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Environmental-mediated relationships between tree growth of black spruce and abundance of spruce budworm along a latitudinal transect in Quebec, Canada

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ABSTRACT

Changes in tree growth and insect distribution are projected due to climate warming. The expected effects of climate change on forest disturbance (e.g., insect outbreak) regime call for a better insight into the growth responses of trees to varying environmental conditions over geographical regions in eastern North America. In this study, the effects of a latitudinal thermal gradient and spruce budworm (SBW) outbreaks on the tree growth of black spruce (*Picea mariana* Mill.) were investigated along a 400 km transect from 48°N to 51°N across the continuous boreal forest in Quebec, Canada. Time series data were analyzed to synchronize climatic factors (temperature and precipitation trends), insect dynamics (SBW population frequency) and tree growth (ring-width chronology). Radial growth resulted as being synchronized with climate patterns, highlighting a positive effect of maximum temperatures on tree growth, especially in the northernmost site. Increasing temperatures and precipitation had a more positive effect on tree growth during epidemic periods, whereas the detrimental effects of SBW outbreaks on tree growth were observed with climate patterns characterized by lowered temperature. The lag between time series, synchrony and/or frequency of synchrony between tree growth and SBW outbreak were considered in order to link the growth of host trees and the dynamics of insect populations. The proposed analytical approach defined damage severity on tree growth in relation to population dynamics and climate fluctuations at the northern distribution limit of the insect. Overall, a decline in tree growth was observed in these boreal forests, due to SBW outbreaks acting in combination with other stress factors.

1. Introduction

In addition to the stressful conditions commonly experienced by boreal trees during extreme events, climate change is modifying disturbance regimes, increasing tree mortality and affecting species composition in boreal ecosystems (Candau and Fleming, 2011). In Canada, spruce budworm (*Choristoneura fumiferana* Clemens) (SBW) outbreaks cause recurrent growth declines of balsam fir (*Abies balsamea* L. Mill.), the main host of this defoliator (Boulanger et al., 2012). However, during epidemic periods, when the SBW population density is higher, other coniferous species, such as white spruce (*Picea glauca* Moench Voss), black spruce (*Picea mariana* Mill.) and red spruce (*Picea rubens* Sarg.), can also be severely defoliated (Simard et al., 2012). In spring, the feeding activity of the larvae is perfectly synchronized with balsam fir needle emergence. However, the currently increasing temperatures could advance insect and plant phenology, mismatching the synchronisms with balsam fir and making black spruce a more suitable host for SBW. This could modify the SBW target host, dramatically increasing outbreak severity in the northern boreal zone, the black spruce domain, whereas the southern parts of the range would become too warm to sustain high SBW population levels (Régnière et al., 2012). In Quebec, Canada, three major SBW outbreaks occurred during the 20th century, in 1915–1929, 1946–1959 (Boulanger et al., 2012) and 1974–1988 (Boulet et al., 1996). The latter caused the defoliation of 55 million ha of black spruce stands. The first outbreak of the 21st century is still ongoing in eastern Canada, where the defoliated area has doubled every year since 2005. In 2012, more than

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2 million ha of forest were affected (Direction de la protection des forêts, 2012).

The SBW periodicity is defined by migrations and local population dynamics (Shlichta and Smilanich, 2012). Jardon et al. (2003) studied this periodicity, synchronism and impact of SBW in Quebec, observing cyclical outbreaks occurring with frequency of 25–28 years at a supra-regional level and lasting 8 years or more (Jardon et al., 2003; Tremblay et al., 2011). Climate is the main factor that drives SBW dynamics, and the range of the outbreaks is predicted to shift beyond the traditional limits as the climate becomes more favorable (Bouchard and Pothier, 2010; Régnière et al., 2012; Zhang et al., 2014). Warmer winter temperatures can lead to overwintering survival, significantly increasing the abundance of insect populations (Han and Bauce, 2000), and longer summers in Eastern Canada may make northern sites more suitable for SBW attacks. The fluctuations in insect survival, caused by a poor synchronism between larval and bud phenology, seem to affect black spruce, whose bud flush is later than that of balsam fir and white spruce (Régnière et al., 2012). An increase in mean annual temperature of 2–5 °C across eastern Canada in the next 50 years, as projected by current climate models (Christensen et al., 2007), may induce phenological changes and trophic interactions among host trees, herbivorous insects and their natural enemies in boreal forests (Pureswaran et al., 2015). Indeed, northern expansion of SBW in Quebec and climate-induced narrowing of the phenological mismatch between the insect and its secondary host may trigger more severe defoliation and mortality in black spruce forests.

