

Tree rings provide no evidence of a CO₂ fertilization effect in old-growth subalpine forests of western Canada

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Abstract

Atmospheric CO₂ concentrations are now 1.7 times higher than the preindustrial values. Although photosynthetic rates are hypothesized to increase in response to rising atmospheric CO₂ concentrations, results from in situ experiments are inconsistent in supporting a CO₂ fertilization effect of tree growth. Tree-ring data provide a historical record of tree-level productivity that can be used to evaluate long-term responses of tree growth. We use tree-ring data from old-growth, subalpine forests of western Canada that have not had a stand-replacing disturbance for hundreds of years to determine if growth has increased over 19th and 20th centuries. Our sample consisted of 5,858 trees belonging to five species distributed over two sites in the coastal zone and two in the continental climate of the interior. We calculated annual increments in tree basal area, adjusted these increments for tree size and age, and tested whether there was a detectable temporal trend in tree growth over the 19th and 20th centuries. We found a similar pattern in 20th century growth trends among all species at all sites. Growth during the 19th century was mostly stable or increasing, with the exception of one of the coastal sites, where tree growth was slightly decreasing; whereas growth during the 20th century consistently decreased. The unexpected decrease in growth during the 20th century indicates that there was no CO₂ fertilization effect on photosynthesis. We compared the growth trends from our four sites to the trends simulated by seven Earth System Models, and saw that most of the models did not predict these growth declines. Overall, our results indicate that these old-growth forests are unlikely to increase their carbon storage capacity in response to rising atmospheric CO₂, and thus are unlikely to contribute substantially to offsetting future carbon emissions.

KEYWORDS

climate change, CO₂ fertilization effect, dendroecology, global warming, old-growth forests, tree growth, tree rings

1 | INTRODUCTION

Global atmospheric CO₂ concentrations increased from 227 ppm in 1750, the beginning of the Industrial Era (Joos & Spahni, 2008), to over 400 ppm in 2017 (Tans & Keeling, 2018). Rising atmospheric CO₂ along with the global warming resulting from it—and other

greenhouse gases—are expected to increase tree growth and forest productivity (Arora et al., 2016; Ciais et al., 2014). A long-standing hypothesis is that elevated CO₂ will stimulate plant photosynthetic rates, which will translate into increased biomass growth, a phenomenon oft called the “CO₂ fertilization effect” (Camarero, Gazol, Tardif, & Conciatori, 2015; Keenan et al., 2013; van der Sleen et al.,

2014). Even small increases in the rate of CO₂ uptake and the amount of C stored in forests could help buffer emission-driven increases in atmospheric CO₂ and mitigate the rate of global climate change (Dymond, Beukema, Nitschke, & Coates, 2016). However, the magnitude of a CO₂ fertilization effect remains uncertain (Friedlingstein et al., 2013; Friend et al., 2014; Girardin et al., 2016; Nabuurs et al., 2013), which poses a persistent challenge for understanding the climate-regulating land-atmosphere feedbacks and has significant implications for climate change policy.

Long-term field studies and manipulative experiments addressing the response of forests to elevated CO₂ have reached inconsistent conclusions. Measurements from permanent sample plots distributed across North America indicate increasing biomass increments with elevated atmospheric CO₂, but also suggest this positive effect could be offset by droughts [e.g. (Hember et al., 2012; McMahon, Parker, & Miller, 2010; Wu et al., 2014)] or nutrient limitation [e.g. (Norby, Warren, Iversen, Medlyn, & McMurtrie, 2010; Oren et al., 2001)]. Growth chamber experiments have demonstrated a positive effect of elevated CO₂ on tree growth that was enhanced by nutrient additions (Johnson, Ball, & Walker, 1997; Winter, Aranda, Garcia, Virgo, & Paton, 2001), but the results of these studies are only relevant to small trees. Free-Air CO₂ Enrichment (FACE) experiments have also shown that, on average, elevated CO₂ stimulates tree growth (Jones, Scullion, Ostle, Levy, & Gwynn-Jones, 2014). However, most FACE studies have been conducted in young stands, which may respond differently than old-growth forests (Leuzinger et al., 2011; Norby & Zak, 2011); the few studies that have experimentally increased CO₂ levels in mature stands have found no increase in tree growth (Bader et al., 2013; Klein et al., 2016; Körner et al., 2005; Sigurdsson, Medhurst, Wallin, Eggertsson, & Linder, 2013). Although initially growth may be enhanced by elevated CO₂, nutrient limitation is a likely explanation for both the diminishing magnitude of response frequently observed in young stands (Norby et al., 2010), and the lack of a CO₂ fertilization effect in mature forests [e.g. a boreal forest stand (Sigurdsson et al., 2013)].

On a global scale, long-term responses of forests to elevated atmospheric CO₂ are often derived from Earth Systems Models (ESMs) and Dynamic Global Vegetation Models (DGVMs), nearly all of which predict that rising atmospheric CO₂ will stimulate tree growth and the rate at which forest biomass is accumulated [e.g. Friend et al. (2014)]. However, most models are hampered by limited data, rely on a large set of model assumptions, and are unable to adequately parameterize the complex interacting ecological processes that regulate growth, including the constraining effects of drought and nutrient availability (Kolby Smith et al., 2015). In addition, models can propagate errors leading to large uncertainty in predictions (Magnussen, Köhl, & Olschofsky, 2014).

The uncertainty in the effect of increasing CO₂ on tree growth indicates the need for further data that can provide insights into growth responses as well as causes of their variability. Tree rings can be a helpful source of data for testing the effects of CO₂ fertilization on tree growth (Battipaglia et al., 2015) because, unlike growth chamber and FACE experiments, they store the historic responses of

trees to changing environmental conditions (Babst, Alexander et al., 2014; Babst, Bouriaud et al., 2014; Gedalof & Berg, 2010). Tree-ring widths can be converted to basal area increments, a proxy for growth, to evaluate long-term temporal trends in productivity and its relationships with environmental variables (Camarero et al., 2015; Klesse, Etzold, & Frank, 2016; Peters, Groenendijk, Vlam, & Zuidema, 2015). Ring width analysis can complement both inventory and experimental studies by extending growth records further into the past (Babst, Bouriaud et al., 2014; Gedalof & Berg, 2010; Klesse et al., 2016). Tree rings can also be useful for model validation, because their interannual variability closely resembles that of forest net primary productivity (Gower, Vogt, & Grier, 1992; Graumlich, Brubaker, & Grier, 1989; Xu et al., 2017) as well as development of individual-based vegetation models (Zuidema, Poulter, & Frank, 2018).

