



Tree-ring widths and isotopes of artificially defoliated balsam firs: A simulation of spruce budworm outbreaks in Eastern Canada

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ABSTRACT

Defoliation by insects is a major disturbance influencing the forest dynamics in many ecosystems and can affect forest productivity worldwide. The main objective of this research was to further investigate the potential use of tree-ring widths and isotopic compositions to identify different degrees of past spruce budworm defoliation episodes. A secondary objective was to understand the responses of trees to defoliation episodes using carbon isotopes as a proxy to provide insights into subsequent physiological changes. Tree-ring widths, carbon and oxygen isotopic compositions in wood cellulose and gas exchange measurements were compared among 288 balsam fir (*Abies balsamea* Mill.) seedlings grown in a controlled experiment that involved different intensities of defoliation. Observations were performed over four growing periods. Moderate to heavy-defoliated seedlings showed reduced radial growth and enriched their cellulose carbon isotopic composition probably as a result of mobilized stored carbohydrates enriched in ¹³C. Less severely defoliated seedlings did not show significant reductions in growth and ¹³C enrichments. The gas exchange observations and wood cellulose oxygen isotope compositions do not suggest photosynthetic compensation in the remaining needles although a positive trend in the response of both assimilation rate (*A*) and stomatal conductance (*g_s*) to defoliation was observed in the first growing period. Thus it remains open as to which mechanisms were employed to compensate for the reduced carbon source in the mildly defoliated seedlings. While further investigations are advised, the results of this study still help promote the utilization of tree-ring widths in combination with carbon isotopic compositions for reconstructing severe past defoliation events.

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1. Introduction

Defoliation affects forest ecosystems worldwide through a variety of causes. Occasional defoliation episodes related to spruce budworm (SBW, *Choristoneura (Archips) fumiferana* Clem.) outbreaks are one of the main disturbances influencing the forest dynamics of the boreal forest of eastern North America. By feeding on both developing and old needles (during times of high insect population density) of balsam fir [*Abies balsamea* (L.) Mill.], white spruce [*Picea glauca* (Moench) Voss] and black spruce [*Picea mariana* (Mill.) B.S.P.] (Morin, 1994) SBW can severely reduce forest productivity thereby decreasing growth and even causing significant tree mortality (Bouchard et al., 2007; MacLean et al., 1996).

Identifying and reconstructing past defoliation episodes on both short and long-term scales is necessary for a better understanding of the fundamentals of SBW outbreaks and related forest dynamics as a whole. Moreover, in a context where ecosystem based management is generally considered the most promising approach to the maintenance of healthy and resilient forest ecosystems, it is essential to better assess the natural long-term variability of insect related disturbances (Gauthier et al., 2008).

Long-term annually resolved SBW outbreak records can be derived through a dendrochronological approach using tree rings. Since these insects feed on developing and old needles of boreal forest tree species they can and do invoke both physiological and chemical responses that are recorded in annually produced rings (Blais, 1983; Leavitt and Long, 1986a; Simard et al., 2008). Tree-ring records from living trees, sometimes in combination with historical timbers (Boulanger and Arseneault, 2004; Krause, 1997) and/or sub-fossil trees (Simard et al., 2011) therefore offer the potential for extended records of SBW outbreaks.

Specifically by reducing photosynthetic biomass, defoliation episodes impact the source/sink balance in trees which can trigger internal reactions to maintain an equilibrium between sources

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(photosynthetic tissues or tissues from where carbohydrate remobilization can occur) and sinks for the carbon required for normal growth and maintenance (Pinkard et al., 2011). Following defoliation, trees can respond in several ways. One way is to mobilize reserve carbohydrates stored as starch (Eyles et al., 2009) to supply the carbon required. Another strategy to compensate for source limitation is to increase the rate of photosynthesis in the remaining needles until a source/sink balance is re-established (Chen et al., 2001; Lavigne et al., 2001; Little et al., 2003; Reich et al., 1993; Vanderklein and Reich, 1999; Welter, 1989). Increased photosynthetic rates in response to defoliation may be achieved through different ways. Increased stomatal conductance following enhanced water availability, increased photosynthetic carbon fixation following increased flow of nitrogen to remaining leaves (a large proportion of N is in chlorophyll and Rubisco), or increased Rubisco activity (rather than a change in quantity) in response to greater light reaching the remaining needles, have been observed (Turnbull et al., 2007). All these responses are known to result in chemical changes (enrichment in the carbon isotopic composition) (Farquhar et al., 1982; Francey and Farquhar, 1982). In the case of increased photosynthetic activity in response to defoliation, assimilates enriched in ^{13}C as a consequence of reduced isotope discrimination against the heavier carbon ($^{13}\text{CO}_2$ vs $^{12}\text{CO}_2$), would also isotopically enrich the molecular components (hemi-cellulose, cellulose, lignin) of the tree-ring wood. Similarly, remobilization and use of stored carbohydrates enriched in ^{13}C could also lead to ^{13}C enriched tree-ring components formed during and after defoliation events (Brugnoli et al., 1988; Damesin and Lelarge, 2003; Helle and Schleser, 2004; Le Roux et al., 2001).

