

Net aboveground biomass declines of four major forest types with forest ageing and climate change in western Canada's boreal forests

HAN Y. H. CHEN and YONG LUO

Faculty of Natural Resources Management, Lakehead University, 955 Oliver Road, Thunder Bay, ON P7B 5E1, Canada

Abstract

Biomass change of the world's forests is critical to the global carbon cycle. Despite storing nearly half of global forest carbon, the boreal biome of diverse forest types and ages is a poorly understood component of the carbon cycle. Using data from 871 permanent plots in the western boreal forest of Canada, we examined net annual aboveground biomass change (Δ AGB) of four major forest types between 1958 and 2011. We found that Δ AGB was higher for deciduous broadleaf (DEC) (1.44 Mg ha⁻¹ year⁻¹, 95% Bayesian confidence interval (CI), 1.22–1.68) and early-successional coniferous forests (ESC) (1.42, CI, 1.30–1.56) than mixed forests (MIX) (0.80, CI, 0.50–1.11) and late-successional coniferous (LSC) forests (0.62, CI, 0.39–0.88). Δ AGB declined with forest age as well as calendar year. After accounting for the effects of forest age, Δ AGB declined by 0.035, 0.021, 0.032 and 0.069 Mg ha⁻¹ year⁻¹ per calendar year in DEC, ESC, MIX and LSC forests, respectively. The Δ AGB declines resulted from increased tree mortality and reduced growth in all forest types except DEC, in which a large biomass loss from mortality was accompanied with a small increase in growth. With every degree of annual temperature increase, Δ AGB decreased by 1.00, 0.20, 0.55 and 1.07 Mg ha⁻¹ year⁻¹ in DEC, ESC, MIX and LSC forests, respectively. With every cm decrease of annual climatic moisture availability, Δ AGB decreased 0.030, 0.045 and 0.17 Mg ha⁻¹ year⁻¹ in ESC, MIX and LSC forests, but changed little in DEC forests. Our results suggest that persistent warming and decreasing water availability have profound negative effects on forest biomass in the boreal forests of western Canada. Furthermore, our results indicate that forest responses to climate change are strongly dependent on forest composition with late-successional coniferous forests being most vulnerable to climate changes in terms of aboveground biomass.

Keywords: Aboveground biomass decline, boreal forest, climate change, drought, global warming, tree mortality, water availability

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Introduction

Annual net aboveground biomass change of forest ecosystems (Δ AGB) is critical to understanding forest carbon balance (Lewis *et al.*, 2009; Pan *et al.*, 2011). Boreal forests contain nearly half of the global forest ecosystem carbon due to the slow decomposition rate of dead biomass in cold climates, playing a critical role in the global carbon cycle (Dixon *et al.*, 1994). Compared with spatially extensive observational networks used to examine Δ AGB and its possible associations with climate change in tropical and temperate forests (Lewis *et al.*, 2009; Phillips *et al.*, 2009; McMahon *et al.*, 2010; Thomas *et al.*, 2010), few studies have examined Δ AGB using ground inventory data in boreal forests. For example, previous attempts focused on only a part of

the forests, that is trembling aspen dominated forests (Hogg *et al.*, 2002, 2008; Michaelian *et al.*, 2011) or old forests (stand age \geq 80 years old) (Ma *et al.*, 2012). The extent and the degree to which climate change may affect Δ AGB remain unclear for the boreal forests due to their diverse types (Gower *et al.*, 2001) and the fact that the majority of these forests are younger than 80 years old because of the high frequencies of stand-replacing disturbance such as wild fire (Weir *et al.*, 2000).

The assessment of climate change effects on Δ AGB is far from straightforward due to difficulty in disentangling the effects of temporal climate change drivers from temporal endogenous processes (Magnani *et al.*, 2007). Net biomass change is strongly driven endogenously by forest development. With forest ageing, both aboveground and belowground forest growth increase initially and peak at intermediate ages, followed by a decline or possibly becoming stable at later stages (Ryan *et al.*, 1997; Law *et al.*, 2003; Luysaert *et al.*, 2008;

Correspondence: Han Y. H. Chen, tel. 807 343-8342; fax 807 343-8116, e-mail: hchen1@lakeheadu.ca
Both authors contributed equally.

Coomes *et al.*, 2012; Yuan & Chen, 2012; Taylor *et al.*, 2014). Mechanisms for the age-related declines are many and include possible hydraulic and nutrient limitations (Ryan *et al.*, 1997; Yuan & Chen, 2012), increases in mortality due to tree ageing (Luo & Chen, 2011) and/or steeper declines in photosynthesis than in respiration (Tang *et al.*, 2014).

Recent climate changes can also affect ΔAGB . The western boreal region of Canada, for example, has experienced persistent increases in atmospheric CO_2 concentration and temperature and decreases in water availability (Scheffer *et al.*, 2012; Diffenbaugh & Field, 2013), but has had little change in nitrogen deposition (Reay *et al.*, 2008). While the increase in atmospheric CO_2 concentration can potentially produce a CO_2 fertilization effect, regional warming and decreasing water availability-associated increases in tree mortality have been observed in these forests (Peng *et al.*, 2011; Luo & Chen, 2013). This situation may be further jeopardized by a decrease in tree growth associated with regional warming and decreasing water availability (Barber *et al.*, 2000). However, decreased growth of surviving trees could be compensated for by an increase of ingrowth from new recruitments, stimulated by growing space and resources released by increased tree mortality (Phillips *et al.*, 2004).

