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Vital rates and their multidecadal trends in the fir-beech old-growth forest of Badínsky prales

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Abstract: The study aimed to quantify annual mortality and recruitment rates on permanent research plots in the Badínsky prales old-growth forest. The data measured in four stands originate from six censuses, which together cover a 48-year period. The mean annual mortality rate reached 4.2% (*DBH* > 2 cm) or 2.3% (*DBH* > 8 cm). The mortality peaked in the first part of the observation period, probably indicating an intermediate disturbance activity, and the subsequent declining trend led to minimum annual mortality during the last 20 years. We found substantially higher fir mortality in comparison with beech, primarily during the first decades of the measurement period. Among three size categories, the stems with *DBH* 2–8 cm showed the highest mortality rate. We detected the minimum fir recruitment rate throughout the observation period; on the other hand, the beech recruitment rate was relatively high responding to the open canopy. Standing and lying deadwood volumes indicated similar trends like mortality did, and high values of fir standing deadwood observed during the first decades can signify that a relatively high proportion of mortality was related to the fir decline caused by air pollution.

Keywords: beech; deadwood; fir; mortality; old-growth forests; recruitment

The dynamics of beech or mixed-beech old-growth forests is generally viewed as continuous opening and closing of relatively small canopy gaps, which are typically created by the death of single or several trees (Kucbel et al. 2010; Feldmann et al. 2018). Besides the characteristic small-scale gap dynamics, the less common intermediate disturbances (Nagel et al. 2014; Frankovič et al. 2021) can affect the tree demography to a large extent. In temperate old-growth forests in Europe and North America, Woods et al. (2021) found considerable variation of mortality rate, which they attributed to larger disturbances and non-equilibrium dynamics of these forests. Impacts of higher mortality open larger gaps which create substantially different conditions (Muscolo et al. 2014) and release less shade-tolerant regeneration than smaller gaps (Nagel et al. 2014; Jaloviar et al. 2020).

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Even though the higher mortality rate has a considerable impact in the long run, this type of dynamics is rather infrequent in beech old-growth forests.

However, the climate change is expected to alter patterns of mortality and recruitment in forests worldwide (McDowell et al. 2020), whereas even minimum changes in mortality can have a significant impact on resulting forest dynamics (McMahon et al. 2019). To capture deviations from what has been taken as a standard we need the long-term data. The studies covering the long-term variability of vital rates are therefore essential (Nagel et al. 2021; Woods et al. 2021) and can shed light on the dynamics of beech old-growth forests in the changing environment.

We attempted to use the data covering 48 years to explore demography and its connection with changes in species composition in the National Nature Reserve (NNR) Badínsky prales (Šumichrast et al. 2020). Since the data needed to calculate vital rates were less robust, we also incorporated the volume of standing and lying deadwood measured on larger plots into this study. The main aim of our research was to analyse the annual mortality and recruitment rates on four permanent plots in the Badínsky prales reserve. We explored their changes through time and identified differences between two main species and diameter categories.

MATERIAL AND METHODS

The study was conducted in a fir-beech old-growth forest in the NNR Badínsky prales (Kremnické vrchy Mts., Slovakia, 48.6836°N, 19.0515°E), which covers 30.03 ha. The reserve is situated at the altitude between 700 m a.s.l. and 850 m a.s.l. on the NW to NE facing slopes. The mean annual air temperature is 5.3–5.8 °C, and annual precipitation ranges between 800 mm and 1 000 mm. The main soil types in the study area are Cambisols developed on andesite conglomerates covered by lava flows of pyroxenic andesite with breccias (Bublinec, Pichler 2001). Except the dominant beech (*Fagus sylvatica* L.) and fir (*Abies alba* Mill.), there is an admixture of other tree species including sycamore (*Acer pseudoplatanus* L.), European ash (*Fraxinus excelsior* L.) and elm (*Ulmus montana* With.). Since 1970, the Department of Silviculture (Technical University in Zvolen) has been conducting research on four rectangular permanent research plots (0.5 ha each). We have included data from six measurements from the last 52 years (1970, 1977, 1986, 1996, 2007 and 2018) in this study.

