Title: The legacy of disturbance on individual tree and stand-level aboveground biomass accumulation and stocks in primary mountain *Picea abies* forests

Authors: Volodymyr Trotsiuk^{1,2,*}, Miroslav Svoboda¹, Pascale Weber², Neil Pederson³, Stefan Klesse^{2,4}, Pavel Janda¹, Dario Martin-Benito⁵, Martin Mikolas¹, Meelis Seedre¹, Radek Bace¹, Lenka Mateju¹, David Frank^{2,4}

¹*Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, 165 21 Prague, Czech Republic*

²*Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland*

³*Harvard Forest, Harvard University, 324 North Main St., Petersham, Massachusetts 01366, USA*

⁴*Oeschger Centre for Climate Change Research, University of Bern, Zähringerstrasse 25, CH-3012, Switzerland*

⁵*Forest Ecology, Institute of Terrestrial Ecosystems, Department of Environmental Systems Science, ETH Zurich, Universitätsstrasse 22, 8092 Zurich, Switzerland*

Email addresses: Trotsiuk V. (trotsiuk@fld.czu.cz)*, Svoboda M. (svobodam@fld.czu.cz), Weber P. (pascale.weber@alumni.ethz.ch), Pederson N. (neilpederson@fas.harvard.edu), Klesse S. (stefan.klesse@wsl.ch), Janda P. (jandap@fld.czu.cz), Martin-Benito D. (dario.martin@usys.ethz.ch), Mikolas M. (mikolasm@fld.czu.cz), Seedre M. (seedre@gmail.com), Bace R. (bace@fld.czu.cz), Mateju L. (lmateju@fld.czu.cz), Frank D.C. (david.frank@wsl.ch)

***Corresponding author:** Volodymyr Trotsiuk, Faculty of Forestry and Wood Sciences, Czech

University of Life Sciences Prague, Kamýcka 129, 165 21 Prague, Czech Republic, tel.:

+420224383795, email: trotsiuk@fld.czu.cz

Abstract

Disturbances, both natural and human induced, influence forest dynamics, ecosystem functioning, and ecosystem services. Here, we aim to evaluate the consequences of natural disturbances on the magnitude and dynamics of tree- and stand-level biomass accumulation from decadal to centennial scales. We use tree-ring data from 2301 trees and biometric data from 4909 trees sampled in 96 plots (each 1000 m²) to quantify the influence of mixed severity disturbance regimes on annual aboveground biomass increment (AGBI) and total aboveground biomass accumulation (AGB) across a mountainous monotypic Norway spruce (*Picea abies* (L.) Karst.) primary forest. We hypothesise that the multiple internal and external factors constraining tree growth will cause differences in tree and stand-level biomass trajectories in these natural forests.

Although we found that tree-level AGB growth increases with tree size, we also found that tree age and disturbance legacies plays a crucial role for AGB in the investigated Norway spruce forests.

Importantly, while younger trees of the same diameter class have an average current AGBI rate that is ~225% higher than older trees (300-400 years), we find trees that have been suppressed for up to 120 years can respond vigorously when competition is reduced. On average, post disturbance AGBI was ~400% greater than pre-disturbance AGBI. Growth of suppressed trees, independent of their age, followed similar trajectories after canopy accession. While aboveground biomass generally increased through time, the time since disturbance and disturbance severity are important co-predictors for stand-level AGBI and AGB. These forests regained most of the above ground living biomass over short interval (~50 years) after low intensity disturbances. The highest stand-level living AGB was observed

on plots that experienced >40% canopy removal 160-190 years ago, whereas the highest AGBI occurred in plots disturbed recently within the past 40-50 years.

Our results emphasize the importance of including both individual tree age and disturbance legacies to accurately characterize biomass dynamics and trajectories in forest ecosystems. Importantly, the period of time that a tree is in the canopy, and not tree age, modulates the trajectory of tree level AGBI.

Growth rates begin to decline after ~30 years (tree-rings width) and ~100 years (AGBI) in the canopy.

We demonstrate that even late-seral forests can rapidly regain biomass lost to low intensity disturbance.

Keywords: Carbon sequestration; Carpathians; Competition; Forest development; Old-growth forest; Tree rings.

1. Introduction

Primary forest ecosystems constitute approximately 36% of the Earth's total forested area (Mackey et al., 2015) and are responsible for at least 10% of the global net ecosystem productivity (Luyssaert et al., 2008). Recent efforts to quantify dynamics and drivers of productivity in forested ecosystems have included comprehensive overviews of the global biomass variability among different biomes and climatic regions (Burrascano et al., 2013; Keith et al., 2009; Luyssaert et al., 2008), as well as the establishment of comprehensive growth models for managed forests (e.g., Weiskittel et al., 2011). Yet, much work is still needed to understand and quantify biomass dynamics and the influence of disturbances in the more remote and less well investigated primary forests (Keeton et al., 2011; Taylor et al., 2014). Most research on the impacts of disturbance on the carbon balance in primary forests has focused on stand replacing disturbances (Magnani et al., 2007; Pregitzer and Euskirchen, 2004) where forest responses have been shown to be highly analogous to those in the better investigated managed forest ecosystems (Bradford et al., 2008; Chen and Luo, 2015). This leaves many unanswered

questions about the long-term biomass dynamics in primary forests characterized by complex developmental pathways and/or mixed-severity disturbance regimes (Stueve et al., 2011; Woods, 2004).

