Temporal declines in tree longevity associated with faster lifetime growth rates in boreal forests

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Abstract

Global change has been linked to significant increases in tree mortality in the world’s forests. Reduced tree longevity through increased growth rates has been suggested as one of the mechanisms responsible for the temporal increases in tree mortality, but this idea has not been directly tested. Here we explicitly defined two testable hypotheses: (i) the probability of ageing driven tree mortality increases with global change and (ii) the mortality probability associated with global change is higher for faster growing trees. To test these hypotheses, we examined the temporal changes of tree mortality probability in 539 permanent sample plots monitored from 1960–2009, with ages greater than 100 years at initial censuses, across the boreal region of Alberta, Canada. As expected, we found an overall temporal increase in tree mortality probability, indicating a loss in tree longevity with global change. We also found that trees with faster lifetime growth rates experienced higher temporal increases in mortality probability compared to slower growing trees. An analysis of the responses of tree mortality probability to increasing atmospheric carbon dioxide and temperature and decreases in water availability indicated that increasing atmospheric carbon dioxide and decreasing water availability were the major drivers of declining longevity. Our results suggest that tree longevity may further decline with the expected increase of atmospheric carbon dioxide and decreasing water availability in the region.

Introduction

Anthropogenic global change has been linked to extensive tree mortality worldwide (Allen et al 2010, 2015). The major interdependent mechanisms causing this increase include hydraulic failure and carbon starvation, often attributed to direct heat stress, lowered water availability, pest and pathogen outbreaks, or intensified tree-to-tree competition, with their relative importance dependent on tree species and region-specific temporal climatic trends (McDowell et al 2011, 2015, Peng et al 2011, Anderegg et al 2012, Luo and Chen 2013, 2015, Rowland et al 2015, Hember et al 2017, Chen et al 2017b). Reduced tree longevity due to global change has been hypothesized as a mechanism for increased biomass loss associated with global change at the stand level (Brienen et al 2015). While studies have shown temporally increasing tree mortality rates (van Mantgem et al 2009, Peng et al 2011), the hypothesis that global change reduces tree longevity (here defined as the lifespan of an organism) has yet to be directly tested. Examining whether mortality probability has increased (i.e. longevity has decreased) for stems in older stands where trees are reaching their longevity (Burns and Honkala 1990, Chen and Popadiouk 2002, Luo and Chen 2011), would enable directly testing if global change has reduced tree longevity.

The negative relationship between lifetime tree growth rates and longevities has been well documented. Among plant species, longevities are negatively related to lifetime growth rates due to the
investment tradeoff between defence and growth (Herms and Mattson 1992) or smaller sizes at older ages being less susceptible to stresses (Mencuccini et al. 2005). Size tends to have a greater impact on tree mortality probabilities than age (Mencuccini et al. 2005, Thomas 2013, Mencuccini and Munne-Bosch 2017, Schmid-Siebert et al. 2017). At larger sizes, trees are more susceptible to hydraulic and mechanical constraints (Ryan et al. 2006) and pest and pathogen outbreaks (Haas et al. 2016). It is plausible that faster lifetime growth rates lead to trees reaching larger sizes more quickly, leaving them more exposed to size-related mortality, and reducing their longevities. This relationship holds within species across spatial gradients of environmental conditions, where tree longevity also has been negatively associated with quicker early (Bigger and Veblen 2009) and lifetime tree growth rates (Di Filippo et al. 2015).

Under a temporally changing climate, modelling studies suggest that global change-induced growth stimulation leading to greater sizes more quickly may reduce tree longevity (Bugmann and Bigger 2011, Hember and Kurz 2018). Global change events such as droughts that coincide with bark beetle outbreaks have been shown to cause larger reductions in short-term growth and higher mortality probabilities in larger trees compared to smaller trees (Bennett et al. 2015), although evidence of taller trees having higher mortality probabilities during droughts without co-occurrence of bark beetle outbreaks is mixed and species-specific (Hember et al. 2017). Since trees can increase their growth rates in response to positive global change drivers such as warming, increased atmospheric CO2, and nitrogen deposition (Pretzsch et al. 2014, Brienen et al. 2015, Chen et al. 2016, Schulte-Uebbing and de Vries 2018) when not limited by water availability (Jump et al. 2006, Korner 2015, Girardin et al. 2016), reduced longevity due to increased lifetime growth rates may contribute to the observed global change-induced increases in tree mortality. While previous studies have inferred reduced longevity from positive relationships between stand level productivity and mortality (Brienen et al. 2015), direct proof of this mechanism should come from individual stem level data. We note that trees that eventually die from long-term accumulated stresses have reduced recent growth rates prior to death (Cailleret et al. 2017).

