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# Disturbance legacies and climate jointly drive tree growth and mortality in an intensively studied boreal forest

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## Abstract

Most North American forests are at some stage of post-disturbance regrowth, subject to a changing climate, and exhibit growth and mortality patterns that may not be closely coupled to annual environmental conditions. Distinguishing the possibly interacting effects of these processes is necessary to put short-term studies in a longer term context, and particularly important for the carbon-dense, fire-prone boreal forest. The goals of this study were to combine dendrochronological sampling, inventory records, and machine-learning algorithms to understand how tree growth and death have changed at one highly studied site (Northern Old Black Spruce, NOBS) in the central Canadian boreal forest. Over the 1999–2012 inventory period, mean tree diameter increased even as stand density and basal area declined significantly. Tree mortality averaged  $1.4 \pm 0.6\% \text{ yr}^{-1}$ , with most mortality occurring in medium-sized trees; new recruitment was minimal. There have been at least two, and probably three, significant influxes of new trees since stand initiation, but none in recent decades. A combined tree ring chronology constructed from sampling in 2001, 2004, and 2012 showed several periods of extreme growth depression, with increased mortality lagging depressed growth by ~5 years. Higher minimum and maximum air temperatures exerted a negative influence on tree growth, while precipitation and climate moisture index had a positive effect; both current- and previous-year data exerted significant effects. Models based on these variables explained 23–44% of the ring-width variability. We suggest that past climate extremes led to significant mortality still visible in the current forest structure, with decadal dynamics superimposed on slower patterns of fire and succession. These results have significant implications for our understanding of previous work at NOBS, the carbon sequestration capability of old-growth stands in a disturbance-prone landscape, and the sustainable management of regional forests in a changing climate.

**Keywords:** boreal forest, carbon cycling, climate change, dendrology, disturbance, forest mortality, machine learning

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## Introduction

The interaction between ecosystem disturbance, vegetative succession, and carbon balance has been the subject of research for many decades (Odum, 1969; Pastor & Post, 1988; Heimann & Reichstein, 2008). More recently, networks of eddy covariance sites – in particular FLUXNET (Baldochi *et al.*, 2001) – have provided a wealth of information about the ‘fast’ response of forests to biotic and abiotic drivers, with hourly to interannual processes in forests a particular focus. Analyses of global data such as atmospheric CO<sub>2</sub> have provided further constraints on biome-level responses to climate (Randerson *et al.*, 1999). These data have in turn been invaluable in drawing larger scale inferences about

ecosystem function (e.g., Mahecha *et al.*, 2010), and provide quantitative measures for testing global land models (Stöckli *et al.*, 2008).

One key finding of model and flux data comparison studies is the poor representation of ecosystem processes that occur or integrate over interannual to decadal time periods (Keenan *et al.*, 2013), a perhaps predictable consequence of most models being fundamentally built upon short-term processes and observations, while used for longer term predictions (Schwalm *et al.*, 2010). Indeed, as longer datasets have been slowly acquired, it appears that older, more biologically and structurally complex forests contain surprises – in particular, unexpected multi-decadal oscillations that may represent important phenomena not currently represented in regional to global models. For example, net ecosystem production (NEP) in the ~100-year-old Harvard Forest has more than doubled in the last

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18 years (Keenan *et al.*, 2012); a similar trend was observed in the 150+ year Canadian boreal forest studied here (Dunn *et al.*, 2006). More broadly, recent syntheses of North American forests found no evidence for a decline in NEP with age (Amiro *et al.*, 2010). Such results suggest that old-growth forests could be global carbon sinks (Zhou *et al.*, 2006; Luyssaert *et al.*, 2008). If true, the implications are significant, as forests sequester on the order of 10% of current fossil fuel emissions in the northern hemisphere alone (Goodale *et al.*, 2002), and play a central role in the global carbon cycle (Pan *et al.*, 2011a).

A critical question, however, is to what extent these decadal dynamics represent normal slow oscillations that are the product of current conditions and past disturbances, and/or new dynamics potentially driven by climate changes (McMahon *et al.*, 2010). To distinguish these factors, it is critical to understand how the legacies of past disturbances, which can have significant and large-scale influences on the carbon cycle (Pan *et al.*, 2011b; Williams *et al.*, 2012), interact with shorter term drivers (Gough *et al.*, 2007). These drivers, including global and regional climate changes, will have both positive (CO<sub>2</sub> fertilization, longer growing seasons) and negative (water stress, increased pests, and pathogens) effects, ultimately affecting tree growth and death (mortality).

Mortality is rising in many forests worldwide (van Mantgem *et al.*, 2009; Anderegg *et al.*, 2012; Williams *et al.*, 2013), increases frequently ascribed to a changing climate (Allen *et al.*, 2010). In this context, the North American boreal forest, which is subject to frequent disturbance and plays a critical role in the global carbon budget (Kurz *et al.*, 2008), is of particular concern. Remote sensing studies have documented landscape-level changes in forest productivity at high latitudes (Bunn *et al.*, 2005; Goetz *et al.*, 2007; Beck & Goetz, 2011). Field studies have been more equivocal. Peng *et al.* (2011) used long-term inventory data to report increases in tree mortality along the southern edge of the Canadian boreal forest, a region generally seen as vulnerable to drought (Hogg, 1994). Conversely, tree growth and death in the central boreal forest have been linked to successional and structural changes from disturbance, with little or no climate effect (Girardin *et al.*, 2012; Silva & Anand, 2012; Thorpe & Daniels, 2012). These latter findings suggest that mortality changes may be driven more by stand dynamics than climate per se, since as forests age they generally decline in productivity, carbon use efficiency, and carbon sequestration (e.g., Goulden *et al.*, 2011).

The goals of this study were to examine how tree growth and mortality have changed at one highly studied boreal forest stand, and understand the interaction

between long-term disturbance legacies and short-term abiotic drivers. Specifically, we used tree cores, inventory data, and climate records to understand how growth and mortality rates have changed over time; how the two are related spatially and temporally; and what climate or other factors drive structural and functional changes in this disturbance-prone, old-growth boreal forest.

