (Bernadzki 1998 et al., Matuszkiewicz 2007). Following the authors' argumentation, the old pines could be relicts of poorer forest types, e.g. the *Melitti-Carpinetum* association, and do not regenerate at all, meaning that they will be eliminated in the long-term from these forest types. Habitat eutrophication could thus have led to the process of colonization of hornbeam and lime trees into formerly poorer sites, together with an increase of eutrophic species. As a consequence, the share of *T-C* forests expands in BNP (Sokołowski 1991, 1999) on the cost of Scots pine.

Characteristics of *P. sylvestris* in *Tilio-Carpinetum*

Density

In the study sites Scots pines grow in higher densities on ablation plateaus and higher elevated areas with more sandy soils. To put pine density in relation to densities of other tree species in *T-C* stands of secondary origin, data from a study of Faliński (1988) was used. The density of pines according to my calculations was 3,1 trees per hectare. Compared to values for other tree species (oak (12,5), maple (7,5), lime (177,5), hornbeam (555) and spruce (32,5)), the recorded pine density is very low in the studied areas. In combination with the data on regeneration it is clear that pine is a species disappearing from this forest type.

Age and DBH structure

As confirmed by Bernadzki et al. 1998, the diameter distribution of the recorded Scots pines is in a typical shape of an aging tree population. Since several decades, there have been no established pine saplings growing in the studied *T-C* areas. All small diameter trees were found to be dead, standing suppressed under a closed canopy with little light penetration. If saplings would recruit under very favourable conditions by coincidence, their number would be too few to ensure a continued presence of Scots pines in their current habitats.

Fire history

Historic utilization of fire, a factor favouring *P. sylvestris*

The finding of open charred multiple fire scars (up to 10 consecutive scars) is a good evidence of fire being an important factor in the history of the studied stands. Many of the fire scars had been chipped for resinous wood since fires-scarred trees were the best source for tinder to start camp fires, light and for splints to smoke bee-swarms (Samojlik 2006). Pines in *T-C*

communities are distributed in a belt-like structure, running in the direction East-West in site 1 “Dziedzinka” and site 2 “Orłowska” or North/South in site 3 “Paharelec” parallel to major roads. This spatial pattern could be caused by underlying soil factors as e.g. the prevailing occurrence of the soil types of Cambisols (Prusinkiewicz & Michalczuk 1998), soil-water conditions etc.

In historic records, scripts appear which tell about forbidden burnings in BF around 1700 (August II the Mighty). These rules indicate that fire risk was recognized or that people were igniting on purpose (Samojlik 2005). Fires were frequent and probably associated with the intensive production of charcoal, tar and potash industries situated in pine forests (Mitchell & Cole 1998). Brincken (1826) emphasizes the role of fire in pine forests in BF, which happen almost every year, mostly ignited by lightning. Irregular spatial distribution and differences in age classes of pines could indicate patchy burnings and prevailing low intensity fires during the centuries. As a catastrophic event besides storms and forest pests, fires could have promoted the exceptional even-aged and very dense pine stands. According to Brincken, local people were also aware of the use of fire, its dangers and possibilities of control, with measures known in Lithuania and Poland since a long time. Brincken’s descriptions also reveal that regeneration of Scots pine was obviously rich and successful at the beginning of the 19th century in the vicinity of older pines and in entanglements of dead wood.

The catastrophic fire of 1811 had a significant effect of following forest dynamics in the stands affected, e.g. the cohort regeneration of *P. sylvestris* (Faliński 1986).

Effects of fire on forest regeneration and dynamics

The degree of removal of spruce, deciduous trees and the field layer is largely dependent on fire presence or absence. If canopy closure remains dense due to little mortality of older trees during very low intense ground fires or their absence, pine regeneration will be less (Zin 2007, Niklasson et al. 2010). Following this argumentation, cohort regeneration of pine in *T-C* communities could derive from fires burning in high intensities, in combination with recurrent fires. From this study no cohort regeneration of Scots pine can be found after the turn of the 19th century. If fires are not occurring anymore, Norway spruce rapidly may become abundant because of its better competitive ability under low light conditions. Such stand replacement can also take place with broadleaved species. As a consequence pine dominance regressed in BF even in mixed and coniferous forests. In combination with increasing grazing pressure in the 19th until the beginning of the 20th century, periodically spruce expanded but is nowadays replaced by various broadleaved species due to decreasing grazing pressure (Bernadzki et al. 1998, Mitchell 1998; Samojlik 2006). The combination of fire with low grazing pressure would explain the recent development of succession in site 1 “Dziedzinka”, which could have been favoured by heavy selective cuttings at the beginning of the 20th century (Michalczuk 2001). High fuel loads of slash deriving from pruning and dead wood favoured single burnings, probably carried out by farmers and Russian convicts, during war times from 1915 to 1945 (Koop 1989). Self-seeded pioneer tree species are replaced by

broadleaved species such as lime, hornbeam and maple, while regeneration of pine and spruce is almost absent.