The boreal forest is an ideal candidate to examine how tree longevity might have been affected by global change since the prevalence of stand-replacing wildfires, and consistent seasonality, allows for accurate tree age determination. In western North American boreal forests, trees of all species are recruited simultaneously following wildfire (Gutsell and Johnson 2002). This leads to evenly-aged, though not evenly-sized, stands that can be used to exclude age effects while analysing growth-mortality relationships. Evidence for global change-induced alterations in growth rates are mixed in the boreal forest with no change or declines at the individual tree level reported in dendrochronological studies (Girardin et al. 2016, Hogg et al. 2017, Chen et al. 2017a, 2017b) and increases in young stands but no change in older stands (i.e. 140 years and older) at the stand level (Luo and Chen 2015, Chen et al. 2016). Here, we use data from 539 permanent sample plots (PSP) established in the western boreal forest of Canada to examine whether tree longevities have been shortened in the past 50 years. We specifically tested whether: (i) annual mortality probabilities have increased temporally for trees in stands older than 100 years, when boreal tree species begin to reach their longevity (Chen and Popadiouk 2002, Luo and Chen 2011); and, (ii) relatively larger trees within a stand (i.e. trees with faster lifetime growth rates) have higher increases in global change related mortality probabilities than relatively smaller trees. To understand whether a specific global change driver was the cause of differences in temporal longevity, we examined the relationships between tree mortality and changes in atmospheric CO2, temperature, and water availability.

Datasets and methods

Study area and long-term repeatedly measured sample plots

The PSPs used in this study were established throughout Alberta starting in 1958 by the provincial government. The PSP data is available upon request to the forestry department of the Alberta government. The PSPs were established in visually homogenous well-stocked stands greater than 1 ha in size, at least 100 m from any openings to minimize the impacts of edge effects. A total of 539 PSPs were compiled from the networks for use in our study, using the following data selection criteria: (i) PSPs with a known origin date of stand-replacing wildfire, and unmanaged; (ii) PSPs with all trees marked and tagged with diameter at breast height (DBH) and species identification tracked accurately over multiple censuses (stems with any negative growth observations were removed from all analyses); (iii) plot spatial location was available and plots were within the boreal zone as defined by Natural Resources Canada (Brandt 2009); and, (iv) plots had a minimum of three censuses and a minimum of two censuses with an average age greater than 100 years. These plots range in latitude from 51.5° to 59.6° N, in longitude from 119.7° to 114.0° W, and in elevation from 291 to 1784 m above sea level (see figure S1 in supplementary information, available online at stacks.iop.org/ERL/13/125003/mmedia). Across space and time, annual temperatures ranged from −5.74 °C to 11.67 °C, and annual precipitation ranged from 187–881.9 mm between 1957–2009, obtained by using the BioSIM 10 software (Régimére et al. 2014).

Wildfire is the dominant forest-replacing disturbance with fire return intervals that vary temporally
and spatially, from 15–90 years in the study area (Weir et al. 2000). To examine whether longevity has been reduced (through higher mortality probability in older organisms) and to minimize the effects of competition-induced mortality, which is a driving factor for individuals smaller than the average tree size in a stand particularly in young boreal forests (Chen et al. 2008, Luo and Chen 2011, 2015), we selected only stands older than 100 years, when boreal tree species begin to reach their longevity (Burns and Honkala 1990, Chen and Popadiouk 2002).

Tree species left after selection for age included *Picea glauca* (Moench) Voss. (41.9% of total stems), *Pinus contorta* (Douglas) (24.6%), *Populus tremuloides* (Michx.) (13.2%), *Abies balsamea* ((L.) Mill) (8.2%), *Picea mariana* (Mill.) (7.4%), *Populus balsamifera* (L.) (3.0%), and other species including *Betula papyrifera* (Marshall), *Picea engelmannii* (Parry ex Engelm), *Abies lasiocarpa* ((Hooker) Nuttal), *Larix laricina* ((Du Roi) Koch), and *Pinus banksiana* (Lamb.), accounting for a total of 1.7% of the total number of stems (table S1).

