Recent climatic drying leads to age-independent growth reductions of white spruce stands in western Canada

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Abstract
Since 2001, climatic conditions have been notably drier than normal across large areas of the western Canadian interior, leading to widespread impacts on the forests of this region. This poses a major concern for the future, given climate change projections for continued warming and drying. We conducted tree-ring analysis in 75 pure stands of white spruce (Picea glauca) across Alberta and west-central Saskatchewan to examine the effects of recent climatic drying on the growth of this important boreal tree species. Allometric equations were used to calculate annual growth in aboveground tree biomass (G_{BM}) from ring width measurements. Results showed an increasing trend in G_{BM} from the 1960s to the 1990s, followed by a sharp decline during the severe drought of 2001–2002. Of the 75 stands, only 18 recovered sufficiently to cause an increase in mean G_{BM} from the predrought decade of 1991–2000 to the subsequent decade of 2001–2010. The remaining 57 stands exhibited a decline in mean G_{BM} between these decades. Climatic drying was a major cause of the growth decline, as shown by the significant stand-level relationship between percentage change in decadal mean G_{BM} and the change in decadal mean values of a climate moisture index from 1991–2000 to 2001–2010. Subsequent analyses of boreal stands sampled across Alberta during 2015 revealed that white spruce growth had declined even further as drought conditions intensified during 2014–2015. Overall, there was a 38% decrease in mean G_{BM} between 1997 and 2015, but surprisingly, the percentage decrease was not significantly different for young, productive stands compared with older, less productive stands. Thus, stand ageing cannot explain the observed decline in white spruce growth during the past quarter century, suggesting that these forests are at risk if the trend towards more frequent, severe drought continues in the region.

KEYWORDS
biomass increment, boreal forest, conifer, drought, Picea glauca, productivity, tree rings, white spruce

INTRODUCTION

Drought-induced forest decline has emerged as a critical climate change concern for forests around the world (Allen et al., 2010), including forests in the North American boreal zone (Beck et al., 2011; Price et al., 2013). In western Canada, recent analyses of permanent sample plot (PSP) networks have revealed long-term increases in tree mortality (e.g. Peng et al., 2011; Thorpe & Daniels, 2012; Luo & Chen, 2013) along with reductions in net growth of aboveground biomass (e.g. Ma et al., 2012; Chen & Luo, 2015).
across a wide range of boreal tree species since measurements began in the 1950s and 1960s. Interpretations differ as to the causes of these multidecadal trends, with some studies showing an important role of climatic warming and drying (e.g., Ma et al., 2012; Chen & Luo, 2015) and others pointing to stand development and competition as the primary drivers (e.g., Thorpe & Daniels, 2012; Zhang, Huang, & He, 2015).

Although uncertainties remain as to whether drought-induced forest dieback and decline has escalated at the global scale (Steinkamp & Hickler, 2015), there has been a notable proliferation of research and reporting on this topic since the turn of the 21st century (Allen et al., 2010; Allen, Breshears, & McDowell, 2015). One of the best-documented examples in North America is the "sudden aspen decline" that followed the exceptionally severe subcontinental drought of 2001–2002 (Worrall et al., 2013; Anderegg, Anderegg, Abatzoglou, Hausladen, & Berry, 2013). This drought led to massive, multidecadal mortality of trembling aspen (Populus tremuloides) stands across extensive areas in the southwestern US (Worrall et al., 2013) and in the Prairie Provinces of western Canada (Michaelian, Hogg, Hall, & Arsenault, 2011) along with regional-scale, multidecadal reductions in stand-level growth and net biomass increment (Hogg, Brandt, & Michaelian, 2008).

For aspen in the western Canadian interior, quantification of these drought impacts was made possible by the prior establishment of a comprehensive, multiscale study (CIPHA) that included analyses of tree rings (Hogg, Brandt, & Kochtubajda, 2005; Hogg, Barr, & Black, 2013) coupled with repeated, tree-level measurements across a regional network of ground plots (Hogg et al., 2008). Unfortunately, no comparable study has been conducted on the other major tree species of this region. One of these is white spruce (Picea glauca), a major upland tree species with a wide distribution spanning the North American boreal zone (Nienstaedt & Zasada, 1990; Brandt, 2009). White spruce is important both ecologically and commercially in western Canada where it commonly grows as a late-successional species in mixed wood stands with aspen.