Hard-wood dominated communities in the lowlands with an open grassy understorey, may support high-frequency, low-intensity fire regimes (Abrams 1992). Pedunculate oaks are associated with Scots pines in the study sites and it is known that oaks are able to survive low intensity ground fires. Their thick bark, ability to compartmentalize rot and for young saplings to resprout after periodic surface fires make it possible to persist enduring as a broadleaved tree species in forest stands with a light fire regime (Brose et al. 2001). Mitchell & Cole (1998) confirmed with the method of soil hollow analysis a substantial increase of *Gramineae* pollen around 1750 A.D. in BNP, indicating open canopy coverage and lighter conditions on the forest floor.

During the 19th century *P. sylvestris* could have dominated forest stands as described above, as a result of fire. Later, after active suppression measures spruce regenerated well. The successional changes in those *Melitti-Carpinetum* (M-C) forest associations in the absence of fire and animal grazing have altered forest composition and structure in ways that have greatly diminished flammability, and therefore fire likelihood across whole BNP (Kwiatkowski 1994; Matusziewicz 2007). It can be suggested that the studied *T-C* forest stand in compartment 344 with high Scots pine density was in former days similar to the “*Lado forest*”/drier *M-C* type and that this part was therefore explicitly integrated into the protection plan of BNP in 1921 (Okolow 2009). Nowadays the described forest types are in the process of recession.

Regeneration

Regeneration of Scots pine under competition and browsing pressure in *T-C* communities

Today, the development of Scots pine regeneration is not favoured in the studied *T-C* sites. The complete lack of seedlings and saplings of *P. sylvestris* in the studied sites as a result of the micro- and macro-scale inventory confirms the regeneration problems of this tree species in BNP. Although wide ranges of vegetation coverage, light penetration/canopy closure, soil disturbances and distance to potential seed tree occurred in the sampled plots, even those seemingly favourable conditions did not promote the establishment of pine seedlings during the last years. As earlier studies revealed, there has been no recruitment of pines in BNP with DBH > 5cm since the last 60 years, neither in typical pine habitats nor in *T-C* communities. Simultaneously, densities of old pine trees are in rapid decline in all forest types in BNP (Bernadzki et al. 1998; Sokołowski 1999). According to the authors study results, the tree species of spruce, oak, maple and pine are diminishing in abundance in BNP. In contrast, the species are described as climax species with a continuous regeneration under their own canopy. Although tree species regeneration was found to be rich for maple, ash and oak in this study in the seedling and young sapling stage, with recruiting hornbeam and rowan, the influence of high zoogenic pressure with intensive browsing is crucial for survival and

recruitment. If trees reach the height of the browsing line, they are heavily damaged and altered in increment and vitality. Scots pine is a tree species preferred by browsing ungulates and at the same time very susceptible to browsing damages. Even in *Pinus* dominated stands in northern BNP (compartments 287, 317, 318) its regeneration seems to be sparse and restricted to the successful establishment of single trees, e.g. within dead wood entanglements (personal observations June 2010). The saplings will be damaged with high probability when reaching the browsing line by game and die off after a couple of years (Kopryk et al. 2004). Fallen logs or other woody material in larger gaps can be interpreted as a mechanism of forest ecosystems to maintain the balance of regeneration versus foraging pressure of herbivores. Those protective entanglements prevent penetration and browsing by ungulates in some areas of the forest, where young trees successfully regenerate as observed for broadleaves and spruces. They may safely grow and exceed the browse line before the CWD completely decays. In the past this mechanism could have worked for pine seedlings after occurrence of a fire, for example in entanglements of spruces killed by fires, fungi and insects. Pines occur in the study sites often in groups as quasi “little islands” in a not associated forest type, which could be a general picture in natural forests with small scale dynamics and high spatial diversity (Bobiec et al. 2005).