## Materials and methods

### Study site

This study was conducted at the former Northern Old Black Spruce (NOBS) site (55.88°N, 98.48°W) west of Thompson, Manitoba, Canada. The NOBS site was established in 1993 as part of NASA's Boreal Ecosystem-Atmosphere Study and was the central northern site for this project that examined atmosphere-biosphere interactions in the boreal forest (Sellers *et al.*, 1995). The site is an old-growth (est. 163 years in 2013) single-species black spruce (*Picea mariana* (Mill.) BSP) forest with a leaf area index of ~4.5 (Bond-Lamberty *et al.*, 2002b). The forest soil is imperfectly drained, with peat-rich clay soils derived from glacial Lake Agassiz (Harden *et al.*, 1997), with a continuous moss (mostly *Pleurozium schreberi* and *Sphagnum* spp.) ground cover and discontinuous permafrost in low areas. The study area is situated in the low-relief Boreal Shield Ecozone, near the northern limit of the continuous boreal forest (Brandt, 2009). The climate is continental, and the Thompson airport weather station, ~40 km from the research site, has 1971–2000 mean air temperature and annual total precipitation means of –3.2 °C and 517 mm, respectively. A number of complete descriptions of the site, and the larger complex in which it sits, have been published (Halliwell & Apps, 1997; Harden *et al.*, 1997; Bond-Lamberty *et al.*, 2004; Dunn *et al.*, 2006; Goulden *et al.*, 2006).

### Forest inventories

We used inventory data starting in 1999 (Bond-Lamberty *et al.*, 2002b) and subsequently updated in 2002, 2007, and 2012. These data were based on tree inventories (recording species, live/dead, standing/down) taken using standard mensuration techniques (Gower *et al.*, 1997) in four randomly located 50 m<sup>2</sup> plots. All trees were permanently tagged at 1.37 m height, and diameter at breast height (DBH) measured with a precision of 0.1 mm immediately above the tag in the initial and all subsequent inventories. The 2002 inventory recorded only live/dead and standing/down information, not tree diameters. Per-year mortality rate was calculated using an assumption of constant annual mortality rate between inventories, based on the trees that died during each time interval, on both a basal area and stem basis. Biomass and leaf area were calculated using the allometric equations and specific leaf area data of Bond-Lamberty *et al.* (2002a,b).

To estimate the effect of mortality on forest carbon accumulation, we constructed an alternate 'zero mortality' scenario.

This was done by applying the 1999–2012 tree growth rates, with trees binned by 3-cm DBH classes, to the 1999 live tree inventory, producing an estimated 2012 distribution if no mortality had taken place. Standard distributional statistics, as well as leaf area and biomass based on previous site-specific allometry (Bond-Lamberty *et al.*, 2002a,b), were then calculated for this scenario. Here and below, all calculations and statistics (unless otherwise noted, based on  $N = 4$  plots and critical level  $\alpha = 0.05$ ) were performed using R version 3.0.1 (R Development Core Team, 2013).

### Tree cores

We used tree cores taken at the NOBS site in 2001, 2004, and 2012. In all years, two cores were taken from each sample tree at breast height, generally on the north and west sides; air dried; mounted into boards; sanded with progressively finer sandpaper; inspected for injuries, reaction wood, and other unusual features; and scanned using a flatbed scanner. Sample trees varied in diameter and age, but all were healthy and mature.

The 2001 ('UW' data set) tree core protocol was described by Bond-Lamberty *et al.* (2004). Cores were embedded into protective boards, sanded, and scanned at 800 dpi (using an Epson Expression 1600, Epson America Inc., Long Beach, CA, USA). Wood annual increment was measured using WinDendro 2000 (Regent Instruments Inc., Canada). In all 77 trees were cored in October 2001, generally 10–100 m to the east and south of the eddy covariance tower.

The 2004 ('UCI') tree core protocol was described by Rocha *et al.* (2006). A total of 88 trees from 300 m west of the tower were cored in September 2004. Cores were glued onto grooved masonite boards, and scanned at 1200 dpi with a Microtek ScanMaker i900 (Microtek USA, Carson, CA, USA). Ring widths were determined using the Lignovision system (Rinntech, Heidelberg, Germany).

In May 2012 ('PNNL'), 32 cores were taken from 16 trees, distributed randomly 5–30 m around the former tower location. These cores were glued into softwood boards, scanned at 1200 dpi using an Epson WorkForce 840 (Epson America Inc., Long Beach, CA, USA), and ring widths measured using CooRecorder 7.6 (<http://www.cybis.se/forfun/dendro/>).

Cores were visually cross-dated to identify common marker years and ring width patterns (in 2001 and 2004) and using the pointer-year method (Yamaguchi, 1991) (in 2012). Both the raw measurements and cross-dating were checked statistically using the *dplR* package (Bunn, 2010) in R. Individual data-set and combined site chronologies (Fritts, 2001), isolating the climate-driven growth indices, were constructed by using spline detrending and prewhitening (using the default autoregressive model) in *dplR*, and computed standard dendrochronological statistics (Bunn, 2010).

### Climate data

We used NCEP/NCAR reanalysis climate data (Kalnay *et al.*, 1996; Kanamitsu *et al.*, 2002), accessed and aggregated using the *RNCEP* package (Kemp *et al.*, 2011) in R, to examine the

influence of local climate on stand dynamics. These data included 2 m air temperature (monthly mean, minimum, maximum), precipitation (P), and relative humidity; following earlier studies (Dunn *et al.*, 2006; Rocha *et al.*, 2006), we computed a Climate Moisture Index as P-PET, based on the simplified potential evapotranspiration (PET) calculation described by Hogg (1997). Each ring width observation was paired with data from that ring's year of growth, as well as data from up to 4 years previously, that is, a given observation from year  $t$  was associated with temperature and precipitation anomalies from years  $t, t - 1, \dots, t - 4$ . This was done because multi-year carbon pools, in particular late-season photosynthetic assimilates stored for next year's earlywood growth (Kagawa *et al.*, 2006), may decouple observed carbon fluxes (e.g., tree growth) from ambient abiotic drivers at this site (Dunn *et al.*, 2006; Rocha *et al.*, 2006).