White spruce appears to be less prone to exhibit the highly visible signs of crown dieback and massive mortality that commonly occur in aspen stands following severe drought (Worrall et al., 2013). Nevertheless, analyses of long-term PSP results from western Canada have revealed a relatively large decline in biomass increment of white spruce and other late-successional conifers (Chen & Luo, 2015), along with a trend towards decreased abundance relative to other tree species (Searle & Chen, 2016). Although these and related analyses have shown that climatic factors are likely contributors to these long-term trends, the period between PSP re-measurements (typically 5–10 years or more and not synchronized among PSPs) limits their usefulness in linking forest responses to specific climatic events such as extreme drought.

As an alternative approach, tree-ring analysis provides a relatively low-cost method that enables the retrospective assessment of forest growth variation on an annual time step that is more conducive for identifying factors causing growth reductions such as drought and insect defoliation (e.g., Hogg et al., 2005). In some regions, white spruce is prone to periodic, severe damage from multiyear outbreaks of spruce budworm (Burleigh, Alfaro, Borden, & Taylor, 2002), spruce beetle (Berg, Henry, Fastie, De Volder, & Matsuoika, 2006) and/or other insects, thus posing a challenge for assessing climatic effects from tree rings. For white spruce, an additional challenge is that as a late successional species, its early growth is often strongly modified by shading and other effects induced by overstory aspen and other deciduous trees. Fortunately, many tree-ring studies have been conducted on white spruce stands that have been relatively free of both insect damage and competition from other tree species. From these studies, there is strong evidence that moisture is the most important factor affecting radial stem growth variation in white spruce across a wide range of sites in western Canada, including southern Yukon (Hogg & Wein, 2005; Griesbauer & Green, 2012) and the Canadian Prairie Provinces (e.g., Larsen & MacDonald, 1995; Sauchyn & Skinner, 2001; Hogg & Schwartz, 2001; Chhin, Wang, & Tardif, 2004; Chen et al., 2017). However, a major knowledge gap has emerged as to how the growth of white spruce stands have been impacted by the exceptional drought conditions that have affected large portions of western Canada since the turn of the 21st century.

During the decade following the severe drought of 2001–2002 there was a strong divergence of climatic conditions across the Prairie Provinces. Portions of Saskatchewan and Manitoba became wetter than normal whereas most of Alberta remained drier than normal (Mbogga, Hamann, & Wang, 2009; Hanesiak et al., 2011; Wang, Hogg, Price, Edwards, & Williamson, 2014; Figure 1). Severe droughts affected parts of northern and central Alberta during 2009–2010, followed by an extreme, province-wide drought that developed during 2014–2015 (Agriculture and Agri-food Canada 2015).

Although most tree-ring research relies on the analysis of variation in radial stem growth (ring widths) or basal area increment, the expression of tree growth in units of annual biomass increment provides a more relevant measure for assessing climate impacts on forest productivity and carbon cycling (Babst, Bouriaud, Alexander, Trouet, & Frank, 2014; Hember, Kurz, & Metsaranta, 2015). Thus, the first objective of this study was to investigate the effects of recent climatic drying on growth of aboveground biomass (GBM) in white spruce-dominated stands distributed across Alberta and west-central Saskatchewan, where GBM was estimated using allometric equations from tree-ring measurements. Specifically, we postulated that regional variation in the proportional decline in mean decadal GBM would be strongly affected by spatial variation in the magnitude of climatic drying from the decades 1991–2000 to 2001–2010. Previous studies have shown age-related differences in growth-climate relationships of white spruce (Szeicz & MacDonald, 1994) and other boreal tree species (Girardin, Guo, Bernier, Raulier, & Gauthier, 2012; Chen, Luo, Reich, Searle, & Biswas, 2016), and plot-based analyses show that growth in aboveground biomass tends to decline naturally in older stands (e.g., Hogg et al., 2008; Chen & Luo, 2015). Thus, the second objective was to examine the relative responses of younger and older white spruce stands in terms of their proportional decline in GBM during the recent extended dry period.
2 | MATERIALS AND METHODS

2.1 | Study areas and field sampling methods

The study was conducted across a network of 23 study areas in Alberta and west-central Saskatchewan, Canada (Figure 2). The study region encompassed a large area of boreal forest in northern Alberta, valleys in the Rocky Mountains and foothills of western Alberta, as well as the climatically drier transition zone near the southern range limit of white spruce in south-central Alberta and Saskatchewan. The study region has a continental climate, with mean January temperatures (period 1981–2010) ranging from −10°C to −20°C and mean July temperatures of 15°C to 18°C. Mean annual precipitation ranges from 370 to 600 mm, including 100–200 cm of snowfall. Over the period 1951–2010, mean annual temperature within the study region has increased by about 1.7°C based on spatial interpolations of Environment Canada climate observations (Régnière & St-Amant, 2008). The predominant soils of the region include grey luvisols in the boreal forest and black chernozems in the more southerly transition zone between forest and prairie (Soil Classification Working Group, 1998).