North American boreal forests contain various forest types primarily depending on successional stage and topography (Frelich & Reich, 1995; Chen & Popadiouk, 2002). For example, in the early stages of succession, forests on rocky, sandy drier sites are more frequently dominated by early-successional coniferous species such as *Pinus banksiana*, whereas forests on mesic sites are colonized by deciduous broadleaf species such as *Populus tremuloides*. At the late-successional stage, forests become dominated by late-successional coniferous *Picea* spp. The responses of ΔAGB to recent climate changes may depend on species composition and forest ageing (Vayreda *et al.*, 2012; Coomes *et al.*, 2014).

Here, we examined ΔAGB and addressed how ΔAGB has changed with forest ageing and climate change for major forest types in the western boreal forest of Canada. We used 871 permanent sampling plots (170.6 ha), monitored between 1958 and 2011 (Table 1). These plots were established by the Alberta and Saskatchewan governments to monitor forest growth, using stratified random sampling to cover four forest types and a wide range of age classes (ranging from 17 to 210 years old). We quantified annual net aboveground biomass change (ΔAGB) as the difference between the sums of annual growth of surviving trees and annual ingrowth from recruitment ($\Delta\text{AGB}_{\text{CI}}$) and annual biomass loss from mortality ($\Delta\text{AGB}_{\text{M}}$). As observed trends in

Table 1 Summaries (mean \pm standard deviation with range in the brackets) of the characteristics of the various forest types. ΔAGB , $\Delta\text{AGB}_{\text{CI}}$ and $\Delta\text{AGB}_{\text{M}}$ were annual net aboveground biomass change, the sum of annual biomass growth of surviving trees, annual ingrowth biomass from new recruitments, and annual biomass loss by mortality, respectively. MAT and CMI represent mean annual temperature and annual climate moisture index, respectively

Variable	Deciduous broadleaf forests		Early-successional coniferous forests		Mixed forests		Late-successional coniferous forests	
	262	210	210	139	260	260	260	
Number of plots								
ΔAGB ($\text{Mg ha}^{-1} \text{Year}^{-1}$)	1.45 \pm 2.56 (-12.21 to 7.25)	1.44 \pm 1.20 (-8.60 to 4.60)	0.82 \pm 1.81 (-8.77 to 5.49)	0.59 \pm 2.25 (-17.47 to 5.18)	2.36 \pm 0.81 (0.05–8.80)	1.77 \pm 1.98 (0.00–17.53)	116 \pm 36.9 (44.5–205.5)	
$\Delta\text{AGB}_{\text{CI}}$ ($\text{Mg ha}^{-1} \text{Year}^{-1}$)	3.94 \pm 1.25 (1.04–9.80)	2.18 \pm 0.85 (0.29–4.70)	2.79 \pm 0.78 (0.20–5.98)	2.36 \pm 0.81 (0.05–8.80)	1.77 \pm 1.98 (0.00–17.53)	116 \pm 36.9 (44.5–205.5)	1984 \pm 9.4 (1964–2002.5)	
$\Delta\text{AGB}_{\text{M}}$ ($\text{Mg ha}^{-1} \text{Year}^{-1}$)	2.49 \pm 2.09 (0.00–16.97)	0.74 \pm 0.78 (0.00–9.64)	1.96 \pm 1.55 (0.00–10.39)	1.77 \pm 1.98 (0.00–17.53)	1.77 \pm 1.98 (0.00–17.53)	116 \pm 36.9 (44.5–205.5)	0.61 \pm 1.30 (-2.96 to 4.23)	
Forest age (years) ¹	69 \pm 22.9 (26.5–157.5)	76 \pm 28.5 (19.5–169.5)	98 \pm 24.1 (33.5–165.5)	98 \pm 24.1 (33.5–165.5)	116 \pm 36.9 (44.5–205.5)	116 \pm 36.9 (44.5–205.5)	9.88 \pm 10.30 (-7.17 to 43.14)	
Calendar year ²	1987 \pm 8.3 (1962.5–2002.5)	1978 \pm 12.5 (1960.5–2005)	1982 \pm 10.2 (1962.5–2004)	1982 \pm 10.2 (1962.5–2004)	1984 \pm 9.4 (1964–2002.5)	1984 \pm 9.4 (1964–2002.5)	1984 \pm 9.4 (1964–2002.5)	
MAT ($^{\circ}\text{C}$)	1.04 \pm 0.93 (-2.87 to 3.81)	1.20 \pm 1.26 (-1.95 to 4.08)	0.75 \pm 1.30 (-2.80 to 4.08)	0.75 \pm 1.30 (-2.80 to 4.08)	0.61 \pm 1.30 (-2.96 to 4.23)	0.61 \pm 1.30 (-2.96 to 4.23)	0.61 \pm 1.30 (-2.96 to 4.23)	
CMI (cm)	4.82 \pm 6.81 (-8.72 to 32.60)	12.15 \pm 9.90 (-10.49 to 38.54)	8.41 \pm 8.74 (-10.17 to 38.83)	8.41 \pm 8.74 (-10.17 to 38.83)	9.88 \pm 10.30 (-7.17 to 43.14)	9.88 \pm 10.30 (-7.17 to 43.14)	9.88 \pm 10.30 (-7.17 to 43.14)	

¹Forest age is the middle age between two successive measurements of each sample plot (see Materials and Methods).

²Calendar year is the middle point of calendar years between two successive measurements of each sample plot.

longitudinal data reflect both endogenous and exogenous processes (Magnani *et al.*, 2007; Brown *et al.*, 2011; Luo & Chen, 2013), we used Hierarchical Bayesian models to disentangle climate change effects on Δ AGB and its components. These methods are also suited for accounting for uncertainties in sampling, models and parameters associated with observational data (Clark, 2005).

