



Annual tree mortality and felling rates in the Czech Republic and Slovakia over three decades

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Abstract

Although tree mortality is an essential process in forests, tree death still remains one of the least understood phenomena of forest development and dynamics. Therefore, we focused on annual mortality rates together with annual felling rates in the Slovak and Czech forests. We used data from the long-term national monitoring (periods of 1988–2017 in Slovakia and 1992–2017 in the Czech Republic). More than 24.6 thousand trees were assessed together in both countries. We calculated mortality and felling rates derived from two variables: basal area and number of trees. For these purposes, we selected five tree species/genera, specifically: Norway spruce, pines, European beech, oaks and common hornbeam. We recorded large inter-annual fluctuations of mortality rates in all tree species/genera. In both countries, spruce and pines had the highest mortality rates, while beech had the lowest mortality rates. Confrontation of long-term climatic data (especially annual precipitation totals) with mortality data indicated that drought was probably the most relevant factor causing tree death. On the other hand, no significant temporal trend, either increasing or decreasing, in tree mortality was found for any tree species/genera. As for all five selected tree species/genera together, significantly higher mean annual mortality rate derived from the number of trees was found in the Czech Republic (1.09%) than in Slovakia (0.56%). This finding indicates that tree mortality is often caused by combined effects of external unfavourable factors and competition pressure in forest stands.

Key words: tree mortality; felling; inter-annual oscillation; drought; climate change; long-term monitoring

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1. Introduction

Tree development, growth as well as lifespan are determined by a combination of internal (genetic properties) and external factors (e.g. Kozłowski & Pallardy 1997). As for internal factors, large differences in lifespan have been observed not only among tree species, but also within each species (Black et al. 2008). External factors are represented by abiotic environmental conditions (climate and soil properties; Williams et al. 2013), but also biotic factors such as tree density and competition (Das et al. 2011). Moreover, tree life span can be shortened by potential harmful agents acting either mechanically (e.g. Konôpka et al. 2016) or biologically (e.g. Adams et al. 2017).

Large-scale mortality (forest decline or forest die-back) has been recorded across the globe, especially in

the Northern America and Europe (e.g. Krahl-Urban et al. 1988). While in the second half of the last century, a substantial part of forest decline was caused by air pollution (Schulze et al. 1989), in the recent two decades, most incidents have been reported as consequences of climate change. Key factors associated with the latter include increasing incidence of droughts (Sánchez et al. 2008) and severe wind events (Gardiner et al. 2016).

This type of large-scale tree mortality brings significant losses in timber production and affects most forest ecosystem functions. Individual tree mortality affecting trees scattered across the forest stand usually forms a natural part of forest life cycle and is not likely to affect overall stand productivity. For instance, high “natural” tree mortality is frequent in young dense stands that originated from spontaneous natural regeneration.

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Šeben et al. (2017) found annual mortality rates calculated from the number of trees (i.e. ratios between the actually deceased trees and all present trees) in young beech and spruce stands between 10% and 30%, while mortality rates expressed from the basal area were below 10%. Mortality rates of middle-aged and mature forest stands are lower than in younger stands, e.g. Little (1995) presented 2% annual mortality in natural mature forest ecosystems.

Individual tree mortality has typically a positive impact on surrounding trees and thus on a forest ecosystem as a whole. The death of a tree creates space (a proxy resource determining availability of other resources) for neighbouring trees, but also directly provides nutrients that are released from decomposing biomass (e.g. Shortle & Dudzik 2012). However, if tree mortality exceeds a critical threshold, optimal timber production of a stand may be disrupted. Dying and ceased trees can also become a host for pests such as bark beetles and fungi, which can subsequently attack neighbouring trees (e.g. Vakula et al. 2015).

Even today, there are still many unanswered questions concerning interactions between environmental conditions and tree mortality in forest ecosystems and their effects on stand productivity. The scheme of the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP FOREST) operating under the UNECE Convention on Long-range Transboundary Air Pollution (e.g. Ferretti 1997) gathered large data sets about tree mortality over long time. The establishment of forest monitoring in Europe was driven by significant worsening of forest health in the 1980s, mainly due to air pollution. Data gathered during this monitoring programme are unique from the temporal and spatial point of view because unlike forest inventory data and traditional forest growth studies they evaluate tree state at a large scale annually (Neumann et al. 2017). Slovakia (SK) and the Czech Republic (CZ) have been members of this international programme since its inception. While in the previous works that evaluated ICP data much attention was paid to the state of foliage (e.g. Badea et al. 2004; Rautio & Ferretti 2015), development of mortality and subsequent tree harvesting has rarely been studied. The recent study of Neumann et al. (2017) analysed mortality rates at European level and identified regions with the highest mortality over the period 2000–2012. However, they examined mortality only from the point of tree number, which may not convey the full implication for forest growth. For example, mortality of the same number of big trees reduces stand living biomass more than the death of the same number of smaller trees. This type of analyses are of interest not only for the assessment of the forest health state and production, but also for modelling of forest dynamics. For example, Stage and Renner (1988) revealed that the greatest proportion of the variability in predicted volume of temperate forest stands was caused by uncertainty in

mortality estimates. In addition, some process-based models, e.g. Biome-BGC (Thornton 1998), operate at a stand level and do not simulate individual trees, hence information about the summary stand characteristics are more valuable for the model application.

