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Biological and Sportbiological Doctoral School

Stand structure and dynamics of semi-natural hardwood floodplain forests of the Pannonian ecoregion - a forest historical perspective

Theses of Ph.D. Dissertation

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1. INTRODUCTION

"*It is indeed a painful thought that this jewel of nature* [the Slavonian primary floodplain hardwood forest] *is doomed, its days are numbered.*" Anonymus 1911

Hardwood floodplain forests are among the two most endangered forest habitat types (European Commission 2016). River regulation and the expansion of settlements and farmland over the past two centuries have led to the loss or significant conversion of around 90% of habitat in Europe (Klimo és mtsai 2008; Király és mtsai 2011; Biró és mtsai 2018). Thus, primeval floodplain forests practically no longer exist in Europe (Sabatini et al. 2018). However, near-natural/old-growth remnant stands have survived along the great rivers and their tributaries in the Pannonian Ecoregion (Hughes et al. 2012) due to low-intensity forest management (Demeter 2016) and the establishment of strict forest reserves (Bobinac 2000; Vrška et al. 2006; Mikac és mtsai 2018). Near-natural stands are also among our most valuable forest habitats in terms of species richness and structural diversity, and are key areas of European biodiversity (Schnitzler 1994; European Commission 2016). These stands are a particularly important part of our natural heritage and we need to pay more attention to their understanding and conservation.

However, this forest habitat is not only significant from a conservation point of view, but also from an economic perspective, due to the quantity and quality of oak that can be harvested, as the high productivity and the high value of the marketable timber clearly allow for very profitable management. However, current forest management, which is mostly based on rotation systems, is increasingly in conflict with the aims of nature conservation and the principles of sustainable landscape management and close-to-nature forestry (Bauhus et al. 2009; Mölder et al. 2019). A possible solution for the conservation of this habitat would be such forest management that is based on natural processes (Bauhus et al. 2009; Frank and Szmorad 2014).

There is still a scientific debate about the natural structure and dynamics of Europe's lowland forests, which are little or not influenced by human activity. Two distinctly different theoretical and conceptual models have been developed. One is the 'closed forest' theory, the other is the 'wood-pasturet' theory (Vera 2000; Birks 2005). The 'closed forest' theory proposes that humid climate in the temperate plains of western, central and northern Europe will eventually support the development of closed and high forest vegetation. A (primeval) forest free from human impacts is made of the mosaics of spatially separated developmental phases (Mosaic Cycle Concept, Watt 1947; Korpeľ 1958; Czájlik 1997). Each developmental phase varies in size and duration, but each phase has well-defined structural characteristics (e.g. age or diameter distribution, amount of large trees, amount of deadwood; Czájlik 1997, Král et al. 2018).

Little is known about the stand development/regeneration dynamics of natural floodplain hardwood (climax) forests and the natural disturbances influencing them in the absence of primeval riparian forests (Schnitzler 1997). Peterken (1996) and Schnitzler (1997) consider regular flooding and windthrow to be the most important disturbance factors in natural floodplain forests. In their view, regular flooding and high groundwater levels loosen the soil, in which most tree species develop shallow, spreading root systems, so that strong winds can easily blow down large, old trees. The same phenomenon was described by foresters in Slavonian old-growth floodplain oak forests (Gelinek 1880, Fekete 1895, Kuzma 1911), which received regular flooding before the regulation of the Sava river. These data suggest that small-scale windbreaks may have been part of natural forest dynamics. In two old-growth floodplain hardwood forest reserves in the Czech Republic, Král et al. (2014) showed that the stand structure can be described by spatially separated developmental phases (e.g. regeneration, optimum, senescence, collapse). The data series spanning three decades (1973-2006) also showed that the size and proportions of each developmental phase are different and vary over time. According to Czájlik (1997), the results of research in other European hill and mountain forest types (e.g. beech) can only be applied to beech forests in the Pannonian region, and forest dynamics research in oak forests should be based on different theoretical and methodological foundations. Based on my field experience and the literature, I argue that the patterns of stand structure and dynamics of mesic forest types developing in the higher elevations of floodplains of large rivers can be described - at least partially - by the presented mosaic-cycle model and fine-scale gap dynamics. The habitat specificity of patch size and possible developmental trajectories of patches can only be assumed in the absence of primeval hardwood floodplain forest and long-term studies.