The dynamics of aboveground biomass (AGB) accumulation in forests are an aggregate of the AGB of individual trees, including the effect of competition and resource availability, and mortality (Berger et al., 2004; Coomes et al., 2014; Jucker et al., 2014; Odum, 1969). Thus, it is critical to understand the accumulation rate and carbon storage potential of trees considering their age, diameter, and competition status within a stand. In particular, interactions among tree size, tree age, tree life history, and tree lifespan require better quantification for diverse species while considering different disturbance histories (Bigler and Veblen, 2009; Johnson and Abrams, 2009). While the growth of trees as they age has classically been thought to follow an asymptotic sigmoidal curve (e.g., Weiner and Thomas, 2001), recent studies suggest that large trees continually increase their rate of carbon accumulation with increasing size (Stephenson et al., 2014). Investigations of large and/or old trees thus require particularly careful examination, firstly, owing to this interesting recent departure from conventional wisdom, and secondly, because of the disproportionately strong impact large trees have on the carbon dynamics of whole stands (Fauset et al., 2015; Slik et al., 2013).

The broad range of disturbance severities, spatial extent, timing, and return intervals makes it difficult to study and generalize disturbance impacts on forest ecosystems. Moreover, due to the stochastic nature and infrequent occurrences of natural disturbances, many traditional methods (e.g., small permanent plots, short-term remote sensing records) have limited potential to investigate long-time scale processes related to disturbance dynamics. Dendroecological methods have proven to be a useful tool in the long-term and retrospective investigations including both disturbance dynamics (Frelich, 2002; Pederson et al., 2014) and forest biomass dynamics (Babst et al., 2014a; Foster et al., 2014; Halpin and Lorimer, 2016).

In this study, we evaluate the influence of natural disturbances on the magnitude and dynamics of biomass accumulation at decadal to centennial time-scales. The high spatiotemporal variability and wide range of disturbance severities represented in our extensive sampling allow us to draw conclusions on interactions between disturbance characteristics and forest productivity. In particular, we assess: i) individual tree AGB increment (AGBI) trends, and ii) living AGB and AGBI in forest stands in relation to past disturbance. Our study aims to advance understanding of biomass accumulation dynamics from the individual tree to stand-level in primary forest ecosystems. We hypothesise that the tree sizes, tree ages, and disturbance legacies will cause differences in tree and stand-level biomass trajectories. We test this hypothesis in primary forests dominated by Norway spruce in the Carpathians Mountains. Our work is broadly applicable to montane coniferous forest systems in similar temperate and boreal regions.

2. Materials and methods

2.1. Study site and data collection

We conduct our study in upper elevation, monotypic primary forests of *Picea abies* (L.) Karst. in the Ukrainian Carpathian mountains. Using remote sensing data, a review of scientific and popular literature, and visual inspections, we selected six stands that ranged from ~ 15-30 ha. Stands were situated between 1200 and 1500 meters a.s.l., and had no evidence of human disturbance. These stands are protected from selective logging or grazing by poor access and the steep and rocky slopes (for details see Trotsiuk et al., 2014). The mean monthly temperature of the warmest month (July) is + 16.4 °C, and of the coldest (January) is -7.6 °C. Precipitation in the region varies from 850 to 1000 mm/year, peaking in June and July. Leptosols and albic podzols predominate on sandstone bedrock (Chernyavskyy and Shpylchak, 2011; Valtera et al., 2013) .

In each stand, we placed 15-20, 1000 m² (or 500 m² if the density was >800 trees/ha, N=8) circular plots using a stratified random design (Svoboda et al., 2014) for a total of 96 plots. We recorded the

positions and diameters of all living trees with a DBH >10 cm in each plot for a total of 4909 trees. A single increment core from each of 23-25 randomly selected canopy trees in each stand was collected (N=2396). We ensured that the retained increment cores hit or were close to the pith: 49% of all cores hit the pith, 41% were within 0.5 cm of pith, and 10% within 1.5 cm of pith. All tree cores were dried and the surfaces were prepared with a core microtome (Gärtner and Nievergelt, 2010). Ring widths were measured and cross-dated following standard techniques (Stokes and Smiley, 1968) using TSAP-WinTM software (Rinntech, Heidelberg, Germany) and verified with COFECHA software (Holmes, 1983).

2.2. *Tree ring analysis*

We classified canopy accession events into two primary groups: i) rapid early growth rate and ii) abrupt, sustained increase in tree growth (Appendix A; Frelich and Lorimer, 1991; Svoboda et al., 2014). Tree recruitment was characterized as open canopy if average annual radial growth for the first 15 years was >1.3 mm or under a closed canopy for growth rates below that threshold (Fraver and White, 2005; Trotsiuk et al., 2014). We used the boundary line approach to detect release events from tree-ring width series of individual trees (Black and Abrams, 2004, 2003). Release was defined as any growth change in excess of 20% of the boundary line (Black and Abrams, 2003) that was sustained for at least 7 years (Fraver et al., 2009). Tree responses were converted to the proportion of canopy area disturbed in each plot. This served to scale the evidence of disturbance according to each tree's current crown area (Lorimer and Frelich, 1989). Current crown areas were predicted from DBH based on a linear regression fitted to the 485 measured trees (5 per plot). A plot level disturbance chronology was compiled from the annually-resolved percent canopy disturbed area. A kernel density estimation function was fit to the plot level distribution of canopy accession events, with the maximum peak of each density function used to classify the main disturbance event. As a measure of severity, we calculated the percentage of canopy removed during the main disturbance event for each plot (Lorimer

and Frelich, 1989). The study sites are characterized by variability in disturbance histories in terms of timing and magnitude (Figs A1 and A2), with these forests characterized with a prevailing mixed severity disturbance regime. We divide all plots into three groups based on their maximum disturbance severity: low (20-40%, N=36), moderate (40-60%, N=34), and high (60-100%, N=27). More information on sampling and site conditions can be found in Trotsiuk *et al.* (2014).