The main aim of this paper was to estimate annual mortality rates and annual felling rates for the main tree species/genera over approximately three decades using the data obtained within the ICP FOREST in the CZ and SK. Based on these data we quantified inter-annual fluctuations of both rates and examined the differences between the main tree species as well as between the two countries. In addition to Neumann et al. (2017), our paper quantifies mortality rates derived from basal area, covers a longer time period, analyses species-specific mortality rates and their temporal development at a national level of both investigated countries.

2. Material and methods

2.1. Forest monitoring – general scheme

The primary goal of the ICP Forests Programme was to provide a periodical overview of spatial and temporal changes of European forests, particularly with regard to air pollution. In 1987, an international network of plots was established in a 16 × 16 km grid (Fig. 1). During the thirty years of monitoring, methodological approaches have developed, national methodologies were unified, and the surveys were enlarged, which resulted in a unique system that informs about the forests in a wider environmental context. In 1987 and 1988, a regular 16 × 16 km square grid consisting of 112 monitoring plots was established (Pavlenda et al. 2009; see also Fig. 1) in SK. In CZ, a network of plots in 16 × 16 km was established in 1987 consisting of 106 plots situated mainly in spruce and some in pine stands (Fabiánek et al. 2012). Plot establishment followed a methodological concept applied in CZ in the 1950s, when the first monitoring plots for the assessment of air pollution impact on forest stands were established (Fabiánek et al. 2005). In 1991, a denser national network of plots in a grid of 8 × 8 km was established. In 1998, the national network was optimised using both grids with regard to the spatial distribution of forest cover, and this design has been maintained until now. In total, 306 monitoring plots were chosen from the grids 16 × 16 km and 8 × 8 km to ensure representative sampling over the whole CZ (Fig. 1).

In both countries, standard indicators of forest state have been monitored: tree category, its loss and yellowing of foliage, tree felling, occurrence of standing dead trees. As we have already indicated above, the methodologies of national forest state monitoring have gone through the development in both countries. The changes also affected the evaluation of mortality and the substitution of extracted trees. In the original methodology from the end of the 1980s and the beginning of the 1990s,

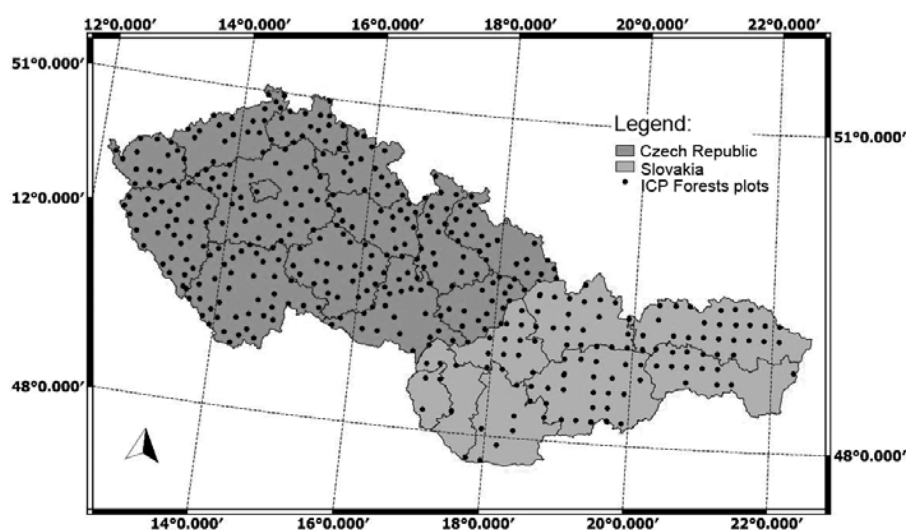


Fig. 1. Location of permanent monitoring plots in the Czech Republic and Slovakia.

not much attention was paid to these trees. In the first years of monitoring, dead trees were only registered in the database, but were not included in the calculations of final defoliation. As the methodologies developed, a new specific tree category for trees with non-evaluated defoliation was created.

Currently, the methodology of the ICP Forests (UNECE, 2016) divides trees to five main categories: living trees, trees felled and extracted, standing living trees with non-evaluated crown parameters (i.e. trees with broken crowns, if more than 50% of crown is missing, leaning or hanging trees), dead standing trees (MS), and uprooted trees (VV). The category of felled trees was divided into dead felled trees (SV) and living felled trees (ZV) based on the defoliation percentage of the tree in the preceding year. If tree defoliation was below 70%, the tree was assigned to ZV category, while a tree with defoliation equal to or greater than 70% was classified into SV category. If the dead standing tree was felled or it fell on the ground, it was reclassified to SV category. According to the international methodology, a dead standing tree is assigned 100% defoliation and the code of mortality cause only during the first evaluation after the tree death. Hence, four different categories of dead trees were defined in the database: MS – a dead standing tree, SV – a dead felled tree, ZV – a living felled tree, and VV – an uprooted tree.

2.2. Data collection in Slovakia

Permanent monitoring plots (PMP) are of a square shape and a size of 50 × 50 m, at which 50 trees were selected at a spacing of 7 × 7 m. The plots were placed in a homogeneous part of a forest remote from the forest edge at a distance of at least one mean height of the main tree species. PMPs were not located in juvenile and thicket stages.

Since the number of assessed trees annually decreases due to the impact of felling, wind disturbance, insect outbreaks and natural mortality, dead trees should be substituted to keep the minimum size of the assessed set. New trees are selected from the dominant and co-dominant trees growing within the plot. This methodology is applied in the case of mortality of individual trees. However, sometimes all trees within a plot are extracted or killed by disturbance. In this case, the plot should remain fixed and not observed until a new stand is established and grown. However, this takes several years during which the number of plots could be reduced substantially.