Long-term ecological thinking: A lack of fires

It can be asked if the driving factor promoting the regeneration of *Pinus sylvestris* in BNP, namely fire, is nowadays simply lacking (Zin 2007) or if a certain combination of different conditions must occur simultaneously to stimulate mass regeneration as it happened apparently several times during the last centuries (Pawlaczyk 2009). Apparently among other tree species, *P. sylvestris* has certain “renewal episodes” from time to time, explaining cohort regeneration with trees in same age classes. A so called “window of renewal opportunity” opens up under a so far unknown combination of ecological conditions. Proposed factors include: 1. Wild boar or red deer rooting/trampling and existence of stump holes/uprooted root plates which leads to bare soil exposure thus reducing competition for light and nutrients of other plants (Bobiec et al. 2005), 2. A drastic fall of ungulate numbers with a decrease of large herbivore (especially red deer) densities in BNP may facilitate tree species diversity and forest dynamics (Kuijper et al. 2010b) 3. Open conditions due to windfalls, snowbreaks and pest outbreaks which create gaps in the stands. The latter are not sufficient to promote a mass regeneration of *P. sylvestris*, as observed neither in coniferous, mixed nor in *T-C* forest communities. A lack of large-scale, “catastrophic” disturbances, e.g. fires, and the missing influence of man from 1921 on in BNP may cause the depression in regeneration of short lived pioneers (aspen, birch, willow) and climax, light demanding tree species like oak and pine. Fire is known as the external factor favouring the regeneration of several *Pinus spp.* around the world, creating high-light and duff-free conditions as typical for burnt areas (Sannikov & Sannikova 1985; Bobiec et al. 2005; Fesenmyer & Christensen 2010). Further investigations are needed on the kind of natural disturbances for Scots pine to remain a climax tree species component in BNP (Bernadzki et al. 1998; Pawlaczyk 2009).

The future of Scots pine in BNP

Nowadays, water resources in BNP shrink with a fall of 40 cm of the water table level over a 17-year study period in fresh and wet habitats. In the past, the water-soil conditions were probably moister. This factor would not be a favoring factor for the former establishment and occurrence of *P. sylvestris* in *T-C* associations. Anthropogenic factors affecting the climate are suspected to cause increased transpiration of plants during the vegetation season and also warmer winters, which will result in smaller volumes of melt water at the beginning of the vegetation period (Malzahn et al. 2009). When this process will continue in the future, the extension of dry habitats and growing and regeneration conditions for xerophilous species, e.g. *P. sylvestris* would be improved, also under the influence of fire due to the higher amount of dead fuel, at least in the short-term. How climate change will affect the future of pine trees in the long-term will also depend on the adaptation of the tree species, e.g. to new pests and diseases. At least the community of *T-C* is expected to increase its role in extension in BNP due to predictions of a warmer climate (Pawlaczyk 2009). To conclude, *P. sylvestris* trees seem to disappear in *T-C* habitats in the coming decades. But the qualities of longevity, durability and pioneer characteristics (when it comes to renewal demands) of the species may profit from more frequent catastrophic events as modeled by current climate scenarios.

Sources of errors, uncertainty of data

The quantity of tree ring cores taken from Scots pines was restricted by the Board of the Białowieża National Park to 30 samples. The small amount of samples makes it difficult to draw conclusions about fire history in the studied stands and furthermore for whole BNP. The quality of the cores taken was partly bad because of decomposition and rot in the material. The problem of dendrochronological analysis in the temperate zone of BF is the weak climate signal in growth patterns (not every tree is recording fires or growth depressions) and that even in the same tree the growth patterns are not uniform. Estimation of germination dates can be biased by coring height and estimated distance to pith by applying a standard height and increment growth for pines in young age. Seven cores taken from trees were rotten, so pith and germination year could only be determined by estimations. A site specific growth curve for juvenile increment growth until 80 years of age of the trees was designed, deriving from average growth for decades in tree cores with pith or close-to-pith rings. That means that for 25% of the sampled trees pith and germination dates can be only roughly determined. However, when comparing later with pointer years in the sample (but it was not possible to use those pointers for cross-dating), estimations seemed quite close to real age.

The data for estimation of tree ages was difficult to compile, as neither tree DBH, height, crown habitus or bark features are good indicators. When estimated age in the field was compared to germination dates estimated in the laboratory of the according cores, only 17% were classified in the same age class. In site 1 “Dziedzinka” tree ages were only underestimated, with values ranging from 30-170 years. Especially the very old trees over 200

years had highest deviations in age. In Orłowska tree age seems to be slightly underestimated by constantly 30 years. In site 3 “Paharelec” trees were overestimated in age by 50-140 years. The low density of seedlings counted during the regeneration study on sample plot base in site 1 “Dziedzinka” could be biased by the early time period at the end of May, when not all seedlings germinated on the forest floor. To improve the quality of comparison between sites, regeneration inventories should be carried out for all sites in a short time period.

To level out extreme differences in the distribution of the values of estimated ground coverage in the regeneration plots due to subjective selection of certain classes, broader classes could be defined before data collection, e.g. in 10% steps, especially for values over 50%.