In each of the 23 study areas, candidate stands were selected according to the following criteria: (a) stands dominated by white spruce (Picea glauca) with other tree species representing <40% of total stand basal area; (b) stand ages of at least 45 years at the 1.3-m height; (c) stands of sufficient size (>100 m in length and width); (d) minimal evidence of recent disturbances; and (e) located on relatively level terrain. All stands were of natural origin (mostly established by seed following fire) with the exception of the planted stand at KEP (Keppel), which is located south of the natural range of white spruce (Figure 2).

A total of 75 stands were sampled during 2010–2015. Where possible, 3–5 stands were selected in each study area within a radius of up to 25 km. Four of the study areas within or near the predominantly agricultural transition zone (BRE, KEP, SMO and SUN) were represented by only one or two stands because of the scarcity of suitable sites. During the selection of boreal stands in August 2015, efforts were made to sample from a wide range of stand ages within each study area to provide a comparison of tree growth responses in younger and older stands having similar climatic regimes and drought histories.

In each stand, five or more white spruce trees were sampled at 1.3-m height for tree-ring analysis. Sampling was conducted on representative, codominant white spruce trees that were free of anomalous damage and located within purely white spruce-dominated portions of the stand that were judged to have been free of significant competition from other tree species during the preceding 25 years or more. Notes were made on the visual evidence and/or reporting of past disturbances such as defoliation by eastern spruce budworm (Choristoneura fumiferana), selective cutting, flooding and...
wind-induced blowdown. Stands showing evidence of major impact by these disturbances were excluded from this study. For each sampled tree, dbh (diameter at 1.3-m height with units in cm) was measured and an increment borer was used to collect core samples from two radii per tree.

2.2 | Tree-ring analysis methods

The collected cores were dried at 70°C, mounted in grooved boards, and prepared for tree-ring analysis by polishing with progressively finer grades of sandpaper. Each annual ring was measured using the Coorecorder/CDendro software suite with a flatbed scanner (Larsson, 2013). The application of the most common cross-dating method (COFECHA) poses challenges for forestry studies in remote areas where suitable master chronologies are lacking, and where tree-ring data sets are built from large numbers of stands of widely differing ages and disturbance histories. Thus, we used the following alternative method for dating and cross-dating tree rings in this study. Dating of tree rings was first conducted on the highest quality cores from each stand, then the remaining cores were initially cross-dated within the CDendro program using graphs of tree-ring series that had been normalized using the P2Yrs (proportion of last 2 years of growth) method (Larsson, 2013; Girardin, Bouriaud et al., 2016). After cross-dating, the two ring width series from each tree were averaged. The tree-level ring width series were then cross-dated within and among adjacent stands. The quality of cross-dating was subsequently confirmed by sequentially creating correlation matrices of normalized tree-ring series among trees within stands, trees within study areas and among adjacent study areas across the region. For this purpose, normalization was conducted using a modified form of the P2Yrs method that gives a value of zero (rather than 0.5) for yearly intervals with no change in ring width as well as for yearly intervals not covered by the tree ring series. Specifically, the normalized change in annual growth (\(d_r\)) was calculated as:

\[ d_r = \frac{R_t - R_{t-1}}{R_{t-2}} \]

FIGURE 2  Locations of 75 white spruce stands sampled within 23 study areas during 2010–2015. Coloured symbols show percentage change in average increment of aboveground tree biomass (kg year\(^{-1}\)) between the decades starting in 1991 and 2001. The dotted line shows the southern/eastern limit of white spruce’s natural range (Zoltai, 1975; Hogg, 1994) and hatching shows portions of its range within the transition zone between predominantly continuous forest (green shading) and the climatically drier prairie.
where \(RW_y\) and \(RW_{y-1}\) are ring widths (mm) for the current and previous years, and \(k\) is a constant (set to 0.1 mm in the current analyses) that is required to prevent division by zero errors during periods with missing or absent rings. The constant \(k\) also serves to dampen the spuriously high variation in \(d_r\) that may otherwise occur during periods containing years with extremely narrow or missing rings.

