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Long-term tree mortality patterns in the natural forest stands of Białowieża National Park in northeast Poland

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ABSTRACT

Natural tree mortality is an important element of the long-term dynamics of strictly protected forest stands. This study aimed to analyse tree mortality patterns in Białowieża National Park over a 80 year period (1936-2012) using an extensive data set from five permanent sample plots (total area=15.44 ha, a sample of ca. 10,000 trees with DBH \geq 5 cm \times 6 census intervals). Mean annual mortality rates for particular tree species for the whole study period ranged between 1-3% \cdot y $^{-1}$. The smallest (ca. 1% \cdot y $^{-1}$) values of mortality rates occurred for hornbeam and pine, and the largest (ca. 3% \cdot y $^{-1}$) for aspen, birch, ash and spruce. The mortality rates varied significantly between census intervals, suggesting the occurrence of two basic types of mortality, *i.e.* regular (baseline) and catastrophic mortality. While the regular mortality was clearly the most prevalent, episodes of catastrophic mortality occurred as well (for ash, elm, spruce, aspen and birch trees). For the smallest trees (5-15 cm DBH) a strong, negative correlation between mortality rates and the degree of shade tolerance was observed (the lower the tolerance, the higher the mortality rate). In general, trees representing intermediate diameter classes were distinguished by lower values of mortality rates than the smallest and largest trees. The average residence time, calculated from mortality rates, varied strongly among individual tree species (from ca. 30 years for aspen, birch, ash and spruce to ca. 90-100 years for pine and hornbeam, for trees with DBH \geq 5 cm). Similarly, there were large differences between tree species in respect to the estimated length of time period needed to allow a recent population density to decline below an arbitrary threshold value of 1 ind. \cdot ha $^{-1}$. The value of this parameter was extremely low for aspen (only 3 years). For the remaining species it varied from ca. 60 years for birch to ca. 600 years for hornbeam. In future studies, an attempt should be made to elucidate the impact of the mortality type (regular *vs.* catastrophic, or dispersed *vs.* clumped) on the basic parameters of the recruitment process (composition, intensity). In addition, extending the current methodology of field work by including the most probable causes of tree mortality would help to understand better the underlying mechanisms of the long-term dynamics of natural forests.

KEY WORDS

catastrophic mortality, life history strategy, long-term study, mortality rate, permanent plot, tree population dynamics, regular mortality

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Introduction

Tree mortality is a very important demographic and ecological process which, along with recruitment and growth, determines the long-term dynamic of woodland communities (Franklin *et al.*, 1987; Wolf *et al.*, 2004; Wunder, 2007; Holzwarth *et al.*, 2012). In contrast to managed forests, in which most trees are felled and removed based on silvicultural prescriptions (*i.e.* through intermediate and final cuttings), in natural forest stands the process of tree death has a spontaneous character and is usually the complex outcome of many different factors and agents influencing stand development (Franklin *et al.*, 1987).

Considering the high importance of tree death as an ecological process, it has often been a subject of scientific interest. For example, a review paper by Franklin *et al.* (1987) presented a high complexity of causes, modes and spatio-temporal dynamics of tree mortality in natural tree stands. Among the most important ecological consequences of the process of tree death are altered tree population and community structure, an increase of necromass volume, release of resources (light, nutrients, moisture), the origination of structures and habitats suitable for wildlife (especially for decomposer organisms), damage to neighboring trees, and changes in soil structure (in case of tree uprooting).

Franklin *et al.* (1987) underline also the complexity and diversity of modes and drivers of tree death in natural forests. Among them are both several abiotic (wildfires, lightning discharges, extremely low and high temperatures, droughts, flooding, strong winds, ice storms and volcano eruptions) and biotic (insects, ungulates and fungi) factors. They can lead to slow and gradual or to rapid and massive tree death which allows for the distinction between two basic modes of mortality which are either regular (baseline) or catastrophic mortality (Hann and Hanus, 2001).

Although qualitative knowledge about tree death as an ecological process is rather high, the quantitative data describing this important aspect of population and community dynamics is fairly scarce (Larson and Franklin, 2010). The reason for this is, among other things, a relative rarity of the occurrence of tree death (Flewellling and Monserud, 2002). In this case, a very important source of information on the quantitative aspects of tree mortality are studies conducted over long-term periods on permanent plots established in natural forest stands and involving sufficiently large tree populations.

In this paper, we analyze data collected on permanent study plots established in natural forest stands in the Strict Reserve of Białowieża National Park (BNP) in northeast Poland. Since 1936 till now, seven major tree censuses were conducted on these plots in total (which means six census intervals). During every census, approximately 10,000 trees (representing eleven different species) were measured, among them *ca.* 2,000 dead trees. Here, we use this data to quantitatively describe long-term temporal patterns of natural tree mortality in the Białowieża woodlands subject to long-term strict protection. Our specific research questions are as follows: 1) What are the average mortality rates characterizing local woodland communities? 2) Are there any visible temporal trends in the values of mortality rates? 3) Is there any correlation between the life history of species and mortality patterns? 4) What is the influence of tree size on the mortality rate? 5) What is the relative role of regular and catastrophic mortality in the long-term development of local woodlands?

Study site and data

Białowieża Forest is situated on both sides of the national border between Poland and Belarus. It encompasses in total of 1450 km² (600 km² in Poland and 850 km² in adjacent Belarus). The climate has features of both Continental and Atlantic types (Faliński, 1986). The average annual

temperature is 7.0°C (January average =−4.6°C, July average =18.2°C), total annual precipitation averages 631 mm and snow cover lasts for an average of 92 days. Białowieża Forest is situated on a mostly flat but occasionally undulating terrain ranging from 135 to 190 m a.s.l., created from glaciofluvial sands, gravels and clays (Kwiatkowski, 1994). From the 14th until the beginning of the 20th century, Białowieża Forest served as an extensive royal hunting area, and due to this fact, escaped the widespread colonization and commercial timber extraction that occurred in most European forests of similar climate and topography (Więcko, 1984; Faliński, 1986).