5. CONCLUSIONS

This study confirms that *P. sylvestris* has features of an aging tree population in BNP (Bernadzki et al. 1998), where at least in the studied *Tilio-Carpinetum* forest sites has not been any successful recruitment of pine saplings since several decades. Apparently this early-successional species is not able to regenerate and establish under the prevailing habitat conditions, although areas with concentrated potential seed trees, soil disturbances and high light penetration on a small scale were present in the stands. All trees with $DBH \leq 30$ cm were dead, standing suppressed under a closed canopy, so that initial growth of the species seems to be strongly determined by competition from other species. It is possible that under high game densities in BNP, Scots pine regeneration could happen by coincidence, e.g. in dead wood entanglements. It is questioned if fertility of adult *P. sylvestris* individuals in BNP is secured: seeds derived from cones should be tested on an experimental base for germination ability, growth, sapling vitality etc.

Germination of oak seedlings was more frequent, but no further investigations about the future of this regeneration in *T-C* are made yet. As found in the micro- and macro-scale inventories, shade-bearing mid-successional and climax-species are currently regenerating under their own canopy within a small gap dynamic, first of all *Acer platanoides* was striking abundant in both, seedling and sapling richness.

The high share of Scots pines which were found to be CMTs and the overall low densities of the tree species in the studied stands (which laid in areas where past human activity traces were detected earlier) could indicate that *P. sylvestris* was subjected to heavy utilization pressure until beginning of the 20th century in BNP (Samojlik 2006). According to examined fire scars, fires could burn the same *T-C* areas repeatedly up to at least ten times between the 17th to beginning of the 20th century (since then active fire suppression). The scale of these fires, as well as causes, circumstances, dependence on climate conditions and potential human purposes can only be suspected because of missing written sources but should be object of further investigations as far as practicable and data is available.

Successful establishment of Scots pine saplings in the past seemed to be connected to a fire event, which was intense enough to reduce canopy coverage of other, less fire adapted species in the stand, followed then by fire-free decades. A lack of large-scale disturbances caused by fire (last 1811 on the eastern side of the Park) could be assumed as one main factor missing to stimulate Scots pine regeneration naturally. It could serve as one hypothetical explanation for the appearance of *P. sylvestris* in richer habitats in BNP, which was simultaneously supported by people in the region due to traditional forest utilization. The diminishing influence of man in BNP may cause the depression in regeneration of short lived pioneers and climax, light demanding tree species like Pedunculate oak and Scots pine. In contrast, continuous forest habitat eutrophication during the 20th century due to immission could have led to the expansion of *Tilio-Carpinetum* forests on the cost of poorer forest types associated with now slowly disappearing Scots pines. But the qualities of longevity and durability of *P. sylvestris* as a climax species with pioneer characteristics (when it comes to renewal demands) may profit from more frequent catastrophic events as modeled by current climate scenarios. The recently small-scale burnt sites in BNP should be studied in the long-term with permanent sample plots to investigate fire effects on temperate lowland forests, especially on tree species regeneration. This would contribute to our knowledge about forest dynamics influenced by fire in the region as well as to a deeper understanding of the present vegetation in Białowieża National Park as a result of its history.

REFERENCES

Cited Literature

- ABRAMS, M.D. (1992). Fire and the development of oak forests. *BioScience* 42, pp. 346-353.
- BERNADZKI, E., BOLIBOK, L., BRZEZIECKI, B., ZAJACZKOWSKI, J., ZYBURA, H. (1998). Compositional dynamics of natural forests in the Białowieża National Park, northeastern Poland. *Journal of Vegetation Science* Vol. 9, pp. 229-238.
- BOBIEC, A., GUTOWSKI, J.M., LAUDENSLAYER, W., PAWLACZYK, P., ZUB, K. (2005). *The Afterlife of a Tree*. WWF Poland, Warszawa-Hajnowka, Bieldruk Drukarnia, Białystok.
- BOROWIK, T., BORKOWSKI, J., JĘDRZEJEWSKI, W., unpublished data (2008). In: KUIJPER, D.P.J., CROMSIGT, J.P.G.M., JĘDRZEJEWSKA, B., MIŚCICKI, S., CHURSKI, M., JĘDRZEJEWSKI, W. (2010). Bottom-up versus top-down control of tree regeneration in the Białowieża Primeval Forest, Poland. *Journal of Ecology* 98, pp. 888-889.
- BRINCKEN, J. (1826). *Mémoire Descriptif sur la forêt impériale de Białowieża en Lithuanie*. Varsovie-Chez N. Glücksberg, imprimeur-libraire de l'Université Royale 1826. Annoté et commenté par Piotr Daskiewicz, Bogumiła Jędrzejewska, Tomasz Samojlik. Editions Epigraf Paris 2004.
- BROSE, P. H. & VAN LEAR, D.H. (1998). Responses of hardwood advance regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. *Canadian Journal of Forest Research* 28, pp. 331–339.
- BROSE, P.H., SCHULER, T., VAN LEAR, D.H., BERST, J. (2001). Bringing Fire Back- The Changing Regimes of the Appalachian Mixed-Oak Forests. *Journal of Forestry*, November 2001, pp. 30-35.
- BROWN, P.M., WU, R. (2005). Climate and Disturbance Forcing of Episodic Tree Recruitment in a Southwestern Ponderosa Pine Landscape. *Ecology* 86 (11), 2005, pp. 3030-3038.
- BROWN, P.M. (2006). Climate Effects on Fire Regimes and Tree Recruitment in Black Hills Ponderosa Pine Forests. *Ecology* 87 (10), 2006, pp. 2500-2510.

