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Methods paper

Tree-ring proxies of larch bud moth defoliation: latewood width and blue intensity are more precise than tree-ring width

Estelle Arbellay[1,4,5], Ingrid Jarvis[1], Raphaël D. Chavardès[1], Lori D. Daniels[1] and Markus Stoffel[2,3]

[1]Tree-Ring Lab, Department of Forest and Conservation Sciences, University of British Columbia, 3041-2424 Main Mall, Vancouver, BC V6T 1Z4, Canada; [2]Climatic Change and Climate Impacts, Institute for Environmental Sciences, University of Geneva, Boulevard Carl-Vogt 66, CH-1205 Geneva, Switzerland; [3]Dendrolab.ch, Department of Earth Sciences, University of Geneva, Rue des Maraîchers 13, CH-1205 Geneva, Switzerland; [4]Present address: Department of Biology, University of Victoria, PO Box 3020, Victoria, BC V8W 3N5, Canada; [5]Corresponding author (arbellay@uvic.ca)

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Reconstructions of defoliation by larch bud moth (LBM, *Zeiraphera diniana* Gn.) based on European larch (*Larix decidua* Mill.) tree rings have unraveled outbreak patterns over exceptional temporal and spatial scales. In this study, we conducted tree-ring analyses on 105 increment cores of European larch from the Valais Alps, Switzerland. The well-documented history of LBM outbreaks in Valais provided a solid baseline for evaluating the LBM defoliation signal in multiple tree-ring parameters. First, we used tree-ring width measurements along with regional records of LBM outbreaks to reconstruct the occurrence of these events at two sites within the Swiss Alps. Second, we measured earlywood width, latewood width and blue intensity, and compared these parameters with tree-ring width to assess the capacity of each proxy to detect LBM defoliation. A total of six LBM outbreaks were reconstructed for the two sites between AD 1850 and 2000. Growth suppression induced by LBM was, on average, highest in latewood width (59%), followed by total ring width (54%), earlywood width (51%) and blue intensity (26%). We show that latewood width and blue intensity can improve the temporal accuracy of LBM outbreak reconstructions, as both proxies systematically detected LBM defoliation in the first year it occurred, as well as the differentiation between defoliation and non-defoliation years. This study introduces blue intensity as a promising new proxy of insect defoliation and encourages its use in conjunction with latewood width.

Keywords: blue intensity, earlywood, insect defoliation, insect outbreak, latewood, *Zeiraphera diniana*.

Introduction

Worldwide, tree defoliation by insects is driven by about 20 different families of Lepidoptera (Dajoz 2000). Among the most voracious defoliators of European forests is larch bud moth (LBM, *Zeiraphera diniana* Gn.), which mainly feeds on European larch (*Larix decidua* Mill.). Mass outbreaks of LBM have led to waves of defoliation traveling eastward across the European Alps (Bjørnstad et al. 2002, Johnson et al. 2004). Larch bud moth outbreaks have occurred with remarkable regularity, every 8–9 years for the last 12 centuries (Lynch 2012). The LBM population cycle is influenced by LBM parasitoids (Turchin et al. 2003) and, to a larger extent, by lower foliage nutritional quality after defoliation (Baltensweiler and Fischlin 1988). Even when defoliated >50%, larch trees refoliate within 3–4 weeks, usually in July and August. However, the newly formed late-summer needles and those of the following spring are short and low in starch and nitrogen, which leads to the collapse of LBM populations (Baltensweiler and Fischlin 1988). Historically, LBM outbreaks have shown very little variation in amplitude and periodicity. Nevertheless, mass outbreaks of LBM synchronized throughout the European Alps have not occurred since the 1980s, an absence that has been attributed to ongoing climate change (Johnson et al. 2010, Iyengar et al. 2016).