Since 1921, the best preserved part of Białowieża Forest has been strictly protected within Białowieża National Park (BNP) (52°30′-53°00′N, 23°50′-24°15′E). The park initially included an area of approximately 47 km² (now called the ‘Strict Reserve’). In 1996, the BNP was enlarged (incorporating surrounding, formerly managed forests) to the present area of 105 km². The area of the Strict Reserve has never been intensively managed and has had no management activity since 1921. Consequently, it is often considered to be one of the best preserved remnants of Central European lowland forest (Jones, 1945; Faliński, 1988; Peterken, 1996; Parviainen, 2005).

In 1936, within the Strict Reserve of Białowieża NP, five permanent plots were established to study the long-term dynamics of natural, strictly protected forest stands (Włoczewski, 1954). The plots are transects of varying width (40-60 m) and length (200-1380 m) with a total area of 15.44 ha. So far, the main stand measurements were conducted 7 times on the following dates (the averaged years of observations are given in brackets): 1936, 1955-1959 (1957), 1968-1972 (1970), 1981-1983 (1982), 1991-1993 (1982), 2001-2003 (2002) and 2011-2013 (2012). For every tree with DBH equal to or greater than 5 cm, species identity, stem diameter and spatial coordinates, were measured or determined. Besides this, since the second census date so called ‘recruits’ (trees which have reached a threshold DBH value of 5 cm) and ‘losses’ (trees which have died since the last inventory) were noted as well.

Analysis

To characterize the tree mortality processes taking place on the study plots two indices were used; one absolute and one relative index.

The absolute index is simply a number of ‘losses’, *i.e.* the number of trees which have died in the period between two consecutive records. To enable comparisons, the values obtained for this index were re-calculated per hectare and per year.

The second relative index is annualized mortality or mortality per year, *m* (Sheil *et al.*, 1995):

$$m = \left(1 - \frac{N_1}{N_0}\right)^{\frac{1}{t}} \cdot 100 \quad (1)$$

where:

- m* – annual mortality rate [%·y⁻¹],
- N*₀ – number of living trees at the beginning of census interval,
- N*₁ – number of living trees at the end of census interval (without recent recruits),
- t* – length of census interval [years].

In the next step, annual mortality rates were used to calculate average ‘residence time’, *i.e.* the average life duration of trees which exceeded the threshold value of DBH (5 cm) (Mori *et al.*, 2007):

$$rt = \frac{100}{m} \quad (2)$$

where:

- rt* – residence time [years],
- m* – annual mortality [%·y⁻¹].

Annual mortality rates were also used to calculate the length of time needed for a given tree species population density to fall below an arbitrarily determined level of 1 ind. · ha⁻¹.

All calculations were performed separately for each major study period, tree species and size class. In the latter case, four classes were created as follows (Woods, 2004; Woods *et al.*, 2021):

- 1) 5-15 cm DBH, small trees in the sub-canopy and suppressed unless influenced by a canopy gap;
- 2) 15-30 cm DBH, sub-canopy/sub-dominant trees which may be partially overtopped by other trees or in the canopy, but most are not fully established as canopy trees;
- 3) 30-65 cm DBH, canopy trees which include the majority of individuals forming the forest canopy;
- 4) >65 cm DBH, large canopy trees which, while much less frequent than 30-65 cm canopy trees, can account for a large portion of total biomass.

To investigate the importance of the life history of tree species for mortality patterns, Pearson correlation coefficients and parameters of regression lines between species-specific mortality rates and ranks describing a position of a given tree species on the shade tolerance gradient were calculated (where rank '1' was used for the species with lowest shade tolerance, *i.e.* aspen in this case, and rank '11' for the species with the highest shade tolerance, *i.e.* hornbeam (Table 1)). The calculations were performed by means of Statistica v. 13.1.

Results

ABSOLUTE LOSS RATES. During the entire study period (1936-2012), the greatest number of losses occurred for spruce (Table 1). With a share in the total pool of dead trees close to 50%, spruce clearly topped the list of all tree species. A relatively high number of losses occurred also for lime, hornbeam and birch. On the other hand, the smallest figures were noted for aspen, maple and elm. It is also worth pointing out big differences concerning the total number of losses between particular census intervals. For example, during the 1970s (third census interval) the

Table 1.

The rate of losses (1 ind. · ha⁻¹ · y⁻¹) on 5 permanent study plots in Białowieża NP by tree species and census intervals: 1: 1936-1957; 2: 1957-1970; 3: 1970-1982; 4: 1982-1992; 5: 1992-2002; 6: 2002-2012

| Tree species | English name | Census interval | | | | | | Mean |
|--------------------------------|--------------|-----------------|-------|-------|-------|------|-------|-------|
| | | 1 | 2 | 3 | 4 | 5 | 6 | |
| <i>Populus tremula</i> L. | Aspen | 0.14 | 0.12 | 0.19 | 0.14 | 0.01 | 0.02 | 0.10 |
| <i>Betula</i> sp. ¹ | Birch | 1.09 | 1.09 | 1.20 | 0.74 | 0.31 | 0.48 | 0.82 |
| <i>Alnus glutinosa</i> (L.) G. | Alder | 0.60 | 0.29 | 0.28 | 0.16 | 0.21 | 0.46 | 0.33 |
| <i>Pinus sylvestris</i> L. | Pine | 0.26 | 0.16 | 0.26 | 0.28 | 0.06 | 0.19 | 0.20 |
| <i>Quercus robur</i> L. | Oak | 0.35 | 0.23 | 0.41 | 0.38 | 0.23 | 0.25 | 0.31 |
| <i>Fraxinus excelsior</i> L. | Ash | 0.28 | 0.47 | 0.82 | 0.38 | 0.55 | 1.68 | 0.70 |
| <i>Acer platanoides</i> L. | Maple | 0.17 | 0.12 | 0.10 | 0.12 | 0.07 | 0.06 | 0.11 |
| <i>Ulmus</i> sp. ² | Elm | 0.03 | 0.14 | 0.26 | 0.10 | 0.01 | 0.12 | 0.11 |
| <i>Picea abies</i> (L.) K. | Spruce | 6.03 | 6.65 | 7.99 | 6.21 | 3.12 | 4.29 | 5.72 |
| <i>Tilia cordata</i> Miller | Lime | 0.06 | 1.50 | 3.57 | 2.88 | 2.24 | 2.61 | 2.14 |
| <i>Carpinus betulus</i> L. | Hornbeam | 1.12 | 0.52 | 1.41 | 1.68 | 1.28 | 2.11 | 1.35 |
| Total | | 10.13 | 11.31 | 16.49 | 13.07 | 8.10 | 12.27 | 11.90 |

The sequence of species corresponds to their estimated shade tolerance (Brzezicki *et al.*, 2016)

¹ *Betula pendula* Roth & *B. pubescens* Ehrh (predominantly *B. pendula*)

² *Ulmus glabra* Hudson, *U. laevis* Pallas & *U. minor* Miller (predominantly *U. glabra*)

loss rate calculated for all species together was 2 times higher than in the 1990s (fifth census interval).