- DZIĘCIOŁOWSKI, R., KOSSAK, S., WASILEWSKI, M., PRZYPAŚNIAK, J., WAWRZYŃIAK, P. (1996). Estimating numbers and structure of red deer population in the Białowieża Forest. In: PASCHALIS, P. & ZAJĄCZKOWSKI, S. (Ed.) (1996) Biodiversity protection of Białowieża Primeval Forest- Selected papers. Fundacja Rozwój SGGW, Warszawa, pp. 77-90.
- DYER, M.E., BAILEY, R.L. (1987). A Test of six Methods for Estimating True Heights from Stem Analysis Data. *Forest Science*, Society of American Foresters, Vol. 33, No.1, pp.3-13.
- ELLENBERG, H. (1996). *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht*. Ulmer, Stuttgart.
- FALIŃSKI, J.B. (1986). *Vegetation dynamics in temperate lowland primeval forests*. Geobotany 8. Dr W. Junk Publishers, Dordrecht, The Netherlands.
- FALIŃSKI, J.B., CANULLO, R., BIALY, K. (1988). Changes in herb layer, litter fall and soil properties under primary and secondary tree stands in a deciduous forest ecosystem. *Phytocoenosis Biuletyn Fitosocjologiczny*, Vol.1 (NS), Warszawa-Białowieża 1988.
- FALIŃSKI, J.B. (1994). *Concise Geobotanical Atlas of Białowieża Forest*. In: *Phytocoenosis Supplementum Cartographiae Geobotanicae* Vol. 6, Warszawa-Białowieża 1994.
- FESENMYER, K.A., CHRISTENSEN, N.L. (2010). Reconstructing Holocene fire history in a southern Appalachian forest using soil charcoal. *Ecology*, 91 (3), pp. 662-670.
- JĘDRZEJEWSKA, B., JĘDRZEJEWSKI, W., BUNEVICH, A.N., MIŁKOWSKI, L., KRASIŃSKI, Z.A. (1997). Factors shaping population densities and increase rates of ungulates in Białowieża Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. *Acta Theriologica* No. 42, pp. 399-451.
- KAMLER, J.F., JĘDRZEJEWSKA, B., MIŚCICKI, S. (2004). Red deer- a tale of two deer. Chapter 7 in: JĘDRZEJEWSKA, B., WÓJCIK, J. M. (2004). *Essays on Mammals of Białowieża Forest*. Mammal Research Institute Polish Academy of Sciences, Białowieża, pp. 51-58.
- KECZYŃSKI, A. (2007). Regeneracja grądu *Tilio-Carpinetum* Tracz. 1962 w następstwie dawnego użytkowania lasu w Białowieskim Parku Narodowym (Regeneration of *Tilio-Carpinetum* hornbeam forest (Tracz. 1962) as a follow-up of forest utilization in the Białowieża National Park). *Sylwan* No. 1, pp. 58-65.