The years of LBM defoliation are exceptionally well-documented thanks to a multi-decade larval census initiated in

1949 (Baltensweiler and Rubli 1999) and numerous multi-century tree-ring reconstructions conducted in Switzerland (Weber 1997, Esper et al. 2007, Kress et al. 2009), France (Rolland et al. 2001, Battipaglia et al. 2014, Saulnier et al. 2017), Italy (Nola et al. 2006) and across the European Alps and Tatra Mountains (Büntgen et al. 2009, Konter et al. 2015, Hartl-Meier et al. 2017). Larch bud moth defoliation is identifiable in European larch tree rings by markedly reduced increments over 2–5 years (Nola et al. 2006, Battipaglia et al. 2014). Growth suppression induced by LBM can be occasionally restricted to one single year in European larch (Weber 1997, Weidner et al. 2010), although this is more common in Swiss stone pine (*Pinus cembra* L., Nola et al. 2006, Battipaglia et al. 2014). Insect defoliation influences radial growth negatively in the initial year of the outbreak and over several subsequent years (Kulman 1971). Defoliation diminishes tree photosynthetic capacity and, as a result, suppresses tree growth due to lower carbon assimilation and heavy reliance on carbohydrate reserves to replace foliage (Gleason and Ares 2004, Myers and Kitajima 2007).

In this study, we conducted tree-ring analyses on 105 increment cores of European larch from the Valais Alps, Switzerland. The well-documented history of LBM outbreaks in Valais (e.g., Röthlisberger 1976, Esper et al. 2007, Figures 1 and 2) provided a solid baseline for evaluating the LBM defoliation signal in multiple tree-ring parameters. First, we used tree-ring width measurements along with regional records of LBM outbreaks to reconstruct the occurrence of these events at two sites within the Swiss Alps. Second, we measured earlywood width, latewood width and blue intensity, and compared these parameters with tree-ring width to assess the capacity of each proxy to detect LBM defoliation.

Blue intensity represents the blue light reflectance occurring in latewood (McCarroll et al. 2002). Blue intensity has been established as a surrogate for latewood density, as minimum blue intensity correlates well with maximum latewood density (MXD) measured with X-ray densitometry (McCarroll et al. 2002, Campbell et al. 2007, 2011). At the same time, MXD is deemed a more reliable proxy than tree-ring width to reconstruct past climate (Beck et al. 2013, Konter et al. 2016). Hence, blue intensity has been increasingly used in dendroclimatology to reconstruct past temperature (Björklund et al. 2013, Wilson et al. 2014, Rydval et al. 2017, Fuentes et al. 2018) and precipitation (Babst et al. 2016, Dannenberg and Wise 2016). Blue intensity has also been introduced as a novel proxy in dendroarchaeology (Wilson et al. 2017). In this study, we tested blue intensity as a new proxy of insect defoliation. Evaluating tree-ring parameters other than tree-ring width contributes toward improving insect outbreak reconstructions. Precise tree-ring estimates of insect outbreaks are needed for comparison with climate data to help predict future outbreaks and develop adequate forest management plans. The absence of LBM outbreaks since the 1980s has led to increased growth in European larch, and has helped demonstrate that in high-elevation forests insect outbreaks can have a greater impact on biomass accumulation than climate (Peters et al. 2017).