As could be expected, the absolute loss rate calculated for a given tree species was closely related to the average population size of that species over the whole study period usually meaning the higher the population size, the greater the number of losses (Fig. 1). It was also observed that the loss rates for spruce, birch and ash were disproportionately higher than average. The opposite tendency occurred for hornbeam.

ANNUAL MORTALITY RATE. The average annualized mortality rate calculated for all species and census intervals was close to $2\% \cdot y^{-1}$ (Table 2). This means that every year in the strictly protected woodlands of Białowieża Forest from a pool of 100 trees (with DBH \geq 5 cm) on average of 2 individuals die (approximately 20 trees in 10 years).

During the entire study period, the highest average annual mortality rates (*ca.* $3\% \cdot y^{-1}$) occurred for birch, aspen, ash and spruce (Table 2). On the other hand, the lowest values of mor-

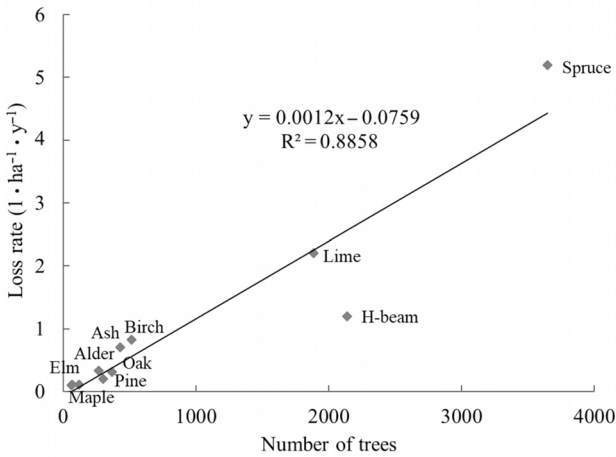


Fig. 1. Relationship between the absolute loss rates and the average tree population sizes during the entire study period (1936-2012)

Table 2.

Annual mortality rates [$m, \% \cdot y^{-1}$] and residence time (rt , years) for trees occurring on permanent study plots in Białowieża NP by tree species and census intervals

| Tree species | Census interval | | | | | | Mean | rt [years] |
|--------------|-----------------|-----|-----|-----|-----|-----|------|-----------------|
| | 1 | 2 | 3 | 4 | 5 | 6 | | |
| Aspen | 2.2 | 2.2 | 4.8 | 6.7 | 0.9 | 1.6 | 3.1 | 33 |
| Birch | 1.9 | 2.6 | 3.8 | 3.9 | 2.2 | 4.8 | 3.2 | 31 |
| Alder | 2.8 | 1.7 | 2.1 | 1.4 | 1.4 | 2.4 | 2.0 | 51 |
| Pine | 1.0 | 0.7 | 1.3 | 1.7 | 0.4 | 1.4 | 1.1 | 91 |
| Oak | 1.1 | 0.8 | 1.7 | 1.8 | 1.3 | 1.7 | 1.4 | 71 |
| Ash | 1.3 | 1.3 | 2.4 | 1.2 | 1.9 | 9.9 | 3.0 | 33 |
| Maple | 1.6 | 1.5 | 1.5 | 1.8 | 1.3 | 1.1 | 1.5 | 68 |
| Elm | 1.1 | 2.0 | 4.8 | 2.2 | 0.1 | 2.6 | 2.1 | 47 |
| Spruce | 1.7 | 2.2 | 3.4 | 3.7 | 2.5 | 4.6 | 3.0 | 33 |
| Lime | 0.4 | 0.9 | 2.0 | 1.7 | 1.4 | 1.7 | 1.4 | 74 |
| Hornbeam | 1.6 | 0.6 | 1.2 | 1.0 | 0.6 | 0.8 | 1.0 | 105 |
| Total | 1.6 | 1.6 | 2.4 | 2.1 | 1.3 | 2.1 | 1.9 | 58 |

Census intervals and the sequence of tree species are as in Table 1. Values greater than the global average ($1.9\% \cdot y^{-1}$) are shown in bold

tality rates (*ca.* $1\% \cdot y^{-1}$) were observed for pine and hornbeam. Also, oak, lime and maple showed rather low mortality rates, amounting to $1.4\text{--}1.5\% \cdot y^{-1}$.

There was a high temporal variation of mortality rates in specific census intervals (from $0.1\% \cdot y^{-1}$ for elm in the fifth period to $9.9\% \cdot y^{-1}$ for ash in the sixth period) (Table 2, Fig. 2). Beyond ash, episodes of high annual mortality ($m > 3\% \cdot y^{-1}$) occurred also in different census intervals for aspen, birch, spruce and elm. In contrast, mortality rates calculated for hornbeam, pine, oak, maple and lime were very stable and never exceeded a value of $2\% \cdot y^{-1}$.

Differences between species in respect to annual mortality rate translated into differences in residence time, *i.e.* average life duration after exceeding a DBH of 5 cm. The values of this parameter for pine and hornbeam were three times higher than for aspen, birch, ash and spruce (Table 2).

Mortality patterns were strongly affected by tree size (Fig. 3). For the smallest trees (DBH 5–15 cm), there was a strong correlation between the degree of shade tolerance and the mortality rate ($r = -0.8558$; $p = 0.0008$). Intolerant tree species at this stage of development showed much higher mortality rates than intermediate and tolerant species (Fig. 3A). This tendency also occurred, although to a much lesser extent, for trees representing the second size/development class ($r = -0.4832$; $p = 0.1321$) (Fig. 3B). For canopy and large canopy trees (two subsequent classes) this correlation practically did not exist (Fig. 3C, D).