In SK, this action was applied in the case of three plots of fast-growing tree species (two poplar and one acacia plots). In other cases, the plot was shifted to another suitable stand in the vicinity (up to 200 m from the original plot). Note that the term “suitable” refers to the perspective of its survival, which should exceed 20–30 years, not to the tree species composition and age. The substitution of the trees should be performed annually, but due to financial constraints it was not performed on a regular basis, which resulted in the reduction of the total number of evaluated trees over the examined period.

2.3. Data collection in the Czech Republic

The plots are of a circular shape with a diameter of 18 m. The plots were selected to represent age and tree species structure of forest stands in CZ. According to the ICP manual, the minimum number of evaluated individuals is 25 per plot. In our case, if the number of individuals in a plot is lower than 100, all trees are assessed. In the case of older stands with more than 100 trees at a plot, only a half of the individuals is assessed annually. In plots where the number of trees falls below 25, additional trees are included from the plot vicinity. In juvenile stages, 25 trees

located in the spiral from the central tree are assessed. If a tree dies, it is substituted by another one to ensure a minimum number of assessed individuals. Similarly to SK, the substitution was not performed regularly, causing a provisional reduction in the number of evaluated trees.

2.4. Data analyses

Natural tree mortality and felling rates were evaluated at a national level for all tree species together (for the periods of 1988–2017 and 1999–2017 in SK and CZ, respectively), and for five tree species/genera (common beech (*Fagus sylvatica*), pine sp. (*Pinus sp.*), oak sp. (*Quercus sp.*), European hornbeam (*Carpinus betulus*), and Norway spruce (*Picea abies*). We assessed their specific annual mortality rates in individual years and mean annual mortality rates over the studied period (i.e. 1988–2017 in SK and 1992–2017 in CZ). Natural mortality in a particular year included the trees assigned the category of dead standing trees (MS) or dead felled trees (SV) in that year. Felling included the trees from the category of living felled trees (ZV). The value of natural mortality was calculated as a ratio of the number of trees that died in the year *n* to the number of living trees in the year *n*–1 in a particular country (SK or CZ). In the case of SK, the mortality ratio was also derived from basal area. Statistical evaluation of the differences in natural mortality and felling rates between species and countries was performed using ANOVA. Homogeneous groups were determined with Fischer LSD test. The calculated tested characteristic was compared with the critical values of the Student t distribution at a significance level of $\alpha = 0.05$, and the comparison of these two values showed if the trend was significant. Student t-test was applied to determine if the differences in the species-specific mean annual natural mortality and mean annual felling rates

between the countries (SK versus CZ) were significant.

3. Results

Data originating from the long-term monitoring of forest health status (1988–2017 in SK and 1999–2017 in CZ) show that felling of living trees is the most important cause of the reduction of trees. Felling of living trees is followed by felling of dead trees, natural mortality resulting in standing dead trees, while uprooting was the least important cause in both countries (Table 1 and 2). Over the whole monitored period, the number of monitored trees regardless of tree species was reduced by 36.9% and 34.4% trees in SK and CZ, respectively. Since the Czech data refer to a shorter monitoring period (by 11 years) in comparison to SK, annual mean reduction of the number of monitored trees was 1.91% per year in CZ, and only 1.27% in SK.

The annual mortality rates of all examined tree species/genera (trees from the categories of “standing dead trees” and “felled dead trees”) varied between the years (Fig. 2). In some years, the values were close to 0, while in other years they reached several per cents, and the differences were observed also between tree species/genera. The highest annual mortality rate of 13.6% was found for oaks in CZ in 1998. In SK, the highest mortality rate derived from basal area was observed for spruce in the year 2012 (5.8%), for pines in 2002 (1.3%), beech in 1999 (only 0.3%), oaks in 1997 (1.2%) and hornbeam in 2017 (0.9%). The highest values of mortality rates calculated from the number of trees for all tree species/genera (except for spruce and oaks) were observed in different years and, in all but one case, they exceeded the rates derived from basal area. The highest mortality rate based on tree number for spruce (3.5%) was recorded in the year 2012, for beech in 1993 (0.8%), and for pines

Table 1. Number of dead and felled trees during the monitored period (years 1988–2017) in Slovakia.

Tree species/genus	Dead felled		Living felled		Dead standing		Uprooted		Monitored set of trees*
	[pieces]	[%]	[pieces]	[%]	[pieces]	[%]	[pieces]	[%]	[pieces]
Black locust	19	10.6	110	61.1	13	7.2	5	2.8	180
Common beech	29	1.8	403	25.1	47	2.9	129	8.0	1,607
Pines	35	7.9	95	21.3	32	7.2	4	0.9	445
Birches	0	0	1	12.5	0	0	5	62.5	8
Elms	7	33.3	2	9.5	1	4.8	0	0	21
Cherry trees	0	0	1	25.0	2	50.0	0	0	4
Oaks	47	8.7	81	14.9	42	7.7	5	0.9	543
Hornbeam	16	3.9	80	19.3	27	6.5	9	2.2	415
Silver fir	17	7.5	71	31.3	8	3.5	5	2.2	227
Alders	1	14.3	1	14.3	1	14.3	2	28.6	7
Ashes	12	10.5	15	13.2	16	14.0	2	1.8	114
Maples	15	18.3	6	7.3	11	13.4	2	2.4	82
Limes	1	12.5	1	12.5	1	12.5	0	0	8
Walnut trees	0	0	0	0.0	1	100.0	0	0	1
Aspen	1	10.0	8	80.0	0	0.0	1	10.0	10
European larch	1	1.4	15	21.4	13	18.6	6	8.6	70
Norway spruce	205	12.7	648	40.2	162	10.1	142	8.8	1,610
Poplars	0	0	89	98.9	1	1.1	0	0	90
Willows	1	33.3	2	66.7	0	0	0	0	3
Total	410	5.5	1,631	22.0	378	5.1	317	4.3	5,439+1,960**

* State in 1998.