### Random forest analysis

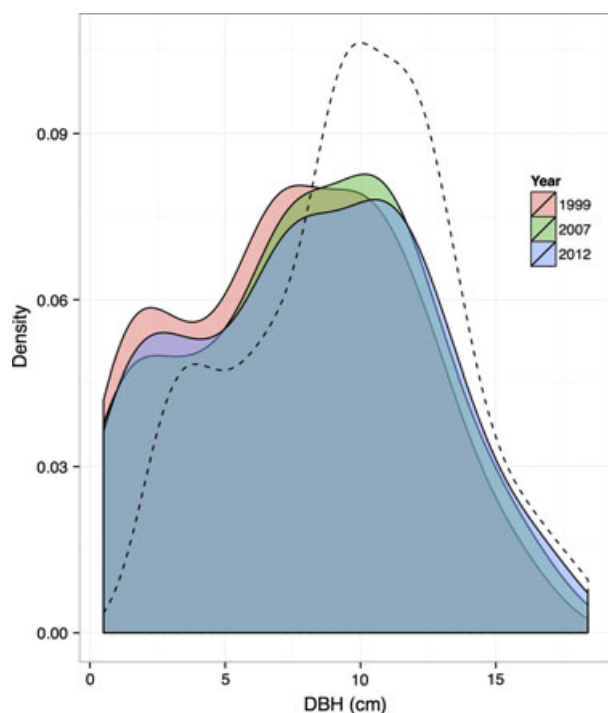
To examine the correlations between ring width and local climate, we used the Random Forest (RF) algorithm (Breiman, 2001), a nonparametric machine learning technique for classification and regression. Biological systems often exhibit characteristics (nonlinearity, autocorrelation) that this algorithm is designed to handle (Evans & Cushman, 2009), even though it is a data-driven methodology that makes no *a priori* assumptions about biological underpinnings. The algorithm calculated variable importance by aggregating regression trees constructed using different random samples of the data, and choosing splits of the trees from subsets of the available predictors, which are randomly chosen at each node (Breiman, 2001). The use of random data and predictor subsets means that data subsets need not be withheld for validation. RF generally produces highly accurate and unbiased estimates and classification, and it is robust against overprediction for 'm > n' (more potential predictor variables than observations) data sets, as was the case here. We used the algorithm's default settings (with one exception: number of trees = 1000), using the *randomForest* package version 4.6-7 in R.

## Results

### Tree growth and mortality from inventory data

Mean tree DBH at this site increased from 7.6 to 8.2 cm (Fig. 1 and Table 1) from 1999 to 2012. Tree recruitment (i.e., saplings attaining 1.37 m and thus entering our inventories) was minimal: three <1.0 cm individuals in the 1999–2007 period, and none between 2007 and 2012.

Tree mortality on a basal area basis was 2.0%, 0.4%, and 1.6%  $\text{yr}^{-1}$  for 1999–2002, 2002–2007, and 2007–2012, respectively, and on a stem basis 2.6%, 0.6%, and 1.4%  $\text{yr}^{-1}$  for the same periods. Over the full 1999–2012 observational period, mortality averaged  $1.3 \pm 0.3\%$   $\text{yr}^{-1}$  and  $1.4 \pm 0.6\%$   $\text{yr}^{-1}$  on a basal area and stem basis, respectively. The 26 trees that died had DBHs from 1.3 to 15.4 cm, but most mortality occurred in



**Fig. 1** Density plot (used instead of a histogram to show clearly the overlapping distributions) of diameter at breast height (DBH) of trees inventoried at the NOBS site in 1999, 2007, and 2012. Dashed line shows distribution of sample trees from which cores (Fig. 4) were taken.

7–9 cm trees (Fig. 2). Snag (i.e., dead tree) density increased from  $650 \text{ ha}^{-1}$  ( $2.2 \text{ m}^2 \text{ ha}^{-1}$ ) to  $1150 \text{ ha}^{-1}$  ( $5.4 \text{ m}^2 \text{ ha}^{-1}$ ) during this period.

The net result of these processes was that from 1999 to 2012 mean live tree basal area dropped 9%, from  $41.3$  to  $37.5 \text{ m}^2 \text{ ha}^{-1}$  (Table 1), a significant decline (one-sided paired  $t$ -test = 2.834,  $P = 0.033$ ). Because mortality primarily occurred in mid-sized trees but leaf area index (LAI) is exponentially related to tree diameter, we calculate that LAI has remained relatively stable (Table 1). Total tree biomass has declined from  $64.8$  to

$61.2 \text{ t C ha}^{-1}$ , although this was not statistically significant ( $t = 1.269$ ,  $P = 0.147$ ). We estimate that stand biomass would have been  $68.8 \text{ t C ha}^{-1}$  in 2012 under an assumption of no mortality. This is 12% higher than the actual value or, expressed in terms of net primary production (NPP) over the time period, an increase in annual NPP of  $58 \text{ g C m}^{-2} \text{ yr}^{-1}$  over the 13 years.

#### Combined chronologies from tree cores

The earliest recorded tree ring, taken from a 12.1 cm tree in the 2012 data set, was 1849, and five other trees had pre-1855 rings. The earliest tree rings across the entire data set reflected an age structure consistent with low recruitment throughout the last century (Fig. 3), but also exhibited two spikes of recruitment, appearing in the record at years  $\sim 1905$  and  $\sim 1950$  (discussed further below). The three chronologies constructed from these data had average 1-year autocorrelations of 0.64, 0.60, and 0.79 (for UW in 2001, UCI in 2004, and PNNL in 2012, respectively), with Gini coefficients (Biondi & Qeadan, 2008) of 0.22, 0.19, and 0.26 and internal correlation (leave-one-out rho) values of 0.19, 0.26, and 0.22. The chronologies were well correlated to each other ( $r > 0.7$ ) except for the UW (2001) and PNNL (2012) chronologies ( $r = 0.45$ ).

