LETTER

Climate change-associated trends in net biomass change are age dependent in western boreal forests of Canada

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Abstract

The impacts of climate change on forest net biomass change are poorly understood but critical for predicting forest's contribution to the global carbon cycle. Recent studies show climate change-associated net biomass declines in mature forest plots. The representativeness of these plots for regional forests, however, remains uncertain because we lack an assessment of whether climate change impacts differ with forest age. Using data from plots of varying ages from 17 to 210 years, monitored from 1958 to 2011 in western Canada, we found that climate change has little effect on net biomass change in forests ≤ 40 years of age due to increased growth offsetting increased mortality, but has led to large decreases in older forests due to increased mortality accompanying little growth gain. Our analysis highlights the need to incorporate forest age profiles in examining past and projecting future forest responses to climate change.

INTRODUCTION

Understanding how climate change impacts forest biomass is critical to assessing the contribution of the world's forests to the global carbon cycle (Dixon *et al.* 1994; Pan *et al.* 2011). Forest annual net biomass change, an indicator for carbon sink change (Pan *et al.* 2011), is the difference between annual growth gain and annual mortality loss (Ma *et al.* 2012; Brienen *et al.* 2015). Climate change has been shown to increase tree mortality rates (Phillips & Gentry 1994; van Mantgem *et al.* 2009; Allen *et al.* 2010; Peng *et al.* 2011; Luo & Chen 2013, 2015; McDowell *et al.* 2015; Zhang *et al.* 2015) and biomass loss from mortality (Ma *et al.* 2012; Brienen *et al.* 2015; Chen & Luo 2015) across a wide range of global forests. By contrast, reported temporal trends in forest growth associated with climate change are inconsistent: increasing (McMahon *et al.* 2010; Hember *et al.* 2012; Coomes *et al.* 2014; Fang *et al.* 2014; Pretzsch *et al.* 2014; Brienen *et al.* 2015), decreasing (Ma *et al.* 2012; Zhang *et al.* 2015) and spatially dependent trends (Charney *et al.* 2016) have been reported. These discrepancies could arise from different responses to climate change associated with forest age and species composition (Luo & Chen 2013; Coomes *et al.* 2014; Fang *et al.* 2014; Chen & Luo 2015) and different growth responses to atmospheric CO_2 (Dawes *et al.* 2011; Camarero *et al.* 2015; Soule & Knapp 2015). Few studies have examined and reported climate change-induced declines in net biomass change; either as a result of a faster temporal increase in tree mortality than growth (Brienen *et al.* 2015) or increased mortality accompanied by little or decreased growth (Ma *et al.* 2012; Chen & Luo 2015).

Endogenous processes associated with forest ageing are known to be critical drivers of forest dynamics (McMahon *et al.* 2010; Luo & Chen 2011, 2013, 2015; Hember *et al.* 2012; Fang *et al.* 2014; Pretzsch *et al.* 2014; Chen & Luo 2015; Zhang *et al.* 2015; Poorter *et al.* 2016). After a stand-replacing disturbance, such as fire in boreal forests, stands develop with or without canopy succession (Oliver & Larson 1990; Chen & Popadiouk 2002; Chen & Taylor 2012). During the stand development processes, growth and net biomass changes are known to decline (Pretzsch *et al.* 2014; Chen & Luo 2015), whereas mortality increases with stand ageing (Luo & Chen 2011). Despite its importance, we still lack a direct assessment of whether climate change-associated temporal trends in net biomass change are dependent on forest age. Because the World's forests consist of diverse ages (Pan *et al.* 2013; Poorter *et al.* 2016), understanding age-dependent responses to climate change in growth and mortality, and hence responses in net biomass change, is important. This is particularly true for boreal forests due to frequent forest-replacing wildfires leading to dominance of young age classes (Larsen 1997; Weir *et al.* 2000).

Here, we sought to examine whether climate change-associated temporal trends in net biomass change, growth and mortality differ with forest age in the western boreal forests of Canada, and if so, to identify possible causes of such differences. To test whether the temporal trends associated with climate change differ with forest age, forest plots of different ages are required to be measured in different calendar years to minimise the collinearity between forest age and temporal trends associated with calendar year. Fortunately, a large

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number of permanent sample plots (871 in total) in Alberta and Saskatchewan, Canada, with various site conditions and species compositions, were established in different years with a large range of forest ages (17–210 years) and monitored from 1958 to 2011 (Figs S1 and S2). We selected trees with diameter at breast height (DBH) ≥ 10 cm to track biomass gain due to growth and recruitment, biomass loss due to mortality and net biomass change at the stand level. We used models that simultaneously accounted for the effects of climate change and forest age and tested whether the temporal trends differed with forest age.