- KOOP, H. (1989). Forest Dynamics. SILVI-STAR: A Comprehensive Monitoring System. Proefschrift, Leersum, Springer-Verlag, Berlin Heidelberg New York, pp. 92-106.
- KOPRYK, W., PALUCH, R., GIL, W. (2004). The possibilities and justification for application of Scots pine natural regeneration on coniferous forest sites. In: Coniferous forest vegetation- differentiation, dynamics and transformations. Brzeg, A., Wojterska, M., Wydawnictwo Naukowe UAM, Seria biologia No. 69, Poznan, pp. 263-267.
- KREPEL, W. (2005). Die polnische Methode der Forstlichen Standortskartierung. Waldoekologie online 2, Freising, pp. 44-48.
- KUIJPER, D.P.J., CROMSIGT, J.P.G.M., CHURSKI, M., ADAM, B., JĘDRZEJEWSKA, B., JĘDRZEJEWSKI, W. (2009). Do ungulates preferentially feed in forest gaps in European temperate forest? Forest Ecology and Management 258, pp. 1528-1535.
- KUIJPER, D.P.J., CROMSIGT, J.P.G.M., JĘDRZEJEWSKA, B., MIŚCICKI, S., CHURSKI, M., JĘDRZEJEWSKI, W. (2010a). Bottom-up versus top-down control of tree regeneration in the Białowieża Primeval Forest, Poland. Journal of Ecology 98, pp. 888-889.
- KUIJPER, D.P.J., JĘDRZEJEWSKA, B., BRZEZIECKI, B., CHURSKI, M., JĘDRZEJEWSKI, W., ŻYBURA, H. (2010b). Fluctuating ungulate density shapes tree recruitment in natural stands of the Białowieża Primeval Forest, Poland. Journal of Vegetation Science 21, pp. 1082-1098.
- KUROWSKI, K.J. (2004). The problem of the naturalness of pine forests- case study Jaksonek nature reserve on the Pilica river. In: Coniferous forest vegetation- differentiation, dynamics and transformations. Brzeg, A., Wojterska, M., Wydawnictwo Naukowe UAM, Seria biologia No. 69, Poznan, pp. 171-177.
- KWIATKOWSKI, W. (1994). Vegetation Landscapes of Bialowieza Forest (map in scale 1:50 000 with comment). In: Phytocoenosis Supplementum Cartographiae Geobotanicae Vol. 6, Warszawa-Bialowieza 1994.
- KWIATKOWSKI, W., GAJKO, K. (2009) (English translation). Geomorphology, Hypsometry, Tree Stands map of BNP. In: Bialowieza National Park. Know it- Understand it- Protect it. Bialowieski Park Narodowy, Bialowieza, Poland, pp. 26-29, 48-49.
- MALZAHN, E., KWIATKOWSKI, W., PIERZGALSKI, E. (2009) (English translation). Inanimate Nature (Chapter 2). In: Bialowieza National Park. Know it- Understand it- Protect it. Bialowieski Park Narodowy, Bialowieza, Poland, pp. 17-36.

- MATUSZKIEWICZ J.M. (Edt.) (2007). Geobotanical Identification of the Development Tendencies in Forest Associations in the Regions of Poland- A Synthetic Survey. Polska Akademia Nauk, Instytut Geografii i Przestrzennego Zagospodarowania im. Stanisława Leszczyckiego, Monografie, 8, Warszawa, pp. 817-848.

- MATUSZKIEWICZ J.M. (2008). Potential natural vegetation of Poland (Potencjalna roślinność naturalna Polski). Polish Academy of Sciences, Department of Geoecology and Climatology. IGiPZ PAN, Warszawa. Official Home Page. [online] (2009-12-23). Available: http://www.igipz.pan.pl/geoekoklimat/roslinnosc/prn_mapa/home.htm#Spatial [2010-12-28].

- MCBRIDE, J. R. (1983). Analysis of Tree Rings and Fire Scars to establish Fire History. Tree-Ring Bulletin, Volume 43, pp. 51-67.

- MICHALCZUK, C., (2001). Forest Habitat Types (map in scale 1:20 000 with comment). Field work done by Biuro Urządzania Lasu i Geodezji Lesnej Oddział w Białymstoku, Michalczuk C., Siedliska i drzewostany Białowieżskiego Parku Narodowego. In: Phytocoenosis Supplementum Cartographiae Geobotanicae Vol. 13, Warszawa-Białowieża.

- MIŚCICKI, S. (1996). Forest regeneration and its damage by herbivorous ungulates in the Białowieża National Park. In: PASCHALIS, P. & ZAJĄCZKOWSKI, S. (Edt.) (1996) Biodiversity protection of Białowieża Primeval Forest- Selected papers. Fundacja Rozwój SGGW, Warszawa, pp. 91-108.

- MITCHELL, F.J.G. (1998). The investigation of Long-term Successions in Temperate Woodland Using Fine Spatial Resolution Pollen Analysis. In: KIRBY, K.J., WATKINS, C. (Edt.) (1998). The Ecological History of European Forests. CAB International, pp. 213-223.

- MITCHELL, F.J.G., COLE, E. (1998). Reconstruction of long-term successional dynamics of temperate woodland in Białowieża Forest, Poland. Journal of Ecology, 86, pp. 1042-1059.

- NIKLASSON, M., ZIN, E., ZIELONKA, T., FEJEN, M., KORCZYK, A.F., CHURSKI, M.; SAMOJLIK, T., JĘDRZEJEWSKA, B., GUTOWSKI, J.M., BRZEZIECKI, B. (2010). A 350-year tree-ring fire record from Białowieża Primeval Forest, Poland: Implications for Central European lowland fire history. Journal of Ecology 98, pp. 1319-1329.