2.3. Aboveground biomass and its increment calculation

To estimate biomass based on a trees' DBH, we considered allometric equations for spruce based upon output parameters (AGB in kg), the species and diameter range used to develop the equation, as well as the geographical location of the allometric study site. The equation developed for the Czech Republic spruce forest (Zianis *et al.*, 2005) was found to be the closest match to our study region. Individual tree diameters were reconstructed back in time based upon the method of Bakker *et al.* (2005). Using these reconstructed diameters, we then computed the historical AGB and AGBI for each tree and year (Babst *et al.*, 2014b). Stand-level AGB and AGBI were calculated as a sum of AGB and AGBI of all living trees on each plot. We define current AGBI as the average growth rate of the last 10 years. AGBI of non-cored trees was derived from the allometric equation fitted to the trees with available AGBI that had a similar DBH and average plot level increment ($r^2=0.51$, RMSE=0.039 Mg, $P<0.001$). This calculation implies some uncertainties due to unknown ages of trees. Cored trees composed on average 71% of the plot level AGB, and the percentage was higher on plots with low severity events, while on recently disturbed plots we lack higher number of small even-aged trees.

2.3. Analysis

We fitted a generalized additive mixed model (GAMM) with a linear combination of smooth functions of DBH and tree age and their interaction as explanatory variables on AGBI, considering random effects (Tree). The pertinence of the random effect and interaction effect was determined by comparing

the different models using the Akaike Information Criterion (AIC) value (Burnham and Anderson, 2002). We calculated significance of the explanatory variables and the overall variance explained by the model. Note, that the size (or age) of a tree in a given year is not independent from the trees previous state. While this still allows for accurate estimates in mean predictions, an underestimation of uncertainty may occur if conventional error analyses are applied. Model fitting and calculations were done using ‘mgvc’ package (Wood, 2011) in the R software (R Development Core Team, 2012). The specific model applied was:

$$\log(m_{ij}) = b_0 + b_i + s_{DBH}(DBH_{ij}) + s_{Age}(Age_{ij}) + s_{DBH*Age}(DBH_{ij}, Age_{ij})$$

$$b_i \sim N(0, S^2)$$

where,

μ_{ij} is the AGBI of tree i at year j

b_i are (independent) random effects of individual tree (i)

$s_{DBH}, s_{Age}, s_{DBH*Age}$ are smooth functions to be estimated (penalized splines are used here)

s_{DBH} reflects the (smooth) marginal effect of tree DBH

s_{Age} reflects the (smooth) marginal effect of tree Age

$s_{DBH*Age}$ reflects the (smooth) interaction of tree DBH and Age (obtained as a tensor product spline).

To describe the trends in stand level AGB and AGBI, we fitted logarithmic regressions with time since main disturbance as the explanatory variable for three levels of disturbance severity (20-40%, 40-60%, and 60-100%). Time since main disturbance and disturbance severity class significantly correlate with stand level AGB and AGBI ($p < 0.05$). We assess the impact of different disturbance severity classes on stand level AGB and AGBI trajectories.

3. Results

3.1. Tree level

Age, DBH, and their interaction had significant effects on the tree level aboveground biomass increment (AGBI) (Tab 1). AGBI varied significantly among trees from different size and age classes (Fig. 2). For a given size, the absolute AGBI is generally largest for younger spruce trees (Fig. 2a,b). Similarly, for a given age, AGBI is higher for larger trees (Fig. 2a,c). Only 40% of the trees showed a positive increase in growth after their diameter exceeded 30 cm. Long-lived individuals had lower biomass growth rates over their entire lifespan. Even though these long-lived trees were large, their annual biomass accumulation is rather low. On average, trees younger than 100 years and with a 30-40 cm DBH, have an AGBI that is ~225% higher than 300-399 year old trees with the same DBH.

Legacies of disturbance strongly influenced the growth patterns and AGBI of the trees (Fig. 3), yet growth followed similar trajectories after the main canopy accession event (Fig. 3b,d). To quantify the legacy of disturbances, we divided all trees based on their duration of suppression into 10-year bins (Fig. 3a,b); more than half (~60%) of the trees originated in open canopy conditions. For those that did not originate in open canopy, long periods of suppression were regularly observed. Seventeen percent of our sampled trees experienced suppression for 50 or more years, with suppression exceeding 100 years in 6% of all cases. Notably, the increase in radial growth after suppression was similarly high, but independent of the duration of suppression period or tree age (Fig. 3c). The average in radial growth after suppression is ~1mm, but with some differences at the individual site (explored below). Even after a prolonged period of suppression (>50 years), spruce trees can abruptly increase radial growth. The AGBI of individual spruce trees peaked approximately 100 years after canopy accession and experienced relatively stable AGBI thereafter (Fig. 3b), indicating a rather constant tree growth behaviour after canopy accession.

3.2. *Stand-level*

Both the severity and timing of disturbance strongly influence the stand AGB and AGBI (Fig. 4, $p < 0.01$). The pools of living stand level AGB increased continuously for at least 200 years following disturbance (Fig. 4a). The rate of AGB increase slowed in time and appeared to become roughly constant about 200-350 year after disturbance. However, we note abilities to accurately assess the trajectory more than 200 years after disturbance are limited in this dataset due to decreases in sample size. Greater percentages of canopy removal (60-100%) were associated with steeper increases in AGB compared to low severity disturbance (20-40%, $p < 0.05$). Concomitantly, the rate of AGBI decreased as AGB increased (Fig. 4b). Minor changes in AGBI were observed for the plots that experienced low severity disturbance (20-40% canopy removed) and were significantly lower ($p < 0.01$) compared to moderate and high severity disturbances (40-60% and 60-100% canopy removed).

Across the entire sites, stand-level living AGB ranged from 141 to 399 $\text{Mg} \cdot \text{ha}^{-1}$ (average 267 $\text{Mg} \cdot \text{ha}^{-1}$), and the current AGBI between 1.5 and 6.1 $\text{Mg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ (average 3.1 $\text{Mg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$). The highest AGB (top 10%) was observed on plots where more than 40% of the canopy was estimated to have been removed 120-190 years ago (median = 176 years). In comparison to more lightly disturbed plots (<40% canopy removal), plots with a higher disturbance severities (>40% of the canopy removed) show 16% greater living AGB 150 years after disturbance and up to 30% higher AGBI 50 years after the disturbance. Much of the AGB (90% of the maximum from fitted regression Fig. 4) in plots influenced by low percentage canopy removal can be regained within a short period (50 years). In more highly disturbed plots, and despite their greater AGBI, this level of recovery takes approximately 110-125 years (Fig. 4).