Vital rates, i.e. the annual mortality rate (m_a) and annual recruitment rate (r_{af}), were quantified using data from four transects of various size (500–1 000 m^2), where coordinates of individual trees ($DBH \geq 2$ cm) were registered, and the history of individual trees could be identified. The annual mortality rate was calculated according to the following Equation (1) (Sheil et al. 1995):

$$m_a = 1 - \left(\frac{N_{ST}}{N_0} \right)^{\frac{1}{T}} \quad (1)$$

where:

N_0 – number of trees at time 0 (the initial census);

N_{ST} – number of trees at time T that were present in the initial census;

T – time of a census period.

and the Equation (2) of the annual recruitment rate was (Sheil 1998; Kohyama et al. 2018):

$$r_{af} = 1 - \left(\frac{N_{ST}}{N_T} \right)^{\frac{1}{T}} \quad (2)$$

where:

N_T – number of trees at time T (the final census).

Next, we considered biases resulting from varying census interval lengths and heterogeneous population, specifically the changing frequency bias and survivorship bias (Kohyama et al. 2018). We calculated the vital rates separately for beech and fir (frequencies of other tree species were not sufficient) and for three diameter classes (2–8 cm, 8–30 cm, > 30 cm). To calculate unbiased total and species-specific means of vital rates, we used the correction approach mentioned by Kohyama et al. (2018).

Since the data from transects might be insufficient to represent demographic processes at the whole-plot scale, we compared them with the deadwood dynamics. Deadwood volume was divided into four categories – standing deadwood (snags) and three decay stages of lying deadwood (logs) which were determined according to Korpeľ (1989). Snags and logs in the first decay stage can be a sign of recent mortality and the other two decay stages can roughly approximate former mortality rates. We expected that the changes in the deadwood volume of tree species and these four categories can indicate demography trends on a larger scale.

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RESULTS AND DISCUSSION

The analysis of vital rates confirmed their considerable temporal variability (Figure 1). Pooling all species and size classes, annual mortality and recruitment rates varied between 0.9–4.3% and 0.29–16.14%, respectively. In the case of trees with *DBH* > 8 cm, these rates varied between 0.41–4.73% and 1.23–3.93%. We also observed the decreasing trend in the annual mortality of trees with *DBH* > 8 cm and in the last two decades we recorded minimum values in this category (ca. 0.4%). The average of the total annual mortality rate was 3.0% (*DBH* > 2 cm) or 2.1% (*DBH* > 8 cm). In comparison with the study from Slovenian mixed-beech old-growth forests, where mean annual mortality ranged from 0.6% to 2.1% (*DBH* > 5 cm; Nagel et al. 2021), or the comprehensive study involving temperate old-growth forests in Europe and North America (Woods et al. 2021), mean annual mortality on permanent plots in the Badínsky prales Reserve reached relatively high values. The mean annual recruitment rate reaching in our study 4.2% (*DBH* > 2 cm) or 2.3% (*DBH* > 8 cm) was also in the upper quartile of the values found in Slovenian old-growth forests (Nagel et al. 2021). These results show that forest stands in Badínsky prales have undergone significant demographic changes in the last 48 years.

