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

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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 AGBI 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-serial forests can rapidly regain biomass lost to low intensity disturbance.

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; Luysaert 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, 2008). 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 disproportionally 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 conducted 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 to 30 ha. Stands were situated between 1200 and 1500 m 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 (Fig. 1). 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 (Gartner and Nievergelt, 2010). Ring widths were measured and cross-dated following standard techniques (Stokes and Smiley, 1968) using TSAP-Win™ software (Rintech, 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 divided 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 (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 ($\text{r}^2 = 0.51$, 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.

2.4. 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 ‘mgcv’ package (Wood, 2011) in the R software (R Development Core Team, 2012). The specific model applied was:

$$\log(\mu_i) = \beta_0 + b_i + s_{\text{DBH}}(\text{DBH}_i) + s_{\text{Age}}(\text{Age}_i) + s_{\text{DBH-Age}}(\text{DBH}_i;\text{Age}_i)$$

$b_i \sim \text{N}(0, \sigma^2)$
where $\mu_{ij}$ is the AGBI of tree $i$ at year $j$

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

$s_{DBH}$, $s_{Age}$, $s_{DBH\times Age}$ 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

$s_{DBH\times Age}$ 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 assessed 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) (Table 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 and b). Similarly, for a given age, AGBI is higher for larger trees (Fig. 2a and 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 $\approx 225\%$ 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 and d). To quantify the legacy of disturbances, we divided all trees based on their duration of suppression into 10-year bins (Fig. 3a and b); more than half ($\approx 60\%$) 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 $\approx 1$ mm, 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 influenced the stand AGB and AGBI ($p < 0.01$). 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 Mg ha\(^{-1}\) (average 267 Mg ha\(^{-1}\)), and the current AGBI between 1.5 and 6.1 Mg ha\(^{-1}\) year\(^{-1}\) (average 3.1 Mg ha\(^{-1}\) 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 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).

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.

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 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 and 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., 2008). 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.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.04.038.

References