METHODS

Forest inventory data

The study area is located in Alberta and Saskatchewan, Canada, where wildfire is the dominant forest-replacing disturbance with fire return intervals that vary temporally and spatially, from 15 to 90 years (Larsen 1997; Weir *et al.* 2000). A total of 2911 permanent sampling plots (PSP) were established to quantify forest dynamics with varying ages in the study area by the provincial governments of Alberta and Saskatchewan. These established plots' areas varied from 0.0405 to 0.8092 ha, and all plots were established in forests (> 1 ha in area), which were visually homogeneous in structure and composition, and were at least 100 m from any openings to minimise edge effects.

To examine the long-term changes in the study forest, we selected PSPs based on the following four criteria: (1) forest that had known forest age (FA, years), originated from wildfire and were not managed (53 plots were removed); (2) plots had at least three censuses and had been monitored for at least 10 years (1802 plots were removed); (3) all trees within sample plots including recruitment trees, whose DBH were defined as ≥ 7.3 cm in Alberta and ≥ 9.7 cm in Saskatchewan, respectively, were marked and their DBH were measured using DBH tapes (169 plots were removed) and (4) each plot had at least 30 trees at initial measurement to ensure that the plot represented the sample forest (16 plots were removed). The last criterion resulted in the exclusion of plots with sizes < 0.06 ha. As the two provinces used different tree size criteria for monitoring, we standardised the data by selecting trees with DBH ≥ 10 cm to eliminate the effect of the different sampling strategies between the two provinces.

In total, 871 plots met our criteria for analyses. The selected plots were geographically distributed from 49°01′ to 59°44′ N in latitude, and from 101°44′ to 119°40′ W in longitude (Fig. S1). Elevation ranged from 260 m to 2073 m above sea level (a.s.l.). The initial census year varied from 1958 to 1993, whereas the final census year ranged from 1972 to 2011 (Fig. S2). The measurement intervals averaged 9.2 years, and the average number of censuses per plot was 3.9. Plots selected for this study ranged in size from 0.06 to 0.81 ha with a mean of 0.20 ha and median of 0.1 ha. Species that made up at least 1% of the total tree biomass across all censuses and plots were *Populus tremuloides* (30.9%), *Picea glauca* (30.8%), *Pinus contorta* (23%), *Populus balsamifera* (5.8%),

Picea mariana (3.2%), *Abies balsamea* (2.6%), *Pinus banksiana* (2.5%) and *Betula papyrifera* (1.3%).

Annual net aboveground biomass change and its components

We calculated forest-level aboveground biomass by summing the biomass of all trees within each sample plot at each census. Individual tree aboveground biomass was estimated by published Canadian national species-specific DBH-based tree aboveground biomass equations for wood, bark, foliage and branches, respectively (Lambert *et al.* 2005). As recommended (Chave *et al.* 2004), these equations were developed based on 207–1534 trees per species with a wide range of sizes, sampled from across Canadian boreal forests. For less frequently occurring *Pseudotsuga menziesii* Mirb. (437 trees), *Pinus flexilis* James (5 trees) and *Picea engelmannii* Parry ex Engelm. (42 trees), we used general equations for softwood or hardwood to estimate their biomass (Lambert *et al.* 2005).

We calculated annual growth (ΔAGB_{GI}) as the aboveground biomass growth of surviving trees and in-growth by new recruitment trees between two successive censuses divided by census length in years. Annual biomass loss due to tree mortality (ΔAGB_M) was the sum of aboveground biomass of all died trees between two successive censuses divided by census length in years. Annual net aboveground biomass change (ΔAGB, Mg ha^{-1} year^{-1}) was the difference between ΔAGB_{GI} and ΔAGB_M, and equalled the difference of aboveground biomass divided by the number of years between two consecutive censuses. We also calculated annual net forest basal area change (m^2 ha^{-1} year^{-1}) and its growth and mortality components. Across all plots and censuses, changes in aboveground biomass and stand basal area are highly correlated (Fig. S3). We subsequently focused our analysis on the changes in aboveground biomass.

Long census intervals may underestimate mortality and growth due to the growth of unrecorded trees that are both recruited and die during the interval (Lewis *et al.* 2004; Brienen *et al.* 2015). To correct for unobserved recruits, we assume that unobserved recruits occurred for trees with DBH between 10 and 15 cm. We first estimated the number of unobserved recruits (U_r) as the number of stems in the plot (N) with DBH between 10 and 15 cm multiplied by the annual recruitment rate (R, calculated as the number of new recruits between two successive censuses divided by census length in years) multiplied by the mean annual mortality rate (M, calculated as the number of trees with DBH between 10 and 15 cm that died between two successive censuses divided by census length in years multiplied by the census interval length (L)): $U_r = N \times R \times M \times L$. To correct for unobserved growth and mortality due to trees that died within a census interval, we assumed that all trees that died during the interval to have died at the midpoint, and assigned growth up to this midpoint, estimated as the median growth of all trees in the plot within the 10–15 cm DBH size class. The biomass associated with unobserved recruits accounted for on average 0.98% and 0.6% of the total growth and mortality, respectively.