4. Discussion

A deeper knowledge of disturbance legacy effects is needed to improve our understanding about the patterns and processes driving biomass development and the fate of primary forest ecosystems. Here

we show the importance of simultaneously considering tree-level and stand-level dynamics to draw an improved picture of development and biomass accumulation over time in the investigated *Picea abies* (L.) Karst. forest ecosystems. We found that prolonged suppression did not reduce trees' potential to attain high growth rates after disturbance. Such trees, independently of their age, can thus follow high trajectories of AGBI after a reduction in competition / canopy accession. Young, large spruce trees had greater rates than older trees of comparable size. At the stand level, sites that experienced minor canopy removal recovered 90% pre-disturbance AGB approximately twice as fast as those stands that experienced major canopy removal. While aboveground biomass generally increased through time, we found that both the time since disturbance and disturbance severity are important co-predictors for stand-level biomass accumulation rate and biomass pool size.

4.1. Tree growth trends and biomass increment

Individual tree AGBI data are required to better understand and model stand and ecosystem level AGBI. Yet key uncertainties remain on the relevant tree-level biomass growth dynamics. Stephenson *et al.* (2014) emphasized the potential of large trees to continuously increase carbon accumulation rates with increasing size. They detailed, for example, how a single large tree can accumulate as much biomass in one year as the total biomass of one mid-sized tree in a stand. This notion, however, contradicts (i) the hypothesis that the growth of organisms will always be constrained by some factor and follow a sigmoidal curve (Weiner and Thomas, 2001), and (ii) various widely applied physiological growth models (Berger *et al.*, 2004; Odum, 1969).

In our investigation of montane monotypic primary Norway spruce forests, we could partially support and partially refine the conclusions from Stephenson *et al.* (2014). While we found that mid-sized trees tended to have larger AGBI, we also found that the age of the tree, a potential constraint of tree growth not factored in Stephenson *et al.* (2014), strongly influences AGBI for a given tree size (Fig. 2).

Considering growth trends of individual trees separately, fewer than half of the trees showed a positive

slope in AGBI after their DBH exceeded 30 cm. Furthermore, for those trees displaying a positive slope in AGBI, the slope was only 23% of that observed for small individuals (DBH<20 cm). So, while we found growth increases in big spruce trees in these monotypic stands, the rate of growth increase was far lower than that observed for smaller trees.

Various lines of evidence provide insights and some explanations for these apparent contradictions. Some elements to consider include: individual tree growth peculiarities and crown architecture (Pretzsch and Schütze, 2005); biases in inferring dynamical processes from inventory snapshots (Bowman et al., 2013; Nehrbass-Ahles et al., 2014); and the potential influence of climate change (Andreu-Hayles et al., 2011; Cole et al., 2009). The rate of tree biomass accumulation is partially dependent on the photosynthetic rate as a function of the crown structure and light use efficiency (Binkley et al., 2010). Norway spruce have a limited ability to laterally expand their crowns and occupy canopy space after entry into the upper canopy layer (Pretzsch and Schütze, 2005). Therefore, spruce trees face constraints to increase their photosynthetic capacity and theoretically have a “predefined” sigmoidal growth after canopy accession (Fig. 3b,d). In comparison to a more diverse stand, competition in a monotypic stands would limit niche space as individuals will mostly compete for a narrow range of resources. In contrast, other tree species have higher ability to expand their crown as they gain better canopy position (Pretzsch and Schütze, 2005; Sillett et al., 2015). In short, the potential to have increasing biomass accumulation rates with tree size may depend on tree species and forest structure (Kunstler et al., 2015). The extent to which such tendencies are related to phylogenetic controls beyond the level of individual species (e.g., early versus late successional or angiosperm versus gymnosperm) requires investigation.

Second, while physiological models are mainly generated for the growth of individual trees, biased assessments will be obtained if population snapshots are assumed to represent the growth dynamics of individuals (Bowman et al., 2013). This is a notable pitfall as it is convenient to assume that, for example, the height-diameter relationships obtained in a single site visit to a forest stand represents the

growth trajectories of the individual trees within the stand (Sumida et al., 2013). Shortly, substituting time by space (Wolkovich et al., 2014). This pitfall may especially be true for trees with the ability to persist in the understory from decades to centuries before reaching a canopy position. Tracing the growth dynamics of individual trees would in reality either require a multi-decade, if not multi-centennial, monitoring campaign or laborious sectioning of a tree (Pensa et al., 2005). The few such (long-term) measurements that are available indeed show the individual growth trajectories are not well represented by population structure (Bowman et al., 2013).

Third, the potential influence of on-going environmental change on tree growth (Andreu-Hayles et al., 2011; Cole et al., 2009; Marshall, 1927) and site conditions change (Boyer, 2001; Monserud et al., 2008) should also be considered. The environmental variation experienced during the past decades includes some monotonic and/or low-frequency variations that can impact tree growth (e.g., CO₂ concentration, increasing temperatures, anthropogenic aerosols, sulphur emissions), but may be difficult to differentiate from contemporaneous trends caused by tree age, size, or changing competitive status and canopy position. Such diverse and contemporaneous growth influencing factors might have influenced patterns observed in existing data and contributed to different conclusions in literature.