**Explanatory variables**

We used the midpoint year of a census (i.e. the average of initial and final measurement years during a census period) to represent overall climatic conditions (van Mantgem et al. 2009, Chen and Luo 2015, Chen et al. 2016), corresponding to each census period of each plot. Using the midpoint year as a proxy for global change encompassed not only the systematic increases in atmospheric CO2 concentrations and temperatures and declines in water availability throughout our study region (IPCC 2013), but also increases in other global change drivers such as insect outbreaks (Chen et al. 2017b).

We used the relative basal area of each stem to the average stem basal area in the prior census period to quantify relative lifetime growth rates within a stand (Luo and Chen 2011). Since all stems are recruited simultaneously following stand-replacing wildfire (Gutsell and Johnson 2002), the larger stems within a stand were also, the faster growing over their lifetime. We also examined absolute size in the prior census period as a potential covariate.

To investigate the sensitivity of tree mortality to increases in temperature and decreases in water availability, we examined the response to climate change drivers by using the annual temperature anomaly (ATA), the annualized standardized precipitation-evapotranspiration index (SPEI), and atmospheric carbon dioxide (CO2) concentration averaged over the census period. The ATA was defined as the average difference between observed mean annual temperatures over the census period and its long-term mean (1957–2013, the length of our study period) at each plot. Similarly, we used the average annual SPEI for each census period as a measure of water availability; SPEI is an excellent indicator of drought conditions and is sensitive to changes in water availability due to global warming (Vicente-Serrano et al. 2010). We calculated SPEI using the SPEI package in R (Vicente-Serrano et al. 2010) using the annual climate moisture index as our measurement of water availability. Both mean annual temperature and the annual climate moisture index (used to calculate SPEI) were generated using BioSIM 10 (Réginère et al. 2014) for the length of our study period. BioSIM uses historical weather data from the nearest weather station to a location and adjusts predictions for differences in elevation, latitude, and longitude (Réginère et al. 2014). Atmospheric CO2 concentration was derived from the Manua Loa Earth System Research Laboratory (http://esrl.noaa.gov/gmd/ccgg/trends/co2_data_mlo.html) and from the Law Dome DE08 and DE08-2 ice cores (http://cdiac.ornl.gov/ftp/tren-ds/co2/lawdome.smoothed.yr20) for measurements before 1959. CO2 values were the average values for each measurement period for each plot. To ensure our use of annual climate variables was appropriate, we also examined the average growing season (1 May–1 September) temperature anomaly and SPEI over the measurement period. Since coefficient estimates were similar (figure S2), we retained annual variables for clarity and to remain consistent with previous literature (van Mantgem et al. 2009, Peng et al. 2011, Luo and Chen 2013).

**Statistical analysis**

Because our measurement intervals varied, similar to Luo and Chen (2013), we scaled the annual mortality probability using the following function:

\[
P_{ijk} = 1 - (1 - p_{ijk,t=1})^{\Delta t},
\]

where \(p_{ijk}\) is the mortality probability of an individual stem for the \(i\)th tree during the \(j\)th census period in the \(k\)th plot, \(\Delta t\) is the length of the census period in years, and \(p_{ijk,t=1}\) is the annual mortality probability of the \(i\)th tree of \(j\)th census period in \(k\)th plot.

We used a generalized mixed-effects logistic model (Chen et al. 2008, Hulsmann et al. 2018) to investigate whether trees with faster lifetime growth rates were more susceptible to global change-induced mortality.

\[
\log it\left(p_{ijk,t=1}\right) = \beta_0 + \beta_1 \times Y_{ijk} + \beta_2 \times f(R_{ij-1\omega}) + \beta_3 \times Y_{ijk} \times R_{ij-1\omega} + \pi_2 + \rho_1 + \varepsilon_{ijk},
\]

where: \(p_{ijk,t=1}\) is the annual probability of mortality of the \(i\)th tree of \(j\)th census period in the \(k\)th plot of the \(l\)th species; \(Y_{ijk}\) is the middle calendar year of census; \(f(R_{ij-1\omega})\) is the best fit function (i.e. linear or logarithmic) of annual tree mortality probability to the previous relative basal area; \(\pi_2\) is the random effect of the \(k\)th plot; \(\rho_1\) is the random effect of the \(l\)th species. We determined the best fit function for relative basal area using a general additive model and AIC selection (table S2). To ensure that our estimate of increasing mortality probabilities with increasing relative size was...
In the response to climate change drivers by substituting the six major species. We then examined the above model to the dataset including all trees and then is natural log transformed relative tree basal area, $D$ is diameter at breast height. Model is defined in equation (2).