A single combined chronology was constructed (leave-one-out rho = 0.24), based on all the tree cores pooled together (ar1 = 0.64, Gini = 0.21); this combined data set covered the entire diameter range of the stand, although over-represented medium-diameter trees (dashed line in Fig. 1). It exhibited a number of interesting features (Fig. 4a), including a two-decade-long growth depression from  $\sim 1920$  to 1940, and less extreme but still significant periods of poor growth from 1885 to 1900 and 1980 to 2000. The period of overlap between the tree ring and inventory data exhibited a  $\sim 5$ -yr lag effect (Fig. 4b), with low growth in the mid-1990s followed by high mortality around 2000; high growth

**Table 1** Tree density, mean basal area (BA), diameter at breast height (DBH), and leaf area index (LAI) collected from forest inventories conducted in 1994, 1999, 2002, 2007, and 2012 at the Northern Old Black Spruce site. Only mortality was measured in 2002

Year	Density ( $\text{ha}^{-1}$ )	BA ( $\text{m}^2 \text{ ha}^{-1}$ )	DBH (cm)	LAI ( $\text{m}^2 \text{ m}^{-2}$ )
1994	5450	35.6	8.5 (2.5–18.6)	4.2 $\pm$ 0.3
1999	7050 $\pm$ 2568	41.3 $\pm$ 8.4	7.6 (0.5–16.7)	3.8 $\pm$ 0.6
2002	6500 $\pm$ 2392			
2007	6100 $\pm$ 2242	39.8 $\pm$ 9.5	8.0 (0.6–17.4)	3.8 $\pm$ 0.7
2012	5500 $\pm$ 1409	37.5 $\pm$ 6.7	8.2 (0.7–17.2)	3.6 $\pm$ 0.3

LAI (hemisphere) was calculated using site-specific allometric equations (Bond-Lamberty *et al.*, 2002a,b). Italicized 1994 data (Gower *et al.*, 1997) were measured on different plots and are not directly comparable to other years. Values are means  $\pm$  plot-to-plot SD ( $N = 4$ ); DBH is given as mean and range.



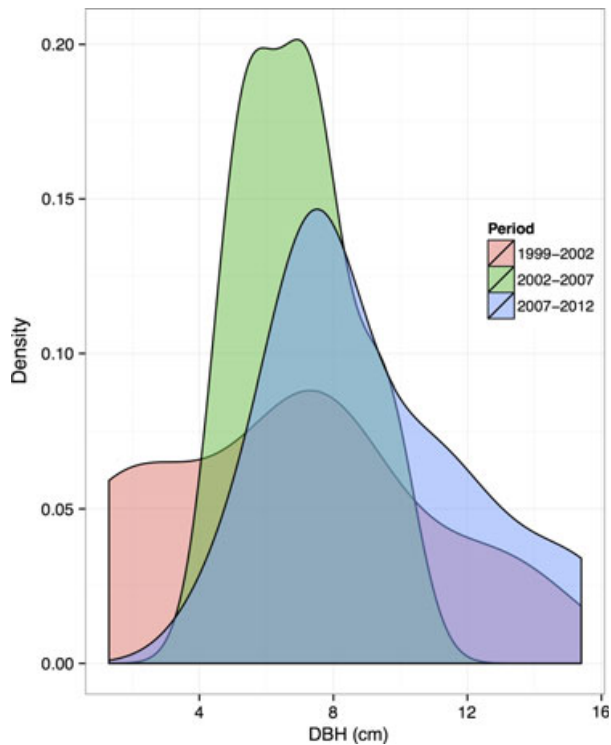


Fig. 2 Density plot of diameter at breast height (DBH) of trees that died during each inventory period.

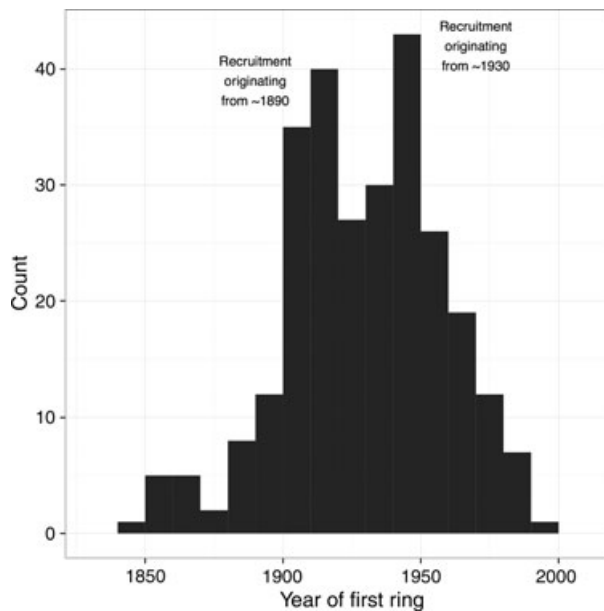


Fig. 3 Distribution of year of first rings in the combined (2001, 2004, 2012) tree core data set. Note corresponding periods (1885–1895 and 1925–1935) of exceptionally poor growth in Fig. 4a.

around 2000 followed by low mortality around 2005; and finally medium growth and mortality in 2005 and 2010, respectively.

The combined chronology was significantly and negatively correlated (adjusted  $R^2 = 0.61$ ,  $P = 0.004$ ) with net ecosystem exchange measured by an eddy covariance tower (Dunn *et al.*, 2006) between 1994 and 2004. Larger ring widths were associated with greater carbon uptake (data not shown).

#### Random Forest analysis of tree cores

Allowing the RF algorithm to ‘look back’ 1 year generally improved the out-of-bag explained variance rate, but using still older data (i.e., 2 years’ previous, three) did not improve the algorithm’s performance. After extensive testing we also removed winter (November to April) months’ weather data from the analysis, as these months resulted explained no extra variability. For all chronologies, higher minimum and maximum air temperature exerted a negative influence on tree growth, while precipitation and climate moisture index had a positive effect (Fig. 5). Typically 1–3 variables were ranked as particularly important by the RF, both monthly (particularly June and July) and annual (for the 2012 chronology only). Subsequent linear models incorporating these variables explained 23–44% of chronology variability (Table 2). There was no unexplained temporal trend in the model residuals (that might indicate, e.g., a  $\text{CO}_2$  fertilization effect).