This method was found to provide a highly sensitive measure for verification of cross-dating accuracy, where correctly dated tree-ring series typically gave mean correlation (\(r\)) for verification of cross-dating accuracy, where correctly dated series that were mismatched by one or more years. In nearly all cases, poorly correlated trees were the result of low core quality, thus leading to the removal of 25 (5.9%) of the trees in the original data set of 425 live white spruce trees. The 25 removed trees were distributed across 19 stands with a maximum of two trees removed per stand. For the 400 trees that were retained, mean \(r\) was .545 among trees within stands and .432 among trees within study areas.

2.3 Estimation of tree age and annual biomass increments from ring width measurements

For cores that missed the pith, the distance from the start of the earliest ring to the centre of the pith (DTC) was estimated (where possible) based on ring boundary curvature, using the “distance to pith” tool in the CooRecorder program (Larsson, 2013). For cores with no apparent curvature of the innermost ring, we used the field dbh measurement to estimate DTC as follows:

\[
DTC = c \times \text{dbh} - \text{sumRW}
\]

where \(\text{sumRW}\) is the sum of all measured ring widths (units in cm) on the dried cores and \(c\) is a constant that is calculated as the mean observed ratio between \(\text{sumRW}\) (i.e. dry stem radius excluding bark) and dbh (fresh stem diameter including bark) for the subset of cores that included the pith. In this study, the mean value of \(c\) was found to be \(0.447 \pm 0.004\) (SE) based on the 52 cores that reached the pith.

Tree ages at 1.3-m height were determined from the increment core measurements using 2010 as the reference year. For the cores that did not include the pith, the number of early missing rings was estimated as DTC divided by the average width of the first 20 rings in the cores from all trees that did include the pith. Actual tree ages were likely 12-15 years older than those recorded at the 1.3-m height, based on a previous study of juvenile white spruce height growth in Alberta (Liefers, Stadt, & Navratil, 1996). Given the uncertainty in estimating actual tree ages, we hereafter report only on tree and stand ages at the 1.3-m height.

For each tree, annual growth in aboveground biomass (\(G_{BM}\)) was estimated from reconstructions of annual dbh using the Canadian national equations of Lambert, Ung, and Raulier (2005) for white spruce. These estimates included the contributions of stemwood, bark, branches and foliage. Stem dbh for each year (\(dbh_y\)) was reconstructed as \((\text{DTC} + \text{cumRW}_y)/c\) where \(\text{cumRW}_y\) is the cumulative sum of measured ring widths prior to and including the given year.

2.4 Assessment of climate-related changes in moisture regimes

A climate moisture index (CMI) was used in the assessment of spatial and temporal variation in moisture regimes and drought severity. This index has been successfully applied in previous studies of drought impacts on growth, dieback and mortality of aspen (Hogg et al., 2005, 2008; Michaelian et al., 2011) and in studies of growth and regeneration of planted white spruce on the prairies (Hogg & Schwarz, 1997, 2001). The CMI has also been used in projections of future climate change impacts on forest distribution and ecosystem functioning in the Canadian Prairie Provinces (Hogg & Hurdle, 1995; Hogg & Bernier, 2005). Monthly CMI values were calculated as precipitation minus potential evapotranspiration (PET), where PET was estimated using the simplified Penman-Monteith method (Hogg et al., 2013). Annual CMI was then determined as the sum of monthly CMI values from 1 August of the preceding year to 31 July of the current year; this 12-month period has been found to give the strongest growth-climate relationships in tree-ring studies of both aspen and white spruce (Hogg & Schwarz, 2001; Hogg & Wein, 2005; Hogg et al., 2005). The BioSIM program (Régnière & St-Amant, 2008) was used to reconstruct annual CMI at each of the 75 white spruce stands over the period 1960-2015, and was also used to generate spatial interpolations of the CMI across the study region (further details given by Michaelian et al., 2011).

2.5 Analyses of growth responses to climatic drying trends

The tree-ring samples from all 75 stands included the growth increments for the year 2010, thus permitting the analysis of changes in annual \(G_{BM}\) during 1960–2010 as well as the change in mean decadal \(G_{BM}\) from 1991–2000 to 2001–2010. Stand-level values of \(G_{BM}\) (kg year\(^{-1}\)) were calculated annually as the average \(G_{BM}\) for the trees sampled in each given stand. Decadal mean values of \(G_{BM}\) were then determined for each stand along with the percentage change in \(G_{BM}\) between the two decades. From this analysis, stands were classified as either “increasers” or “decreasers,” depending on whether the change in decadal \(G_{BM}\) was positive or negative. This enabled a comparison of CMI histories between groups of stands with widely differing growth trajectories. The role of changing moisture regimes was then assessed by conducting a linear regression analysis of percentage decadal change in mean \(G_{BM}\) as a function of the decadal change in mean CMI for the 75 stands. A similar analysis was also conducted using average decadal values of \(G_{BM}\) and CMI for each of the 23 study areas. Subsequently, multiple regression analyses were conducted on these results where mean tree age in each stand was included as a second independent variable. This enabled the assessment of how
stand age in combination with climatic drying affected the observed percentage change in $G_{BM}$ during the decades 1991–2000 and 2000–2010.