In this study, we used tree-ring data from old-growth, subalpine forests of western Canada to determine whether growth changes over the 19th and 20th centuries were indicative of a CO₂ fertilization effect. Our objectives were as follows: (a) to describe long-term trends in growth of trees in old-growth subalpine forests, as indicated by basal area increments, (b) to compare growth trends among species and between two forest types, (c) to test for a relationship between tree growth and annual measurements of atmospheric CO₂, and (d) to compare the trends in tree growth from field observations to downscaled growth predictions for these forests generated from Earth System Models. To address these objectives, we analyzed a large set of tree-ring data collected from 5,858 trees in old-growth forests that have not had a stand-replacing disturbance for hundreds of years.

2 | MATERIALS AND METHODS

2.1 | Study sites

We examined tree growth in four old-growth subalpine forests of British Columbia, Canada: two inland Engelmann spruce–subalpine fir forests and two coastal Mountain Hemlock forests. The two inland stands were at Adams Lake (51°20'N, 119°30'W; 1,900 m elevation; 14-degree west slope) and Damfino Creek (49°52'N, 118°50'W; 1,700 m elevation; <10-degree southeast slope), and were composed almost exclusively of *Abies lasiocarpa* and *Picea engelmannii*, which occurred in all size classes. There was no evidence of major disturbance at Adams Lake and the stand age structure indicated recruitment occurred throughout the stand's history with no major recruitment peaks; this stand appeared to be close to a steady-state forest with a maximum tree age of 462 years (Antos & Parish, 2002b). The Damfino Creek stand was initiated by a stand-replacing fire 330 years prior to sampling; subsequently episodic outbreaks of the 2-year cycle spruce budworm resulted in minor to moderate disturbances, but trees were of all ages since stand initiation (Antos & Parish, 2002a; Parish & Antos, 2002). Both stands contained a large seedling bank, which was dominated by *A. lasiocarpa* but also contained many *P. engelmannii* (Antos, Parish, & Conley, 2000).

The two coastal stands can be considered ancient forests in that they both contained trees exceeding 1,000 years in age (Parish & Antos, 2004, 2006). Mt. Cain (50°14'N, 126°20'W; 1,000 m elevation; 10–15 degree southeast slope) is on northern Vancouver Island and Mt. Elphinstone (49°29'N, 123°32'W; 1,100 m elevation; 10–13 degree southeast slope) is in the Coastal Mountains on the mainland. The Mt. Cain stand contained four tree species: *Abies amabilis*, *Tsuga mertensiana*, *Tsuga heterophylla*, *Callitropsis (Chamaecyparis) nootkatensis* all of which had individuals that exceeded 900 years in age (Parish & Antos, 2004). The Mt. Elphinstone stand contained the same four tree species, although *T. heterophylla* was uncommon; very old individuals were present for all four species (Parish & Antos, 2006). For both coastal stands, there was no evidence of major disturbance and all four species occurred in a wide range of age and size classes (Parish & Antos, 2004, 2006; Parish, Nigh, & Antos, 2008), including a well-developed seedling bank (Antos, Guest, & Parish, 2005).

All four sites occurred in cold, wet climates where deep snowpacks accumulate in winter and last into late spring or early summer. The 20th century averages of annual temperatures were 0.48°C at Adams Lake, 1.59°C at Damfino Creek, 4.63°C at Mt. Elphinstone, and 4.26°C at Mt. Cain (Wang, Spittlehouse, & Hamann, 2015). The coastal sites are very wet with annual precipitation of 3,500 mm or more and snowpacks exceeding 3 m in depth. The interior sites are also wet but have a more continental climate than the coastal sites, with differences between mean winter and summer temperatures of 23°C at Adams Lake, 25°C at Damfino creek, and 16°C at both Mt. Elphinstone and Mt. Cain (Wang et al., 2015). The estimated 20th century averages of Hargreaves climatic moisture deficits for the site locations are 107, 180, 80, and 71 mm/year for Adams Lake, Damfino Creek, Mt. Elphinstone, and Mt. Cain, respectively (Wang et al., 2015).

2.2 | Tree-ring sampling, measurement, and growth calculation

All selected stands were in old-growth forests scheduled for logging. The use of such stands allowed the collection of both predisturbance information and basal discs, which have substantial advantages over increment cores for obtaining age and growth rate data (Antos & Parish, 2002b; Parish & Antos, 2004). In each stand, four 50 × 50 m plots were established in a fairly homogeneous portion of the stand for a total sample area of 1 ha per stand. Prior to logging, all trees ≥4.0 cm in diameter at breast height (1.3 m; DBH) were mapped, tagged, and measured for DBH and height. Trees too small to be of commercial value, which were generally <15 cm DBH, were cut and basal discs obtained prior to the commercial harvesting of the stands; sampling smaller trees is important for obtaining an appropriate sample for growth analyses (Brienen, Gloor, & Zuidema, 2012; Nehrbass-Ahles et al., 2014). For the larger trees, basal discs were cut as close to the ground as possible from the stumps after logging. Basal discs were obtained from most trees but not all, primarily because of damage during logging and lost tags.

Annual rings were measured along one radius for small discs and two to three radii for discs, the diameter of which exceeded 15 cm (Antos & Parish, 2002a; Parish & Antos, 2004) that avoided rot pockets and were assigned to a calendar year. Ring width was measured to the nearest 0.01 mm using a Measu-chron digital positiometer (Micro-Measurement Technology, Bangor, Maine, USA). COFECHA (Holmes, 1983) was used to detect ring dating and measurement errors. Ring measurements were obtained from approximately 1,000 to 1,800 trees per stand (Table 1). For details of the sampling procedures and ring measurements, see (Antos & Parish, 2002a, 2002b; Parish & Antos, 2004, 2006).