Climatic factors play an important role in defining the severity and duration of outbreaks, as well as their synchrony (Gray, 2008; Williams and Liebhold, 2000). The degree of biological synchrony between host (black spruce) and parasite (SBW) depends on the overlap of the potential distribution of trees (as source of needles) and insect populations (Régnière et al., 2012). Therefore, the synchrony between tree growth and SBW dynamics is useful in order to understand the evolution and intensity of outbreaks, and the effect of severe infestation on stand productivity (Boulanger et al., 2012). Using the predictions of the effects of climate change on SBW outbreaks, models are required that describe how SBW defoliation dynamics interact with tree growth patterns across seasons and landscapes, and how they could affect the future productivity of forests (Krause et al., 2012). Moreover, Candau and Fleming (2011) found that the spatial distribution of past defoliation was related to winter and spring temperatures, and stand composition. However, the role of climate in determining the spatial and temporal distribution of defoliation caused by SBW and the interactions with stand productivity are still uncertain, as is the relative importance of the various causes of tree mortality (insect outbreaks vs. drought spells).

An innovative approach was applied in this paper, with the aim of examining the dynamics of black spruce growth in relation to the role of climatic factors in determining the severity and duration of SBW outbreaks, rather than reconstructing the history of SBW outbreaks using dendrochronology. We applied a mathematical function on time series data (Cocozza et al., 2012) to synchronize climatic factors (temperature and precipitation trends), insect dynamics (SBW populations), and tree growth (ring-width chronologies) obtained in black spruce stands along a latitudinal gradient in Quebec. We expected that (1) changes in monthly temperatures and precipitation during the 20th century have progressively amplified the sensitivity of black spruce to SBW incidence, increasing synchrony between time series (tree rings and SBW outbreaks) and growth reduction during outbreaks, and (2) tree growth patterns have also varied along a latitudinal gradient under the influence of changing SBW synchrony, with growth of northern trees benefiting from warming and with greater phenological synchrony between black spruce and SBW in warmer sites.

2. Materials and methods

2.1. Study area

The study was conducted in black spruce stands from 48 to 51°N within the continuous boreal forest of Quebec, Canada (Fig. 1). The climate is subhumid–subpolar continental with mean annual temperatures ranging between −0.9 and 2.0 °C. The region has long winters with temperatures below zero, January being the coldest month with extremes of –47 °C, and short summers with maximum absolute temperatures exceeding 30 °C (Lugo et al., 2012). The landscape is characterized by glacial till deposits and an undulating morphology with many gently-sloping hills reaching 500–700 m a.s.l. (Rossi et al., 2011).

Four permanent sites were selected along a latitudinal gradient, Simoncouche (abbreviated as SIM) at the lowest latitude, Bernatchez (BER) at the highest altitude, Mistassibi (MIS), and Camp Daniel (DAN), the coldest site (Fig. 1) (Lugo et al., 2012).

2.2. Dendrochronological analysis

Fieldwork was carried out in summer 2013. In each site, the trees were selected to maximize the temporal and spatial extent of the time series. Care was also taken to select trees with canopies well separated from each other to reduce the effect of competition on tree growth. Two increment cores were extracted from 21 (SIM), 18 (BER and DAN) and 20 (DAN) black spruce trees with an increment borer 0.5 cm in diameter, at breast height (1.3 m) and at an angle of 120° from one another. Cores were mounted on channeled wood sticks, seasoned in a fresh-air dry store and sanded.

Tree ring widths (TRW) were measured to the nearest 0.01 mm using the LINTAB-measurement equipment at 60× magnifications. The Time Series Analysis Programme (TSAPWin) software package (Frank Rinn, Heidelberg, Germany) was used for statistical analyses on tree rings. TRW chronologies of each tree were cross-dated first visually and then statistically by the percentage agreement in the signs of the first-differences of the two time series (the Gleichläufigkeit, Glk) (Kaennel and Schweingruber, 1995). The Glk is a measure of the year-to-year agreement calculated as the number of times that two series show the same upward or downward trend relative to the previous year. With an overlap of 10 years, Glk becomes significant ($p < 0.05$) at 76% and highly significant ($p < 0.01$) at 87%. In this study, the analyzed time series were mostly longer than 50 years and cross dating was considered successful if Glk was higher than 60%. The statistical significance of the Glk (GSL) was also computed. In addition, the TVBP, a Student's t value, and the cross date index (CDI) were used to investigate the significance of the best match; acceptable comparability is assumed with t-value higher than 3, and values of CDI > 10 were considered as being significant. The TVBP is a statistical tool commonly used to compare and cross-date ring-width series, which determines the degree of correlation between curves and eliminates low-frequency variations within the time series as each value is divided by the corresponding 5-year moving average. The software ARSTAN was used to standardize individual chronologies, producing tree-growth index (TRI) chronologies for each study area (Cook et al., 1990). A spline function with a 50% frequency response of 32 years was fitted to each tree ring raw series, computed by dividing observed by expected values. Mean standard chronologies were then used to analyze climate–growth relationships.

Descriptive statistics were applied to compare key properties of each chronology and included mean sensitivity (MS) and tree