Materials and methods

Study area and the forest inventory data

The study area was located in Alberta and Saskatchewan, Canada. Wildfire is the dominant stand-replacing disturbance with a fire return interval varying temporally and spatially from 15 to 90 years (Weir *et al.*, 2000). Harvesting also plays a role in the southern part of the region (Mkhabela *et al.*, 2009). A total of 2911 permanent sampling plots (PSP) were randomly established to quantify growth of four forest types with varying ages in the study area mostly during 1960s and 1970s by the Alberta and Saskatchewan provincial governments. The plot sizes varied from 405 m² to 8092 m². To ensure a representative sample of the stand, all plots were established in stands (>1 ha in area) that were visually homogeneous in structure and composition and were at least 100 m from any openings to minimize edge effects. The plots were repeatedly measured until 2011 at varying intervals (Table 1).

To examine long-term changes of aboveground biomass, we selected the PSPs based on the following four criteria: (1) stands originated from wildfire with forest age (FA) known 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 was defined as ≥ 7.3 cm in Alberta and ≥ 9.7 cm in Saskatchewan, were marked and their diameter at breast height (DBH) were measured using DBH tapes (169 plots were removed); (4) each plot had at least 30 trees at initial measurement to ensure that the plot represented the sample stand (16 plots were removed). The last criterion resulted in the exclusion of plots with size < 600 m². As each province used different tree size criteria for monitoring, that is ≥ 7.3 cm in DBH in Alberta, ≥ 9.7 cm in DBH in Saskatchewan, we standardized the data by selecting trees with DBH ≥ 10 cm to eliminate the effect of the different sampling efforts between the two provinces. Recruitment trees were defined as those that reached 10 cm DBH between two successive censuses.

In total, 871 plots (170.6 ha) were selected for analyses during the monitoring period (Table 1, Table S1). The first census year varied from 1958 to 1993; the last census year ranged from 1972 to 2011; the measurement intervals averaged 9.20 years; the average number of censuses was 3.91 (Fig. S2). 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). Mean annual temperature and mean annual

precipitation between 1950 and 2011 varied from -2.38 °C to 4.08 °C and from 365 mm to 1184 mm, respectively. Elevation ranged from 260 m to 2073 m above sea level (a.s.l.).

Forest types

Because forest productivity differs strongly among forest types (Gower *et al.*, 2001) and climate change-associated demographic rates such as tree mortality differ among tree species (Luo & Chen, 2013), we examined whether Δ AGB, its components and their systematic trends differ among the forest types that are classified based on the proportions of aboveground biomass of species groups at the first census of each sample plot with similar leaf traits and successional statuses by the Alberta and Saskatchewan governments. Deciduous broadleaf forest type (DEC) consisted of >75% of aboveground biomass of *Populus tremuloides* Michx., *Populus balsamea* L. and *Betula papyrifera* Marsh.; early-successional coniferous forest type (ESC) consisted of >75% of aboveground biomass of *Pinus banksiana* Lamb., *Pinus contorta* Douglas and *Larix laricina* (Du Roi) K. Koch; late-successional conifer forest type (LSC) consisted of 75% of aboveground biomass of *Abies lasiocarpa* (Hooker) Nuttall., *Abies balsamea* (L.) Mill., *Pseudotsuga menziesii* (Mirb.) Franco, *Picea engelmannii* Parry ex Engelm., *Picea glauca* (Moench) Voss and *Picea mariana* Mill.; mixed forest type (MIX) consisted of all stands that did not meet the criteria of the three preceding types (Table S1).

Calculations of annual net aboveground biomass change and its components

We calculated stand-level biomass by summing the biomass of all trees within each sample plot for each census. Individual tree aboveground biomass was estimated using published Canadian national species-specific DBH-based tree aboveground biomass allometric equations, which accounted for tissue sizes and densities, for wood, bark, foliage and branches (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 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 the equations of softwood or hardwood to estimate their biomass (Lambert *et al.*, 2005).

We calculated annual net aboveground biomass change (Δ AGB, Mg ha⁻¹ year⁻¹) as the difference of aboveground biomass divided by the number of years between two consecutive censuses. The Δ AGB included biomass gain by the growth of surviving trees and ingrowth by new recruitment trees (Δ AGB_{GI}) and biomass loss due to tree mortality (Δ AGB_M). Systematic errors in estimating Δ AGB trends could occur when sampling uncertainties associated with the size of study plot and length of monitoring period are not taken into account (Lewis *et al.*, 2004; Talbot *et al.*, 2014). As the measurements varied in plot sizes and intervals of census periods, we corrected the original Δ AGB and its components by accounting for sampling heterogeneity (Appendix S1).

Explanatory variables

Forest stand age for each plot was determined according to a known fire or by coring at least three dominant/codominant trees of each tree species inside or outside 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 age was used to determine time since fire by species-specific relationships between FA and time since fire developed for boreal forests (Gutsell & Johnson, 2002; Vasilias & Chen, 2002). Among 871 selected plots, there were 176 plots that the stand ages were determined by a known fire and 695 plots that the stand ages were determined from cored sections. For these 695 plots, a total of 4024 trees were cored which included 367 *Pinus banksiana*, 455 *Pinus contorta*, 819 *Populus tremuloides*, 28 *Betula papyrifera*, 112 *Populus balsamea*, 334 *Picea mariana*, 1763 *Picea glauca*, 6 *Pseudotsuga menziesii*, 134 *Abies balsamea* and 6 *Abies lasiocarpa* trees.