Twelve of the study areas (total of 46 stands) were sampled during August–October 2015 (see Supporting Information Table S1). Ten of these study areas (total of 40 stands) each included 3–5 stands of widely varying ages, with a difference of >35 years between the youngest and oldest stand in each study area. This enabled an additional analysis of growth responses in older versus younger white spruce stands exposed to the same histories of climatic variation, including the recent drying trend that culminated in the exceptionally severe drought of 2015. For this analysis, paired sample t-tests (Zar, 1999) were used to determine differences in the magnitude and percentage change in mean $G_{BM}$ between the paired sets that comprised the youngest and the oldest stand in each of the 10 study areas.

3 | RESULTS

3.1 | Stand characteristics

All 75 of the sampled stands were dominated by white spruce with an estimated proportional composition of 60%–100% (see Supporting Information, Table S1). Other tree species in the stands included trembling aspen ($Populus tremuloides$), balsam poplar ($Populus balsamifera$), black spruce ($Picea mariana$), balsam fir ($Abies balsamea$), lodgepole pine ($Pinus contorta$) and tamarack ($Larix laricina$). The average dbh of the white spruce trees sampled in each stand ranged from 20 to 45 cm (mean of 32 cm). Stand distribution spanned a latitudinal range from 51.2 to 59.1°N (north-south distance of 880 km) and a longitudinal range from 106.0 to 114.6°W (east-west distance of 870 km).

The average age (1.3-m height) of all 400 sampled trees was 106 years, based on the reference year 2010. Tree ages ranged from 34 to 340 years, with a standard deviation of 50 years. The trees sampled within each stand were generally similar in age, with an average standard deviation of ±12.9 years or 11.8% of the mean tree age within each stand. In the stand-level assessments of age effects, we used the average age of the sampled trees in each stand. The resultant set of stand-average ages (see Supporting Information Table S1) was similar to that based on individual trees (mean and SD of 110 ± 46 years, range 51–289 years). To reduce the skewness induced by a few very old stands, the stand-average ages were log-transformed prior to their inclusion in the regression analyses.

3.2 | Decadal tree growth responses to climatic drying

For all 75 white spruce stands, mean tree-level growth in aboveground biomass ($G_{BM}$) showed an increasing trend during 1960–1990, followed by a period of relatively stable yearly growth ($6.4 \pm 0.5$ kg year$^{-1}$) during the decade of 1991–2000 (Figure 3a). Subsequently there was a sharp reduction in mean $G_{BM}$ from 2000 (6.34 kg year$^{-1}$) to 2002 (3.91 kg year$^{-1}$). This 38% growth reduction occurred during the exceptionally severe regional drought of 2001–2002, when mean CMI for the 75 stands was much lower (−12.7) than in any of the previous years during 1960–2000 (Figure 3b). For all stands, there was a partial recovery of mean $G_{BM}$ during the 3 years following the drought of 2001–2002, but at the decadal scale, mean $G_{BM}$ showed an overall decrease of 16% between 1991–2000 and 2001–2010.

At the stand level, there was considerable variation in the percentage change in decadal mean $G_{BM}$ from the 1990s to the 2000s, but only 18 of the 75 stands (shown with triangle symbols in Figure 2) showed positive changes. These stands, termed as “increasers,” were located in Saskatchewan and near the eastern, northwestern and southwestern boundaries of Alberta (Figure 2). The remaining 57 stands (termed as “decreasers”) showed negative changes; these included all 39 stands in the 13 study areas spanning...
much of Alberta, from Grande Prairie (GRA) and Wabasca (WAB) in the north to Nordegg (NOR) and Sundre (SUN) in the southwest (Figure 2).

