Tree size thresholds produce biased estimates of forest biomass dynamics

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ABSTRACT

Studies that examine forest biomass dynamics often rely on long-term, spatially extensive, repeatedly measured permanent sample plots. Due to the intensive cost of sampling all trees within these plots, an arbitrary size threshold is typically imposed, which leads to only larger trees being sampled. However, it remains unclear whether the sampling of only large trees is representative of the entirety of stands of diverse sizes; the sampling of only large trees may produce biased estimates of biomass dynamics (growth, ingrowth, and mortality). Using a network of 141 permanent sample plots from Manitoba, Canada, with all trees of >1.3 m in height repeatedly measured, we constructed three distinct data sets, with 10 cm, 5 cm, and no diameter at breast height threshold, to illustrate that total productivity and mortality are increasingly underestimated with increasingly larger diameter at breast height thresholds. This effect is particularly significant in young stands, where productivity estimates peak at least 20 years earlier than the determined estimates under large thresholds. We highlight the need to account for smaller trees in long-term observational studies to ensure unbiased estimates of stand level aboveground biomass productivity and loss.

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1. Introduction

Accurate estimates of the changes in forest demographic rates (growth of surviving trees, recruits, and mortality) are essential toward understanding the contribution of forest biomass changes to the global carbon cycle (Pan et al., 2011), climate change impacts on forest biomass (Choat et al., 2012; Brienen et al., 2015; Doughty et al., 2015; Zhang et al., 2015; Chen et al., 2016), and the relationships between tree species diversity and productivity (Liang et al., 2016). Long-term repeatedly measured permanent sample plots (PSPs) are not only essential in the estimation of forest demographic rates, but also for the calibration of remote sensing data when mapping forest biomass distribution (Avitabile et al., 2016). However, these PSPs have been generally restricted to large trees, i.e., diameter at breast height (DBH) $\geq$ 10 cm. Accordingly, national surveys that have been developed to meet the requirements of the Kyoto Protocol often impose thresholds on plots to ease the sampling burden. In the United States of America, for example, woody plants are only considered "trees" if they attain 12.7 cm in DBH (USDA Forest Service, 2010). In Canada's National Forest Inventory, only trees >9 cm in DBH are measured at the full plot size, with all other trees being measured in considerably smaller plots (Canadian Council of Forest Ministers, 2008). These thresholds may lead to technical issues in the estimation of demographic rates. For example, trees that attain a threshold, but die before being measured (i.e., "unobserved recruits") may bias estimates (Talbot et al., 2014). Even studies that rely on increment coring to generate growth estimates tend to core trees >10 cm in DBH (Prior and Bowman, 2014; Stephenson et al., 2014; Elliott et al., 2015). However, it remains untested whether temporal alterations in forest demographic rates observed from large trees represent those that include trees of all sizes.

When measuring stand productivity, an arbitrary DBH sampling threshold can lead to five scenarios. The first occurs when a tree is already at the threshold during the initial and second census, which is an accurate measurement of tree growth. The second is when a tree is below the threshold during the first and second census. This leads to an underestimation of tree growth, as the sampling procedure is "blind" to this tree. The third scenario occurs when the tree is absent during the first census, and achieves, or exceeds, the threshold during the second census, which is an accurate measurement of recruitment. The fourth scenario occurs when the tree is below the threshold during the first census and achieves or exceeds the threshold during the second census. This would lead to an overestimation of tree recruitment, as the threshold

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measurement would count the tree as recruitment, while a no DBH threshold measurement would count the tree, properly, as growth. The final scenario occurs when a tree is absent during the first census and transitions from seedling to sapling, but does not achieve the threshold. This leads to an underestimation of recruitment using a threshold, as the threshold measurement is once again "blind" to the tree.

When using a threshold, total stand growth may only be accurately measured if all trees in a stand represent scenario one; otherwise, growth will be underestimated. Total stand recruitment will be overestimated using a threshold if the biomass from scenario four exceeds the biomass in scenario five; otherwise, if the biomass from trees representing scenario five exceeds the biomass of scenario four, recruitment will be underestimated. Recruitment may only be accurately estimated if all recruited trees represent scenario three. When measuring the biomass lost due to mortality with a threshold, there are only two possible scenarios for a tree. The first is that the tree meets or exceeds the threshold in the first census and is dead at the second census. The second is that the tree is below the threshold at the first census and is dead at the second census. If any trees in a stand align with scenario two, stand biomass lost due to mortality will be underestimated.