#### Discussion

We observed variable and significant tree growth and mortality in the NOBS forest, in both the inventory and tree core records. The contemporary NOBS stand structure is dominated by two – probably three – recruitment events that occurred around 1850, 1910, and 1950. The initial 1850 recruitment event occurred after a stand-replacing fire that occurred in ~1830. Tree ring chronologies from the stand revealed important information about the 1910 and 1950 recruitment events, which lagged (by ~20 years) some of the poorest periods of growth, that is, smallest ring widths, in the combined chronology. The tight coupling between ring width, stand age, and carbon cycling (Rocha *et al.*, 2006) implies that climate and successional processes have interacted with important implications for our interpretation of the historic, current, and future carbon cycling of this system.

#### The importance of climate-driven growth and mortality

Forest growth typically responds strongly and positively to changes in temperature and precipitation (Adams *et al.*, 2004), with the former particularly important at high latitudes (Reichstein *et al.*, 2007). But

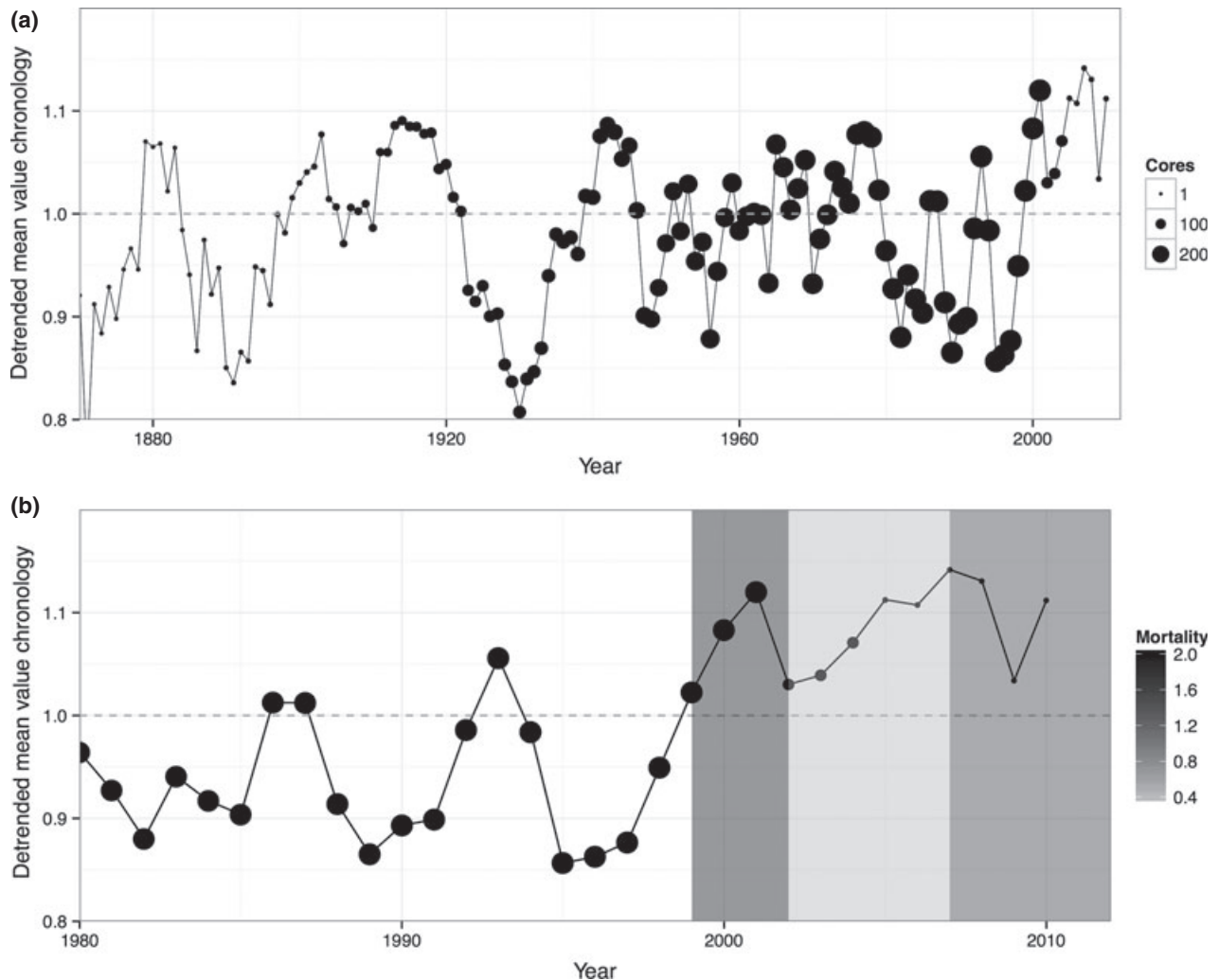
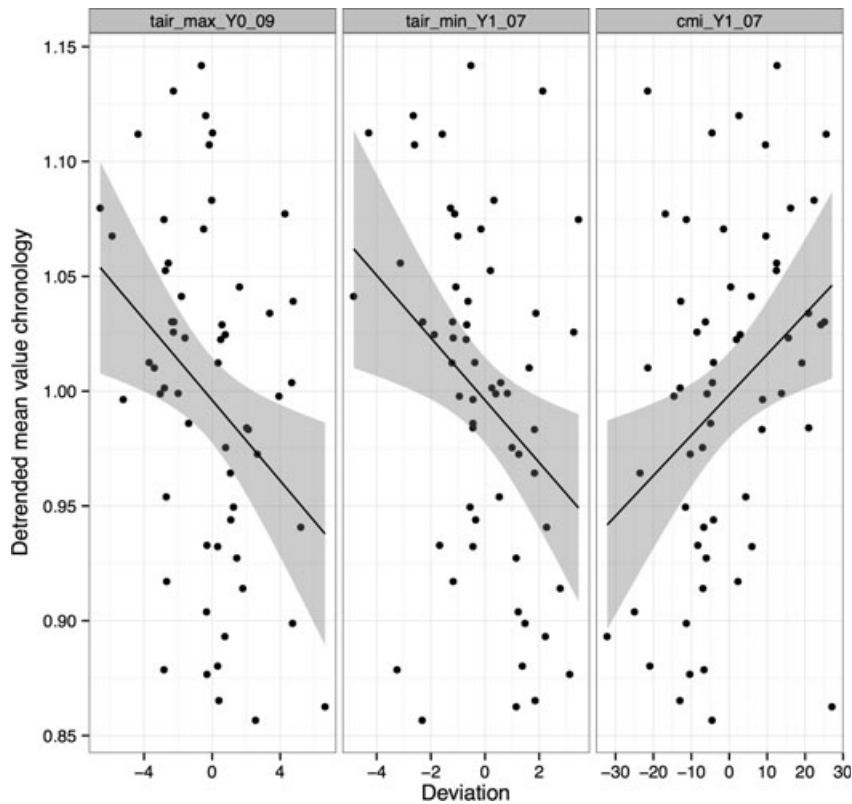