Forest age determination

Forest age for each plot was determined according to a known fire (that cleared the previous forest) or by coring at least three dominant/codominant trees of each tree species inside or outside of the plot at the time of plot establishment. When coring was used, the average ring counts of the tree samples for the species with the oldest ages were used to provide a conservative estimate for time since fire, via species-specific relationships between forest age and time since fire developed for the boreal forests (Gutsell & Johnson 2002). Among the 871 selected plots, the forest ages of 176 were determined by a known fire, whereas 695 were determined from coring. Of these 695 plots, a total of 4024 trees were cored, which included 367 *P. banksiana*, 455 *P. contorta*, 819 *P. tremuloides*, 28 *B. papyrifera*, 112 *Populus balsamea*, 334 *P. mariana*, 1763 *P. glauca*, six *P. menziesii*, 134 *A. balsamea* and six *Abies lasiocarpa* trees.

Climate change drivers

To understand the influence of climate change drivers on growth, mortality and net biomass change, we derived CO_2 measurements from the Mauna Loa Earth System Research Laboratory in Hawaii (http://www.esrl.noaa.gov/gmd/ccgg/trends/co2_data_mlo.html). We obtained mean annual temperature and climate moisture index (CMI) by BioSIM 10 software (Réginère *et al.* 2014). CMI was calculated as the difference between precipitation and potential evapotranspiration for each month, and monthly CMI was then summed for an entire calendar year (from January 1st to December 31st) to obtain annual CMI values as an index for climate moisture availability for our study forests where snow contributes substantially to water availability to plants at the beginning of growing season (Hogg 1997). The climate associated with each census period was calculated as the average of climate values during the period.

Statistical analysis

To determine the contributions of forest age (FA) and temporal trends associated with calendar year (Year) and to test whether the temporal trends of ΔAGB, ΔAGB_{GI} and ΔAGB_M differ with FA, we used the following model:

$$\Delta AGB_{ij} = \beta_1 + \beta_2 \times f(FA_{ij}) + \beta_3 \times Year_{ij} + \beta_4 \times f(FA_{ij}) \times Year_{ij} + \pi_j \quad (1)$$

where *i, j* were i^{th} census period, and j^{th} plot, respectively; β_i are coefficients to be estimated. FA_{ij} and $Year_{ij}$ are the middle forest age and the middle calendar year of a census period, respectively. A random plot effect (π_j) accounted for site-specific spatial climates, local site conditions, species composition and disturbance history. To assess potential nonlinear responses of ΔAGB, ΔAGB_{GI} and ΔAGB_M to forest age, *f* (FA), we compared four alternative models (linear, quadratic, third-order polynomial and logarithm). Based on Akaike information criterion, the logarithmic function was the best fit to describe the forest age-dependent trends of ΔAGB, ΔAGB_{GI} and ΔAGB_M (Table S1), and consequently forest

age was transformed by natural logarithm for further analysis. We modelled the effects of FA, Year and their interactions on biomass dynamics using the *lme4* package (Bates *et al.* 2015). Similar to Brienen *et al.* (2015), each observation was weighted by the product of square root of plot area times the plot total census length. All independent variables were centred to facilitate coefficient interpretation (Cohen *et al.* 2013).

Forest age and calendar year in longitudinal data of repeated measurements from permanent sample plots, in which forest age and calendar year increase simultaneously within each plot between successive censuses, are inherently correlated. In our data, there is a positive collinearity between FA and Year ($r = 0.16$ or $r^2 = 0.027$). There are three possible approaches to disentangle their joint variation. The first is to model their effects simultaneously. The second is to use residual and sequential regressions by assigning the priority to FA and then modelling the effects of Year and its interaction with FA on the residuals (Graham 2003; Cohen *et al.* 2013). The third is to reverse the priority in the second approach. Although these approaches yielded qualitatively similar coefficient estimates for the main FA effects, priority to Year, i.e. ignoring FA effects, produced a contrasting coefficient estimate for growth to other two approaches because the Year coefficient tracked FA effects due to the collinearity between FA and Year (Fig. S4). As we have no logical or theoretical basis for considering any variable to be prior in terms of a hypothetical causal structure of the data (Cohen *et al.* 2013), and assigning priority to FA would marginalise the Year effect, and *vice versa* (Brown *et al.* 2011), we reported the results from simultaneously modelling effects of FA and Year on ΔAGB and its components.