The analysis of mean tree-level growth trends for the two categories of stands showed that “decreasers” were significantly more productive (mean ± SE for \( G_{BM} = 6.85 \pm 0.42 \text{ kg year}^{-1} \)) than “increasers” (5.04 ± 0.60 kg year\(^{-1} \)) during the decade preceding the 2001–2002 drought (\( p = .027 \), two-tailed \( t \)-test); however, the “decreasers” showed a much weaker growth recovery during the years following this severe drought (Figure 3a). Furthermore, these “decreasers” tended to occupy sites that were relatively moist (higher CMI values) during 1960–2000 but where conditions were abnormally dry throughout the subsequent decade (Figure 3b). This is also illustrated by the maps showing spatial variation and temporal change in mean CMI (Figure 1); western and north-central Alberta (where most of the “decreasers” were located) shows relatively high (moist) CMI during 1961–1990 and 1991–2000 but also experienced the greatest drying (decrease in decadal mean CMI) after 2000.

The influence of climatic drying on white spruce growth was further examined through linear regression analysis (Figure 4). At the stand level, the results showed a significant positive relationship (\( r^2 = .392, N = 75 \) stands, \( p < .0001 \)) between mean percentage change in decadal \( G_{BM} \) and mean change in decadal CMI from the 1990s to the 2000s (Figure 4a). This relationship was even stronger when the regression analysis was repeated using average values at the study area level (\( r^2 = .645, N = 23 \) study areas, \( p < .0001 \)).

### 3.3 Potential effects of insect defoliation

Although we avoided stands showing significant visible signs of disturbance, subsequent examination of insect survey records revealed that 9 of the 75 stands (SI Table S1) were located within mapped polygons having one or more years of moderate to severe defoliation by spruce budworm over the period 1937–2015. These records were derived from aerial surveys conducted annually by Canadian federal government agencies (1937–1996) and provincial forest management agencies of Saskatchewan and Alberta (1997–2015). The potentially affected stands included a total of four stands in the DUC and NIS study areas (moderate to severe defoliation during 1995–1998), four stands in the WAB study area (moderate defoliation during 2006–2010) and one stand in the MAN study area (severe defoliation during 1994–1999). Given the possibility that spruce budworm defoliation might confound the observed impacts of climatic drying, the linear regressions were repeated after excluding these potentially budworm-affected stands and study areas (denoted by grey symbols in Figure 4). The results showed that removal of these stands from the linear regressions had little effect on the observed relationships, other than leading to slight decreases in \( r^2 \) values (from .392 to .354 at the stand level, and from .645 to .623 at the study area level).

![FIGURE 4 Percentage change in average increment of aboveground biomass (kg year\(^{-1} \)), plotted as a function of the average change in the climate moisture index between the decades starting in 1991 and 2001: (a) shows average values for each of the 75 stands and (b) shows average values for each of the 23 study areas. Open and closed symbols denote stands or study areas with mean tree age (at 1.3-m height) less than or greater than 95 years, respectively, in the year 2010. Grey symbols indicate stands or study areas where spruce budworm defoliation was recorded from insect surveys during 1991–2010. Also shown are the best-fitting linear regressions for all stands (\( Y = 4.20 X + 9.16; r^2 = .392 \)) and for all study areas (\( Y = 4.43 X + 11.31; r^2 = .645 \)).](image)

### 3.4 Influence of stand age on growth responses to climatic drying

From the analysis of mean tree biomass increment for all 75 stands, \( G_{BM} \) showed significant negative exponential relationships with mean tree age during both decades (Figure 5), suggesting an overall age-related decline in white spruce growth at the stand level. However, there was no evidence of age-related differences in sensitivity to drought and climatic drying over the period 1991–2010. Multiple regression of factors affecting growth responses in these 75 stands (Figure 4a) showed that log-transformed mean tree age had no significant influence (\( t = 1.78, p = .080 \)) on the observed percentage changes in decadal \( G_{BM} \) from the 1990s to the 2000s.
In the second analysis, the influence of stand age on the observed, drought-related growth decline in white spruce was examined across the subset of 10 study areas (total of 40 stands) that were sampled across northern and central Alberta in 2015 (Figure 6a and Table S1). Average tree age for the oldest stands in each study area (in year 2015) was 162 years (range 105–289 years), whereas that of the youngest stands was 79 years (range 51–134 years). On average, the oldest stands (N = 10) and youngest stands (N = 10) had nearly identical climate histories, with mean CMI = +6 for both sets of stands during 1991–2015. For these stands, there was a notable drying trend over this 15-year period (Figure 6b), and drought conditions were even more severe in 2015 (mean CMI = /C0 10) than in 2002 (mean CMI = /C0 5) or 2010 (mean CMI = /C0 3). As expected, mean GBM was consistently greater in the youngest stands (after the 1970s), but the pattern of interannual variation was otherwise similar (Figure 6a). Both sets of stands showed sharp drought-related declines in growth during 1998–2002 and again during 2012–2015. Overall, mean GBM declined by 38% between the moist, pre-drought year of 1997 and the exceptionally dry year of 2015. However, the mean absolute reduction in GBM from 1997 to 2015 was significantly greater (p = .011) in the youngest stands (4.6 kg year−1) than in the oldest stands (1.6 kg year−1) because of the large age-related difference in the magnitude of GBM.