The core idea of the "closed forests" concept is the natural regeneration dynamics. The natural regeneration of tree species is expected to take place in gaps created by canopy disturbance (e.g. windthrow) and natural ageing/dying of trees. However, in a forests made of light-demanding tree species such as floodplain pedunculate oak (*Quercus robur* L.) forests, the natural regeneration of pedunculate oak (in my thesis: pedunculate oak individuals up to 5 cm diameter at breast height - DBH) is almost absent throughout Eurasia. This phenomenon certainly needs an explanation. The above theories strongly dominate ecological and forestry discussion on the dynamics of oak dominated forests, but they ignore a very important factor: the impact of the alien pathogen powdery mldew on seedling and sapling development.

The pathogen oak powdery mildew (PPM) (the most common species in Europe are *Erysiphe alphitoides* (Griffon & Maubl.) U. Braun & S. Takam. and E. quercicola S. Takam. & U. Braun) was first reported in France in 1907 (Hariot 1907), and then rapidly swept across Europe (Kövessi 1910; Woodward et al. 1929). Despite the rapid and extensive accumulation of knowledge about the effects of PPM on the seedling and sapling development in the first years after its epidemic, to date this knowledge has not been adequately integrated into ecological and conservation research and discussions about the natural forest dynamics of pedunculated oak.

2. OBJECTIVES

My general research interest focuses on understanding the structure and dynamics, past, present, and the future of Pannonian semi-natural/oldgrowth hardwood floodplain forests. The overall aim of my thesis is to describe what were the stand structural characteristics and regeneration dynamics in the past when a more natural condition prevailed, and how did the old-growth forests change. My thesis did not aim at a comprehensive evaluation of naturalness of the stands we studied.

My research questions were as follows:

1) Where is the stand structure of some representative semi-natural hardwood floodplain forests of the Pannonian region in the process of forest developmental cycle?;
2) How has forest management systems and the abandonment of management affected the structure of semi-natural forests?;
3) What kind of stand structural and natural regeneration conditions characterised the old-growth hardwood floodplain forests prior to the river regulation and the emergence and invasion of the pathogen oak powdery mildew?
4) How does the alien oak powdery mildew affect the natural regeneration dynamics of pedunculate oak and the natural forest dynamics?

3. MATERIALS AND METHODS

For close-to-nature forest management and restoration ecology, it is important to know how natural the remaining old stands are, where they are in the process of forest development, in what structural elements they differ from natural/near-natural conditions, and what landscape and forest history factors influence the development of stands. However, in the absence of natural reference stands of floodplain hardwood forests and long-term forest dynamics studies, our ability to answer these questions is limited. In my PhD thesis, I attempted to answer these questions by applying a combination of field study, a retrospective historical forest ecological approach and an (interdisciplinary) synthesis of knowledge from related disciplines.

3.1. Field study

3.1.1. Study area

Stand structure of oak-elm-ash forests was studied on two peripheral lowlands of the Pannonian Ecoregion. The Bereg Plain lies on the floodplain of the River Tisza at the foothills of the north-eastern Carpathians in two countries (NE Hungary and W Ukraine). The Drava Plain site belongs to the floodplain of the River Drava in South Hungary. The altitude of the studied landscapes ranges between 96 and 120 m a. s. l. The climate is temperate with an average annual temperature of 9.5–10.4 °C and 600–750 mm of precipitation. The soils can most often be classified as humic alluvial and alluvial meadow soil developed on recent Holocene sandy and clayey sediments on fluvial gravel.