Similar to previous studies (Lewis *et al.*, 2009; Phillips *et al.*, 2009; Luo & Chen, 2013), to examine the systematic trends associated with climate change in ΔAGB and its components, we used the middle calendar year of a census period, that is the period between two successive censuses, to represent climate change drivers as a whole. We calculated two climate anomalies: annual temperature anomaly (ATA) and annual climate moisture index anomaly (ACMIA). Climate anomalies are defined as the departure of means between two sequential measurements from long-term climate means (Clark *et al.*, 2011). The long-term climate mean was defined as the average of each climate variable between 1958 and 2011, during which our plot measurements were taken. The climate associated with each census period was calculated as the average of climate values during the period. The equation for calculating climate anomalies was as follows:

$$\text{Climate_Anomaly}_{ij} = \frac{\text{Annual_Climate}_{ij}}{\text{Annual_Climate}_{1958-2011j}} \quad (1)$$

where $\text{Climate_Anomaly}_{ij}$ was ATA or ACMIA for the i th census period and j th plot; $\text{Annual_Climate}_{1958-2011j}$ was annual mean temperature and annual climate moisture index for the j th plot over the period of 1958–2011, respectively. Annual mean temperature and annual climate moisture index were derived from BIOSIM software (Réginière *et al.*, 2012) (<https://cfs.nrcan.gc.ca/projects/133>), which generates historical scale-free annually or monthly climate data for specific locations based on latitude, longitude and elevation based on linear interpolations of the observations from close climatic stations. The annual climate moisture index was annual precipitation minus annual potential evapotranspiration (PET) in centimetres. The annual PET is annual potential loss of water vapour from a well-vegetated landscape when soil moisture is not limiting and was estimated by the simplified Penman–Monteith equation presented by Hogg (1997). The climate associated with each census period was calculated as the average of climate values during the period.

Statistical analyses

For each forest type, we determined the long-term means of ΔAGB and its components with plot identity as a random factor to account for temporally autocorrelated plot-specific spatial climates, site condition, species composition and disturbance history. Because the observed trends in longitudinal data reflect both forest development and climate change processes, we disentangled the effects of forest development and climate change on ΔAGB and its components using the following model:

$$\Delta\text{AGB}_{ij} = \beta_0 + \beta_1 \times f(\text{FA}_{ij}) + \beta_2 \times \text{Year}_{ij} + \pi_j \quad (\text{Model 1})$$

where i and j were i th census period and j th plot, respectively; π_j represents the random effect of sampling plots. π_j is a normal distribution with a mean of 0; β_0 , β_1 and β_2 are parameters to be estimated. $f(\text{FA}_{ij})$ is the best fit function between ΔAGB and its components and FA among the four selected functions (Table S2). Year_{ij} was the middle calendar year of a census period.

With all data pooled, there was a positive collinearity between FA and Year ($r = 0.16$ or $r^2 = 0.027$). The correlation between FA and Year (r) was -0.024 , 0.345 , 0.337 and 0.199 for DEC, ESC, MIX and LSC forest types, respectively. There are three possible approaches to disentangle the joint variations between forest age and climate change effects. The first approach is to simultaneously model forest age and climate change effects without assigning priority. The second is to use residual and sequential regressions by assigning the priority to FA and then modelling Year effects on the residuals (Graham, 2003). The third is to reverse the priority in the second approach. 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 & Cohen, 1975), assigning priority to FA would marginalize the Year effect, and *vice versa* (Brown *et al.*, 2011), we simultaneously modelled effects of FA and Year on ΔAGB and its components (Tables S3 and S4).

In Model 1, Year represents systematic overall climate change drivers including the systematic increase in ATA, decrease in ACMIA and changes in other unknown climate drivers. To further understand the link between the ΔAGB trends associated with Year and ATA and ACMIA, we modelled the responses ΔAGB and its components to ATA as well as ACMIA by simultaneously accounting for the FA effect (Tables S3 and S4).

To account for uncertainties in sampling, models and parameters, we used the Bayesian Markov chain Monte Carlo methods in the *MCMCglmm* package (Hadfield, 2010) for analyses. All independent variables were centred to speed up convergence. For each model, we evaluated convergence by running three independent chains with different initial values and monitoring the Gelman–Rubin statistic (Gelman & Rubin, 1992). When convergence was confirmed, an additional 10 000 iterations with thinning of half were used to calculate the mean, SD and 95% Bayesian confidence interval (95% CI) for each coefficient from the posterior distribution. We verified and confirmed the normality assumption by examining the posterior distributions of the estimated parameters of all fitted models (Spiegelhalter *et al.*, 2002; Gelman *et al.*, 2003).

Results

For the four forest types, ΔAGB s were significantly higher for DEC and ESC than those for MIX and LSC (Fig. 1). ΔAGB was 1.44 (95% CI, 1.22–1.68), 1.42 (1.30–1.56), 0.80 (0.50–0.1.11) and 0.62 (0.39–0.88) $\text{Mg ha}^{-1} \text{ year}^{-1}$ for DEC, ESC, MIX and LSC, respectively (Fig. 1). Both $\Delta\text{AGB}_{\text{GI}}$ and $\Delta\text{AGB}_{\text{M}}$ were highest for DEC with 3.97 and 2.52 $\text{Mg ha}^{-1} \text{ year}^{-1}$, respectively, followed by MIX, LSC and ESC.

For all forest types, ΔAGB decreased with forest age, reaching zero at approximately age 100–120 years in DEC, MIX and LSC forests, while ΔAGB remained above zero for all ages in ESC (Fig. 2) due to a slower age-dependent declining rate (Table S3). The age-related ΔAGB declines resulted from decreased biomass growth and increased biomass loss from mortality for all forest types (Fig. 2).