Importantly, we found in this study, tree age, which is not always collected in long-term monitoring campaigns, plays an important role in individual tree AGBI estimation in montane Norway spruce. Our work reveals that the amount of time a tree spent in the canopy is important factor in understanding tree level AGBI rates. Omitting tree age in the AGBI modelling of montane Norway spruce in monotypic stands can lead to high uncertainties on the tree-level and thus also on any subsequent up-scaling. A significant part of the forest carbon sequestration models are based on the country level forest inventories data, which often do not include tree age information (Tomppo et al., 2009). More routine and extensive collection of tree cores in forest inventories might greatly improve the models parameterization and AGBI estimation. This is likely especially important in forests with greater species diversity and structural complexity.

4.2. *Stand-level living aboveground biomass dynamics*

Here we used a primary spruce forest to describe natural pathways of the AGB and AGBI dynamics based not only on time since disturbance, but also disturbance severity. We demonstrated that both the timing and severity of disturbance events influence pathways of AGB and AGBI in the primary mountain spruce forest (Fig. 4). Higher disturbance event severity (>40% canopy removal) leads to greater AGBI for approximately 100 years after disturbances and a longer recovery time for living AGB. Such trends of the biomass dynamics are similar to those created by forest management systems oriented towards even-aged stands. Recovery time after severe disturbance events (defined here as regaining 90% of the maximum from fitted regression) fits well with the rotation period for even-aged managed forests in the study region (90-120 years). In addition, our study indicates, that 40-50 years is sufficient for the forest to recover 90% AGB from a simultaneous loss of 20-40% of the canopy, as in group selection forest management (Misson et al., 2003; Nilsen and Strand, 2008).

It is important to separate semi even-aged stands that experienced severe disturbances from those with complex stand and age structure driven by mixed severity disturbances when investigating forest development and biomass dynamics. In this study we could evaluate tree and stand level AGB and AGBI from annual to multi-centennial time-scales. Although we observed a trend of increasing AGB and decreasing AGBI after disturbances, we could not confirm (or refute) that late-seral (old-growth) forest have any trend in AGB at the late developmental stages. Such long-term trends, if present, were below the detection limits in our study. We stress that further discussion on increasing or decreasing of AGB in the old growth forest based upon chronosequences of highly spatially distributed sample units with different stand development history should take into account the past forest disturbance history as an important element in explaining AGB and AGBI trends.

5. Conclusion

Legacies of disturbance history influence both tree and stand-level biomass dynamics by changing local environmental conditions and levels of inter-tree competition. Trees growing in monotypic spruce forests followed a similar sigmoidal trajectory after canopy accession, regardless of age or prior duration of suppression. This finding supports physiological theories and suggests that trees in these types of forest structures might be competing for similar limiting factors. Tree-level AGBI differ between individuals within the same size class demonstrating that both DBH and age data are required for precise tree-level AGBI estimations. While stand characteristics (e.g., time since disturbance, existing biomass, etc.) can explain much of the variability in tree and stand-level AGBI (Coomes et al., 2014; Michaletz et al., 2014), inclusion of the direct and indirect interactions with climatic and physiological factors, together with disturbance regimes, will be required for predictive models of biomass dynamics. Application of the sampling and analytical methods employed herein for other species and in other primary forest ecosystems and biomes will be crucial to refine our knowledge between mixed severity disturbances and long-term terrestrial carbon dynamics.

Acknowledgements

This study was supported by Czech Science Foundation project (GACR 15-14840S), Swiss Scientific Exchange Program (SCIEX-NMS No. 12.255, Czech University of Life Sciences, Prague (CIGA No. 20154316, IGA No. B02/15), and European Union Seventh Framework Programme under grant agreement n° 311970. Members of the WSL team were supported by the Swiss National Science Foundation iTREE-project (CRSII3_136295). We thank Olivier Bouriaud, and Robert C. Morrissey for the discussion on the earlier version of the manuscript, and Marek Brabec for help with statistical analysis.

References

Andreu-Hayles, L., Planells, O., Gutiérrez, E., Muntan, E., Helle, G., Anchukaitis, K.J., Schleser, G.H., 2011. Long tree-ring chronologies reveal 20th century increases in water-use efficiency but no enhancement of