Based on averaged annual tree-ring width measurements, we constructed time series of annual basal area increments for each tree, which were calculated as the difference between basal area at

TABLE 1 Density of living trees sampled and the number of trees used for growth trend analysis, by species, for each of four old-growth, subalpine forests in southern British Columbia: total number of living trees ≥4.0 cm diameter at breast height (DBH) in the 1 ha sample area and the number of trees >4.0 cm DBH with ring data

Site	Species	Total number of living trees >4.0 cm DBH	Number of trees >4.0 cm DBH with ring data
Mt. Adams ^a	<i>Abies lasiocarpa</i>	1,304	938
Damfino Creek ^b	<i>Abies lasiocarpa</i>	1,720	1,528
Mt. Cain	<i>Abies amabilis</i>	938	854
	<i>Tsuga mertensiana</i>	169	140
	<i>Tsuga heterophylla</i>	268	244
	<i>Callitropsis nootkatensis</i>	167	97
Mt. Elphinstone	<i>Abies amabilis</i>	506	460
	<i>Tsuga mertensiana</i>	463	434
	<i>Tsuga heterophylla</i>	35	27
	<i>Callitropsis nootkatensis</i>	408	372

^a69 *Picea engelmannii* were also in the plots. ^b120 *Picea engelmannii* and 17 *Pinus contorta* were also in the plots.

age n and at age $n-1$. For subsequent analyses, basal area and basal area increments were transformed using a logarithmic function and are henceforth referred to as $\ln BA$ and $\ln BAI$, respectively.

2.3 | Detection of a trend in tree growth

To detect a trend in tree basal area increments (our measure of tree growth) related to increasing atmospheric carbon, it was first necessary to remove the influence of tree size and/or age on tree growth. Tree basal area increments ($\ln BAI$) were positively associated with tree basal area ($\ln BA$) (Figure 1a), implying that as a tree grows larger it uptakes more carbon. However, the rate of change in basal area increments slowed down with increasing basal area, indicating that a tree approached its maximum capacity for carbon uptake. Tree age also affects its growth: $\ln BAI$ is negatively related to tree age within all ranges of tree basal area (Figure 1b).

Peters et al. (2015) recommend using Regional Curve Standardization (RCS) or Size Class Isolation (SCI) methods to remove effects of tree size or age in tree-level productivity data. However, we found relationships with both tree size and age; thus, we used multiple regression to remove the effects of both factors and their interactions (see Supporting Information Table S1) on tree biomass increments simultaneously. Slopes of the linear relationships between $\ln BA$ and $\ln BAI$, as well as corresponding intercepts, vary among the individual trees (see point scatter in Figure 1a); therefore, we chose a mixed effects model to account for the effects of tree size on growth. We further explored whether effect of tree age and interactive effect of tree basal area and age on growth varied among the individual trees through comparing the values of Akaike information criterion [AIC (Akaike, 1974)] among model specifications. The

model of $\ln BAI$ at the time t for a tree j with the lowest AIC value (see Supporting Information Figure S1) was:

$$\ln BAI_{tj} = \beta_0 + U_{0j} + (\beta_1 + U_{1j}) \times \ln BA_{tj} + (\beta_2 + U_{2j}) \times \ln A_{tj} + (\beta_3 + U_{3j}) \times \ln BA_{tj} \ln A_{tj} + r_{tj} \quad (1)$$

where $\ln BA_{tj}$ is log-basal area of a tree j at time t ; $\ln A_{tj}$ is log-age of a tree j at time t ; r_{tj} are residuals of $\ln BAI_{tj}$; β_0 is average intercept and U_{0j} is its tree-dependent deviation; β_1 , β_2 , and β_3 are fixed effects of log-basal area, log-age, and their interaction, respectively, and U_{1j} , U_{2j} , and U_{3j} are their tree-dependent deviations. We estimated the parameters in the equation 1 using an R package “lme4” (Bates, Mächler, Bolker, & Walker, 2015; R Core Team, 2018). The model described in equation 1 explained 94% of variability in the observed $\ln BAI$ of *A. lasiocarpa* at Adams Lake, and performed equally well for other species and sites (Figure 1c, Supporting Information Table S2).

After removing the estimated effects of tree size and age on tree growth, we looked for trends in residuals of $\ln BAI$, r_{tj} , (i.e. difference between observed and expected values of $\ln BAI$) in time. We used a linear regression to evaluate the significance of the temporal trend in the residuals:

$$E(r_{tj}) = a + m \times \text{Year}_t \quad (2)$$

where Year_t is the year in which residual r_{tj} occurred; a and m are intercept and slope, respectively. We considered the trend significant if the p -value of m was < 0.05 .

The residuals r_{tj} , or $\ln(BAI_{ij}^{\text{observed}}) - \ln(BAI_{ij}^{\text{predicted}})$, can be expressed as $\ln\left(\frac{BAI_{ij}^{\text{observed}}}{BAI_{ij}^{\text{predicted}}}\right)$, then their exponents will be the factors by

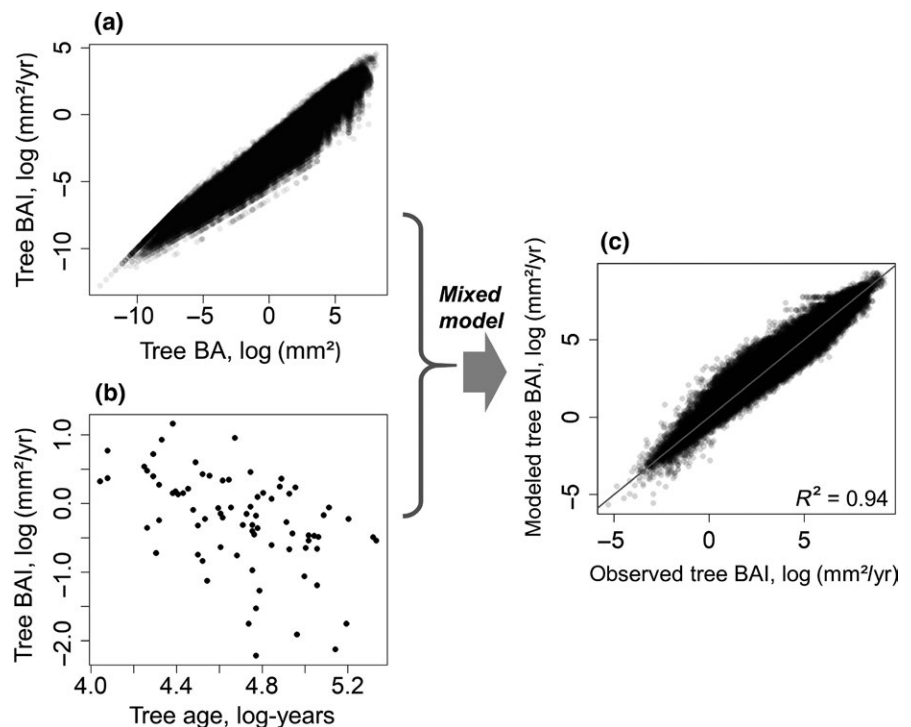


FIGURE 1 Relationship between tree basal area increment and tree basal area (a) and tree age within the basal diameter range of 10–10.02 cm (for demonstration purpose) (b); and fit between the output of a mixed model of the tree age and basal area effects on the tree basal area increments (as specified in Equation 1) and the observed tree basal area increments (c). Tree basal area increments, basal area and tree age data were transformed with a logarithmic function

which the observed BI are above or below the expected, or modeled, BI. Therefore, in a linear regression, where the independent variable is Year_t and dependent variable is $[E(r_{t,j})]$, the slope, m , multiplied by a hundred, will be an approximation of the per cent change in BAI per year. Although the tree-ring data collected from these forests extends back several centuries, we only used data from the last two centuries with a focus on describing the rate of change in $r_{t,j}$ over the 20th century in comparison with the trend during the previous century.