** 1,960 is the number of trees added in the period 1999–2017.

Table 2. Number of dead and felled trees during the monitored period (years 1999–2017) in the Czech Republic.

Tree species/genus	Dead felled		Living felled		Dead standing		Uprooted		Monitored set of trees*
	[pieces]	[%]	[pieces]	[%]	[pieces]	[%]	[pieces]	[%]	[pieces]
Black locust	0	0.0	0	0	0	0	0	0	0
Common beech	25	3.3	63	8.2	26	3.4	4	0.5	767
Pines	319	9.6	694	20.8	257	7.7	23	0.7	3,336
Birches	8	5.2	24	15.6	8	5.2	1	0.6	154
Elms	1	12.5	0	0	1	12.5	0	0	8
Cherry trees	1	14.3	0	0.0	0	0	0	0	7
Oaks	75	7.9	85	9.0	71	7.5	2	0.2	948
Hornbeam	8	3.6	42	18.9	8	3.6	4	1.8	222
Silver fir	2	2.0	7	7.1	4	4.1	0	0	98
Alders	5	3.8	9	6.9	2	1.5	0	0	131
Ashes	20	16.0	24	19.2	5	4.0	0	0	125
Maples	7	4.9	17	11.9	4	2.8	1	0.7	143
Limes	2	1.7	10	8.3	4	3.3	0	0	120
Walnut trees	0	0.0	0	0.0	0	0.0	0	0	0
Aspen	2	13.3	4	26.7	0	0.0	0	0	15
European larch	25	4.3	109	18.7	33	5.7	3	0.5	583
Norway spruce	505	6.8	2,963	39.7	391	5.2	37	0.5	7,468
Poplars	0	0.0	0	0	0	0	0	0	26
Willows	0	0.0	0	0	0	0	0	0	0
Sum	1,005	5.8	4,051	23.5	814	4.7	75	0.4	14,151+3,120**

* State in 1999.