Fig. 4 Combined tree ring chronology, with size of points showing number of cores contributing to each year's datum. (a) Full chronology. (b) Recent decades, with shading indicating annual mortality rate from the inventory data ( $\% \text{ yr}^{-1}$ , basal area basis).

in high-latitude forests, the growth response is complicated by interactions between a lengthening growing season and increasing water stress or even drought. Girardin *et al.* (2008) compared empirical, mechanistic, and hybrid modeling approaches to explain tree ring-width increment (RWI) in central Canada (500 km from the site studied here), and allowed the empirical algorithms to use previous-year data. Their empirical algorithms explained ~50% of the *P. mariana* RWI, slightly more than that explained in our analysis (Table 2). This difference may be due to the higher quality meteorology data available for their further-south site; there are few meteorological stations, and thus higher errors, at high latitudes (Chylek *et al.*, 2009). In addition, tree deformation, biotic and abiotic disturbance, and individual species' phenotypic plasticity can also result in poor correlation between local climate and the tree ring record (Arnan *et al.*, 2012).

The 1920–1940 period of extremely poor growth in the tree ring record is consistent with a known 30-year period of Arctic warming in which the region warmed significantly faster than the rest of the world (Chylek *et al.*, 2009). This period was also marked by significant dry periods in central and eastern Canada (Girardin *et al.*, 2006). We infer that the extremely poor growth in this period resulted in high tree mortality with subsequent canopy gaps and recruitment pulses. Black spruce seedlings take ~18 years after fire to reach breast height in eastern Canada (Vasiliauskas & Chen, 2002). If we assume that it takes 20 years to do so in north-central Manitoba, where the climate is drier and cooler, the timing is right: stressful conditions in 1915–1935 (Chylek *et al.*, 2009), poor growth (Fig. 4a) and presumed high mortality 1920–1940 (i.e., delayed by 5 years consistent with Fig. 4b), and then an influx of new trees in the core record around 1950 (Fig. 3). A similar logic



**Fig. 5** Correlation between tree ring width increment and the three most important variables identified by the Random Forest analysis for the combined (2012) chronology. These variables (expressed as deviation from the overall mean) are, from left to right: maximum daily air temperature, September of current year ('tair\_max\_Y0\_09', °C, relative importance measure = 0.019), minimum daily air temperature, July previous year ('tair\_min\_Y1\_07', °C, importance = 0.018), and climate moisture index, July previous year ('cmi\_Y1\_07', mm, importance = 0.014). Chronology deviation, with higher numbers indicating higher growth, is on *x*-axis. Individual regression lines with error regions are shown to highlight trends.

**Table 2** Summary of three most important weather variables identified in Random Forest analysis, by data type (precipitation, air temperature, and climate moisture index or CMI) and tree-ring chronology

Variable	Chronology			
	2001	2004	2012	Combined
Precipitation	September/0 (0.99)		Annual/0 (1.00)Annual/1 (0.74)	
Min temp	July/1 (0.91)	July/1 (0.83)		July/1 (0.95)
Max temp		Sept/0 (0.85)		Sept/0 (1.00)
CMI	June/0 (1.00)	June/0 (1.00)	Annual/1 (0.79)	July/1 (0.76)
<i>R</i> <sup>2</sup>	0.428	0.440	0.241	0.231

Each table entry gives the month (or 'Annual') of data, followed after a forward slash by 0 (current year) or 1 (previous year), and in parentheses the variable's relative importance in each model (i.e., within a column). The final line summarizes fraction of chronology variance explained by a linear model using the three terms.

applies to the earlier poor growth of 1885–1895 (although there are many fewer cores, and no climate data, for this period), and we suggest that its subsequent recruitment pulse is also visible in Fig. 3.

In this study, we found a lag of ~5 years between low growth (from the tree ring chronology) and increased

mortality (from the inventory records). This is consistent with the physiological and ecological spiral of tree death (Franklin *et al.*, 1987), in which some combination of biotic and abiotic stressors – competition, drought, defoliation – ultimately result in death. These mechanisms interact and result in carbon starvation, hydraulic



failure, or both (McDowell, 2011). The length of this process varies greatly by species and the stressors involved; our 5-year estimate is consistent with a broad range (0–10+ years) reported from forests worldwide (Allen *et al.*, 2010).