When negative forest age effects were simultaneously accounted for, ΔAGB declined in all forest types with the largest decline in LSC by 0.069 $\text{Mg ha}^{-1} \text{ year}^{-1}$ per calendar year, followed by DEC, MIX and ESC at rates of 0.035, 0.032 and 0.021 $\text{Mg ha}^{-1} \text{ year}^{-1}$ per calendar

year, respectively (Fig. 3). Calendar year-associated declines of ΔAGB were primarily driven by increased $\Delta\text{AGB}_{\text{M}}$ (Fig. 3), which was highest for LSC, followed by DEC, MIX and ESC. For MIX and LSC, the declines of ΔAGB also resulted from the declines of $\Delta\text{AGB}_{\text{GI}}$, but $\Delta\text{AGB}_{\text{GI}}$ increased by 0.011 $\text{Mg ha}^{-1} \text{ year}^{-1}$ per calendar year in DEC and it did not change in ESC.

During the study period, mean annual temperature increased by 0.039 $^{\circ}\text{C year}^{-1}$ and annual climate moisture index anomaly (ACMIA) decreased by 0.169 $\text{cm}^{-1} \text{ year}^{-1}$ with calendar year (Fig. 4a–b). With every degree of annual temperature increase, ΔAGB decreased by 1.00, 0.20, 0.55 and 1.07 $\text{Mg ha}^{-1} \text{ year}^{-1}$ in DEC, ESC, MIX and LSC forests, respectively, (Fig. 4c). The ΔAGB decline associated with increasing temperature was a result of simultaneous declines of $\Delta\text{AGB}_{\text{GI}}$ and increases of $\Delta\text{AGB}_{\text{M}}$ in all forest types except ESC, whose $\Delta\text{AGB}_{\text{GI}}$ did not increase with temperature. With every cm decrease of annual climatic water availability, ΔAGB decreased by 0.030, 0.045 and 0.171 $\text{Mg ha}^{-1} \text{ year}^{-1}$ in ESC, MIX and LSC forests, but did not change in DEC forests (Fig. 4d). With decreasing ACMIA, the declines in ΔAGB resulted

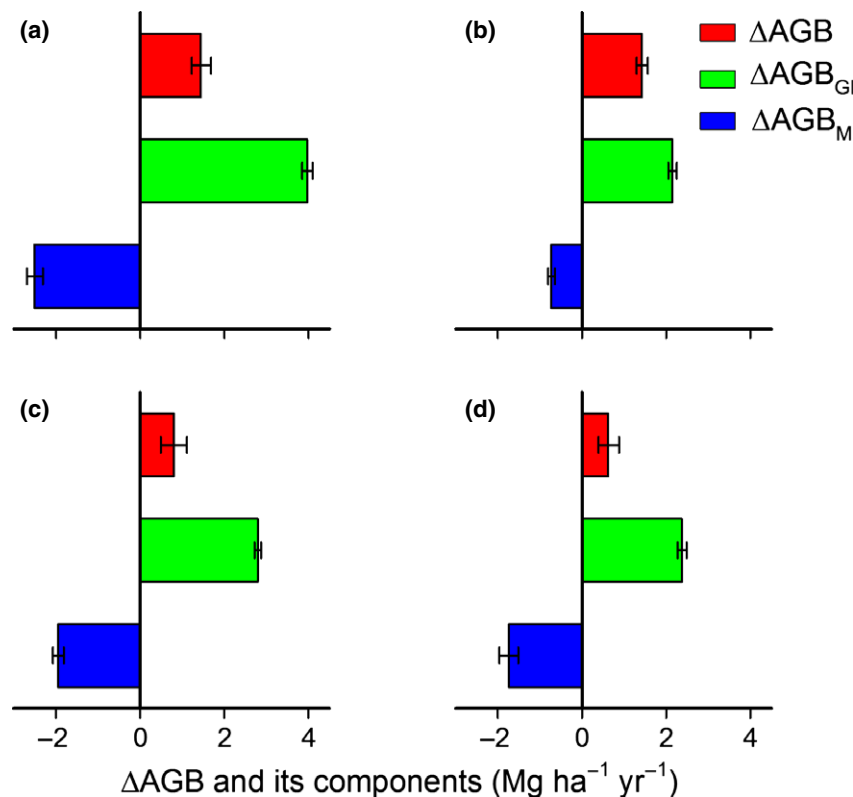


Fig. 1 The average annual net aboveground biomass change (ΔAGB) and its components during the study period (1958–2011) for deciduous broadleaf forests (a), early-successional coniferous forest (b), mixed forests (c) and late-successional coniferous forests (d). Values are means and 95% Bayesian confidence intervals. $\Delta\text{AGB}_{\text{GI}}$ and $\Delta\text{AGB}_{\text{M}}$ represent annual aboveground gain from growth of surviving trees and ingrowth from recruitments and biomass loss through mortality, respectively.