On average, the highest mortality rates were obtained for the first size class (Table 3). The two intermediate-size classes revealed relatively small mortality rates. As expected, mortality rates for the largest trees were higher than for intermediate-size classes.

The percentage of trees which were present on sample plots already in 1936 and were still alive in 2012 (percentage of survivors) depended strongly on species. The corresponding values varied from *ca.* 10% for aspen, birch and spruce to 40–50% for oak, pine, hornbeam and lime (parameter SR in Table 4). For most species the percentage of survival was proportional to the estimated maximum life span with the notable exception of spruce, elm and ash which during some census intervals had catastrophic mortality. The current densities of survivors (AD) do not significantly differ from theoretical density values (TD) which were calculated from the initial density on the basis of mortality rates.

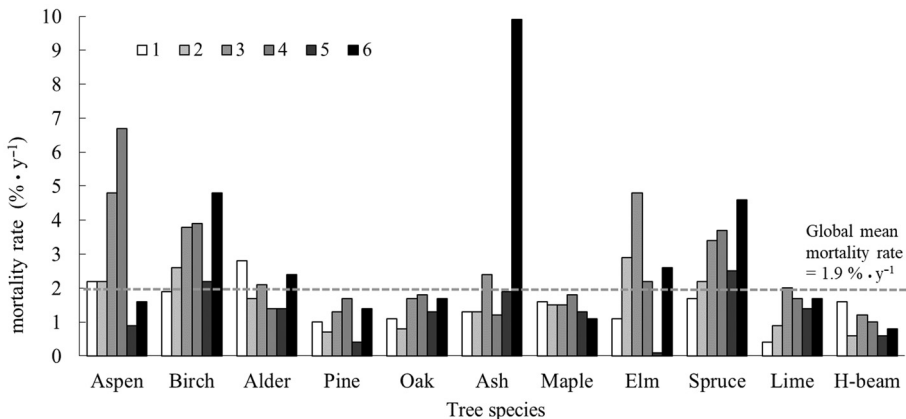


Fig. 2.

Annual mortality rates by species and census interval
Census intervals 1–6 and the sequence of tree species as in Table 1

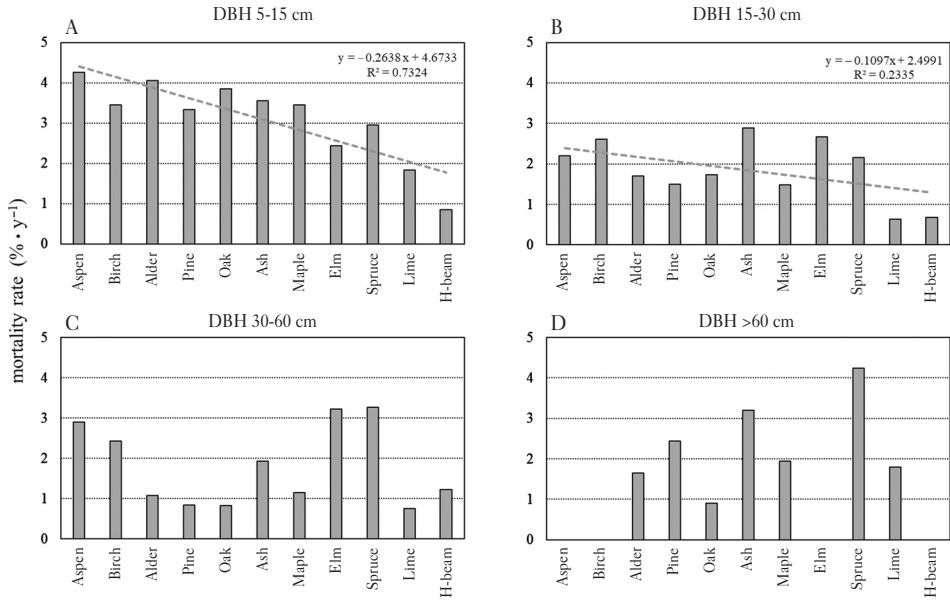


Fig. 3.

Mortality rates of trees in the Strict Reserve of the Białowieża NP by species and four size classes A-D. The sequence of species corresponds to their shade tolerance (Table 1). Missing data for some species for the largest size class (DBH>60 cm) resulted from a limited number of observations

Table 3.

Mean values of annual mortality rates calculated for four tree diameter classes

| Diameter class | 5-15 cm | 15-30 cm | 30-60 cm | >60 cm |
|----------------|------------------------|------------------------|------------------------|------------------------|
| Mortality rate | 3.1% · y ⁻¹ | 1.8% · y ⁻¹ | 1.8% · y ⁻¹ | 2.3% · y ⁻¹ |

Table 4.

Survival rate (SR) and actual, *i.e.* in 2012, density (AD) of trees which were already present on sample plots in 1936; theoretical density of survival calculated by means of annual mortality rates (TD), *m* in Table 2; current total density of trees by species (DTOT); estimated time needed to drop current species densities below an arbitrary value of 1 ind. · ha⁻¹ (ET)

| Tree species | SR [%] | AD [1 · ha ⁻¹] | TD [1 · ha ⁻¹] | DTOT [1 · ha ⁻¹] | ET [years] |
|--------------|--------|----------------------------|----------------------------|------------------------------|------------|
| Aspen | 9 | 0.7 | 0.7 | 1.1 | 3 |
| Birch | 10 | 6.8 | 5.9 | 8.0 | 64 |
| Alder | 24 | 7.0 | 6.5 | 19.4 | 150 |
| Pine | 44 | 12.4 | 12.2 | 12.4 | 227 |
| Oak | 37 | 12.8 | 11.9 | 13.7 | 185 |
| Ash | 20 | 4.9 | 2.3 | 9.1 | 73 |
| Maple | 33 | 4.1 | 4.0 | 4.9 | 108 |
| Elm | 19 | 0.6 | 0.6 | 4.3 | 68 |
| Spruce | 11 | 44.3 | 40.2 | 75.3 | 142 |
| Lime | 50 | 8.7 | 6.2 | 149.5 | 368 |
| Hornbeam | 46 | 37.6 | 39.2 | 311.4 | 598 |
| Total | 19 | 139.8 | 129.8 | 609.1 | |

Annual mortality rates were also used to calculate the length of time which is needed to reduce the current density of trees of a given species below an arbitrary level of 1 ind. · ha⁻¹. The values obtained ranged from 3 years for aspen to almost 600 years for hornbeam (parameter ET in Table 4).