** 3,120 is the number of trees added in the period 1999–2017.

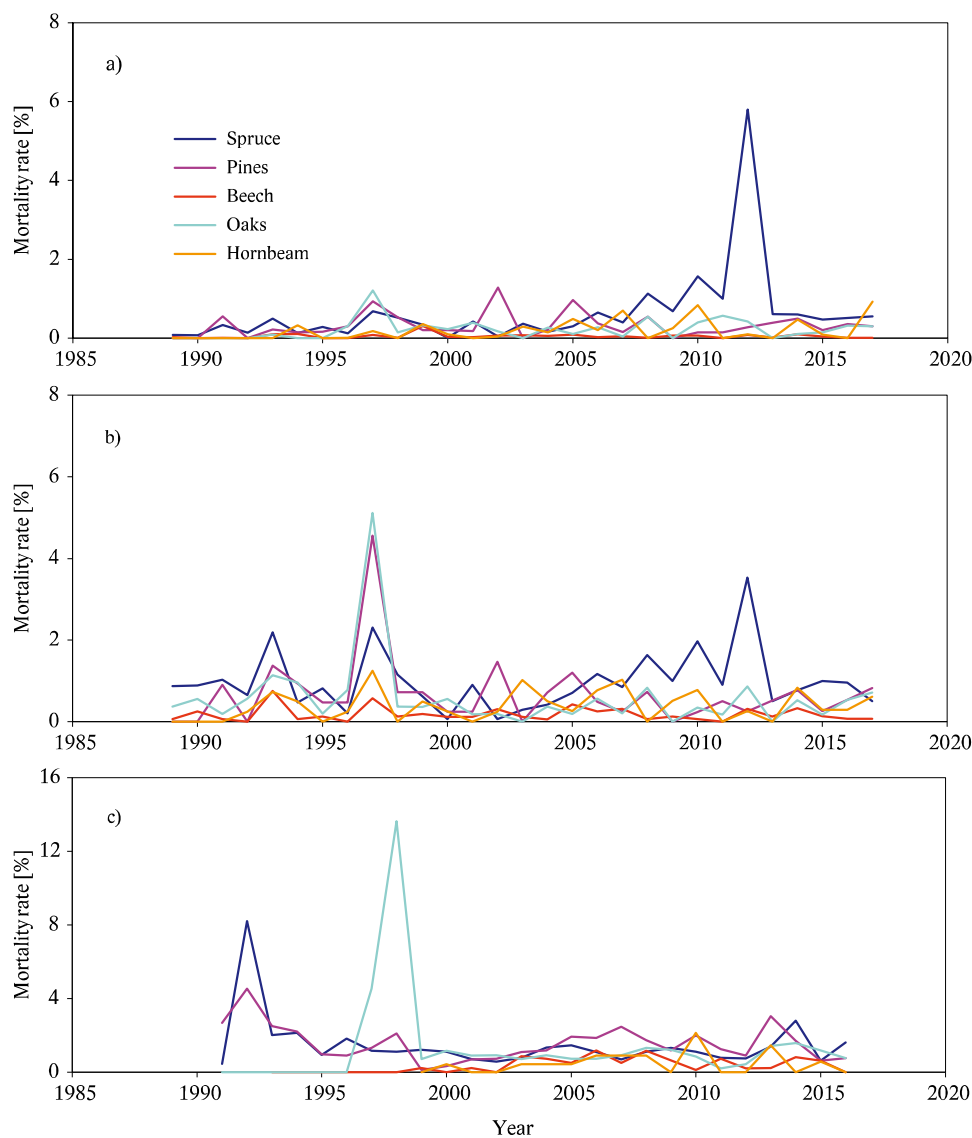


Fig. 2. Species-specific annual mortality rates in Slovakia (a, b) and the Czech Republic (c). Mortality rate derived from basal area (a) or tree number (b, c).

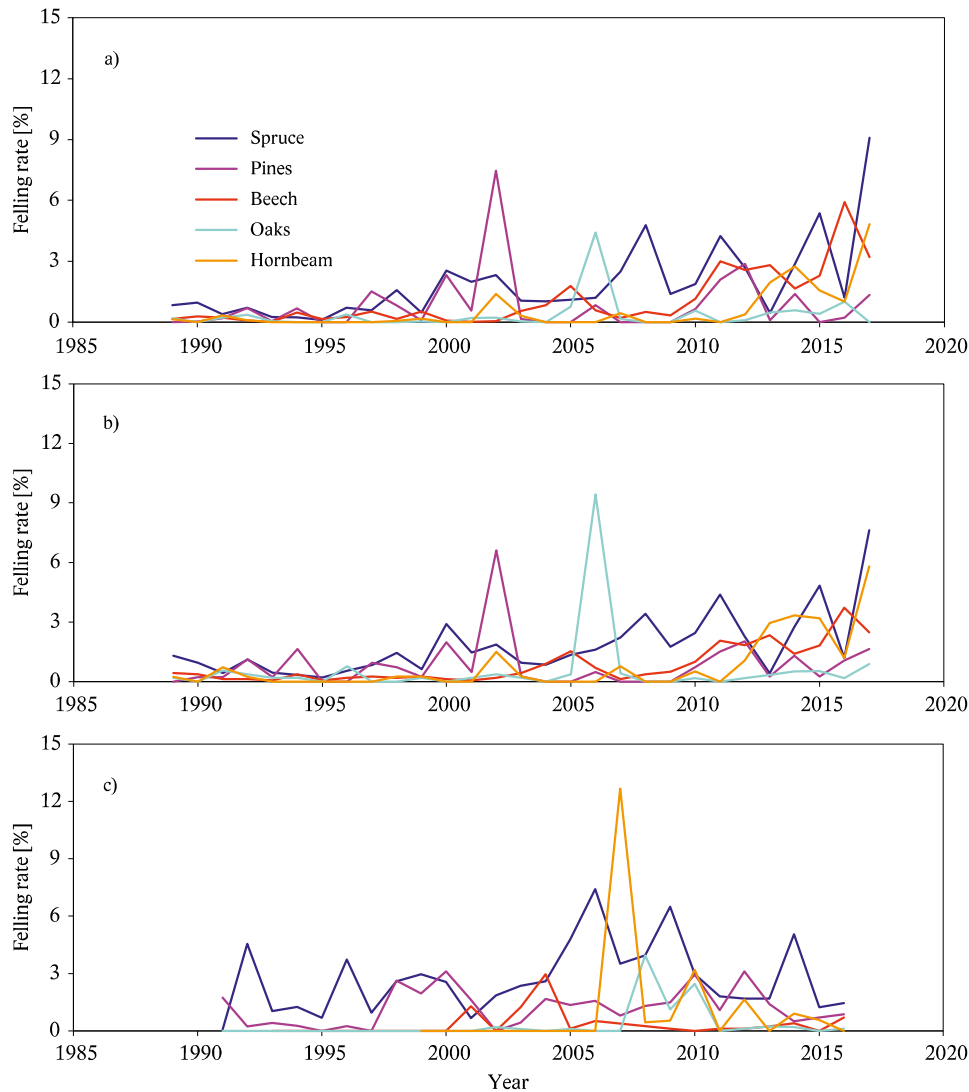


Fig. 3. Species-specific annual felling rates in Slovakia (a, b) and the Czech Republic (c). Mortality rate derived from basal area (a) or tree number (b, c).

(4.6%), oaks (5.1%), and hornbeam (1.2%) in 1997. In CZ, the highest values of the annual mortality rates were recorded in different years than in SK: in the case of spruce (8.2%) and pines (4.5%) in 1992, oaks in 1998 (13.6%), beech in the years 2006 and 2008 (1.2%), and hornbeam in 2010 (2.1%).

Similarly to the annual mortality rates, annual felling rates substantially varied between the tree species/genera and years (Fig. 3). In SK, the highest value of the annual felling rate (9.1%) derived from basal area was found for spruce in the year 2017, followed by pines (7.5% in 2002), beech (5.9% in 2016), hornbeam (4.8% in 2017), and oaks (4.4% in 2006). In the case of annual felling rates based on the number of trees, the observed species-specific maxima in SK were as follows: 7.6% for spruce in 2017, 6.6% for pines in 2002, 3.7% for beech (2016), 9.4% for oaks (2006) and 5.8% for hornbeam (2017). In CZ, the highest value of the annual felling rate was recorded for hornbeam 12.7% (in the year 2007), while

the maximum for spruce was 7.4% (2006), for pines 3.1% (2000 and 2012), for beech 3.0% (2004), and for oaks 4.0% (2008).