- tree growth at five Iberian pine forests. *Glob. Change Biol.* 17, 2095–2112. doi:10.1111/j.1365-2486.2010.02373.x
- Babst, F., Alexander, M.R., Szejner, P., Bouriaud, O., Klesse, S., Roden, J., Ciais, P., Poulter, B., Frank, D., Moore, D.P., Trouet, V., 2014a. A tree-ring perspective on the terrestrial carbon cycle. *Oecologia* 176, 307–322. doi:10.1007/s00442-014-3031-6
- Babst, F., Bouriaud, O., Alexander, R., Trouet, V., Frank, D., 2014b. Toward consistent measurements of carbon accumulation: A multi-site assessment of biomass and basal area increment across Europe. *Dendrochronologia* 32, 153–161. doi:10.1016/j.dendro.2014.01.002
- Bakker, J.D., 2005. A new, proportional method for reconstructing historical tree diameters. *Can. J. For. Res.* 35, 2515–2520. doi:10.1139/x05-136
- Berger, U., Hildenbrandt, H., Grimm, V., 2004. Age-related decline in forest production: modelling the effects of growth limitation, neighbourhood competition and self-thinning. *J. Ecol.* 92, 846–853.
- Bigler, C., Veblen, T.T., 2009. Increased early growth rates decrease longevity of conifers in subalpine forests. *Oikos* 118, 1130–1138. doi:10.1111/j.1600-0706.2009.17592.x
- Binkley, D., Stape, J.L., Bauerle, W.L., Ryan, M.G., 2010. Explaining growth of individual trees: Light interception and efficiency of light use by Eucalyptus at four sites in Brazil. *For. Ecol. Manag.* 259, 1704–1713. doi:10.1016/j.foreco.2009.05.037
- Black, B.A., Abrams, M.D., 2004. Development and application of boundary-line release criteria. *Dendrochronologia* 22, 31–42. doi:10.1016/j.dendro.2004.09.004
- Black, B.A., Abrams, M.D., 2003. Use of boundary-line growth patterns as a basis for dendroecological release criteria. *Ecol. Appl.* 13, 1733–1749.
- Bowman, D.M.J.S., Brien, R.J.W., Gloor, E., Phillips, O.L., Prior, L.D., 2013. Detecting trends in tree growth: not so simple. *Trends Plant Sci.* 18, 11–17. doi:10.1016/j.tplants.2012.08.005
- Boyer, W.D., 2001. A Generational Change in Site Index for Naturally Established Longleaf Pine on a South Alabama Coastal Plain Site. *South. J. Appl. For.* 25, 88–92.
- Bradford, J.B., Birdsey, R.A., Joyce, L.A., Ryan, M.G., 2008. Tree age, disturbance history, and carbon stocks and fluxes in subalpine Rocky Mountain forests. *Glob. Change Biol.* 14, 2882–2897. doi:10.1111/j.1365-2486.2008.01686.x
- Burrascano, S., Keeton, W.S., Sabatini, F.M., Blasi, C., 2013. Commonality and variability in the structural attributes of moist temperate old-growth forests: A global review. *For. Ecol. Manag.* 291, 458–479. doi:10.1016/j.foreco.2012.11.020
- Chen, H.Y., Luo, Y., 2015. Net aboveground biomass declines of four major forest types with forest ageing and climate change in western Canada's boreal forests. *Glob. Change Biol.*
- Chernyavskyy, M., Shpylychak, M., 2011. "Gorgany" nature reserve. Pholiant, Ivano-Frankivsk.
- Cole, C.T., Anderson, J.E., Lindroth, R.L., Waller, D.M., 2009. Rising concentrations of atmospheric CO₂ have increased growth in natural stands of quaking aspen (*Populus tremuloides*). *Glob. Change Biol.* 16, 2186–2197. doi:10.1111/j.1365-2486.2009.02103.x
- Coomes, D.A., Flores, O., Holdaway, R., Jucker, T., Lines, E.R., Vanderwel, M.C., 2014. Wood production response to climate change will depend critically on forest composition and structure. *Glob. Change Biol.* 20, 3632–3645. doi:10.1111/gcb.12622
- Fauset, S., Johnson, M.O., Gloor, M., Baker, T.R., Monteagudo, A., Brien, R.J., Feldpausch, T.R., Lopez-Gonzalez, G., Malhi, Y., ter Steege, H., 2015. Hyperdominance in Amazonian forest carbon cycling. *Nat. Commun.* 6.
- Foster, J.R., D'Amato, A.W., Bradford, J.B., 2014. Looking for age-related growth decline in natural forests: unexpected biomass patterns from tree rings and simulated mortality. *Oecologia* 175, 363–374.
- Fraver, S., White, A.S., 2005. Disturbance dynamics of old-growth *Picea rubens* forests of northern Maine. *J. Veg. Sci.* 16, 597–610.
- Fraver, S., White, A.S., Seymour, R.S., 2009. Natural disturbance in an old-growth landscape of northern Maine, USA. *J. Ecol.* 97, 289–298. doi:10.1111/j.1365-2745.2008.01474.x
- Frelich, L.E., 2002. Forest dynamics and disturbance regimes studies from temperate evergreen-deciduous forests. Cambridge University Press, Cambridge; New York.

- Frelich, L.E., Lorimer, C.G., 1991. Natural disturbance regimes in hemlock-hardwood forests of the upper Great Lakes region. *Ecol. Monogr.* 61, 145–164. doi:10.2307/1943005
- Gärtner, H., Nievergelt, D., 2010. The core-microtome: A new tool for surface preparation on cores and time series analysis of varying cell parameters. *Dendrochronologia* 28, 85–92. doi:10.1016/j.dendro.2009.09.002
- Halpin, C.R., Lorimer, C.G., 2016. Long-term trends in biomass and tree demography in northern hardwoods: an integrated field and simulation study. *Ecol. Monogr.* 86, 78–93. doi:10.1890/15-0392.1
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 43, 69–78.
- Johnson, S.E., Abrams, M.D., 2009. Age class, longevity and growth rate relationships: protracted growth increases in old trees in the eastern United States. *Tree Physiol.* 29, 1317–1328. doi:10.1093/treephys/tpp068
- Jucker, T., Bouriaud, O., Avacaritei, D., Dănilă, I., Duduman, G., Valladares, F., Coomes, D.A., 2014. Competition for light and water play contrasting roles in driving diversity-productivity relationships in Iberian forests. *J. Ecol.* 102, 1202–1213. doi:10.1111/1365-2745.12276
- Keeton, W.S., Whitman, A.A., McGee, G.C., Goodale, C.L., 2011. Late-successional biomass development in northern hardwood-conifer forests of the northeastern United States. *For. Sci.* 57, 489–505.
- Keith, H., Mackey, B.G., Lindenmayer, D.B., 2009. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proc. Natl. Acad. Sci.* 106, 11635–11640.
- Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S.J., 2015. Plant functional traits have globally consistent effects on competition. *Nature*.
- Lorimer, C.G., Frelich, L.E., 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Can. J. For. Res.-Rev. Can. Rech. For.* 19, 651–663. doi:10.1139/x89-102
- Luyssaert, S., Schulze, E.-D., Börner, A., Knohl, A., Hessenmöller, D., Law, B.E., Ciais, P., Grace, J., 2008. Old-growth forests as global carbon sinks. *Nature* 455, 213–215. doi:10.1038/nature07276
- Mackey, B., DellaSala, D.A., Kormos, C., Lindenmayer, D., Kumpel, N., Zimmerman, B., Hugh, S., Young, V., Foley, S., Arsenis, K., Watson, J.E.M., 2015. Policy Options for the World's Primary Forests in Multilateral Environmental Agreements. *Conserv. Lett.* 8, 139–147. doi:10.1111/conl.12120
- Magnani, F., Mencuccini, M., Borghetti, M., Berbigier, P., Berninger, F., Delzon, S., Grelle, A., Hari, P., Jarvis, P.G., Kolari, P., 2007. The human footprint in the carbon cycle of temperate and boreal forests. *Nature* 447, 849–851.
- Marshall, R., 1927. Influence of precipitation cycles on forestry. *J. For.* 25, 415–429.
- Michaletz, S.T., Cheng, D., Kerkhoff, A.J., Enquist, B.J., 2014. Convergence of terrestrial plant production across global climate gradients. *Nature*. doi:10.1038/nature13470
- Misson, L., Vincke, C., Devillez, F., 2003. Frequency responses of radial growth series after different thinning intensities in Norway spruce (*Picea abies* (L.) Karst.) stands. *For. Ecol. Manag.* 177, 51–63. doi:10.1016/S0378-1127(02)00324-9
- Monserud, R.A., Yang, Y., Huang, S., Tchebakova, N., 2008. Potential change in lodgepole pine site index and distribution under climatic change in Alberta. *Can. J. For. Res.* 38, 343–352. doi:10.1139/X07-166
- Nehrbass-Ahles, C., Babst, F., Klesse, S., Nötzli, M., Bouriaud, O., Neukom, R., Dobberty, M., Frank, D., 2014. The influence of sampling design on tree-ring-based quantification of forest growth. *Glob. Change Biol.* 20, 2867–2885. doi:10.1111/gcb.12599
- Nilsen, P., Strand, L.T., 2008. Thinning intensity effects on carbon and nitrogen stores and fluxes in a Norway spruce (*Picea abies* (L.) Karst.) stand after 33 years. *Impacts For. Ecosyst. Manag. Greenh. Gas Budg.* 256, 201–208. doi:10.1016/j.foreco.2008.04.001
- Odum, E.P., 1969. The strategy of ecosystem development. *Sustain. Sustain.* 164, 58.
- Pederson, N., Dyer, J.M., McEwan, R.W., Hessel, A.E., Mock, C.J., Orwig, D.A., Rieder, H.E., Cook, B.I., 2014. The legacy of episodic climatic events in shaping temperate, broadleaf forests. *Ecol. Monogr.* 84, 599–620. doi:10.1890/13-1025.1