Discussion

SPECIES-SPECIFIC, TEMPORAL VARIATION OF MORTALITY PATTERNS: THE ROLE OF REGULAR AND CATASTROPHIC MORTALITY. To quantify the process of tree mortality the number of losses per unit area (usually 1 hectare) and time (usually 1 year) can be used (Peterken and Jones, 1987; Bernadzki *et al.*, 1998). However, the values obtained for this coefficient depend strongly on the population size of a given species. This hinders potential comparisons between different species at the same location as well as between populations of a given species occupying different sites/localities. For this reason, relative indices of mortality should be applied (Sheil *et al.*, 1995; Mori *et al.*, 2007). The annualized mortality index m used in this paper allows for the direct comparison of different sized populations. Also, its advantage is that it does not depend on the length of the census interval (Sheil *et al.*, 1995).

The mean values of annualized mortality rates obtained in this study suggest the existence of two major groups of species. The first group contains hornbeam, pine, oak, lime and maple. Average mortality rates m for this group (1.0 to 1.5% · y⁻¹) do not deviate significantly from data reported in the literature for natural forest stands representing temperate, boreal and tropical conditions (Runkle, 1985; Harcombe, 1987; Peterken, 1996; Condit *et al.*, 1999; Wolf *et al.*, 2004; Larson and Franklin, 2010). The second group contains the remaining species studied, *i.e.* alder, elm, spruce, ash, aspen and birch. The average annual mortality rates for these species ranged from 2.0 to 3.2% · y⁻¹ which was markedly higher than the values obtained for the first group. These results suggest that in the case of the first group of species so called regular mortality was the dominant mode of tree death over the whole study period (Fig. 4A) (Hann and Hanus, 2001). In the case of regular mortality, the process of tree death is rather slow and is caused mainly by allogenic factors such as suppression (caused by competition by dominant neighbors), senescence, and selective and random occurrence of some endemic agents related to the activity of insects and fungi.

In the second group of tree species, average values and temporal variations of mortality rates were much higher. During some census intervals the mortality rate values obtained for species in this group markedly exceed the figures which are typical for regular mortality (1.0-1.5% · y⁻¹). This suggests that in this group the second type of mortality, *i.e.* catastrophic mortality, has played some role as well (Fig. 4B, C) (Hann and Hanus, 2001; Woods *et al.*, 2021). The best example in this regard is for ash. For a lengthy period of the study mortality rates for ash were rather low (1.2-2.4% · y⁻¹). However, ash dieback (Kowalski and Holdenrieder, 2009; Pautasso *et al.*, 2013), which took place during the last census interval (2002-2012), has led to a five-fold increase ('spike') in mortality rate as calculated for this species. Similarly, although not as large, spikes in mortality occurred also for other tree species in the analyzed group. Most of these spikes can be attributed to species-specific disturbance events. For example, a high increase in mortality rate observed for elm during the third census interval (1970-1982) can be attributed to the emergence of the second wave of Dutch elm disease which reached Białowieża Forest at the beginning of the 1970s (Brzeziecki *et al.*, 2012, 2018a). Similarly, high mortality rates for spruce in some census intervals are the direct result of several bark beetle outbreaks which have taken place in Białowieża Forest over the several past decades (Brzeziecki *et al.*, 2018b). In the

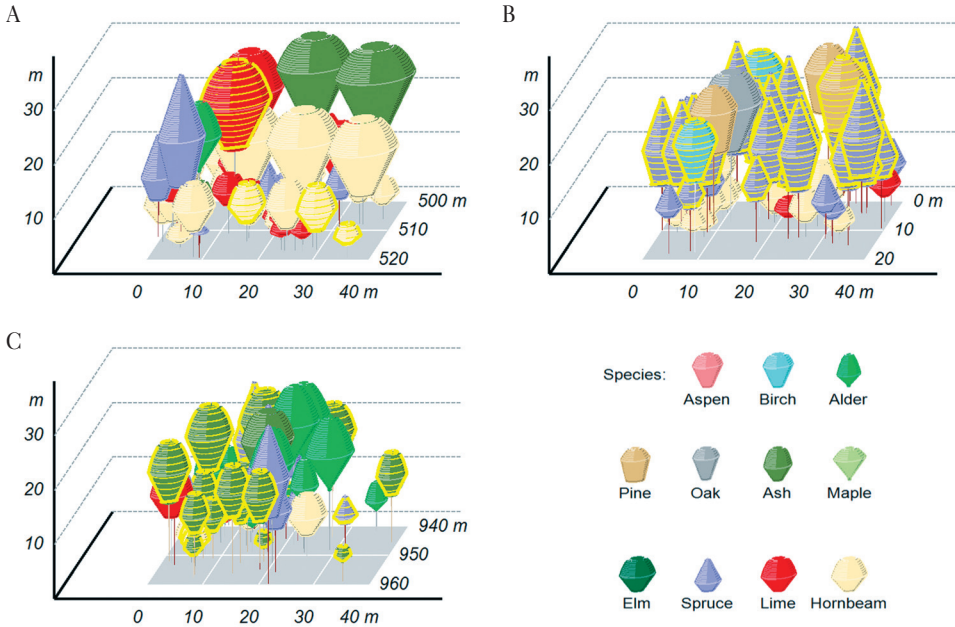


Fig. 4.

Examples of two types of tree mortality occurring in Białowieża stands

A – regular mortality (death of some suppressed hornbeams dominated by neighbouring trees) and of a single lime tree (caused most probably by aging process); B – catastrophic mortality (dieback of several spruce trees killed by bark beetles) accompanied by death of some trees of other species (birch and Scots pine); C – catastrophic mortality (dieback of several ash killed by invasive fungus *Chalara fraxinea*) accompanied by death of some other trees (mainly spruce). Dead trees are shown with yellow contour and yellow hatching. Plot no 4; comp. 318/288/289; census interval: 2001-2011

case of birch, aspen and probably also alder, the causes of strongly elevated mortality as noted during some census intervals were probably different. All three species are shade intolerant and usually establish most easily (and abundantly) after some large-scale disturbances over the course of relatively short periods. As a result, more or less even-aged cohorts of these species develop. This often leads to the simultaneous dieback of several individuals of these species which can be interpreted as a long-term residual signal of past disturbances (Woods, 2004; Woods *et al.*, 2021).