We assessed relationships between, $r_{t,j}$, and atmospheric CO_2 concentration between 1800 and 1997. Global atmospheric CO_2 for the period from 1800 to 1997 was obtained from a compilation of Antarctic ice core data (Etheridge et al., 1998) and data from Mauna Loa in Hawaii after 1959 (Tans & Keeling, 2018). The ice core data provided CO_2 records every 3–5 years, whereas records from Mauna Loa are available annually; we decided to linearly interpolate the ice core records to annual scale to avoid loss of the information from the tree rings in trend analysis. We explored whether the relationship between changes in tree growth and atmospheric CO_2 was linear or nonlinear by fitting a smoothing curve to the noisy responses of $r_{t,j}$ to CO_2 using a “smooth.spline()” function in R (R Core Team, 2018) and visually explored the curve.

We also compared the 20th century growth trends obtained from the tree rings to the growth trends simulated by Earth System Models (ESMs). Such comparisons provide an independent assessment of the capacity of Earth system models to predict local changes in forest growth associated with increased CO_2 and thus their potential for projecting future forest productivity. We extracted the modeled net primary productivity (NPP) estimates for each year from the model grid cells that encompassed our sample sites. Although there are many Earth system models, we used those for which NPP data were readily available: www.earthsystemgrid.org or <http://pcmdi9.llnl.gov/>. The models used for comparison were Community Earth System Model [CESM, (Oleson et al.,)], Max Planck Institute model [MPI, (Giorgetta et al., 2013)], Model for Interdisciplinary Research on Climate [MIROC, (Watanabe et al., 2011)], Institut Pierre Simon Laplace model [IPSL, (Dufresne et al., 2013)], Beijing Normal University model [BNU, (Ji et al., 2014)], Canada's Earth System Model [CanESM2, (Arora et al., 2011)], and Norwegian Earth System Model [NorESM, (Tjiputra et al., 2013)]. In the models, NPP can change due to changes in photosynthesis and/or due to changes in leaf area index (LAI), which is used to upscale the leaf-level photosynthesis estimates and is often programmed to increase with increasing NPP. The growth trends obtained in this study were adjusted for tree size and age, and thus reflected the changes in photosynthetic activity of trees. Because sapwood area has been reported to scale linearly with leaf area (Marchand, 1984; Whitehead, 1978), we assumed that if modeled NPP is adjusted for modeled leaf area, it would reflect photosynthetic activity within a modeled gridcell. Therefore, we also downloaded LAI dynamics for the seven models and divided modeled NPP by modeled LAI to make modeled photosynthetic activity trends comparable to the trends obtained from the tree rings.

3 | RESULTS

3.1 | Trends in tree growth

Growth decreased at all sites during the 20th century. The trends in residual basal area increments, $r_{t,j}$, of *A. lasiocarpa* (the only species with enough individuals for study) were similar in both old-growth subalpine forests sampled at inland sites (Figure 2a,b). *Abies lasiocarpa* $r_{t,j}$ decreased significantly during the 20th century, at a rate of $0.44\% \text{ year}^{-1}$ at Adams Lake and 0.21% per year at Damfino Creek (Figure 2a,b). In contrast, during the previous century (1800 s), $r_{t,j}$ increased significantly at both sites (Figure 2a,b). Although the rate of increase in the 19th century and rate of decrease in the 20th century differed somewhat between the two sites, the pattern was the same with a growth increase in the 19th century followed by a growth decrease in the 20th century. The 20th century trends in $r_{t,j}$ at the coastal sites were also decreasing, and at a greater rate than at the two interior sites, $0.56\% \text{ year}^{-1}$ at Mt. Elphinstone and $0.62\% \text{ year}^{-1}$ at Mt. Cain (Figure 2c,d). During the 19th century, the trend was increasing at Mt. Cain ($0.16\% \text{ year}^{-1}$), but decreasing slightly at Mt. Elphinstone ($0.03\% \text{ year}^{-1}$), albeit at a much slower rate than the decrease in the 20th century.

We explored whether growth trends obtained from the mixed model residuals were consistent with the trends obtained via Regional Curve Standardization (RCS) and Size Class Isolation (SCI; see Supporting Information for details on application of the two methods). In most cases, growth trends as indicated by mixed model residuals were similar to the trends in ring width indices obtained via RCS and SCI (Supporting Information Figure S2): 19th century growth trends were positive, and 20th century growth trends were negative. However, RCS-derived RWI's had a positive 20th century trend at Damfino Creek and nonsignificant 20th century trend at Mt. Elphinstone, which, in turn, was not consistent with the trends in SCI-derived RWI's.

All four tree species in coastal forests exhibited significant decreases in $r_{t,j}$ over the 20th century at both Mt. Elphinstone (Figure 3) and Mt. Cain (Figure 4). However, the rate of decline varied among species. *Tsuga mertensiana* exhibited the greatest rate of decline at Mt. Elphinstone, and was the second fastest declining species at Mt. Cain (0.68 and $0.52\% \text{ year}^{-1}$). The rate of decline of *A. amabilis*, $r_{t,j}$, was somewhat less at Mt. Elphinstone, but greater at Mt. Cain ($0.58\text{--}0.73\% \text{ year}^{-1}$). The rate of decline in *C. nootkatensis* growth at Mt. Elphinstone was $0.41\% \text{ year}^{-1}$, which was substantially less than at Mt. Cain ($0.19\% \text{ year}^{-1}$). Rate of decline in growth of *Tsuga heterophylla* was much lower at Mt. Elphinstone ($0.27\% \text{ year}^{-1}$) than at Mt. Cain ($0.5\% \text{ year}^{-1}$). In contrast to the pronounced growth decreases across the 20th century, during the 19th century growth responses were variable among species. At Mt. Elphinstone, *C. nootkatensis* and *T. mertensiana* had no significant trend in growth, *A. amabilis* decreased slightly, and *T. heterophylla* decreased at a substantial rate (Figure 3). At Mt. Cain, all of the species except *C. nootkatensis* had a significant positive trend in tree growth during 19th century (Figure 4). In all cases, the temporal change in basal area increments was not only negative in the 20th century but notably more negative than in the 19th century (Figures 3 and 4).