The highest mean annual mortality rate (over the period 1988–2017) derived from basal area was found for spruce (0.64%), followed by pines (0.32%), oaks (0.22%), hornbeam (0.19%), and the lowest value was revealed for beech (0.05%; Fig. 4a). Significant differences were found between the mortality rates of spruce and all other tree species, as well as between pines and beech. Mean annual felling rates of selected tree species/genera in Slovakia were slightly higher than their mean annual mortality rates (Fig. 4). Similarly to the mortality, the highest mean annual felling rate was found for spruce (1.88%), followed by beech (1.05%), pines (0.83%), hornbeam (0.54%) and oaks (0.35%). Significant difference in the mean annual felling rate was revealed between spruce and all other tree species (Fig. 4b).

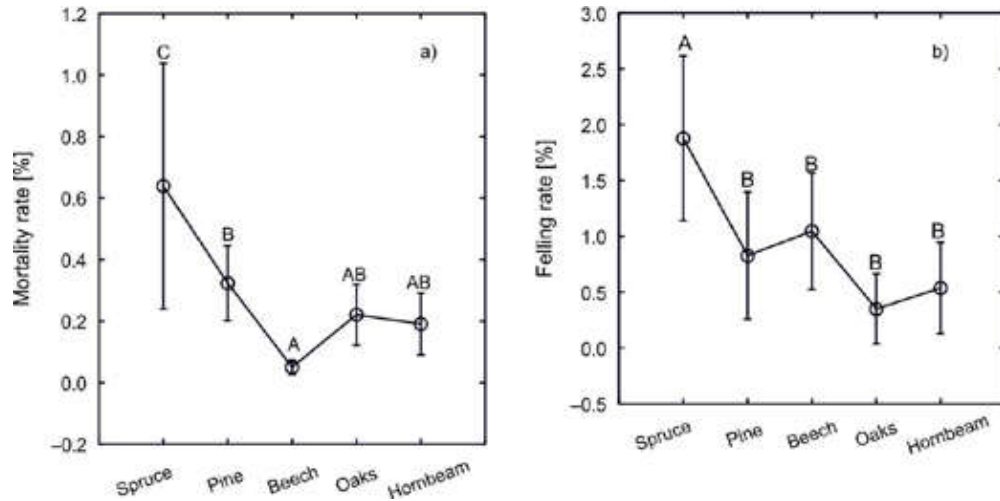


Fig. 4. Species-specific mean (\pm SE) annual mortality rates (a) and felling rates (b) in Slovakia. Rates calculated from basal area for the period between 1988 and 2017. Letters indicate significant differences between tree species/genera (LSD test; $\alpha = 0.05$).

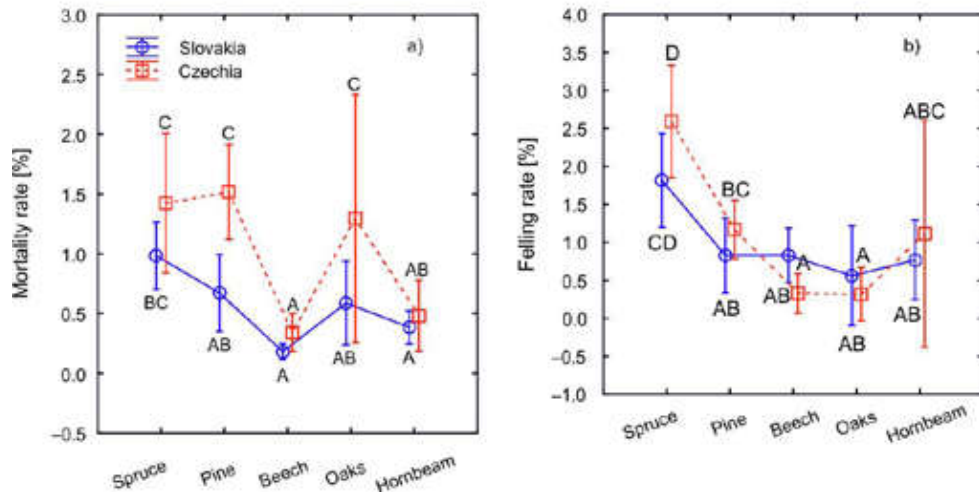


Fig. 5. Species-specific mean (\pm SE) mortality rates (a) and felling rates (b) calculated on the basis of tree number in Slovakia (period of 1988–2017) and the Czech Republic (1992–2017). Different letters indicate significant differences between countries and tree species/genera (LSD test; $\alpha = 0.05$).