In general, the relatively high mortality rates obtained in this study for the second group of species may suggest that some previous estimates of mortality rates (seldom exceeding $1\% \cdot y^{-1}$) probably underestimated the true, long-term mortality rates, at least in old-growth forests in which both regular and catastrophic mortality mortality are present (Hann and Hannus, 2001; Woods *et al.*, 2021).

LIFE HISTORY STRATEGIES OF TREE SPECIES AND CORRESPONDING MORTALITY RATES. When considering the mortality rates obtained at the tree species level, it is rather difficult to find a strong correlation between the type of life strategy represented by a given species and its related mortality rate. It is clear, however, that both species groups mentioned above (differing in respect to mean relative mortality rates m) contain species with very different life histories and succession statuses (*e.g.*, pine *vs.* hornbeam in the first group and aspen *vs.* spruce in the second group).

Nevertheless, the analysis of the data taking into account different tree size classes revealed that there was indeed a correlation between mortality patterns and the degree of shade tolerance which is an important element of life history strategies of trees (Franklin *et al.*, 1987;

Brzeziecki and Kienast, 1994; Brzeziecki, 2000; Lorimer *et al.*, 2001; Wunder *et al.*, 2008; Holzwarth *et al.*, 2012). This correlation was most evident for suppressed and sub-canopy trees (5-15 cm of DBH) and, to a lesser extent, for sub-dominant trees (15-30 cm). In the case of natural forest stands which are often distinguished by diverse vertical structure and in which regeneration processes proceed more or less continuously, the relationship between shade tolerance and the mortality rate is somehow understandable. Under these conditions tree species with greater shade tolerance (hornbeam, lime and spruce) have a better chance to become part of the stand canopy than intolerant species. For larger trees this relationship was much weaker which indicates that other (*i.e.* not related to shade tolerance) mortality factors become more important during more advanced tree life stages.

RELATIONSHIP BETWEEN TREE SIZE AND MORTALITY RATE. Several authors have indicated that there is a correlation between tree size and the mortality rate (Lorimer and Frelich, 1984; Lorimer *et al.*, 2001; Salk *et al.*, 2011). Usually trees of medium size are distinguished by lower mortality rates than smaller and larger trees. Thus, the curve describing the relationship between mortality rate and tree size (tree diameter) is often U-shaped with some authors describing it as a 'boat-shaped' relationship. Our results confirmed this general pattern. On average, the lowest values of mortality rates were obtained for the two intermediate-sized classes, containing trees in the 15-60 cm DBH range. Relatively high mortality rates, as noted for the first size class (5-15 cm), were most likely the result of the low competitive status of such small trees. They are often suppressed by larger trees and have limited access to light and other vital resources, thus, their mortality rates are relatively high. They can also be killed by larger trees when the latter are windthrown, windsnapped or falling after death caused by other factors. In contrast, trees of greater size represent a fraction of the population which managed to achieve at least a co-dominant position in the overstory and to secure access to light and space. Such trees are relatively young and resistant to pests and pathogens as well as to harmful abiotic agents (*e.g.*, strong winds). For the largest trees (DBH>60 cm) mortality rates increase again. Firstly, such large (and old) individuals become more and more susceptible to different environmental stresses, and, secondly, the populations of such large trees are usually relatively small. Thus, even relatively rare episodes of tree death can cause significant population reductions. The U-shaped size-mortality relationship is even more clearly demonstrated when the analysis is performed for each species separately (Salk *et al.*, 2011; Brzeziecki *et al.*, 2016).

HYPOTHETICAL EXTINCTION TIME. Knowing the average mortality rate and the actual population size of a given tree species, it is possible to calculate the time which is needed to reduce current population density below an assumed threshold value (*e.g.*, 1 ind. · ha⁻¹), a parameter which could be called 'a hypothetical extinction time'. Such an analysis assumes a complete lack of new recruits, thus, it is purely theoretical. Nevertheless, the results of such an analysis may have some value. The results obtained in this paper suggest that for most species (except for aspen), a long or very long time would be needed (from 60 years for birch to 600 years for hornbeam) until their density would drop below the assumed density of 1 ind. · ha⁻¹. The large differences between specific species are the outcome of the following two causes: 1) differences in average mortality rates; 2) initial population size (the larger the current population size, the longer the time needed to reach an assumed density). Still, the results of this analysis should be treated with caution. For example, it is rather doubtful that hornbeam trees constituting the current population of this species can live this long as the maximum age of hornbeam trees is usually 250-300 years (Brzeziecki and Kienast, 1994). Moreover, the results obtained are based on the assumption of a constant

mortality rate. It is reasonable, however, to expect that as long as the population is aging the mortality rate will increase (Table 3). Random mortality agents may play some role as well. Yet, one needs to underline the importance of longevity as a key element of the life history strategies of trees (Brzeziecki and Kienast, 1994; Brzeziecki, 2000). The survival probability for trees which manage to reach a dominant position in the forest canopy is usually high (Harcombe, 1987) as confirmed by the results in this study.

CONCLUSIONS AND POSSIBLE FUTURE DEVELOPMENTS. Long-term, permanent research plots established in woodland communities subject to strict protection are an indispensable source of quantitative, detailed information about basic demographic parameters of tree populations, including *inter alia* mortality rates. A good understanding of such parameters is important for improving knowledge on community processes and for developing reliable conceptual and mathematical models of forest dynamics. In this paper by using long-term, permanent plot data, we were able to analyze mortality rates characterizing Białowieża woodland communities which have been strictly protected for over 100 years. At the community level, the average mortality rates were relatively stable varying in different census periods from 1.6 to $2.4\% \cdot y^{-1}$. Thus, our analysis did not support the findings of some other authors suggesting that overall tree mortality rates have been increasing recently as a consequence of climate change (Woods *et al.*, 2021). Nevertheless, at the tree species level several spikes in mortality rates occurred which suggest that at least for some tree species (spruce and ash) there were episodes of catastrophic mortality which might be attributed to the impact of changing environmental and biotic conditions (recurring droughts in the case of spruce and invasive fungus species in the case of ash). Such observations suggest (*inter alia*) that even under conditions of strict protection several forest species are not 'safe', and are subject to many external threats resulting from current changes in global environmental and biotic conditions. A continuation of observations and measurements conducted on permanent study plots is needed to fully understand the importance of such changes for the long-term functioning of Białowieża woodland communities.