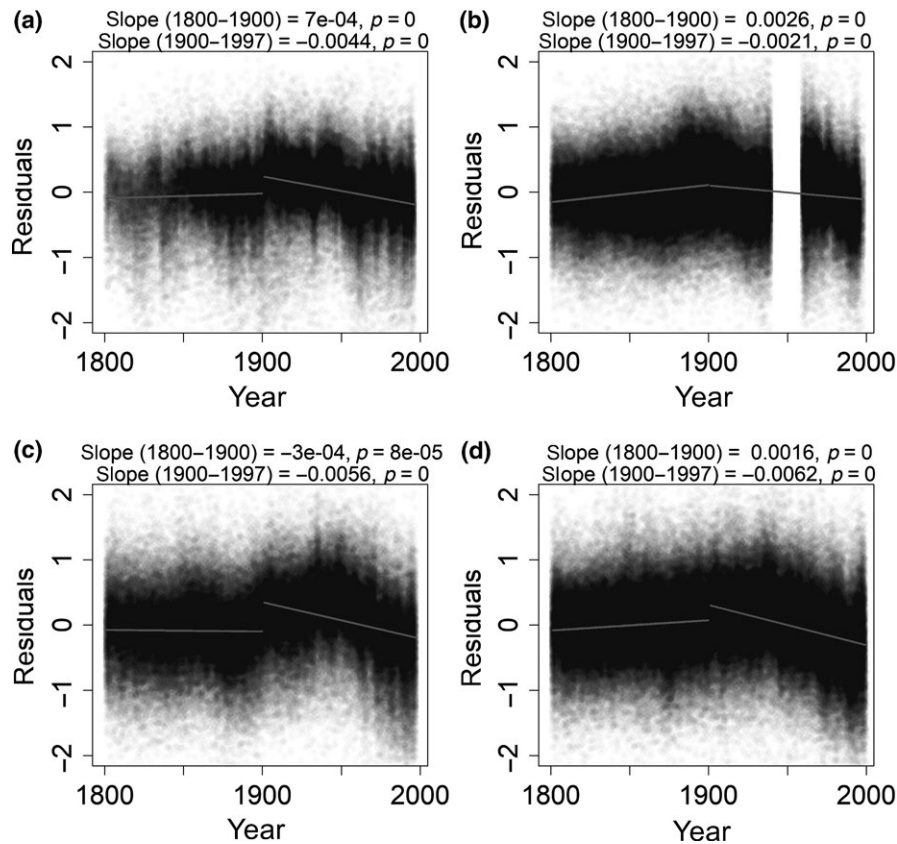


FIGURE 2 Trends in the mixed model residuals of annual tree basal area increments over the 19th and 20th centuries at Adams Lake (a), Damfino Creek (b), Mount Elphinstone (c), and Mount Cain (d) sites. At Damfino Creek, we took out a portion of data in 1940–1960 due to an insect disturbance event that caused a rapid decrease and then an increase in the residuals. The exponents of the residuals are the ratios of observed to expected tree basal area increments; thus, the slopes can be interpreted as fractional change of BAI due to factors other than tree basal area (size) or age. At Adams Lake, tree basal area increments decreased in the 20th century at a rate of 0.44% year⁻¹ (a), in Damfino Creek—0.21% year⁻¹ (b), at Mt. Elphinstone—0.56% year⁻¹ (c), and at Mt. Cain—0.6% year⁻¹ (d). The mixed effects model was specified for each site as $\ln \text{BAI}_{t,j} = \beta_0 + U_{0,j} + (\beta_1 + U_{1,j}) \times \ln \text{BA}_{t,j} + (\beta_2 + U_{2,j}) \times \ln A_{t,j} + (\beta_3 + U_{3,j}) \times \ln \text{BA}_{t,j} \ln A_{t,j} + r_{t,j}$; where $\ln \text{BA}_{t,j}$ is log-basal area of a tree j at time t ; $\ln A_{t,j}$ is log-age of a tree j at time t ; $r_{t,j}$ are residuals of $\ln \text{BAI}_{t,j}$; β_0 is average intercept and $U_{0,j}$ is its tree-dependent deviation; β_1 , β_2 , and β_3 are fixed effects of log-basal area, log-age, and their interaction respectively, and $U_{1,j}$, $U_{2,j}$, and $U_{3,j}$ are their tree-dependent deviations. The model residuals are defined as the difference between observed and modeled $\ln \text{BAI}_{t,j}$.

3.2 | Responses of tree growth to increased atmospheric CO₂

We found a nonlinear relationship between tree basal area increments and atmospheric CO₂ (Figure 5). Basal area increments increased for all species at all sites before global atmospheric CO₂ concentrations reached about 305–320 ppm, which occurred between 1927 and 1965. After that, $r_{t,j}$ decreased steadily with increasing atmospheric CO₂. The threshold point at which increasing CO₂ was no longer positively related to $r_{t,j}$ varied from about 305 to 320 ppm suggesting climate and species-dependent responses.

3.3 | Modeled rates of carbon uptake

Predicted rates of change in productivity over the 20th century at our study sites varied substantially depending on the Earth Ecosystem Model used (Table 2) and were also quite different from the observed change in growth rates derived from tree rings. Only MIROC and CanESM2 predicted a decrease in growth for some of

our study sites. The changes in growth simulated by CanESM2 were most similar to the trend obtained from tree rings at Damfino Creek. The closest predictions to observed growth rates at Adams Lake and Mt. Cain were produced by the MIROC model, but the rates of decline predicted by the model were 3–6 times less than we observed using tree rings.