For the ridge regression using the `lm.ridge` function in the ` MASS` package and a non-parametric model using the `predict.lm` function in the `Rfit` package. For the ridge regression and non-parametric model, we removed the random effects estimated by the simultaneous model prior to model fits and bootstrapped confidence intervals from 1000 bootstrap iterations. To ensure our model specification was correct, we also examined a model including all interactions between each climate driver and relative size (figure S3). Since this did not affect our parameter estimates, we present the two-way interaction model in the Results. Parameter significance for `glmer` models was assessed using an analysis of deviance with Type II sum of squares through the `Anova` function in the `car` package. Alternative to the models with global change drivers simultaneously included, we also ran models with each driver considered separately, similar to previous analyses (van Mantgem et al 2009, Peng et al 2011, Luo and Chen 2013). We generated 95% confidence intervals using the Wald method of the `conint` function within the `lme4` package. To determine if the models properly discriminated trees that died from trees the survived, we used the Area Under the Receiver Operating Characteristic Curve (AUC). A value of AUC > 0.8 indicates that a model has excellent discriminatory power, and a value > 0.7 indicates good discriminatory power (Hosmer and Lemeshow 2000). The AUC was calculated using the `pROC` package (Robin et al 2011). All analyses were implemented in R statistical software, version 3.5.0.

### Results

Across all individuals, annual mortality probability increased significantly over time ($0.471 \pm 0.016$, scaled coefficient estimate $\pm 95\%$ confidence interval, $P < 0.001$) but decreased on average with increasing relative size ($-0.349 \pm 0.016$, $P < 0.001$) (table 1, figure 1). Temporal increases in mortality probability increased with increasing relative basal area ($0.092 \pm 0.014$, $P < 0.001$), but this increase was not large enough to cause larger trees to have higher

### Table 1. Effects of relative size, year, and absolute size on annual tree mortality probability for two alternative models. Values are parameter estimates with 95% confidence interval in brackets. log $R$ is natural log transformed relative tree basal area, $Y$ is calendar year, $D$ is diameter at breast height. Model is defined in equation (2).

| Parameter | Model from equation (2) | Model with $D$ |
|-----------|-------------------------|---------------|
| Intercept | $-3.948 \pm 4.24$ to $3.656$ | $-3.967 \pm 4.247$ to $3.687$ |
| log $R$   | $-0.349 \pm 0.366$ to $-0.333$ | $-0.592 \pm 0.635$ to $-0.548$ |
| $Y$       | 0.471 (0.455–0.486) | 0.448 (0.432–0.464) |
| $D$       | — | 0.320 (0.267–0.372) |
| $D^2$     | — | — |
| log $R \times Y$ | 0.092 (0.079–0.106) | 0.086 (0.073–0.100) |
| AIC       | 97 746.5 | 97 690.2 |
| AUC       | 0.736 | 0.737 |

![Figure 1. Temporal trends in annual mortality probability by relative basal area. Black line represents the response at mean relative basal area.](image-url)

Figure 1. Temporal trends in annual mortality probability by relative basal area.

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mortality probabilities than smaller trees by the end of the study period (figure 1). The AUC of the model was 0.736 indicating a good fit. Temporal trends by individual species were consistent with the model of all trees except for *A. balsamea*. For *A. balsamea*, larger individuals on average had higher mortality probabilities than smaller individuals, and there was no significant interaction effect of relative size and year (figure S4). Alternative models with the DBH as a predictor yielded similar coefficient estimates for the effects of the calendar year, relative tree basal area and their interactions (table 1).

During the study period, atmospheric CO$_2$ and temperature increased, while water availability decreased (figures 2(a)–(c)). The linear mixed effect model that included atmospheric CO$_2$, ATA and SPEI simultaneously as predictors showed that with rising atmospheric CO$_2$ and decreasing SPEI led to on average higher mortality probabilities, while increasing ATA led to on average lower tree mortality probability (table 2, figures 2(d)–(f)). Similar to the response to calendar year, increasing atmospheric CO$_2$ and decreasing SPEI led to higher mortality probability in larger trees than in smaller trees, but the effect of ATA was independent of relative tree size, indicated by the insignificant interaction of ATA and relative basal area (table 2, figures 2(d)–(f)). Ridge regression and non-parametric regression yielded similar coefficient estimates to those of the linear mixed effect model. However, the results from the models that tested global change drivers individually yielded a contrasting effect of ATA (figure 3). In the ATA model, the effect of ATA was confounded with the effect of atmospheric CO$_2$ and SPEI since ATA and CO$_2$ were correlated.