So far, the measurements conducted on the study plots in the 'Strict Reserve' of the Białowieża NP did not include a determination of the possible causes and modes of individual tree deaths. Therefore, this element should be included in future studies as it would enable a deeper understanding of this important process and allow for the interpretation of the mortality patterns (Larson and Franklin, 2010; Holzwarth *et al.*, 2012). Towards this aim, classification schemes used by different authors for natural forests (Chao *et al.*, 2009; Larson and Franklin, 2010; Holzwarth *et al.*, 2012) can be used after some modifications and adaptation to local conditions.

Further future developments in study and analysis could attempt to relate the mode of tree death (regular *vs.* catastrophic or dispersed *vs.* clustered) to regeneration and recruitment processes. It is commonly assumed that the mode of tree death has a significant influence on which tree species and at which rate they regenerate (Whitmore, 1982; Franklin *et al.*, 1987; Woods, 2004; Mori *et al.*, 2007; Larson and Franklin, 2010). The data from permanent study plots in the Białowieża NP collected over a long period (*ca.* 80 years) comprising information on the spatial arrangement of both losses as well as recruits provides an excellent opportunity to empirically verify this commonly accepted hypothesis.

Authors' contributions

B.B. – conceived and designed the investigation, developed research methodology and prepared the manuscript; J.Z. – analyzed and visualized the data and helped in preparation of the manuscript.

Conflicts of interest

The authors declare the absence of potential conflicts of interest.

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STRESZCZENIE

Główne wzorce i prawidłowości wieloletniego procesu zamierania drzew w naturalnych drzewostanach Białowieskiego Parku Narodowego w pń.-wsch. Polsce

Naturalne wydzielanie się drzew jest obok odnowienia i wzrostu jednym z trzech głównych procesów składających się na dynamikę lasów naturalnych. Chociaż wiedza jakościowa na temat przebiegu zjawiska zamierania, głównych czynników oraz ekologicznych konsekwencji tego procesu jest stosunkowo obszerna (Franklin i in. 1987; Hann i Hanus 2001; Wolf i in. 2004; Wunder 2007; Holzwarth i in. 2012; Woods i in. 2021), to konkretnych i wiarygodnych danych liczbowych na ten temat jest stosunkowo niewiele (Larson i Franklin 2010). Wynika to m.in. ze względnej rzadkości tego zjawiska (Flewellling i Monserud 2002). W takiej sytuacji niezwykle ważną rolę odgrywają badania na stałych powierzchniach badawczych o odpowiedniej wielkości, założonych

w lasach naturalnych i obserwowanych w ciągu dostatecznie długiego czasu. Wspomniany warunek spełniają powierzchnie badawcze Katedry Hodowli Lasu SGGW w Białowieckim Parku Narodowym, funkcjonujące od 1936 r. do chwili obecnej. W niniejszej pracy dane zbierane w oparciu o te powierzchnie wykorzystano do ilościowej charakterystyki procesów zamierania drzew w tym obiekcie leśnym, cechującym się wysokim stopniem naturalności.

Obliczenia zostały wykonane z uwzględnieniem gatunków i rodzajów drzew, klas grubości oraz 6 okresów pomiarowych. Wykorzystano 2 wskaźniki zamierania drzew: o charakterze bezwzględny i względny. Pierwszy sposób polegał na obliczeniu liczby drzew, które zamarły w danym okresie (tzw. wypadów), tj. pomiędzy 2 kolejnymi inwentaryzacjami, i na przeliczeniu otrzymanych wartości na jednostkę powierzchni (1 ha) i czasu (1 rok). Drugi sposób polegał na obliczeniu rocznego względnego wskaźnika zamierania drzew (Sheil i in. 1995) (wzór 1). Ponadto na podstawie wskaźników śmiertelności określonych powyższą metodą obliczono tzw. średni czas rezydencji, tj. przeciętną długość życia drzew poszczególnych gatunków po przekroczeniu progu pomiaru pierśnicy – 5 cm (Mori i in. 2007) (wzór 2). Obliczone wskaźniki śmiertelności wykorzystano także w celu określenia długości czasu potrzebnego do spadku aktualnej liczebności populacji badanych gatunków poniżej przyjętego umownego progu (1 szt. · ha⁻¹).

Na podstawie uzyskanych wyników stwierdzono, że w okresie badań (lata 1936-2012) największą liczbą wypadów charakteryzował się świerk, na który przypadła prawie połowa wszystkich drzew, które wydzieliły się w tym czasie (tab. 1). Stosunkowo duża liczba wypadów wystąpiła także u lipy, grabu i brzozy. Najmniejszą liczbę wypadów zanotowano u osiki, klonu oraz wiązu. Zagęszczenie wypadów było skorelowane z wielkością populacji danego gatunku (ryc. 1).

Przeciętne roczne tempo zamierania drzew (w ujęciu względnym) wyniosło niespełna 2%·rok⁻¹ (z uwzględnieniem wszystkich gatunków i okresów pomiarowych) (tab. 2). Największe wartości tego parametru wystąpiły u osiki, brzozy, jesionu oraz świerka (ok. 3%·rok⁻¹), a najmniejsze u sosny i grabu (ok. 1%·rok⁻¹). Stosunkowo niskie wskaźniki zamierania (1,4-1,5%·rok⁻¹) charakteryzowały dąb, lipę i klon. Wskaźniki zamierania dla olszy i wiązu były najbardziej zbliżone do średniej ogólnej i wyniosły ok. 2%·rok⁻¹ (tab. 2). Tempo zamierania drzew poszczególnych gatunków w kolejnych okresach pomiarowych było zróżnicowane (od 0,1%·rok⁻¹ dla wiązu w 5. okresie pomiarowym do 9,9%·rok⁻¹ dla jesionu w 6. okresie pomiarowym) (tab. 2; ryc. 2). Epizody intensywnego zamierania ($m > 3\% \cdot \text{rok}^{-1}$) miały miejsce w różnych okresach pomiarowych w odniesieniu do osiki, brzozy, świerka i wiązu. Wskaźniki zamierania drzew grabu, sosny, dębu, klonu i lipy odznaczały się dużą stabilnością i w żadnym okresie pomiarowym nie przekroczyły 2%·rok⁻¹. Zróżnicowane tempo zamierania drzew poszczególnych gatunków i rodzajów przełożyło się na różnice średniego czasu rezydencji, czyli przeciętnej długości życia drzew po przekroczeniu przyjętego progu wielkości pierśnicy (5 cm). Wartość tego parametru była 3-krotnie większa dla grabu i sosny niż dla osiki, brzozy, jesionu czy świerka (tab. 2).