4 | DISCUSSION

Long-term trends in annual tree basal area increments calculated from tree-ring widths do not support the presence of a CO₂ fertilization effect in old-growth, subalpine forests of British Columbia. Despite dramatic increases in global atmospheric CO₂ over the 20th century, we consistently found no evidence of tree growth stimulation in both subalpine forest types, across all sites, and among all tree species. Our conclusion that a CO₂ fertilization effect was not occurring in these stands is inconsistent with a common expectation that such an effect should be widespread and prominent (Arora et

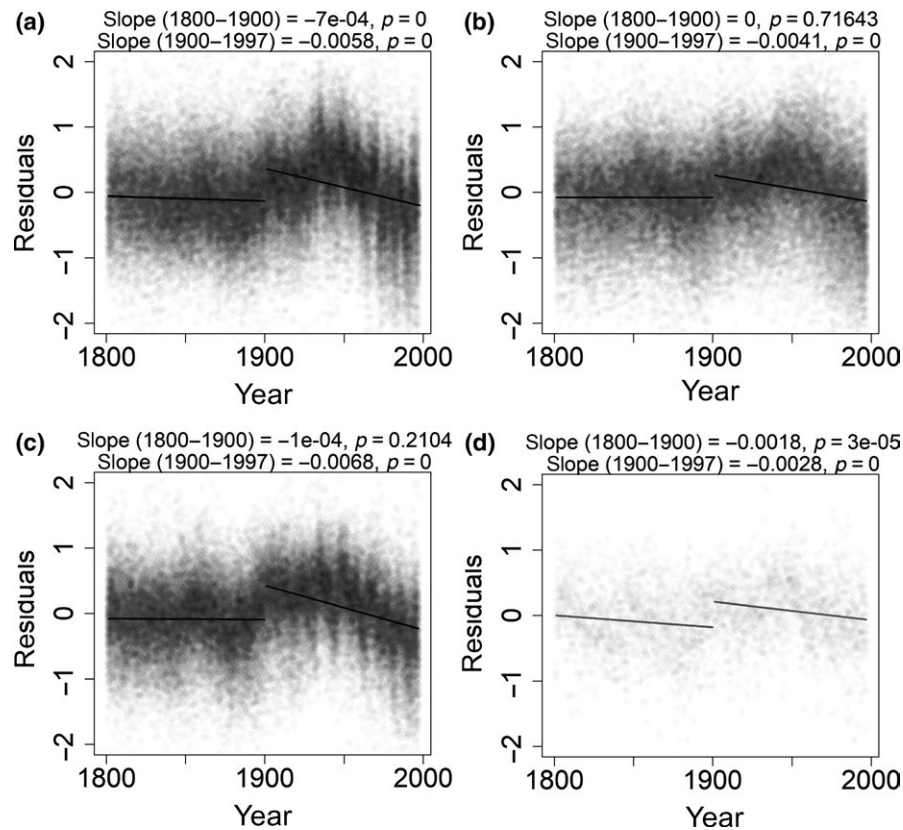


FIGURE 3 Trends in the mixed model residuals of tree basal area increments for *Abies amabilis* fir (a), *Callitropsis (Chamaecyparis) nootkatensis* (b), *Tsuga mertensiana* (c), and *Tsuga heterophylla* (d) in old-growth forest at Mt. Elphinstone. The mixed effects model was specified for each species as $\ln BAI_{t,j} = \beta_0 + U_{0,j} + (\beta_1 + U_{1,j}) \times \ln BA_{t,j} + (\beta_2 + U_{2,j}) \times \ln A_{t,j} + (\beta_3 + U_{3,j}) \times \ln BA_{t,j} \ln A_{t,j} + r_{t,j}$; where $\ln BA_{t,j}$ is log-basal area of a tree j at time t ; $\ln A_{t,j}$ is log-age of a tree j at time t ; $r_{t,j}$ are residuals of $\ln BAI_{t,j}$; β_0 is average intercept and $U_{0,j}$ is its tree-dependent deviation; β_1 , β_2 , and β_3 are fixed effects of log-basal area, log-age, and their interaction, respectively, and $U_{1,j}$, $U_{2,j}$, and $U_{3,j}$ are their tree-dependent deviations. The model residuals are defined as the difference between observed and modeled $\ln BAI_{t,j}$

al., 2013; Luyssaert et al., 2008; Matthews, 2007; Norby et al., 2005; Zhu et al., 2016) as well as with some local and large-scale inventory studies (McMahon et al., 2010; Pan et al., 2011). However, our results concur with the observed lack of a CO_2 -induced growth response in mature natural stands illustrated via manipulative experiment (Körner et al., 2005), inventories (Chen, Luo, Reich, Searle, & Biswas, 2016) and tree rings (Camarero et al., 2015; Gedalof & Berg, 2010; Groenendijk et al., 2015; Reed, Ballantyne, Cooper Leila, & Sala, 2018; van der Sleen et al., 2014). Other recent large-scale analyses reveal a high degree of heterogeneity in growth responses to elevated CO_2 (Charney, D., Babst, F., Poulter, B., Record, S., Trouet, V., M., Frank, D., Evans, M., E., Evans, M., E., Evans, M., E., Evans, M., & E. K., 2016; Girardin et al., 2016; Kelsey, Redmond, Barger, & Neff, 2018; Tei et al., 2017). This, as well as fundamental theory on the limits to tree growth, indicates that a CO_2 fertilization effect is unlikely to be ubiquitous and that making such an assumption might lead to inappropriate predictions.

A nonlinear (parabolic) relationship between the residuals of tree basal area increments and atmospheric CO_2 suggests that the unmanaged old-growth, subalpine forests in our study may have already achieved their probable maximum capacity to assimilate carbon at historic CO_2 concentrations between 305 and 320 ppm.

Nabuurs et al. (2013) report similar responses in tree growth increment, signaling a carbon sink saturation point in European forests. The peak and then decrease in growth residuals with rising CO_2 could, however, be an indirect response to changes in other possible limiting factors such as soil nutrients, altered temperature regimes, or increased dry periods.