- OBERDORFER, E. (1977). Süddeutsche Pflanzengesellschaften. Bd. I-IV, Jena.

- OKOŁOW, C. (2009) (English translation). History of Conservation (Chapter 1). In: Białowieża National Park. Know it- Understand it- Protect it. Białowieżski Park Narodowy, Białowieża, Poland, pp. 9-16.

- PAWLACZYK, P. (2009) (English translation). Forest communities (Chapter 3). In: Białowieża National Park. Know it- Understand it- Protect it. Białowieski Park Narodowy, Białowieża, Poland, pp. 37-58.
- PRUSINKIEWICZ, Z., MICHALCZUK, C. (1998). Soils of the Białowieża National Park. Phytocoenosis Supplementum Cartographiae Geobotanicae Vol. 10, Warszawa-Białowieża.
- PYNE, S.J. (1997). Vestal Fire- An Environmental History, Told through Fire, of Europe and Europe's Encounter with the World, University of Washington Press, Seattle and London, pp. 147-209.
- SAMOJLIK, T. (Edt.) (2005). Conservation and Hunting: Białowieża Forest in the Time of Kings. Mammal Research Institute, Polish Academy of Sciences, Białowieża.
- SAMOJLIK, T. (2006). The grandest tree - a history of Scots pine (*Pinus sylvestris* L.) in Białowieża Primeval Forest until the end of the 18th century. Rocznik Dendrologiczny, Vol. 54, pp. 7-27.
- SAMOJLIK, T. (2007). Antropogenne przemiany środowiska Puszczy Białowieskiej do końca XVIII wieku [Anthropogenic changes of the environment of Białowieża Primeval Forest until the end of 18th century]. Unpublished PhD thesis, Mammal Research Institute, Polish Academy of Sciences, Białowieża, pp. 1-181 (in Polish).
- SANNIKOV, S. N., SANNIKOVA, N. (1985). Ekologija estestvennogo vozobnavlenija sosny pod pologom lesa. Nauka Moskwa, p. 149. In: KOPRYK et al. (2004).
- SCHWEINGRUBER, F.H., BÖRNER, A., SCHULZE, E.-D (2006). Atlas of woody plant stems: Evolution, Structure and Environmental Modifications. Springer-Verlag Berlin Heidelberg, pp. 174-177.
- SOKOŁOWSKI, A. W. (1991). Changes in species composition of forest associations in the nature reserves of the Białowieża Forest. Summary. Zakład Ochrony Przyrody i Zasobów naturalnych polskiej Adademii Nauk, Ochr. Przyr. Ann. 49, cz. II, Krakow, pp. 63-78.
- SOKOŁOWSKI, A. W. (1999). Succession of forest communities in the Starzyna reserve in the Białowieża Forest. Parki nr. Rez. przyr., Białowieża, 18,2, pp. 31-59.
- STOKES, M.A., SMILEY, T.L. (1968). An introduction to tree-ring dating. University of Chicago Press, Chicago.

- STRYD, A. H. (1997). Culturally Modified Trees of British Columbia: A handbook for the Identification and Recording of Culturally Modified Trees. Ministry of Forests, Vancouver Forest Region.
- SVENNING, J.-C. (2002). A review of natural vegetation openness in north-western Europe. *Biological Conservation* 104, pp. 133-148.
- SZAFER, W. (1922). Uwagi o celach i organizacji badan naukowych w polskich parkach natury. *Ochr. Przyr.* 3, pp. 10-15.
- SZCYGIEL, R., UBYSZ, B., ZAWIŁA-NIEDŹWIECKI, T. (2009). Spatial and Temporal Trends in Distribution of Forest Fires in Central and Eastern Europe. In: BYTNEROWICZ, A., ARBAUGH, M., RIEBAU, A., ANDERSEN, C. (Edt.) (2009). *Developments in Environmental Science, Volume 8, Chapter 10*, pp. 233-245.
- UNESCO (2010). Belovezhskaya Pushcha/ Białowieża Forest. Official Home Page. [online] (2010-08-20). Available: <http://whc.unesco.org/en/list/33> [2010-08-20].
- WEBER, H.E., MORAVEC, J., THEURILLAT, J.-P. (2000). International Code of Phytosociological Nomenclature. 3rd edition. *Journal of Vegetation Science* 11, IAVS; Opolus Press Uppsala, pp. 739-768.
- YAMAGUCHI, D.K. (1991). A simple method for cross-dating increment cores from living trees. *Canadian Journal of Forest Research*, 21, pp. 414-416.
- ZIN, E. (2007). Age structure and dynamics of a semi-natural mixed Scots pine (*Pinus sylvestris* L.) – Norway spruce (*Picea abies* L. Karst.) stand in relation to fire regime in the Białowieża Forest (Poland). Examensarbete Nr. 103, Institutionen för sydsvensk skogsvetenskap, SLU Alnarp.