These arbitrary thresholds may alter our estimates of climate change driven responses of forest biomass. Similar to previous studies (Choat et al., 2012; Brienen et al., 2015; Doughty et al., 2015; Zhang et al., 2015; Chen et al., 2016), we consider the changes of demographic rates associated with the calendar year to be driven by climate changes as a whole. Although larger trees add significantly more biomass than do smaller trees, on an individual tree basis (Stephenson et al., 2014), they tend to have higher mortality probabilities during drought (Bennett et al., 2015) and slower growth rates under warmer temperatures (Prior and Bowman, 2014). When aggregated to the stand level, tree mortality rates associated with climate change tend to increase faster in younger forests than those in older forests (Luo and Chen, 2013). It is important to note that when comparing the effects of tree sizes or stand ages, several studies (Luo and Chen, 2013; Prior and Bowman, 2014; Stephenson et al., 2014) have sampled trees of only >10 cm in DBH. Previous investigations using observational data from large trees have found that biomass gain from productivity increased at slower rates than did biomass loss from mortality, leading to an overall net biomass loss associated with climate change over the past thirty years in boreal and tropical forests (Brienen et al., 2015; Chen et al., 2016). If smaller trees within a stand can grow more rapidly and be less susceptible to increased mortality (Bennett et al., 2015), then studies that rely on solely large trees may be underestimating the biomass that is gained from growth, while overestimating biomass loss from increased mortality rates. This may lead to an overestimate of the negative effects of temporal trends associated with climate change on net aboveground biomass change.

The use of DBH thresholds may also alter our predictions of how forest stands respond to stand development. Generally, subsequent to a stand-replacing disturbance, stands are initiated through a high level of recruits, which grow quickly (Oliver and Larson, 1990; Poorter et al., 2016). Once canopy trees attain their maximum longevity, they are replaced by understorey trees. This gap dynamics phase is theorized as biomass gain from the growth of surviving trees and recruits equaling biomass loss from mortality (Oliver and Larson, 1990; Coomes et al., 2012). Sampling trees >10 cm in DBH may lead to higher underestimations of growth and mortality at younger ages. In boreal forests, for example, the majority of aboveground biomass is contained within small trees (<10 cm in DBH) in stands younger than 27 years old, while large trees (≥10 cm in DBH) become the primary reservoirs of aboveground biomass quickly thereafter (Taylor et al., 2014). How DBH

threshold use may bias estimates in the biomass dynamics of regenerating stands is critical to understand, in the face of increasing stand-replacing disturbances (Westerling et al., 2006; Millar and Stephenson, 2015).

Here we used a network of 141 repeatedly measured PSPs, located throughout Manitoba, Canada to assess how DBH thresholds may alter biomass change estimates associated with each of the three demographic rates, and the predictions for their responses to temporal trends associated with climate change and stand ageing processes. These plots were established in stands that regenerated naturally following stand replacing wildfire, and underwent repeated censuses every five years, from 1985 to 2010. During each census, all trees >1.3 m in height were tagged and measured for DBH. The dataset included a total of 54,795 individual trees at least 1.3 m in height and an average of 3.4 recorded measurements per stem.

2. Materials and methods

2.1. Study area and long-term repeatedly measured sample plots

We used permanent sample plots (PSPs) established throughout Manitoba, Canada, commencing in 1985, by the Provincial Government of Manitoba (data is available upon request). The PSPs were located in visually homogenous stands of greater than 1 ha in size, at least 100 m from any openings to minimize edge effect impacts. We selected 141 plots for our study, using the following selection criteria: (*i*) PSPs had a known origin date of stand replacing wildfire, and were unmanaged; (*ii*) PSPs had all trees marked and tagged with diameter at breast height (DBH) and species identification accurately tracked over multiple censuses; and, (*iii*) PSPs had to have a minimum of three censuses with a census length of 5 years. Since the Manitoba government has applied its own threshold of 7.1 cm DBH for all measurements after 2011, only measurements before 2011 were included in this study (i.e., measurements where all trees of ≥1.3 m in height were tagged and measured). Plots ranged from 95.3° to 101.7°W in longitude, 49.0° to 56.99°N in latitude, and from 159 to 406 m above sea level in elevation (Fig. S1). Plots were generally established in forests dominated by *Populus tremuloides* Michx., *Pinus banksiana* Lamb., and *Picea mariana* (Mill.) Britton, Sterns & Poggenb. Species that made up at least 1% of aboveground biomass across all plots consisted of: *Pinus banksiana* (33.6%), *Populus tremuloides* (23.7%), *Picea mariana* (21.7%), *Larix laricina* (Du Roi) K. Koch (5.4%), *Picea glauca* (Moench) Voss (3.7%), *Abies balsamea* (L.) Mill. (3.3%), *Fraxinus nigra* Marshall (3.0%), *Betula papyrifera* Marshall (2.7%), *Fraxinus pennsylvanica* Marshall (1.7%), and *Thuja occidentalis* L. (1.0%). We examined 13 trees that grew more than 2 cm yr^{-1} in DBH for measurement errors. We corrected their growth rate to the mean growth rate of the binned 10 cm growth rate (i.e., 0–10 cm, 10–20 cm, 20–30 cm, etc.).

2.2. Biomass component calculation

Biomass for each individual stem was calculated using species specific equations for stems of below 3 cm in DBH (Bond-Lamberty et al., 2002), and stems above 3 cm in DBH (Lambert et al., 2005), at each census, and summed to obtain total stand biomass. Annual biomass growth was calculated as the amount of biomass added by surviving trees between measurements, divided by the census interval. Annual biomass added due to ingrowth was calculated as the amount of biomass added due to recruits between measurements, divided by the census interval. Annual productivity was the summation of annual growth and annual ingrowth. Annual biomass lost due to mortality was calculated as the quantity of