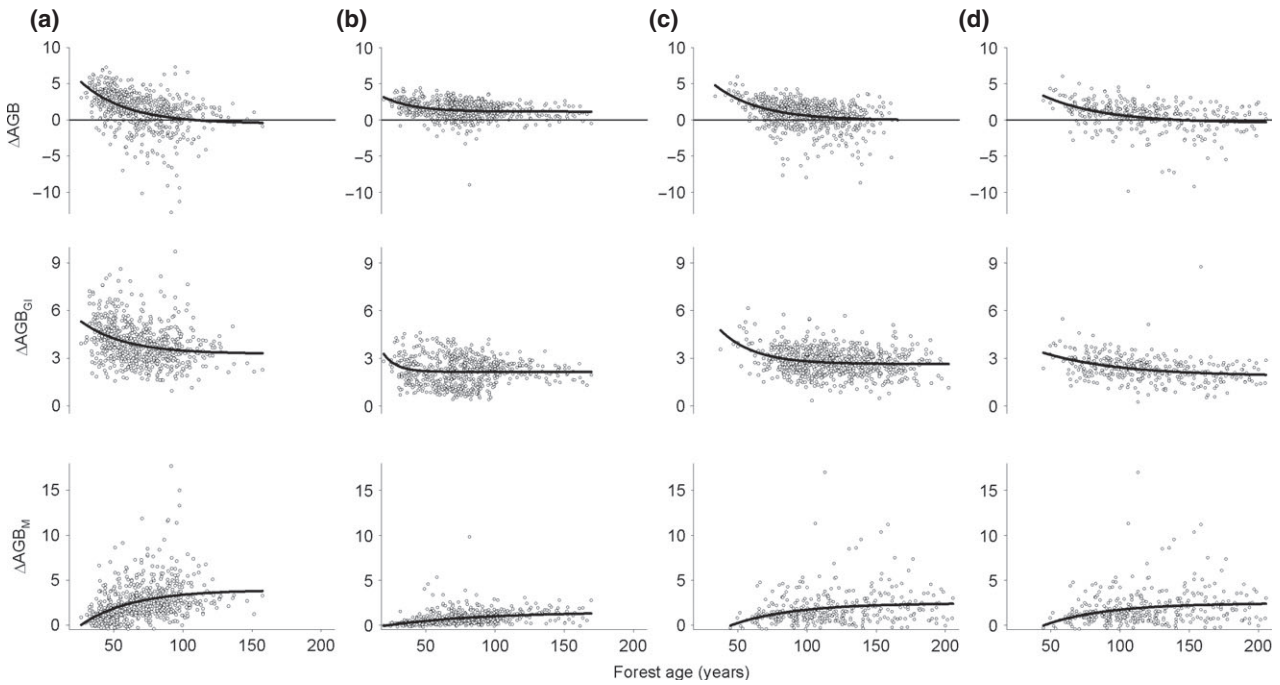


Fig. 2 Annual net aboveground biomass change (ΔAGB) in relation to forest age for deciduous broadleaf forests (DEC) (a), early-successional coniferous forests (ESC) (b), mixed forests (MIX) (c) and late-successional coniferous forests (LSC) (d). The dots represent calendar year effects-corrected ΔAGB and its components, derived by their observed values - $\beta_{\text{Year}} \times \text{Year}$ and the fitted relationships to forest age are in models C in Tables S3 and S4.

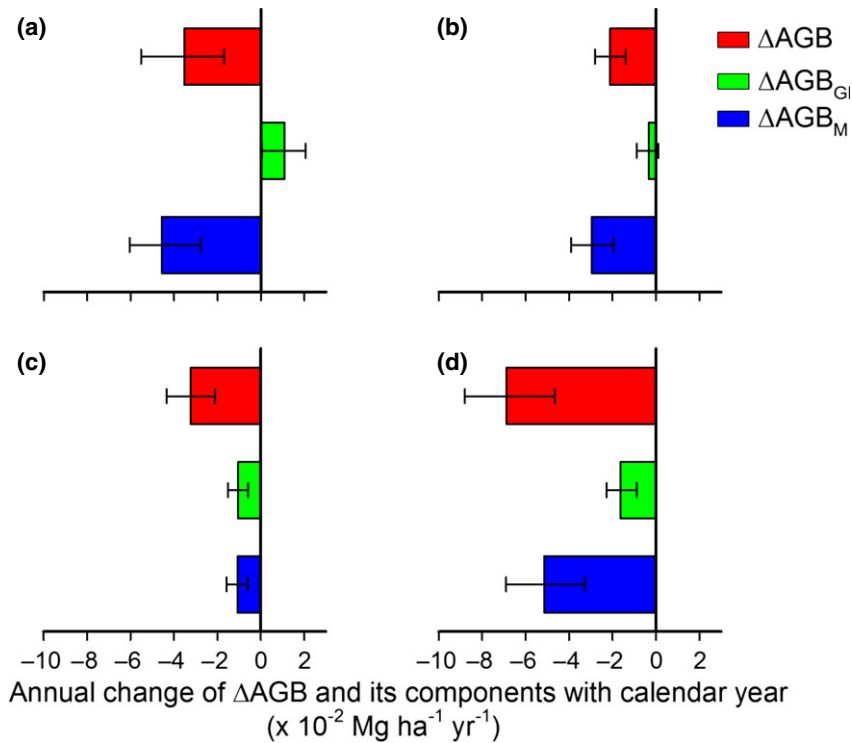


Fig. 3 The response slopes of annual net aboveground biomass change (ΔAGB) and its components associated with calendar year for deciduous broadleaf forests (a), early-successional coniferous forest (b), mixed forests (c) and late-successional coniferous forests (d). Both means and error bars (the 95% Bayesian confidence intervals) are provided in Model Cs in Tables S3 and S4. Abbreviations for $\Delta\text{AGB}_{\text{GI}}$ and $\Delta\text{AGB}_{\text{M}}$ are same as in Fig. 1.