The elevated mortality rate during the first decades could indicate the occurrence of intermediate disturbance events. Depending on the diameter threshold (2 cm or 8 cm), the annual mortality rate prevailed over recruitment until 1986 or 1996, respectively (Figure 1). The pronounced mortality corresponds with the increased disturbance activity in the 1980s reported by Kucbel et al. (2010). A subsequent increase in the recruitment was probably a consequence of the mortality releasing a higher amount of regeneration. The significance of intermediate-severity disturbances in terms of long-term demographic processes was previously mentioned by other authors (Nagel et al. 2021; Woods et al. 2021), and this type of disturbances was also evident from studies on disturbance dynamics in mixed beech old-growth forests in Europe (Firm et al. 2009; Nagel et al. 2014; Frankovič et al. 2021). The lower frequency of these events generally hinders their detection in mortality studies with short observation period resulting in underestimated mortality rates (Woods et al. 2021). Although in our case the presence of intermediate disturbance event is probable [background mortality rate in mixed beech old-growth forests is approximately 1% (Nagel et al. 2021)], we cannot exactly disentangle it from the general mortality rate without recording the mortality mode (standing dead trees vs snapping/uprooting).

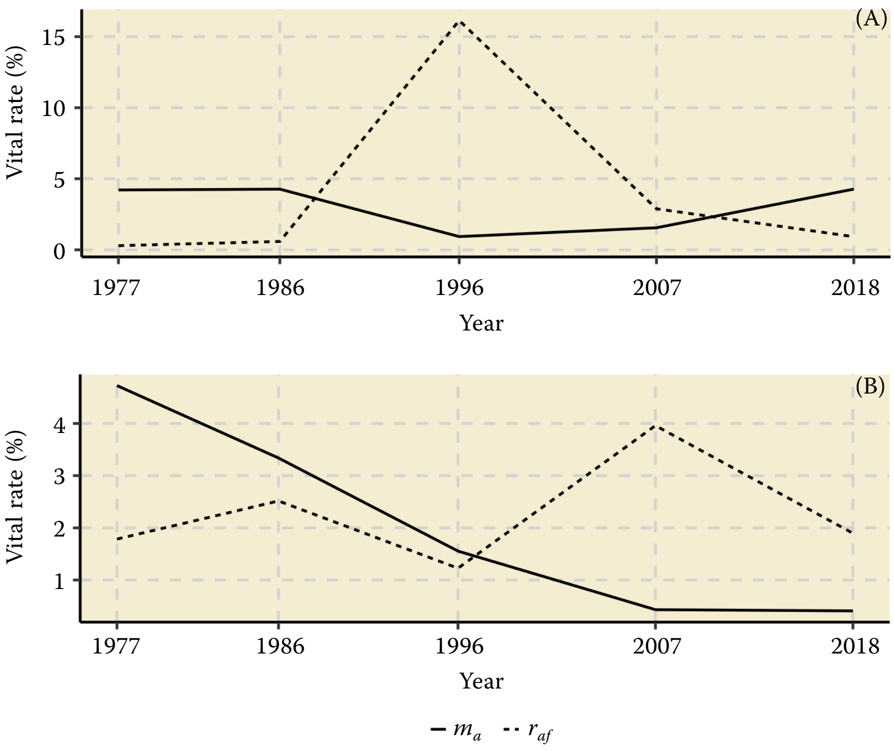

Figure 1. Mean vital rates calculated for diameter thresholds (A) *DBH* > 2 cm and (B) *DBH* > 8 cm

m_a – annual mortality rate; r_{af} – annual recruitment rate

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We registered substantial differences in the vital rates between beech and fir (Figure 2). Throughout the observation period, the annual mortality rate of beech did not exceed 5% or 3% depending on the diameter threshold. On the other hand, the annual mortality of fir reached significantly higher values in the first two decades (8.9–9.3% or 5.8–10.8%) and then it gradually decreased. The relatively high fir mortality in the 1970s and 1980s overlapped with the increased air pollution causing the fir decline in that period (Elling et al. 2009). A higher mortality rate of fir compared to beech was also detected in Slovenian old-growth forests (Nagel et al. 2021).