This analysis is parametric and assumes normally distributed data, while our data on ΔAGB_{GI} are right skewed and those on ΔAGB_M and ΔAGB are left skewed. We thus bootstrapped the fitted coefficients by 1000 iterations (Table S2). Furthermore, we used a rank-based estimator for linear models available from the *Rfit* package (Kloke & McKean 2012). We show that intercepts, slopes for forest age

Table 1 Growth, mortality and net biomass change associated with forest age and calendar year

Fixed effects	Sum of squares	df	*F*	*P*
Biomass gain from growth (Mg ha^{-1} year^{-1})				
ln(forest age)	49.6	1, 755.2	383.2	< 0.001
Year	7.6	1, 2411.1	58.8	< 0.001
ln(forest age) × year	2.8	1, 2330.0	21.6	< 0.001
Biomass loss from mortality (Mg ha^{-1} year^{-1})				
ln(forest age)	35.5	1, 1076.7	72.0	< 0.001
Year	75.0	1, 2539.2	152.2	< 0.001
ln(forest age) × year	0.6	1, 2483.8	1.2	0.278
Net biomass change (Mg ha^{-1} year^{-1})				
ln(forest age)	278.1	1, 1096.2	418.4	< 0.001
Year	28.4	1, 2536.8	42.7	< 0.001
ln(forest age) × year	4.4	1, 2498.5	6.66	0.010

Forest age (years) was transformed by natural logarithm (see Methods). Year = calendar year. Linear mixed-effects model fit tests used Satterthwaite approximations for denominator degrees of freedom.
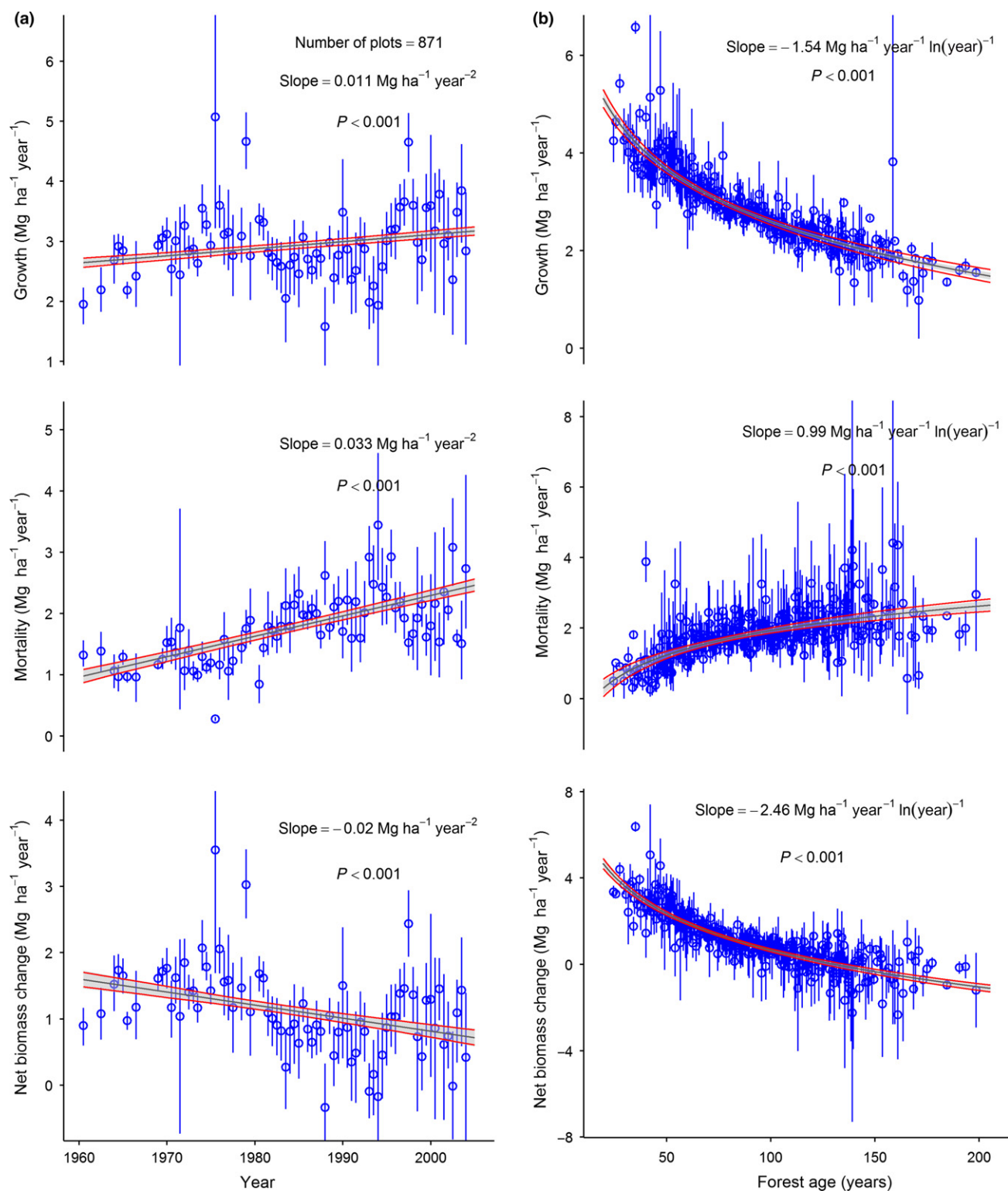
Figure 1 Temporal trends of aboveground growth, mortality and net biomass change across all plots. (a) Temporal trends associated with calendar year with the effects of forest age accounted. (b) Trends associated with forest age with the effects of calendar year accounted (Table 1). Blue dot and error bars show mean and their 95% bootstrapped confidence intervals. The black line and shades are the mean and 95% confidence intervals of the slope fitted by linear mixed-effect models; the red lines represent bootstrapped 95% confidence intervals (Table S1). Grand means for growth, mortality and net biomass change were 2.91, -1.75 and 1.15 Mg ha^{-1} year^{-1}, respectively, across all plots and measurement years.