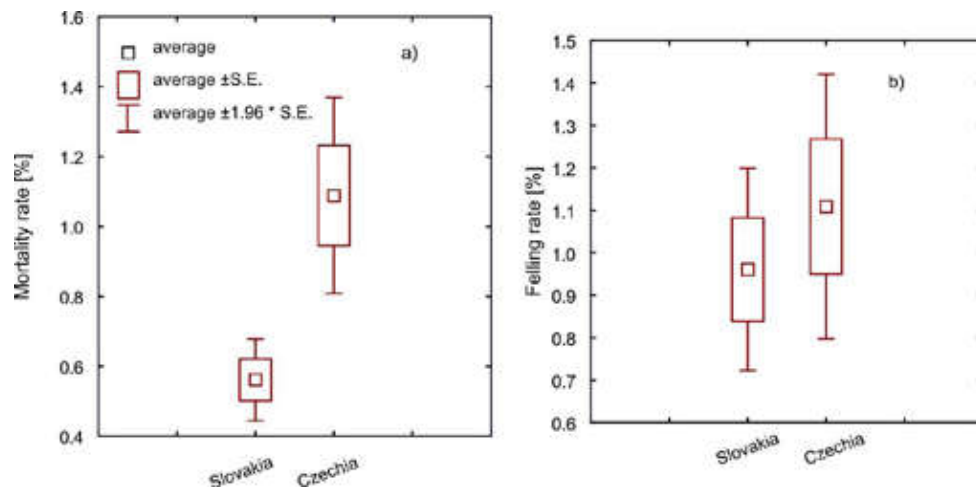


Fig. 6. Mean annual mortality rates (a) and felling rates (b) of five main tree species in Slovakia (period of 1988–2017) and the Czech Republic (1992–2017).

In the case of mean annual mortality rates based on the number of trees, spruce rate was the highest in SK (0.98%) and the rate of pines was the highest in CZ (1.46%; Fig. 5a). The lowest mean annual mortality rates were found for beech in both countries (0.18% in SK and 0.30% in CZ). Significant differences between the countries were found between mean annual mortality rates of pines and oaks. In both countries, the highest mean annual felling rates were found for spruce (1.81% in SK and 2.50% in CZ; Fig. 5b). Similarly, the lowest mean annual felling rates were recorded for oaks in both countries (0.56% in SK and 0.31% in CZ). No tree species/genus manifested significant differences in mean annual felling rates between the countries.

Finally, we compared mean annual mortality rates and mean annual felling rates calculated for all five tree species/genera together between SK and CZ (Fig. 6). Lower values of both indicators were found in SK (0.56% for mortality and 0.96% for felling) than CZ (1.09% for mortality and 1.11% for felling). We revealed significant differences in mortality rates between the countries (Fig. 6).

No significant temporal trend in the annual mortality rates of selected five tree species/genera could be revealed for the analysed monitoring period at $\alpha = 0.05$ significance level, although the calculated t value for spruce mortality rate derived from basal area was close to the critical value of Student t -distribution ($t = 2.050$ vs. $t_{crit} = 2.052$ at $\alpha = 0.05$). However, this is caused by a single high value in the year 2012 due to bark beetle disturbance of monitoring plots in the High Tatras.

4. Discussion

Although tree mortality is an essential process in forest ecosystems, tree death still remains one of the least understood phenomena of forest development and dynamics (Neumann et al. 2017). A number of published focused on short-term “massive” forest decline, usually caused by pests or natural disasters (e.g. Raffa et al. 2008; Nikolov et al. 2014; Svoboda et al. 2014; Trombik et al. 2016), but very few studies have dealt with long term individual or small-scale tree mortality occurring in a scattered pattern within a stand (Franklin et al. 1987). Therefore, we focused on the evaluation of individual tree mortality in Czech and Slovak forests based on the forest health state monitoring data. Initially we intended to derive tree mortality rates from two variables: number of trees and basal area. The basal area approach is a more comprehensive approach to tree mortality calculation than that based on the number of trees, because it accounts for the impact of tree size (see also Šebeň et al. 2017). Hence, mortality of few large trees transfers a higher amount of biomass into the dead biomass than death of a larger number of smaller trees. Moreover, while mortality of suppressed or intermediate trees is frequently related to competition

stress, this is usually not the primary cause of the death of co-dominant and dominant trees. Unfortunately, the measurements of the required input variable, i.e. stem diameter, were available only from the Slovak plots. Therefore, the mortality and felling rates for CZ were derived only from the number of trees. Thus, the comparison of tree mortality between countries was possible only on the base of the number of trees.

Our results showed large inter-annual fluctuations in both mortality and felling rates with no significant trend in time. This is in contrast to van Mantgem et al. (2009), who revealed an increasing trend in non-catastrophic mortality in the western parts of the USA since 1955. While felling rates are prevalently dependent on forestry planning and current decision making of foresters, mortality rates result from the impact of internal (stand properties) and external stress (especially abiotic agents and pests) factors. During the last decade, many papers (e.g. Sánchez et al. 2008; Hogg et al. 2008; Neumann et al. 2017) referred to drought stress, or eventually to climate variability as the most frequent reasons of changing tree mortality (van Mantgem et al. 2009).

In SK, growing season precipitation totals lower than the long-term average (1901–1990) were recorded in 1991–1993, 2000, 2003 (in that year, the lack of precipitation combined with extremely high temperature in summer occurred almost in the entire Europe), 2009, 2012, 2013 and 2015 (see a chart by Lapin 2018). On the other hand, precipitation totals exceeded the long-term normal in 1994–1996, 2001–2002, 2005, 2010 (the wettest year in the observed decades), and 2014 (Lapin 2018). In CZ, the situation was similar, since drought occurred in 2000, 2003 and 2012 (Rožnovský 2014) that were identified as dry years in SK, while floods were recorded in 1997, 2002, 2006, 2010, and 2013 (Rožnovský 2014). No general pattern was found in the annual mortality rates at monitoring plots (Fig. 2a, 2b and 2c) with regard to the precipitation totals in the growing season.