Zbadano też wskaźniki zamierania drzew poszczególnych rodzajów i gatunków z uwzględnieniem 4 klas grubości: 5-15 cm, 15-30 cm, 30-60 cm oraz >60 cm (ryc. 3). W przypadku drzew najcieńszych (5-15 cm) zaobserwowano wyraźną korelację pomiędzy stopniem światłoządności drzew danego rodzaju i wskaźnikiem zamierania ($R^2=0,73$) (ryc. 3A). U drzew reprezentujących drugą klasę wielkości (15-30 cm) ta zależność była jeszcze w pewnym stopniu widoczna, chociaż już wyraźnie słabsza ($R^2=0,23$) (ryc. 3B). U drzew grubych i bardzo grubych zależność między stopniem światłoządności oraz wskaźnikiem zamierania praktycznie nie występowała (ryc. 3C i 3D). Analiza średnich wartości wskaźników zamierania dla 4 rozpatrywanych klas wielkości drzew wykazała, że w przypadku drzew o pośrednich rozmiarach wskaźniki zamierania przyjmują niższe wartości niż u drzew najcieńszych i najgrubszych (tab. 3).

Procent przeżycia drzew poszczególnych gatunków był zróżnicowany: od 9% dla osiki do 50% dla lipy (tab. 4) i z wyjątkiem takich gatunków jak świerk, wiąz czy jesion, w przypadku których wystąpił katastroficzny typ zamierania, raczej dobrze korelował z maksymalną długością życia. Zagęszczenie drzew pozostałych przy życiu w całym okresie badań, obliczone z wykorzystaniem średnich wartości wskaźników zamierania, nie odbiegało znacząco od rzeczywistych wartości tego parametru (tab. 4). Czas potrzebny do tego, aby aktualne zagęszczenie poszczególnych populacji spadło poniżej umownej wartości 1 szt. · ha⁻¹, wahał się w szerokich granicach: od 3 lat u osiki do prawie 600 lat u grabu (tab. 4).

Przeciętne wartości wskaźników zamierania dla poszczególnych gatunków i rodzajów drzew (1-3% · rok⁻¹) mieściły się w ramach podawanych przez różnych autorów (Runkle 1985; Harcombe 1987; Peterken 1996; Condit i in. 1999; Wolf i in. 2004; Larson i Franklin 2010) dla naturalnych lasów strefy umiarkowanej, borealnej i tropikalnej. Najniższym wskaźnikiem zamierania drzew charakteryzował się grab. Na stosunkowo niskim poziomie utrzymywała się także śmiertelność sosny, dębu, lipy, klonu oraz olszy. Sugeruje to, że w przypadku tych gatunków wydzielanie się drzew miało „zwykły” (regularny) charakter i było spowodowane głównie takimi czynnikami jak konkurencja o zasoby i naturalne procesy starzenia (ryc. 4A). Dla pozostałych gatunków, przynajmniej w niektórych okresach badań, wskaźniki zamierania drzew wyraźnie przekraczały wartości standardowe (tj. ok. 3% · rok⁻¹), co sugeruje, że w tych okresach pojawiał się także drugi typ zamierania drzew, określany mianem „katastroficznego” (ryc. 4B i 4C). Taka sytuacja wystąpiła w najbardziej jaskrawej postaci w odniesieniu do jesionu wyniosłego w ostatnim, 6. okresie pomiarowym (lata 2002-2012). Wskaźnik zamierania drzew jesionu osiągnął w tym okresie rekordową wartość, wynoszącą 9,9% · rok⁻¹, 5-krotnie przekraczając wartość średnią dla wszystkich gatunków i całego, blisko 80-letniego okresu badawczego. Katastroficzny typ zamierania wystąpił także w przypadku takich gatunków jak świerk (kolejne gradacje kornika drukarza), wiąz (holenderska choroba wiązków), a także brzoza i osika. U tych dwóch ostatnich gatunków wynikało to prawdopodobnie z nasilenia procesu zamierania mniej lub bardziej jednowiekowych populacji powstałych po wcześniejszych, wielkopowierzchniowych zaburzeniach.

Silna zależność pomiędzy wskaźnikiem zamierania i zdolnością znoszenia ocienienia w młodości przez drzewa danego gatunku (w zakresie grubości 5-15 cm) sugerowała, że w przypadku lasów naturalnych, odznaczających się z reguły urozmaiconą strukturą oraz tym, że przebieg procesów odnowieniowych praktycznie wszystkich gatunków odbywa się pod większą lub mniejszą osłoną większych drzew, największą szansę na przeżycie i awansowanie do wyższych warstw drzewostanu mają gatunki o większej zdolności znoszenia ocienienia (grab, lipa, świerk). W miarę wzrostu rozmiarów drzew zależność ta staje się coraz słabsza, co świadczy o tym, że w późniejszych etapach życia drzew coraz większą rolę zaczynają odgrywać inne czynniki.

W przyszłości warto podjąć próbę wykorzystania danych zgromadzonych na stałych powierzchniach badawczych w celu określenia wpływu sposobu zamierania drzew (zwykły *vs.* katastroficzny, ew. rozproszony *vs.* skupiskowy) na przebieg procesu dorastania (zagęszczenie i skład gatunkowy dorostów). Warto także rozważyć rozszerzenie dotychczasowej metodyki badań o wskazanie najbardziej prawdopodobnej przyczyny wypadków rejestrowanych w kolejnych pomiarach. Pozwoliłoby to w przyszłości na bardziej pogłębioną analizę tego procesu, a tym samym na lepsze zrozumienie mechanizmów rządzących wieloletnim rozwojem lasów naturalnych.