and calendar year, and interaction terms are consistently similar to those from lme4, bootstrapped and nonparametric rank-based estimations (Table S1).

To graphically demonstrate temporal trends of biomass dynamics associated with calendar year from fitted models (Table S2), we used the residuals from modelling eqn. 1 plus the mean intercept coefficient (β_1) plus the Year coefficient (β_3) times Year. The temporal trends represent overall responses (main effect) across all plots after accounting for the effects of forest age. We graphically showed trends by yearly mean and their 95% bootstrapped CIs using 1000 iterations, and plotting fitted partial responses (mean and 95% CIs to Year). Similarly, we derived biomass dynamics associated with forest age (main effect of forest age) using the residuals from modelling eqn. 1 plus the mean intercept coefficient (β_1) plus the ln(FA) coefficient (β_2) times ln(FA). To graphically illustrate how Year effects on biomass dynamics differ with FA, we calculated Year effects as $\beta_3 + \beta_4 \times \ln(FA)$ (Cohen *et al.* 2013) by 20-year FA intervals.

To understand the role of the climatic drivers that may be responsible for observed temporal changes, we replaced *Year* in eqn. 1 by atmospheric CO_2 concentration, annual temperature anomaly or annual climate moisture anomaly. Climate anomalies are defined as the departure from their long-term climate means between 1958 and 2011, during which our plot measurements were taken.

RESULTS

We found that both calendar year and forest age affected annual growth, mortality and net biomass change, with growth more strongly associated with forest age while mortality was more associated with calendar year, indicated by their respective sums of squares (Table 1). On average over the sampling period, across all plots, annual growth was 2.9 Mg ha^{-1} year^{-1} and annual mortality was 1.8 Mg ha^{-1} year^{-1}, resulting in an annual net biomass gain of 1.1 Mg ha^{-1} year^{-1}. With calendar year, growth increased temporally at 0.012 Mg ha^{-1} year^{-1} on average, whereas mortality increased at 0.034 Mg ha^{-1} year^{-1}, leading to a decline in net biomass change of 0.020 Mg ha^{-1} year^{-1} per year (Fig. 1a). This represents a change from 2.62 to 3.24 Mg ha^{-1} year^{-1} in growth, from 0.90 to 2.7 Mg ha^{-1} year^{-1} in mortality and from 1.64 to 0.60 Mg ha^{-1} year^{-1} in net biomass change from 1958 to 2011. In relative terms, annual growth increased by approximately 24%, mortality increased by 200% and the annual rate of net biomass change declined by 63.5% over the study period. Independent of temporal shifts associated with calendar year, growth decreased and mortality increased, leading to a logarithmic decline in net biomass change with forest age (Fig. 1b).