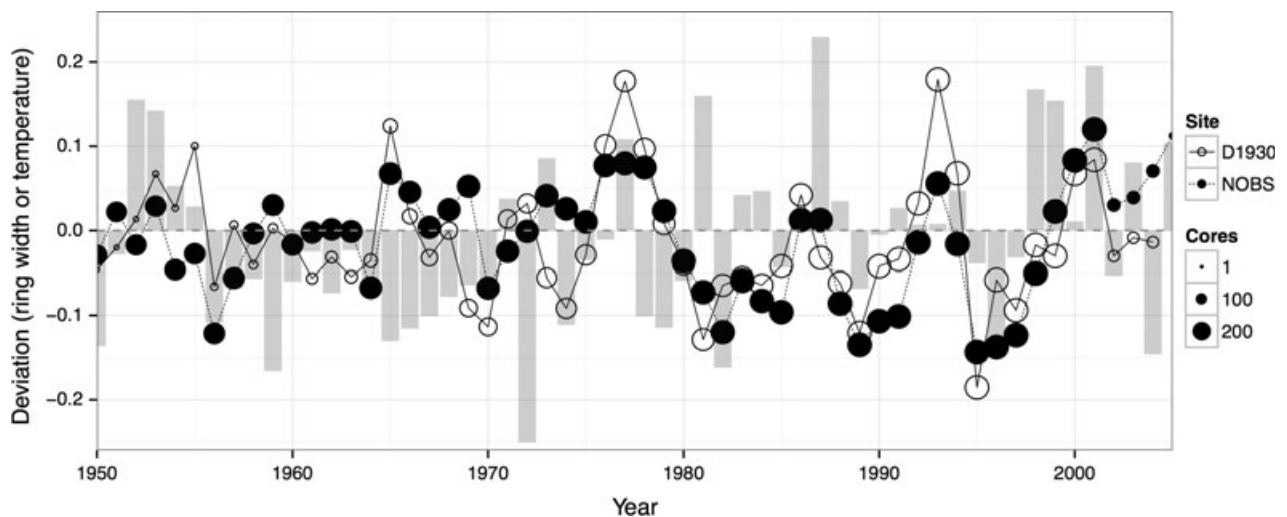
How much spatial coherence exists in these climate-driven growth and mortality patterns? Figure 6 shows how ring-width chronology for this old-growth site compares to a chronology computed, using identical methods, from a nearby 85-year-old site (cf. Figure 1 in Rocha *et al.*, 2006), and how both compare to the air temperature record. The strong cross-site correlation ( $r = 0.55$ ) in Fig. 6, combined with the high degree of scatter in Fig. 5, as well as temporal lags and modest  $R^2$  values in Table 2, together suggest that (i) the forest response to environmental variability is coherent across space, (ii) the system largely buffers against these fluctuations, but (iii) when it is hit hard enough (i.e., multi-decade warming or drought), these buffers are exhausted (Niinemets, 2010). Such a dynamic is consistent with, for example, altitudinal patterns of conifer mortality observed in southern California (Fellows & Goulden, 2012), in which stressful decades are followed by increases in mortality and vegetation redistribution, decadal patterns superimposed on slower patterns of fire and succession.

#### The importance of succession-driven mortality

Mortality fluctuates throughout forest succession, and is typically high among colonizing tree seedlings and during self-thinning (Peet & Christensen, 1987), periods

frequently studied by ecologists. It is less well understood for old-growth forests, in part because lower mortality rates in such forests mean that longer observational periods, and/or larger sample areas, are required (Franklin *et al.*, 1987). Here, we observed that the NOBS forest is clearly undergoing deterioration (Cogbill, 1985), with tree density and basal area dropping even as mean DBH rises (Fig. 1). Interestingly, this mortality is not occurring primarily in the oldest cohort (the original fire-induced population), or is this cohort the only one present. This unexpected age and structural diversity has implications for how well old-growth forests might sustain their production and carbon sequestration capabilities, and whether such forests are modeled correctly. Most modeling studies at this site (e.g., Amthor *et al.*, 2001; Bond-Lamberty *et al.*, 2006), for example, have assumed an even-aged stand with constant mortality. How mortality is treated can have large effects on model skill (Pietsch & Hasenauer, 2006), and it seems doubtful that most models could reproduce the dynamics observed here.

We observed higher mortality in intermediate-diameter trees, in contrast to an old-growth *Picea abies* stand in Sweden (Fraver *et al.*, 2008) and the general expectation that the oldest (largest) and youngest (suppressed and vulnerable) trees would have higher mortality. One reason may be the proclivity of older *P. mariana* trees to reproduce vegetatively, as the resulting small-diameter clones grow more quickly (Morin & Gagnon, 1992), and have access for a period to the non-structural carbohydrate stores of their parents trees (Niinemets, 2010).



**Fig. 6** Mean annual air temperature and combined tree ring chronologies for old-growth NOBS and nearby (5 km distant) 80-year-old stand 'D1930'. Both sites are single-species *Picea mariana*. Chronologies have been adjusted to a zero mean (cf. Fig. 4); size of points shows number of cores contributing to each year's datum. Bar graph shows mean annual air temperature deviation, that is, relative to overall dataset mean, and has been rescaled by a factor of 0.1 for ease of comparison.

Together, these factors probably result in lower mortality than that experienced by saplings from seed.

The earliest tree ring (1849) in the data set, coupled with the time-to-DBH assumption outlined above, implies a best estimate of the NOBS site's age (time since catastrophic fire) of ~1830. This is older than typically reported and has implications for age-based analyses of the pools and fluxes of this site (e.g., Bond-Lamberty *et al.*, 2004) as well as multi-site syntheses (Coursolle *et al.*, 2012). It is also consistent with the newly understood multi-cohort nature of the stand, and implies that a combination of successional and demographic processes, along with abiotic drivers, continue to affect this forest.

#### *Does climate- or succession-driven mortality dominate carbon cycling?*

The current balance of recruitment and mortality observed here is unsustainable, and will halve the stand density in a few decades. Although LAI and biomass have remained relatively constant, stem density has dropped significantly, and the functional effect of mortality is significant, resulting in a NPP difference of ~25% of total production at this site (Bond-Lamberty *et al.*, 2004). Such relatively (compared to previous decades) high mortality has, however, occurred in the past, and currently follows a relatively poor decade (the 1990s; Fig. 4) for growth. Although we cannot unambiguously distinguish climate from purely successional effects, as this is an observational, not manipulative, study, the combination of a senescing stand and normal decadal climate dynamics seem sufficient to explain the mortality patterns observed here.