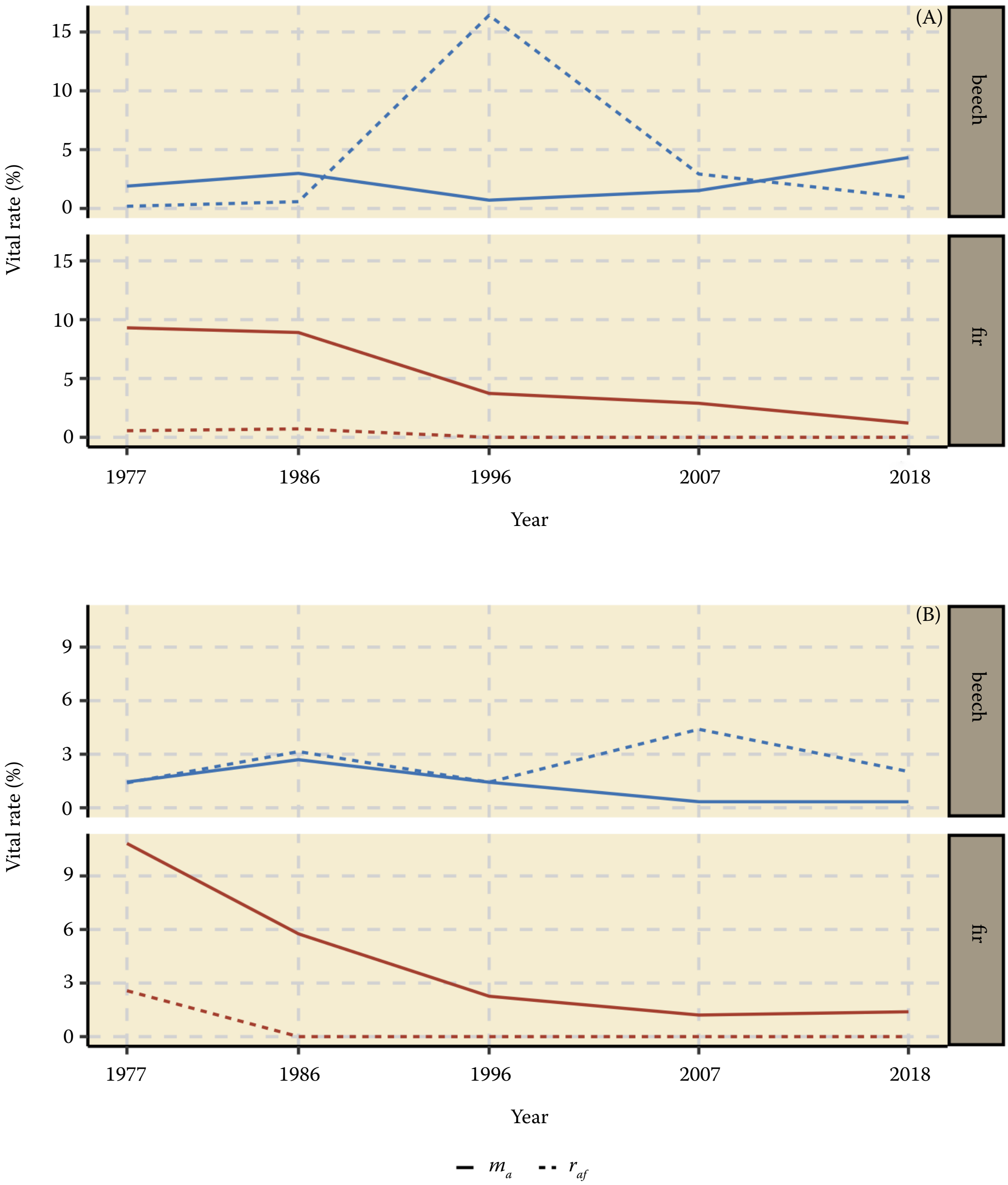

Figure 2. Vital rates of beech and fir calculated for diameter thresholds (A) *DBH* > 2 cm and (B) *DBH* > 8 cm