Materials and methods

Sample procurement

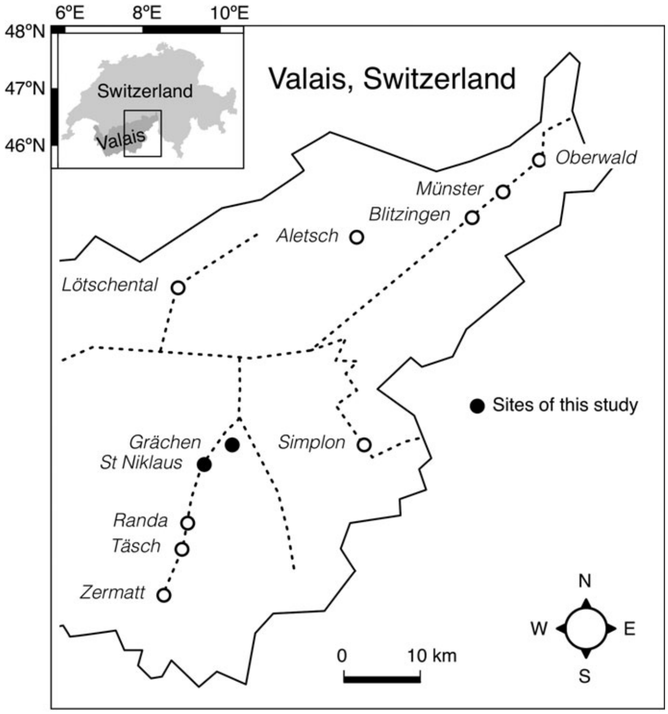
The 105 increment cores of European larch evaluated in this study were collected in Grächen (46°11′N, 7°49′E, Stoffel et al. 2008) and St Niklaus (46°10′N, 7°47′E, Bollschweiler et al. 2008). Both study sites are located in the Zermatt Valley in Valais, Switzerland (Figure 1). In addition to sampling trees disturbed by past debris-flows, Stoffel et al. (2008) and Bollschweiler et al. (2008) also cored trees not impacted by these events to build a reference chronology. Growth curves of disturbed trees were crossdated with the reference chronology to separate debris-flow-induced disturbances from other environmental influences on tree growth, such as climate and insect outbreaks (Cook and Kairiukstis 1990, Vaganov et al. 2006). Each increment core evaluated in the current study is from a different reference tree that was either sampled between November 2000 and May 2001 (Stoffel et al. 2008) or in November 2005 (Bollschweiler et al. 2008). Average tree age is 179 ± 77 years. Data on the innermost ring vary from AD 1507 to 1939. We analyzed tree growth over the period AD 1850–2000, where >50% of the sampled trees were present.

Sample analysis

An Epson Expression 10,000 XL scanner calibrated with EZcolor 2.6.5 software and an IT8.7/2 calibration target was used to produce a color image of each increment core (24-bit, 2400 dpi, BMP). No resin extraction was performed prior to scanning, as samples were previously mounted on wooden supports and sanded. We measured tree-ring width (hereafter referred to as total ring width), earlywood width, latewood width and blue intensity on each captured image using CooRecorder 7.4 software (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden). Boundaries between earlywood and latewood were determined with a threshold of 70 (Larsson 2011). Blue intensity was calculated in a latewood window with a frame width of 40, frame position of 0, maximum frame deepness of 40 and percentage of 'dark' latewood of 75 (Larsson 2011). These values were chosen to best control for resin, discoloration and artefacts, such as cracks and rough edges. Following Rydval et al. (2014), raw blue intensity data were inverted to facilitate comparison with the other tree-ring parameters.

Reconstruction of LBM outbreaks

Larch bud moth outbreaks were reconstructed by means of tree-ring analyses and regional records of outbreaks. First, total ring-width chronologies were screened for pointer years or years of extreme ring widths (Schweingruber et al. 1990). Pointer years associated with LBM defoliation correspond to tree rings



Regional records	**Study sites**
Röthlisberger 1976	Zermatt and Täsch
Schweingruber 1979	Münster
Weber 1997	Blitzingen, Münster and Oberwald
Gers 1998	Täsch and Randa
Baltensweiler and Rubli 1999	Various locations (incl. Zermatt)
Schneuwly 2003	Täsch
Esper et al. 2007	Lötschental, Aletsch and Simplon
Kress et al. 2009	Lötschental and Simplon
Weidner et al. 2010	Lötschental

Figure 1. Study sites of historical LBM outbreaks in Valais, Switzerland.

showing a relative width reduction of >40% (Weber 1997, Rolland et al. 2001, Weidner et al. 2010). The relative width reduction was calculated by comparing total ring width in each tree ring with the mean value of the four previous years (Rolland et al. 2001). A year was only considered a pointer year when the reduction was observed in >8% of the trees (Rolland et al. 2001). When pointer years were identified in several successive years, the first year defined the start of defoliation and was used to date the outbreak. Second, pointer years were compared with LBM outbreaks derived from regional records of the Zermatt Valley and beyond (e.g., Röthlisberger 1976, Esper et al. 2007, Figures 1 and 2). Regional records report 67 LBM outbreaks in Valais between AD 1850 and 2000 (Figure 2). A pointer year was only considered an outbreak when the year was confirmed in more than one record. In our dataset, the pointer years of 1868, 1884 and 1933 correspond to years where no LBM defoliation is known according to regional records, and were therefore not considered outbreaks. These years are hereafter referred to as non-defoliation years.