The temporal growth trends differed with forest age, whereas those of mortality were similar across all forest ages (Table 1 and Fig. 2). The temporal increase in growth was smaller in older forests, and was restricted to forests < 120 years of age, and highest in the youngest forests. As a result, temporal trends in net biomass change varied with forest age with no or slight positive temporal trends in forests ≤ 40 years, and increasingly negative trends in older forests (Fig. 2).
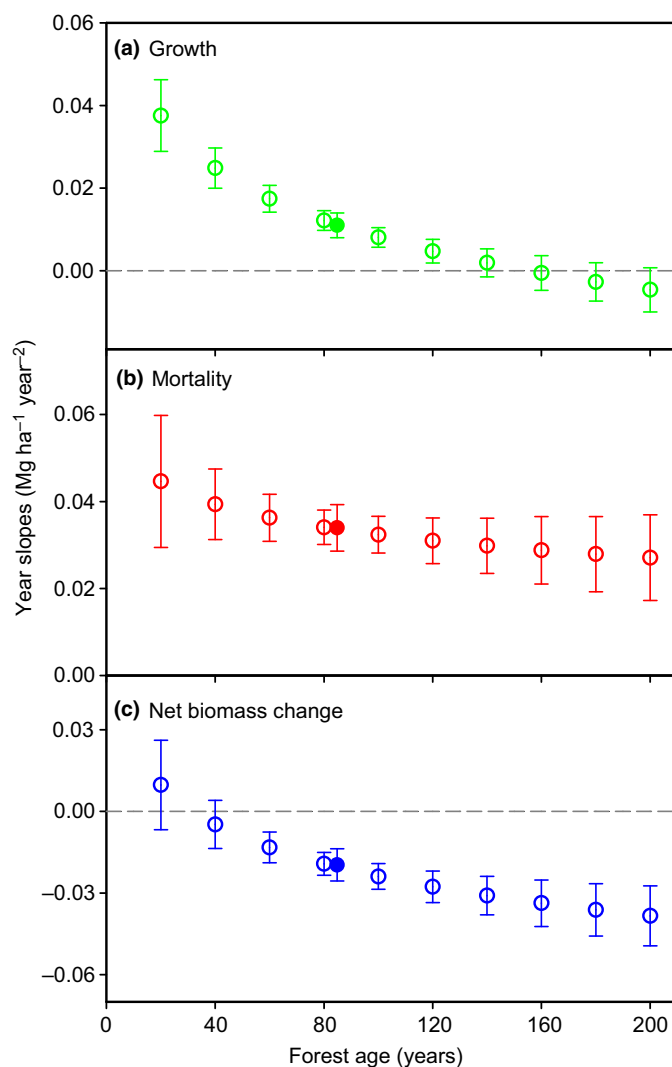

Figure 2 Forest age-dependent temporal trends of aboveground growth, mortality and net biomass change. (a–c) Values (means and bootstrapped 95% confident intervals) represent the temporal trends (Year slopes) for given age classes. Filled symbols are the Year slope across all plots (mean forest age = 84.8 years), which are illustrated in Fig. 1.