m_a – annual mortality rate; r_{af} –annual recruitment rate

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The annual recruitment rate of fir reached significantly lower values than that of beech (Figure 2). Unlike the fir, beech recruitment was able to flexibly respond to the higher mortality in preceding decades. In fact, we noticed virtually no recruitment of fir during the entire observation period. The fir regeneration was probably affected primarily by ungulates, whose artificially elevated populations in Badínsky prales have been reported since the beginning of the observation (Korpeľ 1958; Saniga et al. 2012). Ungulate populations inhibiting fir recruitment were reported from various parts of Europe (Vrška et al. 2009; Diaci et al. 2011; Nagel et al. 2021), and with other anthropogenic factors they led to considerable changes of the tree species composition in European old-growth forests (Diaci et al. 2011; Šumichrast et al. 2020; Diaci et al. 2022).

The annual mortality rate changed also depending on a tree dimension expressed by diameter classes (Figure 3), although these differences were not confirmed as significant. Within all three categories, fir mortality was evidently higher than that of beech during most of the observation period; however, the last decades were probably affected by a relatively small number of remaining fir trees (Table 1). Regardless of the tree species, the lowest layer (< 8 cm) mostly had the highest annual mortality throughout the entire observation period (beech 0.4–5.4%; fir 0–12.7%), and the canopy layer (> 30 cm) generally reached slightly higher values than the middle layer (8–30 cm). Higher values of mortality in the lowest category were presumably caused by stronger competitive conditions characteristic of this category, and also by overbrowsing. Nagel et al. (2021) also found the higher annual mortality for subcanopy trees in comparison with canopy trees (> 30 cm) in Slovenian old-growth forests. In temperate old-growth forests in Europe and North America, mor-

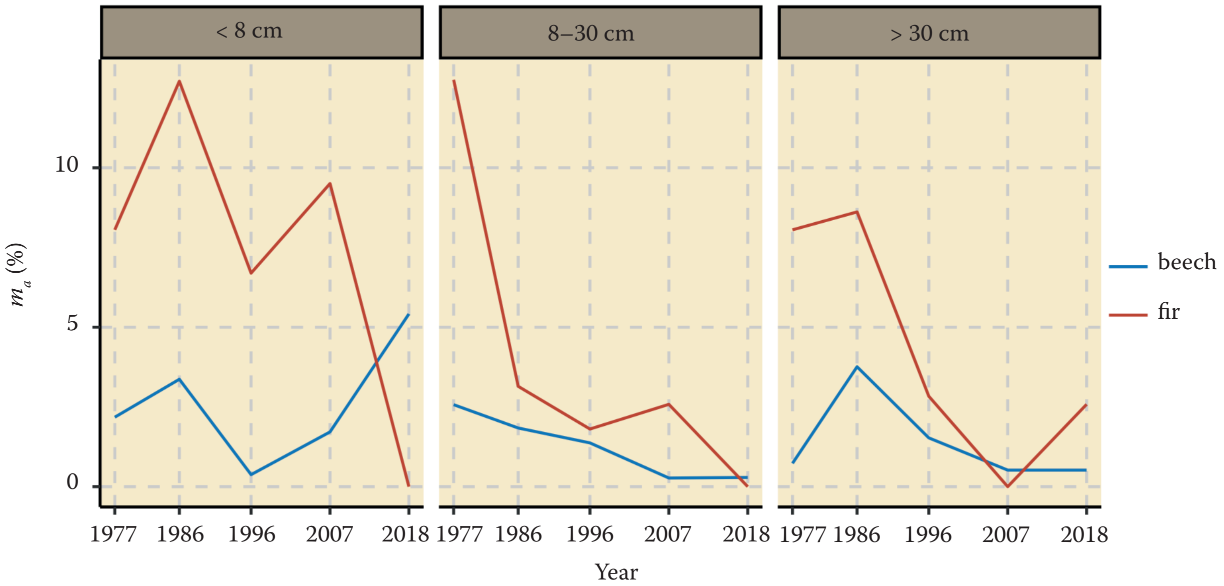

Figure 3. The annual mortality rate (m_a) of beech and fir divided into three diameter classes