3.1.2. Studied management systems

Actively managed and abandoned stands were sampled in two management types, forming four different a priori categories: sanitary selection (ManSel), rotation (ManRot), abandoned sanitary selection (AbnSel), and abandoned rotation forests (AbnRot).

3.1.3. Sampling design and stand structural variables

We studied 16 fporests and the oldest stands from each of the forests were selected according to the forest management plans. In each forest, separate rectangular or linear clusters of permanent sampling plots (SPs) were established, measuring 50 by 50 m, containing 4, 6, 8, 12 or 16 circle-shaped SPs, and representing 1–4 hectares of typical old stands. A total of 135 SPs were surveyed for stand structure according to the long-term monitoring methodology and protocol of Hugarian Strict Forest Reserve Program (Horváth 2012; Horváth és mtsai 2012). There were three modules of data acquisition:

1. *General description of forest stand*. Stand canopy closure, percentage cover of lower and upper canopies, percentage cover of shrub and regeneration layer were visually estimated in circle-shaped SPs (area=250 m^2; r = 8,92 m).
2. *Living and standing dead trees, shrubs and standing broken trees* were identified and recorded at all SPs with a combination of circular plot sampling and horizontal point (angle-count) sampling with a basal area factor k = 2.

3. *Lying dead wood* was estimated using the line intercept sampling method. We established three sampling lines (each 20 m in length) radiating from the centre of the SP in the directions of 0 (North), 120 and 240 degrees.

We analysed a total of 26 old-growth forest structural variables in three groups: 15 live tree structural indicators (LTSIs), 9 dead tree structural indicators (DTSIs), and 2 gap-related structural indicators (GRSIs)

3.1.4. Statistical analyses

For each of these variables, the average was calculated by the four management categories from the values measured at the sampling point or calculated for the sampling point. Multiple comparisons of the four site subsets to each other were made by ona-way ANOVA and Tukey post hoc test for all 26 variables to examine the management effect. The significance level (α) was set to 0.05.

Principal component analysis (PCA) was performed on the 22 old-growth indicators that were retained to reduce dimensionality and to calculate the significance of the studied variables. Non-metric Multidimensional Scaling (NMDS) was selected to study whether the 135 sampling plots are separated according to their management history (i.e., four management categories) in the two-dimensional ordination space of the 22 retained stand structure variables, using the Bray–Curtis dissimilarity measure.

The diameter distribution of living trees was studied with regression for the management categories. All the studied species were aggregated and the mean prevalence (trees/ha) was calculated for all DBH classes (at 5 cm intervals). The self-thinning rule-based power function model (stem density = ax^{-2}, where x: DBH class, and a: density of DBH1cm) was selected as the theoretical reference for comparison of DBH-class distributions. According to Shimano (2000), this clearly represents the patch-mosaic structure of natural deciduous broad-leaved forests.

Analyses of stand structure and species composition data were conducted in R statistical software (R Core Team 2017), using the packages ‘vegan’ for PCA and NMDSordination, ‘agricolae’ for Tukey’s HSD test, ‘tidyr’ for data transformation, and ‘ggplot2’ for graphic display.

3.2. Historical forest ecology approach

Since 1862, foresters have regularly published landscape, forest and stand-scale forest descriptions from many parts of the Pannonian region in the Hungarian forestry journal, Erdészeti Lapok. In my thesis, I conducted a systematic review of the historical forestry literature to identify old (>70 years old) hardwood forests that existed prior 1930. It can be assumed that before or around large-scale river regulation and the spread of rotation forestry, these stands may have been more natural than today's stands, and thus may provide good reference for certain stand structure variables. Reading through the table of contents of all issues of the journal from 1862 to 1930, I downloaded articles whose titles referred to hardwood floodplain forests or landscapes where the habitat was likely to occur (130 articles in total). All issues of the journal are freely available and searchable online (http://epa.niif.hu/01100/01192).