![Figure 2](image-url)

**Figure 2.** Trends in global change drivers and the response of annual mortality probabilities. (a) Atmospheric CO$_2$ concentration, (b) mean annual temperature anomaly (ATA), and (c) mean standardized precipitation-evapotranspiration index (SPEI) in relation to calendar year. Dots and error bars show the mean and their 95% bootstrapped confidence intervals. Blue line is a fitted linear model with 95% confidence bands in grey. (d)–(f) Change in annual mortality probability according to global change drivers by relative basal area: (d) atmospheric CO$_2$, (e) ATA; and (f) SPEI. Black line represents the response at mean relative basal area.
Our results show consistent temporal increases in annual mortality probabilities (i.e. reduction in survival probabilities) for trees older than 100 years during the past half-century in our study region, indicating that tree longevity declined over time. We found that annual mortality probabilities increased temporally faster for larger trees although larger trees on average had lower annual mortality probabilities. Lower mortality probabilities for dominant trees is consistent with previous literature in the boreal forest (Luo and Chen 2011). This suggests that some suppression still occurs in these stands and is significant enough to outweigh increases in mortality due to faster lifetime growth rates on average. Species-level responses were similar with the exception of A. balsamea. Large individuals of A. balsamea died more frequently than smaller individuals of the species, and there was no difference in temporal trends between large and small individuals. This may be attributable to the fact that A. balsamea rarely grows to dominate these stands (average relative basal area across all stands was 0.700 ± 0.009) and is highly susceptible to insect outbreaks (Fleming and Volney 1995).

Our climate change driver analysis suggests that rising atmospheric CO$_2$ and decreasing water availability increased annual tree mortality probabilities, confirming work done by other studies in the region (Peng et al 2011, Luo and Chen 2013, Hember et al 2017). Our analysis with global change drivers individually modelled corroborated the result that warming increased tree mortality probability (van Mantgem et al 2009, Peng et al 2011, Luo and Chen 2013). However, with all three global change drivers accounted simultaneously, our mixed effect model, non-parametric model, and ridge regression model, all of which equally split the shared variations among correlated predictors (Legendre and Legendre 2012) showed that increasing temperature on average decreased annual tree mortality probability. It remains unknown whether warming by 1 °C (figure 2(b)) during the past decades in our region has led to an effect on tree mortality independent from rising atmospheric CO$_2$ and decreasing water availability since our observational data showed that changes in temperature correlated positively with atmospheric CO$_2$ and decreasing water availability. A study to the east of our region, using a space-for-time methodology, shows that warming at higher than 2 °C had a negative effect on trees, but warming at a lower temperature could have a positive effect (D’Orangeville et al 2018).

In agreement with our second hypothesis, we found that reductions in longevity due to increasing
atmospheric CO\textsubscript{2} and decreases in water availability were stronger in trees with faster lifetime growth rates. Reduced longevity due to increasing CO\textsubscript{2} could be attributable to an acceleration in tree life cycles: higher atmospheric CO\textsubscript{2} promotes tree growth, causing trees to grow larger, and leading them to be more susceptible to size-related mortality (Brienen et al 2015). On the other hand, it could be related to concurrent increases in pest and pathogen pressures, which are expected to affect larger trees more than smaller trees (Haas et al 2016). Increasing mortality probabilities as water availability declines and trees grow larger could be caused by requirements of larger investments in rebuilding xylem post-drought in bigger than in smaller trees (Trugman et al 2018) or due to increases in path length putting increased hydrological pressure on larger individuals (Hember et al 2017).

We demonstrate that decreases in tree longevity in the western boreal forests of Canada are associated with trees that have higher lifetime growth rates. Our climate change driver analysis suggests that rising atmospheric CO\textsubscript{2} and reduced water availability are the major drivers of reduced longevity for larger trees in our study area, and that tree longevity may be further reduced with an expected on-going increase in atmospheric CO\textsubscript{2} and decrease in water availability in the region.

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