Table 1. Number of fir and beech stems in 5 censuses (divided into three diameter classes)

Census	Beech			Fir			All		
	< 8 cm	8–30 cm	> 30 cm	< 8 cm	8–30 cm	> 30 cm	< 8 cm	8–30 cm	> 30 cm
1970–1977	56	12	20	27	13	9	83	25	29
1977–1986	49	26	24	17	8	9	66	34	33
1986–1996	27	31	21	6	6	4	33	37	25
1996–2007	375	34	18	3	4	4	378	38	22
2007–2018	417	64	18	1	3	4	418	67	22

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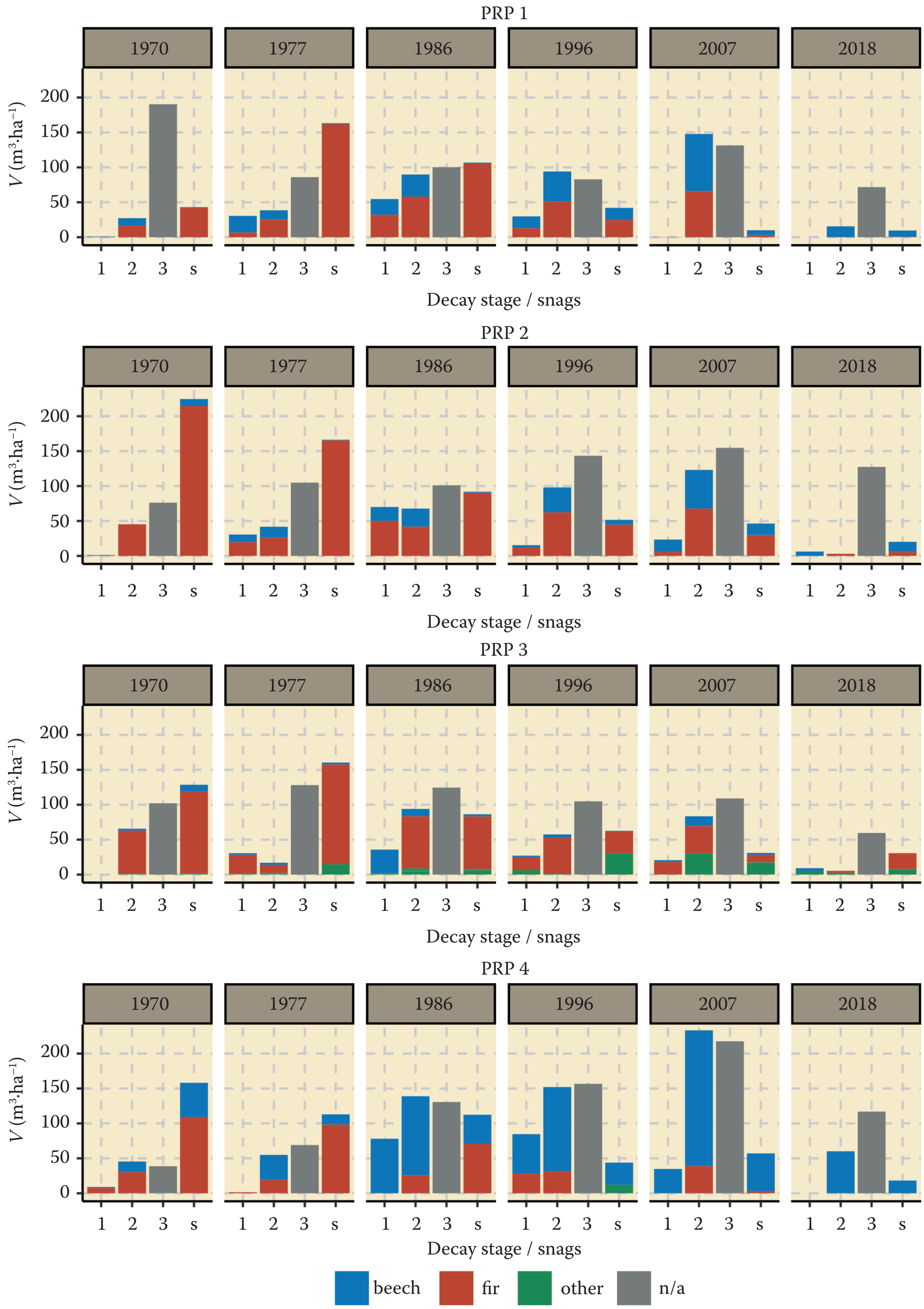