I read each article carefully and selected the articles that could be analysed. I kept the articles in which I found qualitative descriptions and/or quantitative data on the following topics:

1. stand structural variables (e.g. mixed ratio of tree species, total number of trees or timber volume per hectar, number of very large trees),
2. forest management system,
3. natural regeneration or management approaches based on natural regeneration.

3.3. Synthesis of knowledge from different scientific fields

Identification of the recent and historical literature on the impacts of the pathogen oak powdery mildew on the development of seedlings or saplings of pedunculated oak and its natural regeneration dynamics has been done from two directions. First, we identified the key literature from my personal collection and from the collections of those colleagues who were the co-authors of one of the paper on which this thesis is based on. Further articels were identified using the snowball method. Second, searchable database of journal was also studied. Articles published in Hungarian about PPM impacts were searched using the archive of Erdészeti Lapok (published since 1862) and Erdészeti Kísérletek (https://adt.arcanum.com/hu/collection/BME_ErdeszetiKiserletek/ - published between 1900 and 1932). In this search we used the following broad search string: ‘oak’ AND ‘mildew’ (in Hungarian).

Recent scientific papers were searched in the Web of Science, Scopus and Google Scholar Databases using the following search string: "pedunculate oak" AND "powdery mildew". I found a total of 602 paper (GoogleScholar – 516; Scopus – 30; Web of Science – 65). Findings were refined based on the title and abstract, to identify publications focusing on the ecology and dynamics of pedunculate oak forests, their natural regeneration, and the influence of oak powdery mildew, including its pathology, taxonomy and distribution. The reference lists and citations of these publications were also checked to identify further relevant papers. Altogether, we collected and analysed 254 papers and books in English, Hungarian, French, German, Romanian. The relevant information is presented using narrative literature analysis and flow charts.

4. RESULTS

4.1. Management impacts on the structure

The effects exerted by management on diameter distribution are quite obvious. The empirical diameter distributions for every group were greatly similar to the rotated sigmoid curve. However, the rotation and abandoned rotation groups exhibited stronger kurtosis among diameter classes between 25 and 55 cm. On the other hand, the distribution of sanitary selection and abandoned sanitary selection stands fitted Shimano's reference model more closely and with lower kurtosis than their rotation counterparts (Figure 1). Both the thinnest (5–20 cm DBH) and thickest (>80 cm DBH) diameter classes had a lower density than predicted by the model that indicated the lack of innovation and degradation developmental phases.

Whereas there were five significant differences in the old-growth structural characteristics/variables between the abandoned rotation stands and their managed counterparts (only deadwood related variables like standing dead wood and total amount of dead wood), in the case of abandoned and managed sanitary selection stands, there were ten (five live tree variables such as the number of very larg trees and five deadwood related variables such as lying deadwood). The greatest number of significant differences in stand structural variables, 13 in total, were between the abandoned sanitary selection group and the managed rotation group. However, the sanitary selection forests were significantly older than their rotation counterparts.