During the study period, atmospheric CO_2 concentration and annual temperature anomalies increased, whereas climate moisture anomalies decreased (Fig. 3a). As calendar year and CO_2 concentration were strongly correlated ($R^2 = 0.99$), the responses of growth, mortality and net biomass change atmospheric CO_2 concentration largely mirrored those to calendar year (Fig. 3b). The negative effects of warming on growth, mortality and net biomass change were consistent across all forest ages, as indicated by insignificant interaction effects of forest age and annual temperature anomaly (Table S4). With every degree increase in temperature, growth on average decreased at 0.1 Mg ha^{-1} year^{-1} and mortality increased 0.5 Mg ha^{-1} year^{-1}, leading to a decrease in net biomass change at 0.6 Mg ha^{-1} year^{-1} (Fig. 3b). With every 10 cm decrease in climate moisture, growth on average decreased at 0.15 Mg ha^{-1} year^{-1} and mortality increased 0.3 Mg ha^{-1} year^{-1}, leading to
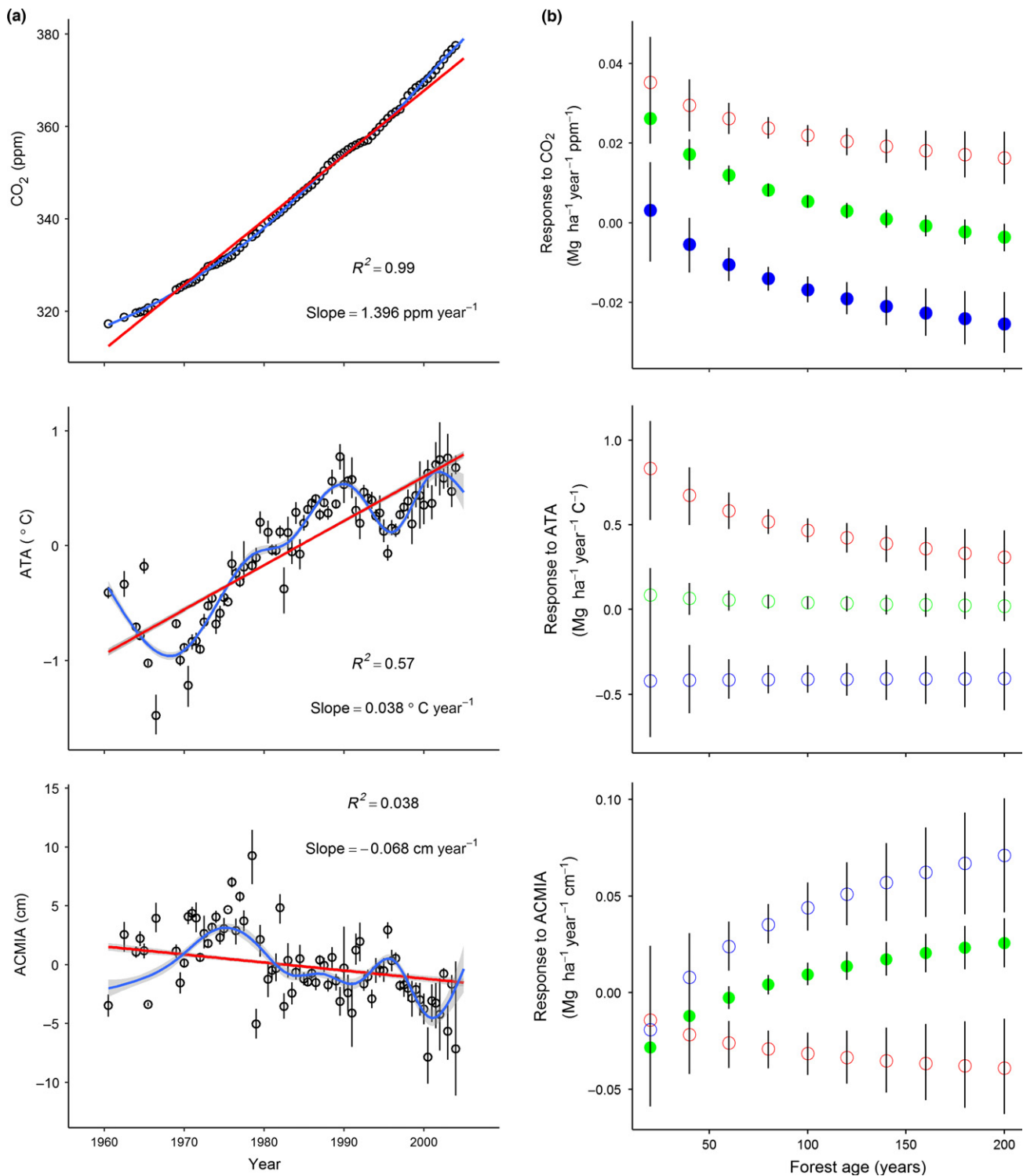
Figure 3 Trends in climate change drivers and the responses of growth, mortality and net biomass change. (a) Atmospheric CO_2 concentration, mean annual temperature anomaly (ATA) and annual climate moisture index anomaly (ACMIA) in relation to calendar year. Dots and error bars show yearly mean and their 95% bootstrapped confidence intervals. Red line is the fitted linear effect with 95% confidence intervals in grey shade. LOESS smooth lines are in blue with 95% confidence intervals in grey. (b) Forest age-dependent response slopes (mean and 95% bootstrapped confidence intervals) to individual climate change drivers. Green, red and blue represent growth, mortality and net biomass change, respectively. Solid dots indicate significant difference ($P < 0.05$) in response slopes across forest ages (Table S3).

a decrease in net biomass change at 0.45 Mg ha^{-1} year^{-1}. However, while the negative effects of decreasing climate moisture were similar across forest ages, growth reduction was more pronounced in old forests than young forests, resulting in more negative responses in net biomass change to decreasing climate moisture availability with forest age (Fig. 3b).