- Pensa, M., Salminen, H., Jalkanen, R., 2005. A 250-year-long height-increment chronology for *Pinus sylvestris* at the northern coniferous timberline: A novel tool for reconstructing past summer temperatures? *Dendrochronologia* 22, 75–81. doi:10.1016/j.dendro.2005.02.005
- Pregitzer, K.S., Euskirchen, E.S., 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. *Glob. Change Biol.* 10, 2052–2077. doi:10.1111/j.1365-2486.2004.00866.x
- Pretzsch, H., Schütze, G., 2005. Crown Allometry and Growing Space Efficiency of Norway Spruce (*Picea abies* [L.] Karst.) and European Beech (*Fagus sylvatica* L.) in Pure and Mixed Stands. *Plant Biol.* 7, 628–639. doi:10.1055/s-2005-865965
- R Development Core Team, R.C., 2012. R: A language and environment for statistical computing.
- Sillett, S.C., Van Pelt, R., Carroll, A.L., Kramer, R.D., Ambrose, A.R., Trask, D., 2015. How do tree structure and old age affect growth potential of California redwoods? *Ecol. Monogr.* 85, 181–212. doi:10.1890/14-1016.1
- Slik, J.W.F., Paoli, G., McGuire, K., Amaral, I., Barroso, J., Bastian, M., Blanc, L., Bongers, F., Boundja, P., Clark, C., Collins, M., Dauby, G., Ding, Y., Doucet, J.-L., Eler, E., Ferreira, L., Forshed, O., Fredriksson, G., Gillet, J.-F., Harris, D., Leal, M., Laumonier, Y., Malhi, Y., Mansor, A., Martin, E., Miyamoto, K., Araujo-Murakami, A., Nagamasu, H., Nilus, R., Nurtjahya, E., Oliveira, Á., Onrizal, O., Parada-Gutierrez, A., Permana, A., Poorter, L., Poulsen, J., Ramirez-Angulo, H., Reitsma, J., Rovero, F., Rozak, A., Sheil, D., Silva-Espejo, J., Silveira, M., Spironelo, W., ter Steege, H., Stevart, T., Navarro-Aguilar, G.E., Sunderland, T., Suzuki, E., Tang, J., Theilade, I., van der Heijden, G., van Valkenburg, J., Van Do, T., Vilanova, E., Vos, V., Wich, S., Wöll, H., Yoneda, T., Zang, R., Zhang, M.-G., Zweifel, N., 2013. Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Glob. Ecol. Biogeogr.* 22, 1261–1271. doi:10.1111/geb.12092
- Stephenson, N.L., Das, A.J., Condit, R., Russo, S.E., Baker, P.J., Beckman, N.G., Coomes, D.A., Lines, E.R., Morris, W.K., Rüger, N., Álvarez, E., Blundo, C., Bunyavejchewin, S., Chuyong, G., Davies, S.J., Duque, á., Ewango, C.N., Flores, O., Franklin, J.F., Grau, H.R., Hao, Z., Harmon, M.E., Hubbell, S.P., Kenfack, D., Lin, Y., Makana, J.-R., Malizia, A., Malizia, L.R., Pabst, R.J., Pongpattananurak, N., Su, S.-H., Sun, I.-F., Tan, S., Thomas, D., van Mantgem, P.J., Wang, X., Wiser, S.K., Zavala, M.A., 2014. Rate of tree carbon accumulation increases continuously with tree size. *Nature* 507, 90–93. doi:10.1038/nature12914
- Stokes, M.A., Smiley, T., 1968. An introduction to tree-ring dating. Chicago, University Press.
- Stueve, K.M., Perry, C.H. (Hobie), Nelson, M.D., Healey, S.P., Hill, A.D., Moisen, G.G., Cohen, W.B., Gormanson, D.D., Huang, C., 2011. Ecological importance of intermediate windstorms rivals large, infrequent disturbances in the northern Great Lakes. *Ecosphere* 2, art2. doi:10.1890/ES10-00062.1
- Sumida, A., Miyaura, T., Torii, H., 2013. Relationships of tree height and diameter at breast height revisited: analyses of stem growth using 20-year data of an even-aged *Chamaecyparis obtusa* stand. *Tree Physiol.* 33, 106–118. doi:10.1093/treephys/tps127
- Svoboda, M., Janda, P., Bače, R., Fraver, S., Nagel, T.A., Rejzek, J., Mikoláš, M., Douda, J., Boublík, K., Šamonil, P., Čada, V., Trotsiuk, V., Teodosiu, M., Bouriaud, O., Biriş, A.I., Sýkora, O., Uzel, P., Zelenka, J., Sedlák, V., Lehejček, J., 2014. Landscape-level variability in historical disturbance in primary *Picea abies* mountain forests of the Eastern Carpathians, Romania. *J. Veg. Sci.* 25, 386–401. doi:10.1111/jvs.12109
- Taylor, A.R., Seedre, M., Brassard, B.W., Chen, H.Y.H., 2014. Decline in Net Ecosystem Productivity Following Canopy Transition to Late-Succession Forests. *Ecosystems* 17, 778–791. doi:10.1007/s10021-014-9759-3
- Tomppo, E., Gschwantner, T., Lawrence, M., McRoberts, R.E., 2009. National Forest Inventories: Pathways for Common Reporting. Springer.
- Trotsiuk, V., Svoboda, M., Janda, P., Mikolas, M., Bace, R., Rejzek, J., Samonil, P., Chaskovskyy, O., Korol, M., Myklush, S., 2014. A mixed severity disturbance regime in the primary *Picea abies* (L.) Karst. forests of the Ukrainian Carpathians. *For. Ecol. Manag.* 334, 144–153. doi:10.1016/j.foreco.2014.09.005
- Valtera, M., Šamonil, P., Boublík, K., 2013. Soil variability in naturally disturbed Norway spruce forests in the Carpathians: Bridging spatial scales. *For. Ecol. Manag.* 310, 134–146. doi:10.1016/j.foreco.2013.08.004
- Weiner, J., Thomas, S.C., 2001. The nature of tree growth and the “age-related decline in forest productivity.” *Oikos* 374–376.
- Weiskittel, A.R., Hann, D.W., Kershaw, J.A., Vanclay, J.K., 2011. Forest Growth and Yield Modeling. Wiley.