Regionally, our 1999–2012 mortality estimate of 1.4% yr<sup>-1</sup> is commensurate with mortality reported in a much larger study across Canada by Peng *et al.* (2011), and almost identical to rates observed in Scandinavia (Rouvinen *et al.*, 2002). Thorpe & Daniels (2012) used long-term inventory records, from an Alberta forest including *P. mariana*, to calculate mortality rates of 0.8% yr<sup>-1</sup> for 1990–2007 (but much lower rates in the decades before this), inferring that mortality was driven by stand development and not climate changes. More broadly, the rates observed here are roughly in the middle of the relatively small number of studies that have measured background mortality in natural boreal stands (Table 3).

Finally, no trend in the tree-ring and inventory data consistent with a CO<sub>2</sub> fertilization effect was observed, although we note that tree-ring and inventory studies on this subject are subject to numerous potential sampling biases (Brienen *et al.*, 2012). Many modeling

**Table 3** Summary of studies reporting background mortality, that is, with no recent major disturbance, in mature boreal forests. Data include age of forest when available, observation period, and tree mortality rate

Ecosystem	Age	Period (year)	Mortality (% yr <sup>-1</sup> )	Ref.
<i>Pinus sylvestris</i> , Fennoscandia	>90	1	0.43	1
<i>Picea abies</i> , Sweden		72	0.45	2
<i>P. abies</i> , Russia	>250	15	0.49	3
<i>P. sylvestris</i> ( <i>Vaccinium-Myrtillus</i> ), Fennoscandia	198	3	0.6*	4
<i>P. sylvestris</i> ( <i>Empetrum-Calluna</i> ), Fennoscandia	198	3	0.6*	4
<i>P. abies</i> , Sweden	379	18	0.60	5
<i>Pinus contorta</i> , <i>Picea glauca</i> , <i>P. mariana</i> , Alberta, Canada		18+	0.2–0.8	6
<i>P. abies</i> , Sweden	~200	53	1.12	7
<i>Betula pubescens</i> , Sweden	163	18	1.15	5
<i>Picea mariana</i> , Quebec, Canada		10	1.2	8
<i>P. sylvestris</i> ( <i>Empetrum-Vaccinium</i> ), Fennoscandia	198	3	1.2*	4
<i>P. mariana</i> , Manitoba, Canada (this study)	160+	13	1.4 ± 0.6	
<i>P. mariana</i> , Manitoba, Canada	77	8	1.4 ± 1.0	9
Various, southern boreal forest, Canada	>80	45	0.3–3.0	10
Mixed, Québec, Canada		10	1.8	8
<i>Abies balsamea</i> , Quebec, Canada		10	2.3	8
<i>Picea glauca</i> , Quebec, Canada	150	~50	4.0	11
<i>Populus tremuloides</i> , Québec, Canada		~50	5.9	11

References: 1. Siitonen *et al.* (2000). 2. Linder (1998), based on calculation in #4. 3. Aakala *et al.* (2011). 4. Rouvinen *et al.* (2002). 5. Fraver *et al.* (2008). 6. Thorpe & Daniels (2012). 7. Hyttborn *et al.* (1991). 8. Aakala *et al.* (2007). 9. Bond-Lamberty & Gower (2008). 10. Peng *et al.* (2011). 11. Senecal *et al.* (2004).

\*Volume basis. All other reported rates on a stem basis.

studies have not predicted a significant CO<sub>2</sub> fertilization effect for North American boreal forests, given these ecosystems' water, nutrient, and other constraints (Chen *et al.*, 2000; Bond-Lamberty *et al.*, 2007; Thornton *et al.*, 2007; Balshi *et al.*, 2009). Our results are also consistent with a recent temperate-to-boreal transect study in Ontario that found increased water stress leading to

growth declines, with little evidence for a CO<sub>2</sub> growth effect (Silva *et al.*, 2010).

### Implications for forest management

Almost 85% of the Canadian boreal forest is under management (Natural Resources Canada, 2009; Payeur-Poirier *et al.*, 2012), including the Manitoba region in which the NOBS site sits, and climate change has been recognized for decades as a forest management challenge (Singh & Wheaton, 1991; Spittlehouse & Stewart, 2003). This has typically focused on the risks of wildfire (Bergeron *et al.*, 2004) and the potential for increased forest growth (Girardin *et al.*, 2008). Our results, however, emphasize two additional, interactive, and potentially under-appreciated factors.

First, forest management – particularly fire suppression – may be pushing this stand and region significantly outside of historical successional processes, resulting in an older and slower-growing landscape. This is in contrast to Canada's eastern boreal forest, where harvest has created a younger landscape than the historical norm (Cyr *et al.*, 2009). The NOBS site studied here is in an active fire suppression zone. Second, changes in background mortality are not well understood or accounted for by management plans. Such mortality is included, implicitly or explicitly, in foresters' regional yield tables (Sharma *et al.*, 2008), ecosystem models, and thus stand- to national-level management. But even a slightly warming and drying climate could significantly raise trees' mortality risk (Choat *et al.*, 2012) and thus the background mortality rate (Table 3), altering the forest structure and function in unexpected ways. Both greenhouse (Way & Sage, 2008) and field (Peng *et al.*, 2011) studies have shown that black spruce is vulnerable to drying-induced mortality. Such a mortality increase could interact strongly with the fire-suppression factor noted above, as thinning, over-mature forests that are 'ready to burn' increase their snag and dead wood loads. This could potentially result in a quickly thinning yet more-flammable forest.

In summary, our results support the hypothesis that these forests' responses to climate 'are dependent on demographic and species traits via their mediation of temperature and water stress constraints' (Girardin *et al.*, 2012), while emphasizing that demography is significantly complicated by the legacies of past disturbances (Gough *et al.*, 2007). We observed significant temperature- and precipitation-driven patterns in ring width superimposed on slower patterns of recovery from past disturbance. The uneven-aged and rapidly senescing character of the NOBS forest, the result of past disturbances whose effects continue to be felt in the stand's mortality patterns and carbon cycling, has

implications for our understanding and management of such old-growth forests and their responses to a changing climate.

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