A recent dendro-isotopic survey of SBW outbreaks (1950–1960; 1970–1980), from mature host and non-host conifers from the boreal forest, shows carbon isotope enrichment signatures (relatively high isotope values) in both severely and more lightly defoliated trees (Simard et al., 2008). Higher carbon isotope values of host-trees and reduced ring widths directly corresponded with the two last SBW outbreaks in the area. Altogether, very few studies have investigated the effects of defoliation on the $\delta^{13}\text{C}$ composition in tree ring cellulose (Kress et al., 2009; Leavitt and Long, 1986a; Weidner et al., 2010) and the results varied among the studies. Investigations on European larch (*Larix decidua* Mill.) in relation to larch budmoth (LBM, *Zeiraphera diniana* Gn.) defoliation showed no relationship between tree-ring $\delta^{13}\text{C}$ variations and outbreak periods (Kress et al., 2009; Weidner et al., 2010). However, high $\delta^{13}\text{C}$ values and reduced ring widths in tree rings of evergreen conifers formed during a western SBW outbreak were observed by Leavitt and Long (1986a). Kress et al. (2009) proposed the difference in life cycles between SBW and LBM as a possible explanation for the different signals in tree-ring $\delta^{13}\text{C}$ in LBM-European larch and SBW-black spruce/balsam fir systems (Simard et al., 2008). LBM defoliation events last for one vegetation period and reoccur with a periodicity of 8–10-year intervals while SBW outbreaks appear in decadal scale frequencies (30–40-year intervals) which can last for more than five years. The impact of a one-year-long defoliation outbreak compared to a five-year repeated defoliation event is likely much lower and might explain the discrepancies observed between the two studies.

The fact remains that understanding causes vs consequences in dendrochronological studies is challenging. For example, it is not clear from the studies of Simard et al. (2008) and Leavitt and Long (1986a) if the wood cellulose $\delta^{13}\text{C}$ values increased in response to defoliation, or if the trees were experiencing some situation (e.g. localized drought) that increased their $\delta^{13}\text{C}$ values and also lead to greater susceptibility to insect attack. The present study helps address this issue by inducing a “cause” (defoliation) and measuring the “consequence” in a controlled manner.

The objective of this research is to further investigate the potential use of tree ring widths and isotopic compositions for identifying different degrees of past SBW defoliation episodes. A controlled experiment involving different intensities of defoliation on balsam fir seedlings was conducted. This study was designed to determine the relation between defoliation intensities and annual tree-ring widths, cellulose carbon and oxygen isotopic compositions and plant physiology (CO_2 assimilation rate and stomatal conductance) over four growing periods. Oxygen isotopic compositions were also measured because they are linked to water source, evaporative demand and stomatal conductance (Barbour and Farquhar, 2000; Saurer et al., 1997). Linking both isotopes could therefore help to further understand the mechanisms responsible for the carbon isotopic compositions of the defoliated seedlings (Scheidegger et al., 2000). The research also aims at understanding what tree responses are to outbreaks by using $\delta^{13}\text{C}$ to determine if they rely on starch reserves to continue growth and metabolic activities or if they undergo other physiological changes.

Based on the evidence from Leavitt and Long (1986a) and Simard et al. (2008), carbon isotopic enrichment of the balsam fir tree-ring cellulose is expected with increased levels of defoliation due to the mobilization of ^{13}C enriched stored carbohydrates for xylem cell production and/or increased carbon fixation as a compensatory mechanism to defoliation. Accompanying tree-ring width reductions are also expected in the ring series of the most severely defoliated seedlings. The oxygen isotope composition of the tree-ring cellulose is expected to respond independently to artificial defoliation (Simard et al., 2008).

2. Material and methods

2.1. Plant material

To test the effects of different degrees of defoliation on tree-ring widths, and tree-ring cellulose $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, a growth experiment was conducted in a greenhouse setting. Two hundred eighty-eight (288) container-grown five-year-old balsam fir (*A. balsamea*) seedlings of uniform height (26.7 ± 4.1 cm) and diameter (7.8 ± 1.2 mm) were obtained from a nursery in the Lac Saint-Jean (Quebec, Canada) area. The seedlings were planted in plastic pots containing peat moss (15.2 cm diameter, ~ 2.44 l of peat moss/pot) in springtime and allowed to adapt to the new rooting environment during that initial summer before starting the defoliation experiment.

2.2. Experimental design

Seedlings organized in a randomized block split-plot design were subjected to one to four growing periods or “pulses” of growth (i.e. time as the main plot), four different intensities of current-year needle defoliation (CYD; 0, 33%, 66%, 99%) and two intensities of old-needles defoliation (i.e. all other age-class needles except the currently developing ones; OND; 0% and 50%) (i.e. defoliation as the subplot). The experiment was replicated within three blocks. Pulse of growth refers to a growing episode between two dormancy periods. Dormancy between pulses of growth was applied by exposing the seedlings to a cold environment protected from snow at or below 0°C for a period of four to six weeks (Dubuc, Canadian Forest Service, Pers. Comm.). Growing period 1 (end of December 2004 to mid of March 2005) was simulated by increasing the greenhouse temperature and irrigating the seedlings (details provided below). Dormancy was then again initiated by a cold treatment between mid March and end of May (2005). Growing period 2 was initiated between June and September (2005) followed by another cold treatment for dormancy between October and December (2005).

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