DISCUSSION

We found that growth of young forests increased more significantly with climate change than old forests, while the responses of net biomass change and its components to forest age to be similar to those expected from theory (Oliver & Larson 1990; Chen & Popadiouk 2002) and empirical evidence (Pretzsch *et al.* 2014; Chen & Luo 2015). The age-dependent growth responses are in part due to the different responses to climate change associated with species compositional changes through succession (Bergeron 2000; Coomes *et al.* 2014; Chen & Luo 2015). The temporal increase in growth in young forests is at least partially the result of increasing atmospheric CO_2, which has been shown to increase tree productivity through both increased carbon supply and increased resource use efficiency (Norby *et al.* 2005; Keenan *et al.* 2013). Our analysis also suggests that the greater increase in growth in young forests is attributable to its lower sensitivity to decreasing climate moisture availability. This is probably because young forests consist of a large portion of drought-tolerant *Pinus* spp. Our analysis indicates that little growth increase in old forests is a result of their lower sensitivity to rising CO_2, but greater sensitivity to decreasing climate moisture availability as our statistical models have simultaneously accounted for the effect of forest age. This finding suggests that large trees, which have proportionally greater maintenance costs, might have benefited less from increasing atmospheric CO_2 or suffered more from the stress of decreasing water availability (Prior & Bowman 2014). It is also possible that increased growth resulted from resources released from increased mortality (Brienen *et al.* 2015; Luo & Chen 2015).

While the growth and net biomass change response to climate change was significantly more positive in younger forests than older forests, we found a similar increase in biomass loss from tree mortality associated with all drivers of climate change across all forest ages. This result indicates that, even in cases where higher climate change-induced temporal increases in mortality rates have been observed in the younger forests (Luo & Chen 2013), their contribution to biomass loss is similar to that in old forests because biomass loss from each tree is far less in young forests than in old forests as average tree size increases markedly with age (Stephenson *et al.* 2014). Moreover, larger trees within a stand tend to suffer most during drought (Bennett *et al.* 2015). In addition, large trees have been shown to be more susceptible to pest and pathogen outbreaks (Haas *et al.* 2016), which can increase during drought (Bennett *et al.* 2015) and under warming temperatures (Altizer *et al.* 2013). Our analysis of the mortality sensitivity to warming and climate moisture availability indicates that increased biomass loss from mortality resulted from warming-induced decreasing water availability, as suggested by previous studies in western North America (van Mantgem *et al.* 2009; Peng *et al.* 2011; Ma *et al.* 2012; Luo & Chen 2013; Williams *et al.* 2013; Chen & Luo 2015). However, we note that the increasing rates of tree mortality and associated biomass loss could occur under warming without a temporal decrease in water availability (Phillips & Gentry 1994; Brienen *et al.* 2015; Luo & Chen 2015; McDowell *et al.* 2015), likely driven by increased competition associated with increased growth (Luo & Chen 2015) and shortened tree longevity (Brienen *et al.* 2015). We find that climate change has led to a decline in net biomass change on average across all forest plots. However, our analysis shows that the response of net biomass change to climate change is highly dependent on forest age, with little or even positive response in forests < 40 years of age, but pronounced negative responses in older forests. This forest age-dependent response in net biomass change is a result of climate change-induced growth gain offsetting mortality loss in young forests, but little growth increase or even growth decrease accompanying mortality loss in old forests. These age-dependent responses may be primarily due to the differences in growth response to rising atmospheric CO_2 and decreasing water availability between young and old forests.

It is important to note that the climate drivers in our studied forests are intrinsically linked. Although we speculate on the importance of CO_2 to the temporal trends associated with calendar year, it could be due to its tight correlation with warming ($r^2 = 0.58$). Much of our current knowledge surrounding growth responses to atmospheric CO_2 come from studies examining individual trees, and clearly indicate species-specific (Dawes *et al.* 2011; Soule & Knapp 2015) and age-specific (Camarero *et al.* 2015) responses. It may be problematic to scale up the responses of demographic patterns and processes (e.g. local competition and individual tree size) at the individual tree level to the stand level or to make inferences from the stand level to the individual tree level. Long-term experiments that can manipulate individual climate drivers across stands (such as the Free-air concentration enrichment experiments) are required to provide definitive evidence for the influences of individual climate change drivers on stand biomass changes and offer linkages between the responses at the individual tree and stand levels.

By accounting for both endogenous and exogenous drivers (Brown *et al.* 2011), we show evidence that temporal trends in growth and net biomass change are forest age dependent, suggesting that temporal trends estimated from mature or old-growth forests cannot be used to represent those for younger forests. Moreover, we show that although warming has pronounced effects on biomass loss from mortality across all forest ages, young forests appear to be more resilient by increasing growth to offset increased mortality, possibly due to their greater growth sensitivity to rising CO_2 and less sensitivity to decreasing climate moisture availability than old forests. Our analysis highlights the need to incorporate forest age profiles in examining past and projecting future forest responses to climate change.

AUTHORSHIP

H.Y.H.C. and Y.L. designed the study; Y.L. compiled the data; H.Y.H.C., Y.L., P.B.R. and E.B.S. analysed the data; H.Y.H.C., Y.L., P.B.R., E.B.S. and S.R.B. wrote the manuscript.

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