Nutrient limitation is widespread in forest ecosystems, especially old-growth forests (Ellsworth et al., 2017; Körner, 2006, 2009; Oren et al., 2001; Sigurdsson et al., 2013) and might generate this pattern of growth in relation to rising atmospheric CO_2 (Cotrufo, Ineson, & Scott And, 2002; Luo et al., 2004; Norby et al., 2010), with the possible exception of some northern and high-elevation regions, where there are high nitrogen (N) inputs from rock (Houlton, Morford, & Dahlgren, 2018). On the global scale, foliar N concentrations have declined by 9% in the past 37 years (Craine et al., 2018), indicating that N supply is not meeting plants' N demand under increasing CO_2 . However, even when nutrients are enhanced through experimentation, mature trees of some species exhibit no stemwood growth stimulation in response to continued rising CO_2 as trees eventually changed their biomass allocation strategy and shifted extra carbon to roots and mycorrhizal associations, or increased carbon export to soil (Bader et al., 2013; Callaway, DeLucia, Thomas, & Schlesinger,

FIGURE 4 Trends in the mixed model residuals of tree basal area increments for *Abies amabilis* fir (a), *Callitropsis* (*Chamaecyparis*) *nootkatensis* (b), *Tsuga mertensiana* (c), and *Tsuga heterophylla* (d) in old-growth forest at Mt. Cain. The mixed effects model was specified for each species as;

$$\ln \text{BA}_{t,j} = \beta_0 + U_{0,j} + (\beta_1 + U_{1,j}) \times \ln \text{BA}_{t,j} + (\beta_2 + U_{2,j}) \times \ln A_{t,j} + (\beta_3 + U_{3,j}) \times \ln \text{BA}_{t,j} \ln A_{t,j} + r_{t,j}$$

where $\ln \text{BA}_{t,j}$ is log-basal area of a tree j at time t ; $\ln A_{t,j}$ is log-age of a tree j at time t ; $r_{t,j}$ are residuals of $\ln \text{BA}_{t,j}$; β_0 is average intercept and $U_{0,j}$ is its tree-dependent deviation; β_1 , β_2 , and β_3 are fixed effects of log-basal area, log-age, and their interaction, respectively, and $U_{1,j}$, $U_{2,j}$, and $U_{3,j}$ are their tree-dependent deviations. The model residuals are defined as the difference between observed and modeled $\ln \text{BA}_{t,j}$.

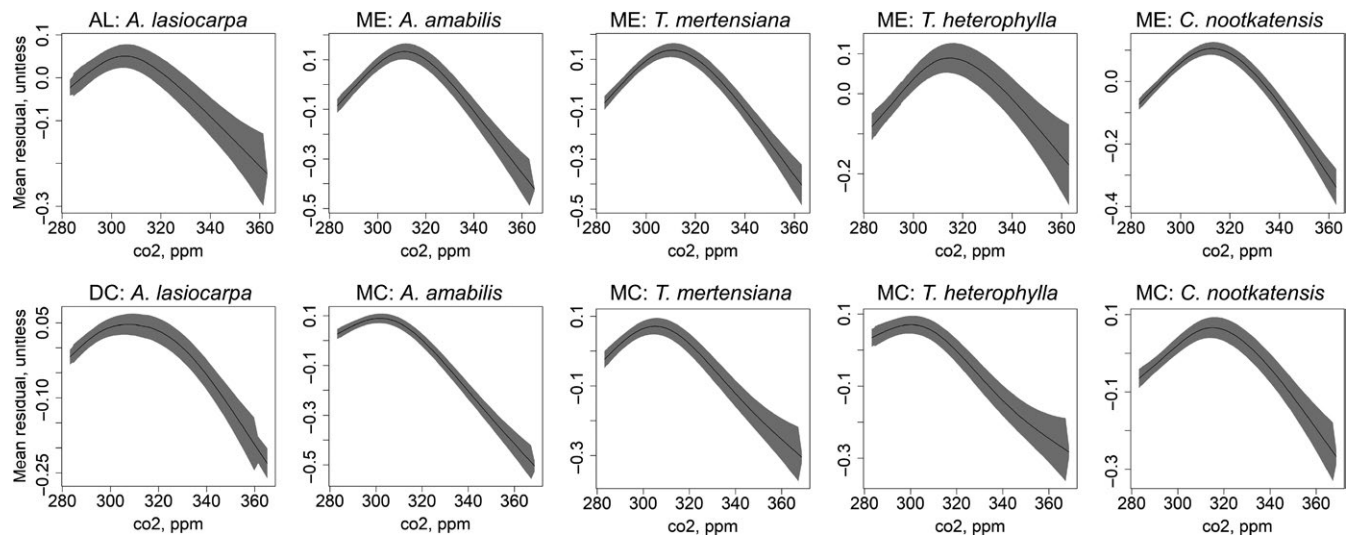
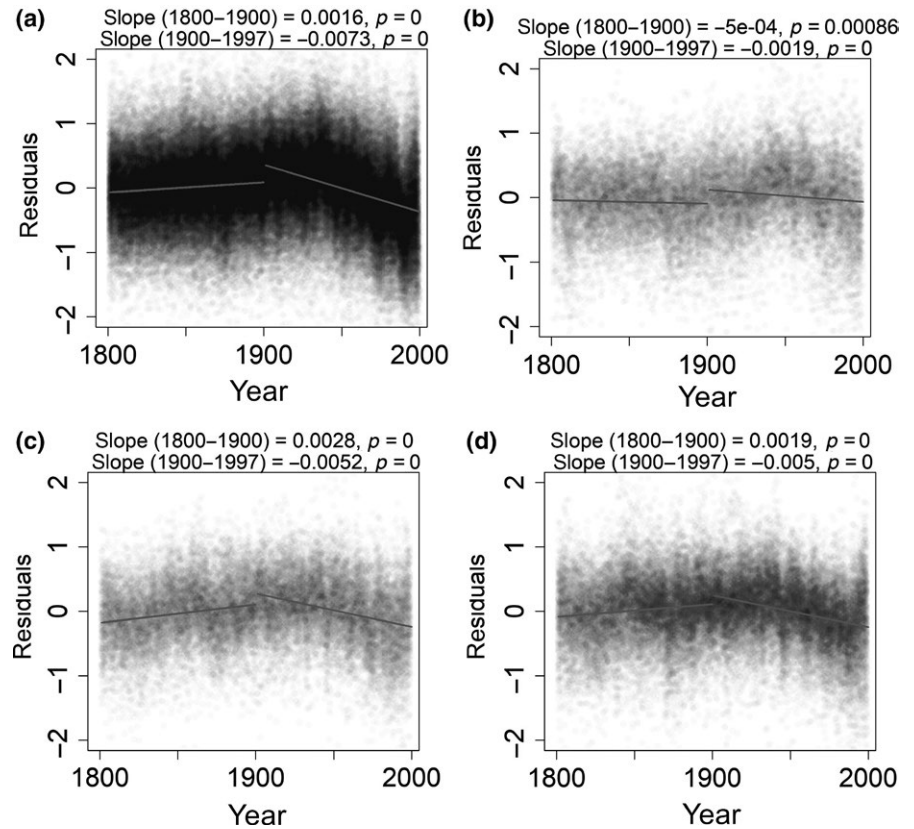


FIGURE 5 Comparison of basal area increment residuals ($r_{t,j}$), in log-fraction of the expected values, with atmospheric CO_2 concentrations (1800–1997) obtained from ice cores and measurements at Mauna Loa, for each tree species at each site. Trends in residuals have been smoothed with a R function “smooth.spline()”, and shaded areas are 95% confidence intervals of the smoothed residuals

1994; Ceulemans & Mousseau, 1994; Fatichi & Leuzinger, 2013; Poorter et al., 2011; Suter, Frehner, Fischer Bernt, Nösberger, & Lüscher, 2002).