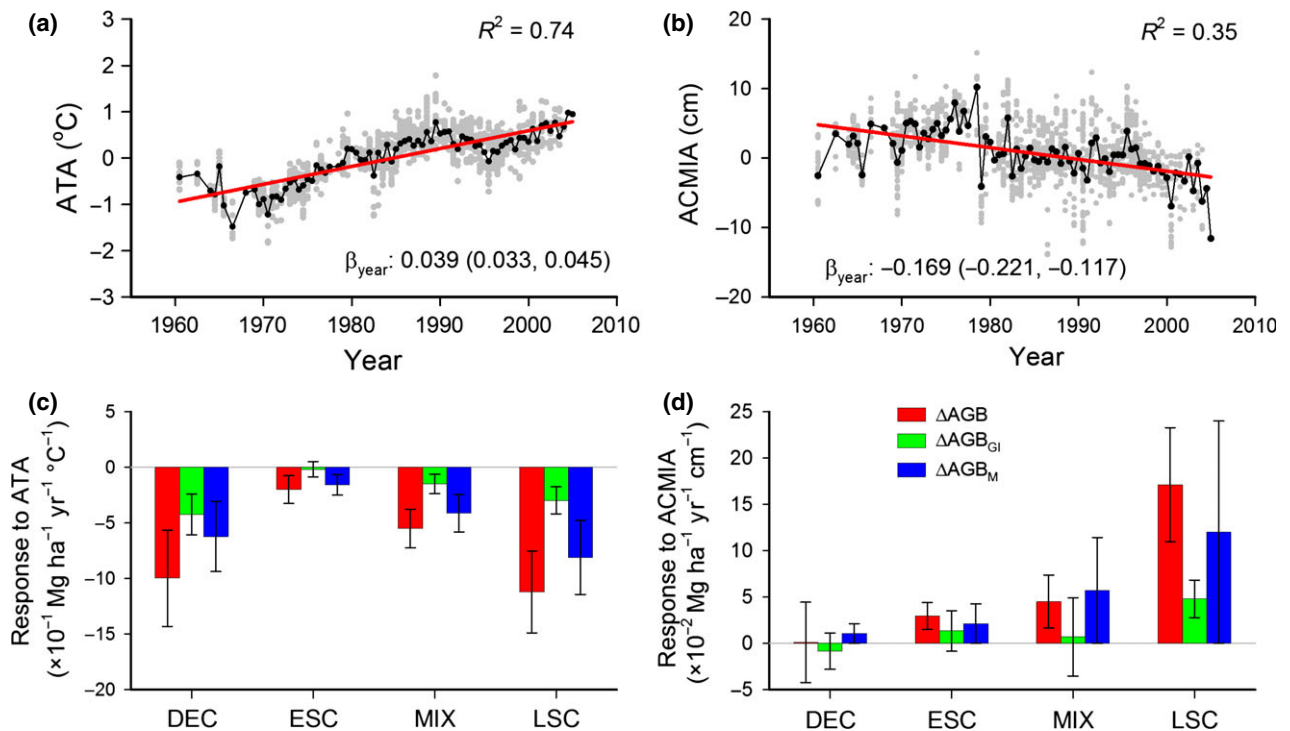


Fig. 4 Temporal trends of climatic anomalies and the sensitivities of annual net aboveground biomass change (ΔAGB) and its components to climate anomalies. Temporal trends of annual temperature anomaly (ATA) (a), annual climate moisture index anomaly (ACMIA) (b), and the sensitivity of forest age-corrected ΔAGB and its components to ATA (c), and ACMIA (d). In Figure 4a–b, the grey dots were the plot-level observations. Black dotted lines were the summarized annual means. Red lines were fitted trends using Hierarchical Bayesian linear model with R^2 . And β_{Year} was the fitted slope, with mean and its 95% Bayesian confidence intervals in brackets. The values in Fig. 4c–d are provided in models D and E in Tables S3 and S4.

from primarily the increases in ΔAGB_M in all forest types except LSC, whose ΔAGB_{GI} also decreased.

Discussion

The net aboveground biomass change reported in this study was based on a spatially extensive observational network (170.6 ha) in boreal forests of diverse types and ages. Similar to previous studies (Gower *et al.*, 1997; Coomes *et al.*, 2014), we found that net aboveground biomass change varied with species composition with higher net aboveground biomass changes in deciduous broadleaf and early-successional coniferous forests than mixed and late-successional coniferous forests. However, the similarly high net biomass change in deciduous broadleaf and early-successional coniferous forests resulted from different demographic rates – higher biomass gain from growth accompanied by higher biomass loss from mortality in deciduous broadleaf forests than early-successional coniferous forests.

Net aboveground biomass change, after standardization for climate change effects, decreased with age, as a result of decreases in biomass growth and increases in biomass loss from mortality in all forest types. The

age-dependent patterns in net aboveground biomass change were similar to those reported in previous boreal and temperate studies (Gower *et al.*, 2001; Law *et al.*, 2003; Magnani *et al.*, 2007; Yuan & Chen, 2012; Taylor *et al.*, 2014). However, net aboveground biomass change of old forests dominated by *Pinus* spp. declined at a slower rate than the other three forest types and remained positive after 120 years of age, similar to *Pinus ponderosa* forests (Law *et al.*, 2003). In the other three forest types, which reflect different successional stages of boreal mixedwood (Chen & Popadiouk, 2002), net aboveground biomass change of stands older than 120 years was approximately zero, that is nearly half of the stands had negative changes and the other half had positive changes. The different net aboveground biomass change rates among old stands reflecting their variation in disturbance regimes and recruitments indicate the need for a large sample size such as is used in this study to determine overall trends in net biomass change.

After accounting for forest age effects, the climate change-associated declines in net aboveground biomass change not only occurred in previously reported deciduous broadleaf forests (Hogg *et al.*, 2008) and

late-successional forests (Ma *et al.*, 2012), but in all forest types, providing evidence of long-term systematic climate change effects (Parmesan & Yohe, 2003) on the western boreal forests. The greatest decline was in late-successional coniferous forests dominated by shallow-rooted *Picea* spp. at a rate of -0.069 (95% CI, -0.088 to -0.047) $\text{Mg ha}^{-1} \text{ year}^{-1}$ per calendar year, which is similar to the previously estimated decline rate of old forests in the region (Ma *et al.*, 2012). However, the rates of decline are much lower in other forest types with the least in early-successional coniferous forests dominated by drought stress-tolerant *Pinus* spp.