Used handbooks

- DYTHAM, C. (1999). *Choosing and Using Statistics: A Biologist's Guide*. Blackwell Science Ltd. Oxford, London.

APPENDIX I

Common system of classification of forest vegetation types

Vegetation types are models of a certain composition of plant species dependent on site conditions. The forest types classified in Białowieża and used in this study are related to syntaxa traditionally used by phytosociologists. In phytosociology, plant associations are the basic unit of systematic. Higher hierarchical orders are alliances, orders and classes. The described associations are unique and therefore clearly to identify because of their typical species composition. The name of an association consists of one or two character species names and the ending typical for the syntaxonomical level, in the case of associations –*etum* (International Code of Phytosociological Nomenclature ICPN). If a forest site is described newly, its vegetation type will be abstracted to an ideal type and then compared and set in order with known plant associations. Furthermore, associations can be divided in subassociations, variants, fazies etc. with the help of differential species (Oberdorfer 1977; Faliński 1986; Ellenberg 1996; Weber et al. 2000).

Forest site mapping in Poland

Forest site mapping in Poland via the basic unit of ecological forest types (polish: siedliskowy lasu). The classification concept of the site survey has two dimensions: 1. Natural forest region and altitudinal zone, 2. Site analysis on local scale of soil water, soil nutrient regime, type of substrate, current form of stocking and natural vegetation unit with tree species present. The forest site types give information about the forest association as well as nutrient and water conditions. Examples of given abbreviations of forest site type names in BF are listed below (Krepel 2005).

Type of association:

- B: *bory* (coniferous forests)
- Bm: *bory mieszane* (mixed coniferous forests)
- Lm: *lasy mieszane* (mixed deciduous forests)
- L: *lasy* (deciduous forests)
- las legowy* (riparian forests) with
- Ol: *ols* (alder floodplain forests)
- OlJ: *ols jesionowy* (alder-ash-streamside forests)

Water conditions:

- s: *suchy* (dry)
- sw: *swiezy* (fresh)
- w: *wilgotny* (moist)
- b: *bagienny* (swampy)

Latin name of association	Polish forest sites	English name of community type
<i>Calamagrostio arundinaceae-Quercetum</i>		Acidophilous oak forest
<i>Carici elongatae-Alnetum</i>	Ol	Swampy alder fen forest
<i>Circaeo-Alnetum</i>	Lmb	Marshy alder woods
<i>Ficario-Ulmetum</i>		Deciduous floodplain forest
<i>Fraxino-Alnetum</i>	OIJ	Riparian alder and eutrophic alder-ash forest
<i>Ledo-Sphagnetum magellanicum</i>	Bb	Raised bog complexes with Scots pine
<i>Melitti-Carpinetum (M-C)</i>	LMsw	Dry thermophilous oak-hornbeam “grond” forest with admixture of Scots pine, Norway spruce, birch and aspen on ablation moraines
<i>Peucedano-Pinetum</i>		Scots pine forest with admixture of Norway spruce
<i>Pino-Quercetum/Quercopiceum</i>	BMw	Mesotrophic oak-pine mixed forest
<i>Sphagno-Betuletum suspecantis</i>	BMb	Birch swamp forest on peat
<i>Sphagno girgensohnii-Picetum</i>	LMw	Lowland sub boreal spruce forest
<i>Tilio-Carpinetum caricetosum remotae</i>	Lw	Humid <i>T-C</i> with remote sedge
<i>Tilio-Carpinetum circaeetosum</i>	Lw	Poorest of the humid <i>T-C</i> with reed grass
<i>Tilio-Carpinetum stachyetosum silvaticae</i>	Lsw	Floristically richest form of <i>T-C</i>
<i>Tilio-Carpinetum typicum (T-C)</i>	Lsw	Eutrophic lime-oak-hornbeam forest with Norway spruce
<i>Potentillo albae-Quercetum</i>		Subxero- thermophilous dry-mesic oak forest and pine-oak forest
<i>Quercopiceum</i>	BMw	Humid oak-spruce forest
<i>Vaccinio myrtili Picetum</i>	BMsw	Fresh coniferous mixed forest with Norway spruce
<i>Vaccinio myrtili Pinetum</i>	Bw	Pine forest on poor aeolic sands

All communities concern middle or east European (continental/subboreal) vegetation communities. English forest community names of corresponding latin names for forest associations were taken from Matuszkiewicz (2008).