The mean annual temperature at our study sites has risen steadily over the 20th century to about 0.5–1°C higher than it was in 1900 (Supporting Information Figure S3a). Increased temperatures could have detrimental effects on growth via increased respiration (Amthor, 2000; McDowell et al., 2011), or stimulate growth via

accelerated nitrogen mineralization (Bonan & Cleve, 1992; Rustad et al., 2001). The mixed model residuals at our sites were positively related to temperature (Supporting Information Table S3), which might indicate that tree productivity in these old-growth forests is temperature limited. Soil moisture deficits can constrain growth in cold regions, despite rising temperatures and CO_2 concentrations (Girardin et al., 2016; McDowell et al., 2011; Tei et al., 2017; Williams, 2014), and there is evidence of growth declines related to

TABLE 2 Comparison of the rates of change in carbon uptake over 20th century (expressed in fractional change over 100 years) obtained from tree rings and seven Earth system models at the locations of the experimental sites. Because the Earth system models had coarse resolution of output, we calculated the trends in carbon uptake for the whole gridcell, within which the experimental sites were located

	Tree rings	CESM	MPI	MIROC	IPSL	BNU	CanESM2	NorESM
AL	-0.45***	-0.033	0.16***	-0.15***	0.267***	-0.1	0.0008	0.05
DC	-0.21***	0.12***	0.2***	-0.003	0.21***	0.09	-0.3**	0.03
ME	-0.55***	0.12***	0.23***	0.48***	0.09***	-0.1	0.0009	0.06**
MC	-0.41***	0.14***	0.2***	-0.07	0.07***	-0.04	0.03	0.01

** $p < 0.1$. *** $p < 0.05$.

water stress in subalpine forests (Carrer & Urbinati, 2004; Reed et al., 2018). Moisture deficits are possible at our sites, but they are unlikely, because mean summer precipitation (MSP) had increased in the 20th century at all sites except Mt. Cain, where it did not change significantly (Supporting Information Figure S3b). Also, water use in old-growth forests tends to be less than in young stands (Perry & Jones, 2016), which decreases to some extent the probability of drought as a major limiting factor in our old-growth stands. Mixed model residuals were not correlated with MSP at Adams Lake, but were positively related with MSP at Damfino Creek, and negatively—at the two coastal sites (Supporting Information Table S3). Negative relationships of tree growth (represented by mixed model residuals) and MSP at the coastal sites might indicate the waterlogging effect (Kozłowski & Pallardy, 1984), which was evident at some patches of the sites (Parish & Antos, 2004, 2006).

Increasing tree age and changing stand density, for example, due to disturbance by defoliating insects, can explain declining growth trends (e.g. Carrer & Urbinati, 2004), but are unlikely causes of negative trends at our sites because we compensated for tree effects by accounting for tree-specific random effects on the relationship between basal area increments, tree age and size in the mixed effects model. In addition, the stands were very old with no evidence of major disturbance for centuries, implying stable tree density (Antos & Parish, 2002b; Parish & Antos, 2004, 2006). Although the specific causes are unknown, growth declines could relate to subalpine trees becoming increasingly maladapted as the environment changes (Aitken, Yeaman, Holliday, Wang, & Curtis-McLane, 2008).

Our results are consistent with Williams (2014) argument that Earth System Models may provide an overly optimistic view concerning CO₂ fertilization effects on forest growth. We found that the growth trends derived from tree rings in our study were substantially different from the trends simulated by seven CMIP5 models, which also were not unanimous in their output. The consistent decreasing growth observed in all four of our old-growth forests, compared to increasing growth predictions among most models, reinforces Williams' (2014) supposition and implies some important processes are inadequately represented in the models, such as the effects of nutrient limitations on growth and the inability of trees to acclimate to increasing water stress (Anav et al., 2013; Tei et al., 2017; Williams, 2014). Incorporating tree-ring data into model development and parameterization could help reduce model uncertainty about forest growth responses to increasing atmospheric CO₂.

Understanding how old-growth forests respond to increasing atmospheric CO₂ concentration is a key element for accurate predictions of global carbon dynamics and carbon budgeting (Bugmann & Bigler, 2011; Luyssaert et al., 2008; van der Sleen et al., 2014). Although elevated CO₂ generally increases growth and rates of carbon accumulation in developing forests that are undergoing succession (Miller, Dietze, DeLucia, & Anderson-Teixeira, 2016), the effect of elevated CO₂ on old-growth forests is equivocal. Some studies indicate that forests can store increasingly more carbon to offset some anthropogenic fossil fuel emissions (Pan et al., 2011; Peng et al., 2014; Pretzsch, Biber, Schütze, Uhl, & Rötzer, 2014), but many studies show no recent growth increases despite increased atmospheric CO₂ (Camarero et al., 2015; Feeley, Joseph Wright, Nur Supardi, Kassim, & Davies, 2007; Groenendijk et al., 2015; Klein et al., 2016; van der Sleen et al., 2014). Although old-growth forests often contain large stores of carbon, they may have reached a steady-state in biomass. Long-standing theory indicates that ecosystem biomass accumulation rates should reach an asymptote, leveling off in the absence of major disturbance (Odum, 1969). Our results reinforce the generalization derived from much of the literature on CO₂ effects on forests (Bader et al., 2013; Ellsworth et al., 2017; Feeley et al., 2007; Girardin et al., 2016; Klein et al., 2016; Norby & Zak, 2011; Sigurdsson et al., 2013)—old-growth forests in many regions are unlikely to provide a further carbon sink beyond the large amounts of carbon they already contain. The lack of a fertilization effect in the old-growth forests, however, does not negate their value; the persistence of old-growth forests on landscapes translates into massive and long-term carbon storage, which is important to mitigating climate change.

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