4 | DISCUSSION

4.1 | Growth responses to recent climatic drying

The results showed a notable reduction in the growth of white spruce across the study region that coincided with the onset of anomalously dry conditions at the start of the 21st century. For all 75 stands, mean decadal GBM declined by 16% between the 1990s and the 2000s, and the decline exceeded 40% in 12 of the sampled stands in central and northern Alberta (Figure 2). Based on our analysis, climatic drying was an important factor driving spatial variation in the observed percentage growth declines at both the stand and study area levels (Figure 4). These results are consistent with previous tree-ring studies showing that yearly variation in radial growth of white spruce is primarily governed by moisture at many locations across western Canada (e.g. Chhin et al., 2004; Hogg & Wein, 2005). This study, however, is one of the first to report on the impact of prolonged drought conditions on the growth of a boreal conifer using a measure (aboveground biomass increment) that is directly relevant to forest ecosystem functioning, carbon cycling and commercial forestry applications. From the 40 boreal stands that were sampled in 2015, we have documented a 15-year period of drought-related decline in tree-level growth of white spruce growth across a
large area of northern and central Alberta (Figure 6). This poses a concern for the productivity and health of white spruce in this region, especially given that the period 2012–2015 was the driest on record in more than 50 years (Figure 6).

4.2 Role of stand age as a potential driver of the recent growth decline

One of the challenges in identifying long-term (multidecadal) impacts of climate change on forests is that stand biomass dynamics tend to vary as a function of time following stand-replacing disturbances such as fire or clearcutting. For example, previous analyses of plot-based measurements show a significant age-related decline in annual biomass increment for several major forest types in the western Canadian boreal zone (Chen & Luo, 2015; Chen et al., 2016). Such declines may be expected to occur in the absence of climate change, thus requiring the application of analytical techniques to distinguish the effects of external factors such as drought versus internal factors associated with stand development (Thorpe & Daniels, 2012; Zhang et al., 2015; Chen & Luo, 2015).

In this study, we found that at the tree level, GBM declined significantly as a function of stand age (Figure 5). There was also an indication that in the younger stands, predrought values of GBM in the 1990s were greater than the maximum values achieved historically in the older stands. Nevertheless, the average inter-decadal decline in GBM for all 75 stands was notably greater (16%) than that expected from 10 years of stand-ageing (3%–4%) based on the best-fitting growth-age relationships (Figure 5). For the 40 boreal stands that were sampled in 2015, the 38% decrease in average GBM during 1997–2015 was similarly much greater than the expected growth decline from stand-ageing over this 18-year period (estimated at 5%–7% from the relationships shown in Figure 5). Thus, we conclude that climatic drying (rather than stand-ageing) was the main cause of the decline in white spruce growth that was observed in this study.

Previous tree-ring studies of boreal conifers have shown that differences in stand age can affect tree growth responses to climatic factors such as temperature and soil moisture (e.g., Szeicz & MacDonald, 1994; Girardin et al., 2012). In a recent global analysis, Bennett, McDowell, Allen, and Anderson-Teixeira (2015) found that droughts consistently had more detrimental impacts on the growth and mortality of larger trees, which might lead to the expectation that the growth of older white spruce stands should be the most strongly impacted by recent severe droughts and climatic drying in Alberta. However, our results show no significant effect of stand age on the magnitude of growth decline when expressed as percentage decline in GBM from the 1990s to the post-2000 period (Figures 4 and 6). When expressed in terms of the absolute change in GBM (with units in kilograms of biomass increment per year), there was actually a greater growth decline in the younger stands because of their higher productivity relative to the older stands (Figure 6).