The LBM outbreaks reconstructed in this study were classified according to the three typical tree-ring patterns defined by Weber (1997), which are used as a measure of outbreak intensity. Type 1 outbreaks show maximum growth reduction in the first year of the outbreak. Type 2 outbreaks show this reduction in the second year of the outbreak. Type 3 outbreaks are similar to type 1, but only last a single year (Weidner et al. 2010). Outbreak intensity decreases from type 1 to type 3.

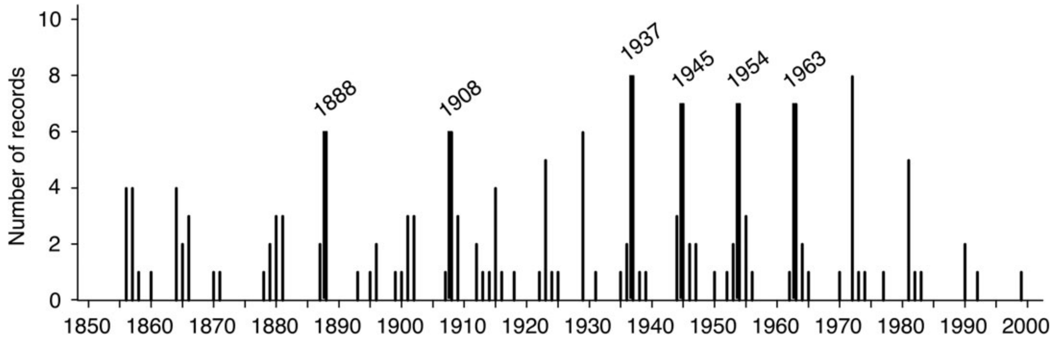
Comparison of tree-ring parameters

A multilevel model (Qian 2016, 2017) was used to determine whether LBM defoliation elicited significant changes in total ring width, earlywood width, latewood width and blue intensity. The multilevel analysis showed significant differences in the four tree-ring parameters before and after defoliation (Qian 2017), with latewood width and blue intensity resulting in the lowest and highest level of uncertainty, respectively. The Kruskal–Wallis test was then used to further investigate the nature of these differences. Pairwise comparisons were run for each tree-ring parameter to quantify differences between individual years of LBM defoliation and the 2 years prior. An individual year had to be significantly different ($P < 0.05$) from both prior years to reject the null hypothesis. Results were compared amongst the four tree-ring parameters in regard to the type of change, either decrease or increase, as well as the severity of change, including its magnitude and duration following initiation. Furthermore, similar analyses were conducted in the three non-defoliation years (1868, 1884 and 1933) where total ring width was nonetheless reduced by >40% during that single year. These events could therefore be mistaken for type 3 outbreaks.

Results

Reconstruction of LBM outbreaks

Tree-ring analyses of 105 increment cores of European larch allowed the reconstruction of six LBM outbreaks in Grächen and St Niklaus between AD 1850 and 2000: 1888, 1908, 1937, 1945, 1954 and 1963 (Table 1). These pointer years coincided with LBM outbreaks derived from regional records of the Zermatt Valley and beyond, and each were confirmed in six to eight records (Figure 2). Outbreaks lasted 2–4 years and affected 11–36% of the sampled trees present at the time of the outbreak (Table 1). Classification of tree-ring patterns associated with LBM defoliation (Weber 1997) indicated type 1 outbreaks (1937, 1945 and 1954) and type 2 outbreaks (1888, 1908 and 1963), although the 1963 outbreak actually showed maximum growth reduction in the third year of the outbreak. However, our tree-ring data did not show evidence of the other frequently recorded outbreaks of 1923, 1929, 1972 and 1981.