Meteorological records show that July 1997 had extremely high precipitation events, which caused floods in SK and especially in CZ (Rožnovský 2014). Such unfavourable conditions might have not only increased mortality rates of some forest tree species in SK (Fig. 2), but could explain high mortality rates of oaks in CZ in the subsequent year (1998, Fig. 2). High mortality rates of oaks might also be coupled with gradation of defoliating and sucking insects on oak species, which was observed in the period 1993–1998 (Kunca et al. 2016).

We found differences in mortality rates derived from basal area measurements from those calculated using the number of trees (data for the Slovak monitoring plots, Fig. 2). In most examined years, the mortality rates derived from the number of trees exceeded those expressed from the basal area. As for SK, the largest differences between the mortality rates derived from the two variables (i.e. basal area versus number of trees), were for almost all tree species/genera recorded in 1997. Higher mortality rate

derived from the number of trees indicates that mortality of intermediate and suppressed trees prevailed over dominant and co-dominant trees. Similar results were presented by Lutz and Halpern (2006), who revealed that mortality resulting from tree suppression dominated and occurred more frequently than mortality due to mechanical damage. The opposite relationship was revealed for spruce in the year 2012, when the mortality rate calculated from the basal area was almost 6%, while the mortality rate derived from the number of trees was less than 4% (Fig. 2). These values represented extreme values in the whole examined period, and were caused by bark beetle disturbance in the High Tatras resulting in local catastrophic mortality.

Nevertheless, as can be seen in Fig. 2, in most cases annual mortality rates did not exceed 2% that was stated by Little (1995) as an annual mortality rate in natural mature forest ecosystems. Mortality rates in CZ were frequently higher than in SK, since the applied sampling design included stands of all age categories, while in SK pre-mature stands were not monitored within this scheme.

Our results for Slovak conditions showed that the long-term species-specific averages of annual mortality rates did not exceed 1% (spruce 0.6%, pines 0.3%, beech 0.1%, oaks and 0.2%). These values are slightly lower than those derived from the National Forest Inventory (NIL) data (spruce 0.7%, pines 0.5%, beech 0.3%, oaks 0.4%, hornbeam 0.3%; Šebeň 2017) because of different stand age class frequencies in the two data sets. While the monitoring was performed in the stands aged over 30 years, the NIL included all age classes, i.e. also initial and young growth stages. Young stands, especially over-dense complexes originating from natural regeneration, are typical with very high mortality rates due to competition for resources, mainly light (Larson et al. 2015; Šebeň et al. 2017).

However, statistical differences between the countries were found only for pines and oaks (Fig. 5). In both countries, the highest mortality rates were recorded in spruce and pines, while the lowest was found in beech. These inter-specific differences are related both to ecological demands of species (climate and soil conditions) and their sensitivity to disturbance. In the temperate continental zone at lower elevations, spruce is probably one of the tree species most threatened by climate change, while beech seems to be the most resistant one (Lindner 2008). Concerning the susceptibility of tree species to a variety of pests, spruce and pine are generally prone to biotic damage, while beech is infested by pests relatively rarely (Stolina et al. 1985; Kunca et al. 2017).

Our analyses of the felling rates show that the values were larger than mortality rates (Fig. 4–6). In our case, the felling rate included not only regular thinning but also sanitary cuts. In both countries, the highest felling rates were recorded for spruce, the values were two to three times higher than the rates of other tree species.

This may indicate higher interest of forest users to harvest and utilise spruce wood, as well as its worsened health conditions due to its occurrence outside its natural range (Hlásny & Sitková 2010). Although the priority of this paper was to analyse species or genera-specific mortality rates in forest stands, the information about felling rates indicates that forest management substantially affects stand density in Central European forest ecosystems. The values of felling rates expressed from basal area and number of trees were in most cases similar (Fig. 3). That indicates that unlike mortality, felling affected all tree sizes in stands.

The ratio between the reduction of tree number caused by felling (i.e. felling of living trees) and mortality (i.e. dead felled trees + dead standing trees) was for SK equal to 1.47 (1,631 to 1,105 trees from Table 1). In CZ, the ratio was 2.14 (4,051 to 1,894 trees from Table 2). It means that in SK, “intentional” reduction of trees exceeded the “non-intentional” natural mortality by 47%, while in CZ it was much higher, by 114%. This result indicates that Czech forests are managed more intensively than Slovak forests.

The information about mortality and felling provides us not only with a more detailed picture of forest state and development, but also with valuable data for modelling forest dynamics. Individual tree mortality is one of the most difficult to predict since it is affected by a wide range of factors and their interactions. The simplest approach assumes constant annual mortality rate, e.g. Biome-BGC (Thornton 1998) uses 0.5% annual regular mortality rate for forests, which was derived from a single large-scale field experiment (White et al. 2000). Our results confirm that this is a reasonable value applicable to many managed forest stands in Central Europe. In addition, the derived mortality and felling rates can be used as species-specific inputs for modelling at national levels. This type of long-term annual records of tree survival and mortality is valuable, especially if it can be linked to inter- and intra-annual climate fluctuations, weather extremes (Neumann et al. 2017), site and stand conditions, and biotic disturbances (Das et al. 2016). More detailed evaluation of these relationships can improve our knowledge and understanding of tree mortality, and subsequently enhance the representation of this process in forest growth models.

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