4.3 Sources of uncertainty in the estimation of forest growth trends

Several approaches have been used to address questions as to how boreal ecosystems and forest dynamics are being affected by recent climatic warming and associated changes in moisture regimes. These include the analysis of radial growth patterns within individual trees (e.g., Girardin, Hogg et al., 2016), long-term monitoring of tree growth and mortality within ground plot networks (e.g., Chen et al., 2016), and satellite observations of change in vegetation “greenness” indicators such as the Normalized Difference Vegetation Index (NDVI, e.g., Sulla-Menashe, Friedl, & Woodcock, 2016). Regardless of which approach is used, there are inherent challenges and sources of uncertainty in measuring vegetation changes across large heterogeneous landscapes, and in attributing the causes of these changes. Such challenges are evident from the divergent interpretations that have been reported as to the extent of recent “greening” and “browning” of northern forests from satellite observations (e.g., Alcaraz-Segura, Chuvieco, Epstein, Kasischke, & Trishchenko, 2009; Sulla-Menashe et al., 2016) and in determining the role of climatic change and variation as a driver of observed changes in forest stand dynamics from plot-based measurements (e.g., Ma et al., 2012; Zhang et al., 2015).

Uncertainties also arise in the application of tree-ring analysis to the study of climate-induced changes in forest growth over periods of several decades or longer, where differing interpretations may arise from the choice of standardization method or model that is used (e.g., Sullivan, Pattison, Brownlee, Cahoon, & Hollingsworth, 2016; Girardin, Bouriaud et al., 2016; Girardin, Hogg et al., 2016). Although this study was also based on tree ring measurements, we circumvented some of the limitations of traditional approaches (Hember et al., 2015) by reporting directly on changes in above-ground biomass increment (GBM, with units of kg tree⁻¹ year⁻¹), where allometric equations (Lambert et al., 2005) were used to obtain annual estimates of GBM from the original ring width chronologies. Another important source of uncertainty is the scaling of tree-level measurements to the stand level. As in most tree-ring studies, our reporting of growth trends was based on the sampling of living trees and thus cannot account for the past growth contributions made by trees that died prior to the year of sampling (i.e., mortality bias). Also, the sampling of representative trees above a certain size threshold does not capture any growth contributions made in recent years by seedlings and saplings in the forest understory (i.e., recruitment bias). These sources of potential bias are counteracting, where neglecting past mortality would lead to an underestimation of the recent decline in stand-level growth while neglecting recruitment would lead to an overestimation. In this study, field observations suggested that there has been only minimal recent recruitment in the sampled stands, and only four of the 75 stands showed signs of recent, elevated mortality (Table S1).

Overall, our tree-based estimates of GBM should be robust indicators of change in stand-level growth, given that we restricted our analysis to the most recent 20–25 year period. If there is a bias, it
seems likely that our results are giving a slightly conservative estimate of growth decline at the stand level, given that on a per stem basis, white spruce mortality (ca. 0.5%–1.5% year\(^{-1}\)) has exceeded recruitment (<0.5% year\(^{-1}\)) over the past few decades based on a recent analysis of plot measurements across western Canada (Zhang et al., 2015). Nevertheless, there are many remaining challenges in quantifying the impacts of recent droughts and climatic drying on the productivity and decline of white spruce and other boreal forest types at the stand to regional scale.

At the stand level, applying a combination of tree-ring analysis and repeated, plot-based measurements (e.g. Hogg et al., 2008) could provide a more reliable approach for reconstructing tree biomass (and carbon) gains and losses at an annual resolution over periods of several decades. Alternatively, reconstructions spanning several decades can be achieved through the comprehensive sampling and analysis of tree rings in all living and dead trees (both standing and fallen) within fixed area plots (Metsaranta & Lieffers, 2010). Such approaches are likely to be useful in distinguishing the effects of factors other than climate (e.g. inter-tree competition) on forest growth trends over multidecadal time periods (e.g. Metsaranta & Lieffers, 2010). However, these methods are labour intensive and/or can only be conducted in forest types represented by plot networks with long-term measurement histories. Furthermore, the assessment of landscape- to regional-scale forest responses to drought and climatic drying requires consideration of interactions with disturbance regimes (Schneider, Hamann, Farr, Wang, & Boutin, 2009), notably fire (Johnstone, McIntire, Pedersen, King, & Pisaric, 2010) and damaging insects such as spruce budworm (Régnière & St-Amant, 2012) and spruce beetle (Hart, Veblen, Eisenhart, Jarvis, & Kulakowski, 2014). In this respect, drought-related failure of white spruce to regenerate naturally from seed (Hogg & Schwarz, 1997; Johnstone et al., 2010) could become an even greater concern for this species under a future scenario of continued climatic drying, especially if combined with increased frequency and extent of stand-replacing disturbances (Schneider et al., 2009; Price et al., 2013).

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REFERENCES


SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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