Regional records	Outbreak history	1888	1908	1937	1945	1954	1963
Röthlisberger 1976	1548–1972	x	x	x	x	x	x
Schweingruber 1979	1784–1970	x		x	x		
Weber 1997	1474–1990		x				
Gers 1998	1556–1992	x		x		x	x
Baltensweiler and Rubli 1999	1820–1981		x	x	x	x	x
Schneuwly 2003	1598–1999	x		x	x	x	x
Esper et al. 2007	844–1981	x	x	x	x	x	x
Kress et al. 2009	1660–1981	x	x	x	x	x	x
Weidner et al. 2010	1908–1981		x	x	x	x	x

Figure 2. Historical LBM outbreaks during the period AD 1850–2000. Labeled years (and thicker bars) indicate LBM outbreaks reconstructed in this study.

Table 1. Characteristics of reconstructed LBM outbreaks.

N	Initial year	Defoliation period	Length (years)	Defoliated trees (%)	TRP
1	1888	1888–1890	3	11	2
2	1908	1908–1909	2	19	2
3	1937	1937–1939	3	36	1
4	1945	1945–1946	2	26	1
5	1954	1954–1955	2	18	1
6	1963	1963–1966	4	32	2

TRP, tree-ring pattern associated with LBM defoliation, as defined by Weber (1997).

Comparison of tree-ring parameters

Larch bud moth defoliation caused substantial reductions in total ring width, as well as in earlywood width, latewood width and blue intensity (Figure 3). Significant to highly significant results were found in the 1888, 1908, 1937, 1945 and 1963 outbreaks, but all results were non-significant in the 1954 outbreak (Table 2). Growth suppression induced by LBM was, on average, highest in latewood width (59%), followed by total ring width (54%), earlywood width (51%) and blue intensity (26%). In type 1 outbreaks (1937 and 1945), the four tree-ring parameters detected significant impacts of LBM defoliation starting in the first year of the outbreak (Table 2). However, in type 2 outbreaks (1888, 1908 and 1963), only latewood width and blue intensity detected significant impacts of LBM defoliation in the first year of the outbreak. Significant reductions in total ring width and earlywood width were initiated in the second year of the outbreak.

The 1908 outbreak serves to illustrate these observations (Figure 4). In 1908, growth suppression induced by LBM was, on average, highest in latewood width (67%), followed by total ring width (50%), earlywood width (45%) and blue intensity (24%). However, significant reductions in total ring width and earlywood width were initiated in 1909 only, the second year of the outbreak, with decreases of 69% and 71%, respectively. In contrast, significant reductions in latewood width and blue intensity occurred in both 1908 and 1909. Latewood decreased by 67% in both 1908 and 1909, while blue intensity decreased by 24% in 1908 and by 25% in 1909.

The three non-defoliation years (1868, 1884 and 1933) also showed reductions in the four tree-ring parameters (Table 3). Results were mostly non-significant. Growth suppression was, on average, highest in earlywood width (51%), followed by total ring width (49%), latewood width (42%) and blue intensity (6%).