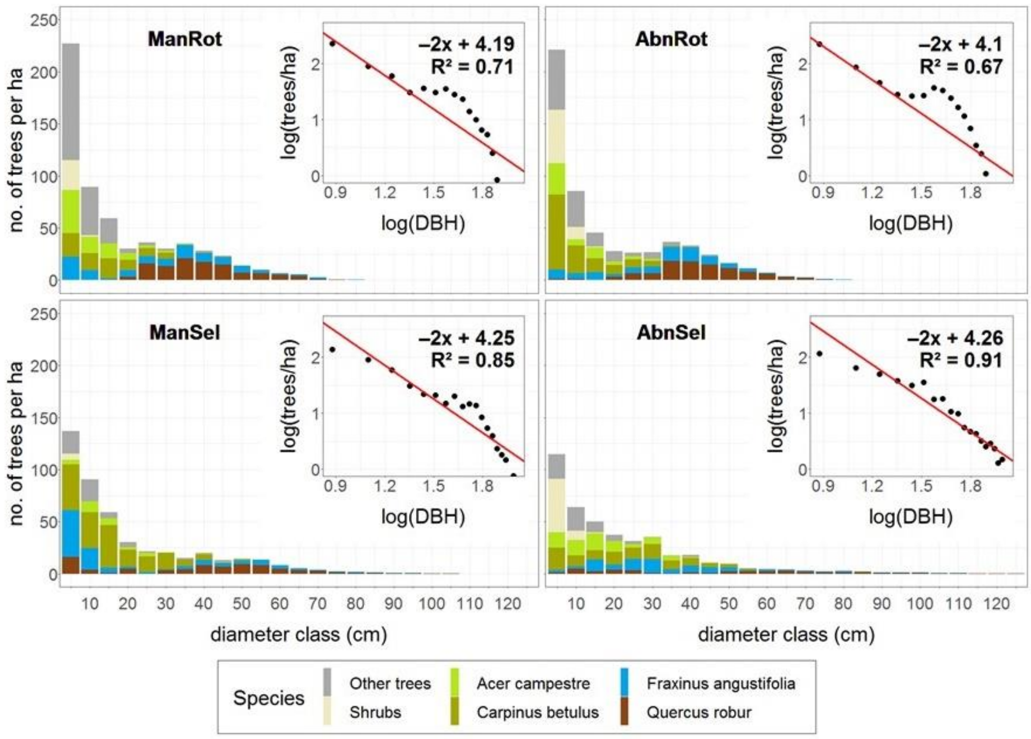

Figure 1. Diameter distribution of studied management categories with the fitted negative power function model. Legend: ManRot – managed rotation, AbnRot – abandoned rotation, ManSel – managed sanitary selection, AbnSel – abandoned sanitary selection.

4.2. Stand structure and forest management in the historical literature

In total, 266 qualitative and quantitative historical descriptions/data on stand structure, forest management, natural regeneration or artificial regeneration were collected from 67 forests or forested areas in 14 landscapes.

In our field surveys, the thickest tree (135 cm DBH) was recorded in a 179-year-old forest called Györke, located on the floodplain of the River Borzha (Ukraine), where the sanitary selection management was abandoned 20 years ago. In this stand, the number very large trees (>80 cm DBH) varied from 9 to 32 tree (average 16) per ha. In old hardwood forests (200-300 years old) along the Sava River, before river regulation and the spread of rotation forestry, the number of very large trees varied from 40 to 60 tree per ha. The thickest trunks could exceed >2 m DBH, in exceptional cases even reaching 3 m DBH. Studies reported individuals with 200-260 cm DBH in recent semi-natural stands in the Stara Vratična Reserve (Serbia), Prašnik Reserve (Croatia), and Cahnov-Soutok Reserve (Czech Republic). The number of very large trees in these stands varies between 17 and 25 tree/ha (Bobinac 2000; Vrška et al. 2006; Mikac et al. 2018). Taking into account all these historical and recent data, I concluded that even in the oldest stands studied in the Pannonian region, the degradation phase has not developed, based on the number of very large trees and potential diameters at breast height.

In the semi-natural old stands described in the historical literature, the proportions of the five main tree species may have been significantly different than today. One of the most striking differences was the higher proportion and size of elm species (*Ulmus* spp.) in the canopy. In recent stands we studied, elm species (*U. minor* and *U. laevis*) were only the fifth taxon in the total sample based on the mixed ratio by basal area, with 14.5 cm average diameter at breast height. The second most common tree of the canopy in the floodplain hardwood forests of the Sava floodplain was elm (Kozarac 1886). Róbert Bokor (1912) reported that in a Slavonian stand harvested in 1892, 23% of the total timber volume (m^3) was elm. In a 100-acre stand (~175 ha) described by Kuzma (1911), the average diameter harvested 1265 elm trees was 70 cm at breast height. While Bokor (1912) measured 143 cm DBH for an elm tree left at the edge of a clearcut area.