- Wolkovich, E.M., Cook, B.I., McLauchlan, K.K., Davies, T.J., 2014. Temporal ecology in the Anthropocene. *Ecol. Lett.* 17, 1365–1379. doi:10.1111/ele.12353
- Woods, K.D., 2004. Intermediate disturbance in a late-successional hemlock-northern hardwood forest. *J. Ecol.* 92, 464–476.
- Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. R. Stat. Soc. Ser. B Stat. Methodol.* 73, 3–36.
- Zianis, D., Muukkonen, P., Mäkipää, R., Mencuccini, M., 2005. Biomass and stem volume equations for tree species in Europe. *Silva Fenn. Monogr.* 4, 1–213.

Tables

Table 1 Results of GAMM for influence of DBH and Age and their interaction on tree AGBI.

Figures legends

Fig. 1 Geographical location and period of occurrence of maximum disturbance severity (color gradient) of the 96 study plots (0.1 ha each). The reconstructed disturbance history is based on the growth pattern of 23-25 randomly selected trees per plot. Source of digital elevation model: <http://www.reverb.echo.nasa.gov>; country boundaries: <http://www.diva-gis.org>. Updated from Trotsiuk *et al.* (2014).

Fig. 2 Predicted aboveground biomass increment (AGBI) from generalized additive mixed model based on the ca. 342000 yearly resolved tree DBH, Age and their interaction (a). Black lines show examples of growth trajectories and change in AGBI during lifespan for selected trees. AGBI is significantly higher for younger trees within same DBH class (b), and larger trees within same Age class (c).

Fig. 3 Tree-level aboveground biomass increment (AGBI) and ring-width increment (TRW) in relation to age (a, c) and time since main canopy accession event (b, d). All trees were grouped based on the duration of suppression period into 10 years step classes (colour gradient) and the average chronology was truncated when the sample depth drops below 15 individuals. Trees show similar growth trends in both AGBI and tree-ring increment after main canopy accession event (b, d). Dashed lines (c) were

fitted to the TRW values shortly before and after the canopy accession event from each curve, and show a steady potential for growth increase over tree age.

Fig. 4 Living aboveground biomass (AGB) and current aboveground biomass increment (AGBI) expressed by the time since main disturbance and severity of the main disturbance event (% of canopy removed, as colour of points/lines). Majority of the AGB (90% from the level at 200 years, indicated by arrows) can be recovered within ca. 50 or 120-130 years after respectively moderate or heavy/extreme disturbances. Solid lines show logarithmic models fit [$y = a * \ln(x) - b$] for the different disturbance severities.

Table 1

Response variable	Explanatory variable	Estimated degree of freedom	Chi.sq	p-value
AGBI ($r^2=0.83$)	Random effect of Tree	2305.4	36	<0.0001
	Smooth main effect of DBH	4.0	1646	<0.0001
	Smooth main effect of Age	4.0	473	<0.0001
	Interaction between main effects	16.0	847	<0.0001

Figure 2

(Figure 3)

Figure 4