Figure 4. Volume (V) of standing and lying deadwood on four permanent research plots (PRP) between 1970–2018

1, 2, 3 – three decay stages; s – snags; n/a – not available

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tality was generally higher in the lowest layer and in the largest trees (Woods et al. 2021).

We attempted to employ the data on standing and lying deadwood from entire research plots (Figure 4) and compare them with the detected mortality rate, as deadwood can approximately indicate the history of mortality. From 1970 to 2018, the volume of total deadwood on individual research plots fluctuated between 97 $m^3 \cdot ha^{-1}$ and 543 $m^3 \cdot ha^{-1}$. The overall mean value calculated from four research plots reached the maximum in 1986 (370 $m^3 \cdot ha^{-1}$), whereas the minimum mean value was recorded in 2018 (138 $m^3 \cdot ha^{-1}$). The minimum total deadwood volume in 2018 was underlined by an extremely low volume of standing deadwood and logs in the first and second decay class. The volume of standing deadwood peaked between 1970 and 1977, and then it gradually decreased on each plot. We also found an apparent predominance of fir within standing deadwood in the first half of observation period and a subsequent decrease in the fir deadwood share.

The abovementioned trends of deadwood volume can be viewed as a rough confirmation of the investigated annual mortality rates. The maximum mean deadwood volume in 1986 could reflect the high annual mortality rate detected before that year. Next, the distinctively low deadwood volume in 2018 can be viewed as the result of the continually declining annual mortality rate and its relatively low values in the last two decades. A slightly delayed decrease in deadwood volume is a consequence of the decomposition time which can vary due to environmental conditions (Stokland et al. 2012), deadwood dimension (Herrman et al. 2015) or tree species (Weedon et al. 2009; Seibold et al. 2021). The dominant proportion of fir deadwood, primarily in the first part of the observation period, was caused by pronounced fir annual mortality recorded until 1986. This also overlapped with the most significant decrease of fir in the species composition in the Badínsky prales Reserve reported by Šumichrast et al. (2020). A relatively high proportion of fir deadwood in later measurements could be the result of longer decay times of coniferous deadwood (Weedon et al. 2009; Seibold et al. 2021). The high amount of fir standing deadwood in the 1970s and 1980s could corroborate the assumption that the air pollution was a key mortality factor which largely contributed to fir decline in the corresponding time (Elling et al. 2009; Dobrowolska et al. 2017). Thus, the dynamics of the deadwood volume provided an important insight into demography and made the results obtained from the transect data more relevant.

CONCLUSION

The analysis of the vital rates revealed their substantial changes during the last five decades. The deadwood volume dynamics showed trends similar to annual mortality and helped to understand the results better. High annual mortality in the first part of the observation period suggests the occurrence of an intermediate disturbance activity and was probably the result of increased natural and anthropogenic disturbances. Subsequently, the open canopy released considerable amounts of beech recruitment, but fir recruitment failed. The deficiency of fir recruitment was presumably caused by overbrowsing. The results suggest that the vital rates in the NNR Badínsky prales have been largely affected by anthropogenic factors.

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