In the historical forestry literature, a total of 86 forests or forest compartment have been described in terms of their management system, the methods of final felling and regeneration. The vast majority of the forests described in the articles were managed as high forest, harvested with some form of clear-cutting (clear-cut, clear-cut with tree retention or shelterwood cutting). In 17% of the forests/forest compartments mentioned in the descriptions, selection forestry was applied. Three times more data (67%) were found for forest regeneration based on natural regeneration than on acorn sowing and five times more than for forest regeneration by planting. In historical sources we also found sporadic descriptions of the successful regeneration of pedunculate oak in canopy gaps in stands managed by irregular selective logging, if they were protected from overgrazing (e.g. Beregi plain, Bodrogköz; Fekete1890a, 1890b). Foresters reported that it was easy to regenerate hardwood floodplain forests by shelterwood cutting based on natural regeneration, with only the timely thinning of mixed tree species (e.g. hornbeam or elm species) and the prohibition of grazing (Timis Plain - Divald 1886; Slavonia - Kozarac 1885).

4.3. Impact of the pathogen oak powdery mildew on pedunculate oak seedlings

After infection of young, developing leaves with PPM, various damage types were reported: (1) Severe foliar infection can lead to seedling mortality, especially when coinciding with other damage (e.g. insect defoliation, game browsing or late frost) (Vadas 1917; Woodward et al. 1929; Lonsdale 2015); (2) Severe shoot infection can diminish cold resistance by altering bud hardening and dormancy (Kövessi 1910; Marçais and Desprez-Loustau 2014); (3) PPM may parasitize nutrients from the living cells of their hosts (Hewitt and Ayres 1976, Desprez-Loustau et al. 2014). 4) Heavy infection of leaves by E. alphitoides can lead to a 50–70% reduction in the net assimilation rate (Lonsdale 2015). The direct consequence of altered nutrient uptake by PPM and the reduced carbon assimilation may lead to a significant decrease in both vertical and radial growth in seedlings (Woodward et al. 1929; Igmándy 1972; Desprez-Loustau et al. 2014; Bert et al. 2016). (5) Although saplings can produce up to 4–5 new shoots a year under favourable light conditions, PPM infection is more severe in these shoots, which renders them unable to compensate for diminished vertical growth (Roth 1915; Lonsdale 2015; Desprez-Loustau et al. 2019). Thus, the growth potential of the seedling is compromised during this crucial growing period.; (6) Leaf lifespan and shade-tolerance are significantly reduced by severe infection in the shade of the parent tree (Hajji et al. 2009); (7) PPM infection in young leaves results in increased transpiration and water loss (Hewitt and Ayres 1975). Infected seedlings and saplings may thus be more light-demanding, less drought-tolerant and less competitive with the surrounding vegetation (Hajji et al. 2009; Marçais and Desprez-Loustau 2014; Lonsdale 2015). Considering all these impacts, PPM can seriously impede the natural regeneration of pedunculate oak, especially in shade and when competition is high (Figure 2.).