The climate change-associated declines in net aboveground biomass change are primarily driven by biomass loss from increased tree mortality, which have been previously reported for western North American forests (Van Mantgem *et al.*, 2009; Peng *et al.*, 2011; Luo & Chen, 2013), as well as reduced growth in mixed and late-successional coniferous forests. Our finding of reduced growth provides stand-level evidence for reduced growth reported for *Picea glauca* at the individual tree level (Barber *et al.*, 2000). However, in deciduous broadleaf forests, a large biomass loss from mortality was accompanied by a small increase in growth. Our observed net aboveground biomass change declines associated with calendar year is in contrast to net aboveground biomass increases in tropical forests where biomass gain from growth is larger than biomass loss from mortality (Phillips *et al.*, 2004; Coomes *et al.*, 2014).

Net aboveground biomass declined with warming, a result from increased mortality and reduced growth associated with warming for all forest types except early-successional coniferous forests. With decreasing water availability, net aboveground biomass declined in all forest types except deciduous broadleaf forests. In deciduous broadleaf forests, decreased growth associated with warming is in contrast to increased growth associated with calendar year, indicating that warming is not the cause of calendar year-associated increased growth. The increased growth is likely the result of the resource release from large increases of mortality in *Populus* forests associated with insect outbreaks (Hogg *et al.*, 2002). Among forest types, net aboveground biomass change, biomass growth and biomass loss from mortality of late-successional forests are most sensitive to warming and decreasing water availability, whereas deciduous broadleaf forests appear to be more responsive to warming than decreasing water availability.

Our results could not be attributable to our use of Canadian tree biomass allometric equations because annual net changes in stand basal area and aboveground biomass had similar responses to forest age and climate change (Table S5). Additionally, while correcting

for census length is well justified because of increased underestimation of demographic rates with increasing census length (Lewis *et al.*, 2004; Talbot *et al.*, 2014), climate change effects may be altered if census length changes over time as the correction would also account for climate change effects. We examined whether climate change effects might differ without correcting census length and found that climate change effect remained qualitatively similar to those after census length correction (Table S6 vs. Model C in Table S3). Furthermore, we examined whether inclusion of standing biomass as a predictor altered climate change effects and found that climate change effects on net aboveground biomass change, biomass gain from growth and biomass loss from mortality did not differ between the models with or without standing biomass as a predictor (Tables S3 and S4). Our data are based on measurements of large trees (DBH ≥ 10 cm) that were the measurement threshold for historical permanent sample plots, which have been critical to demonstrating direct evidence for climate change impacts on forest ecosystems (Lewis *et al.*, 2009; Phillips *et al.*, 2009; Van Mantgem *et al.*, 2009; Ma *et al.*, 2012; Luo & Chen, 2013; Coomes *et al.*, 2014). Although trees greater than this diameter threshold account for $\geq 95\%$ stand biomass in mature boreal forest stands (Popadiouk *et al.*, 2003), trees smaller than this threshold would account for greater stand biomass in younger stands and their mortality and turnover rates may be higher (Luo & Chen, 2013). Hence, large diameter thresholds could lead to underestimation of both growth and mortality rates and introduce uncertainties for estimating net biomass change. Future forest monitoring should consider including small trees.

We present evidence that, unlike other forests where increased nitrogen deposition and rising atmospheric CO_2 increase forest growth (Magnani *et al.*, 2007; Reay *et al.*, 2008; Lewis *et al.*, 2009; McMahon *et al.*, 2010; Thomas *et al.*, 2010), the net aboveground biomass change of the boreal forests has declined in all forest types but at different rates. The reduced aboveground biomass inputs coupled with increased soil respiration associated with climate warming (Bond-Lamberty & Thomson, 2010) and increased stand-replacing fire activities in western North American forests (Westerling *et al.*, 2006) present challenges to the carbon accumulation function of the western boreal forests. As warming and decreasing water availability are expected to continue (Diffenbaugh & Field, 2013), the negative impacts of climate change on the carbon accumulation function of the forests are anticipated to escalate. In addition to endogenous forest succession that favour early-successional species with increased stand-replacing fire activities (Chen *et al.*, 2009), different

sensitivities to warming and decreasing water availability among forest types suggest that climate change has shifted to higher dominance of early-successional species. As current climatic trends continue (Differbaugh & Field, 2013), the region will likely shift to even higher dominance of early-successional species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Correcting sampling heterogeneity for annual net biomass change (ΔAGB) and its components.

Fig. S1. Plot locations of 871 plots of western boreal forests of Canada.

Fig. S2. Frequency distribution of sample plots and measurements.

Table S1. Definitions of forest types and associated sampling efforts.

Table S2. Comparisons of Deviance Information Criterion (DIC) among functions describing forest age-dependent responses.

Table S3. Alternative models for annual net biomass change (ΔAGB) for four forest types.

Table S4. Models for annual net biomass change components (ΔAGBGI and ΔAGBM) for four forest types.

Table S5. Parameter values estimated from simultaneously modelling the effects of forest age and calendar year on annual net change of stand basal area ($\text{m}^2 \text{ha}^{-1} \text{year}^{-1}$).

Table S6. Net biomass change (ΔAGB) for four forest types analysed by observed data without correcting for sampling heterogeneity associated with census length.