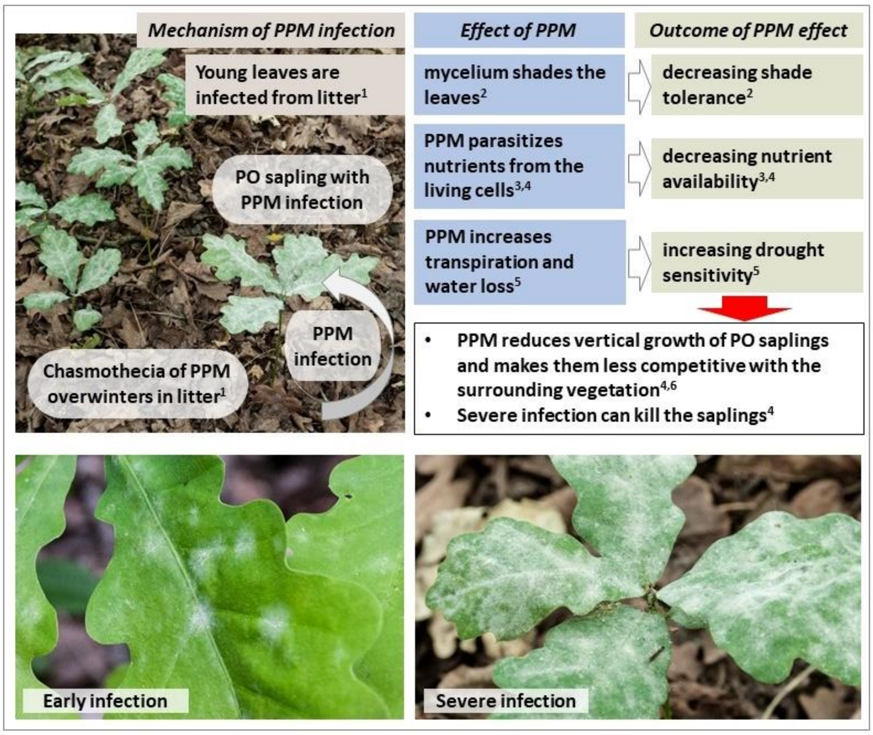

Figure 2. The effects of pathogen powdery mildew (PPM) on pedunculate oak seedling (PO). References: [1]Marçais és mtsai 2009; [2]Hajji és mtsai 2009; [3]Hewitt és Ayres 1976; [4]Desprez-Loustau és mtsai 2014; [5]Hewitt és Ayres 1975; [6]Igmándy 1972. Photo: Molnár Ábel Péter

5. SUMMARY AND NOVEL FINDINGS

1. I collected and published basic stand structure data from 16 semi-natural recent hardwood floodplain forests of the Pannonian region. I collected and analysed historical forestry literature on stand structure, management and natural regeneration of Pannonian hardwood floodplain forests.
2. Based on the number of very large trees, the naturalness of the diameter distribution and the potential diameter at breast height, I found that most of the stands are in the optimal or ageing forest development phases. Even the oldest stands we examined are not old enough to show patches that are in the degradation and innovation phases. The oldest stand in the sample (189 years old) still needs at least 50-100 years of uninterrupted development for patches of degradation and innovation developmental phases to appear and become more frequent, unless the forest is subject to some kind of severe disturbance.
3. The sanitary selective logging management system is better to promote the development of late developmental phases than the rotation system.
4. In both forest management systems, abandonment of management promotes fast regeneration of standing deadwood, but the lying deadwood increases more rapidly only after the abandonment of the sanitary selective logging system.
5. By analysing the historical literature, I have found that the species composition of the recent hardwood floodplain forest stands has changed substantially over the last 100 years. The most striking change is the reduction of the proportions of stem number of elm species (*U. minor* and *U. laevis*) by at least half in the canopy layer, the almost complete disappearance of the species from the upper canopy leyer and the many-fold reduction of the timber volume of the species compared to those described in the second half of the 19th century.
6. The management system of hardwood floodplain forests has changed significantly over the last 150 years. Selection forestry and shelterwood forest management has declined and rotation forestry based on clear-cuts has become more widespread. Forest regeneration based on natural regeneration, which dominated the forestry practices at the turn of the 19th and 20th centuries, has now declined remarkably.
7. Over the past 150 years, the structure of the vast majority of the hardwood floodplain forests has been significantly altered by socio-economic drivers such as the shift to rotation forestry and the introduction and spread of several alien fungal species (Dutch elm disease and oak powdery mildew).
8. In my thesis, I collected, reviewed and synthesized the recent and historical literature on the impact of the oak powdery mildew on (1) seedling development and (2) natural regeneration of pedunculated oak, and I developed the pathogen mildew hypothesis. The hypothesis states that the disease caused by introduced alien fungal species reduces the vertical growth and survival of seedlings and saplings to such an extent that it is, among other biotic and abiotic environmental conditions, one of the most important factors of the natural regeneration failure of pedunculate oak.

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7. PUBLICATIONS

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