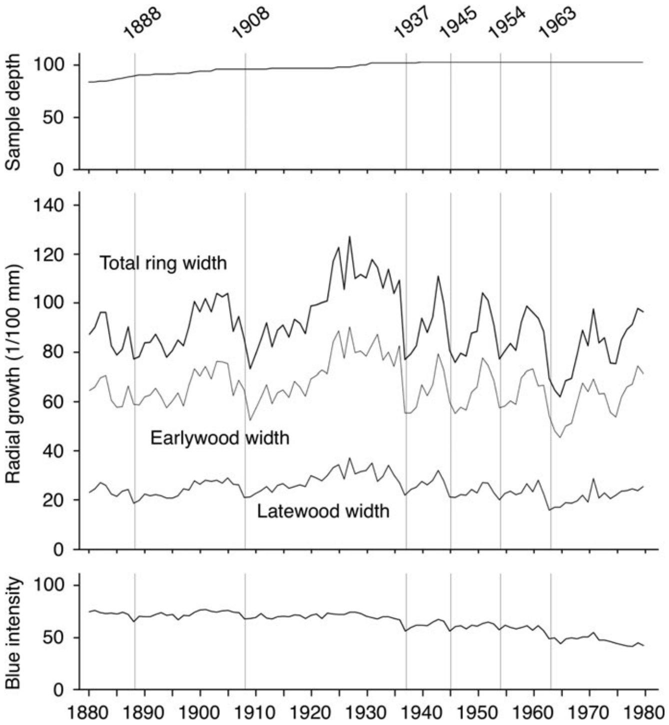


Figure 3. Sample depth, radial growth and blue intensity during the period AD 1880–1980. Radial growth includes total ring width, earlywood width and latewood width. Labeled years (and vertical lines) indicate LBM outbreaks reconstructed in this study.

Discussion

Reconstruction of LBM outbreaks

European larch tree rings revealed occurrence of six LBM outbreaks in Grächen and St Niklaus between AD 1850 and 2000: 1888, 1908, 1937, 1945, 1954 and 1963. Comparison of these pointer years with LBM outbreaks derived from regional records demonstrated that outbreaks have occurred uniformly over the upper part of the Valais canton. High outbreak synchrony in Valais is congruent with widespread LBM outbreaks in valleys with continental climates (Nola et al. 2006), as well as the western Alps in general (Baltensweiler and Rubli 1999, Bjørnstad et al. 2002). Nevertheless, we report that trees in Grächen and St Niklaus did not record the well-known outbreaks of 1923, 1929, 1972 and 1981. The 1923 and 1929 outbreaks are described as 'light' and 'weak' (type 3) outbreaks (Weber 1997, Baltensweiler and Rubli 1999, Weidner et al. 2010). The 1972 and 1981 outbreaks are considered 'medium' outbreaks in Valais in general (Baltensweiler and Rubli 1999), but in the Lötschental are classified as more severe (type 1) in 1972 and less severe (type 3) in 1981 (Weidner et al. 2010). In contrast to the Lötschental, the 1972 outbreak was 'weak' in the Goms Valley (Weber 1997). Regional differences in outbreak intensity therefore exist in the upper part of the Valais canton. We suggest that the 1923, 1929, 1972 and 1981 outbreaks were all low-intensity outbreaks in Grächen and St Niklaus, and were consequently not captured in tree rings.

Tree-ring analyses substantiated that LBM defoliation negatively influences radial growth of European larch in the initial year of an outbreak and over several subsequent years (Weber 1997, Rolland et al. 2001, Weidner et al. 2010). Growth suppression induced by LBM was manifest over 2–4 years, including the initial year of the outbreak and 1–3 subsequent years, which is consistent with previous observations (Nola et al. 2006, Battipaglia et al. 2014). The 1937, 1945 and 1954 outbreaks are high-intensity outbreaks (type 1) showing maximum growth reduction in the first year of the outbreak, whereas the 1888, 1908 and 1963 outbreaks are medium-intensity outbreaks (type 2) showing this reduction in the second or third year of the outbreak. We are the first to discuss outbreak intensity for the 1888 outbreak. Results for the other outbreaks concur with those of nearby Lötschental, except for the 1963 outbreak, which is classified as more severe (type 1) in that valley (Weidner et al. 2010). We here demonstrate the existence of regional differences in outbreak intensity in the upper part of the Valais canton, which may stem from regional differences in land-use affecting host abundance, connectivity between forest stands and thereby outbreak intensity (Johnson et al. 2004, Battipaglia et al. 2014, Hartl-Meier et al. 2017).

Comparison of tree-ring parameters

Larch bud moth defoliation significantly reduced total ring width, as well as earlywood width, latewood width and blue intensity. We support that growth loss is an important ensuing effect of insect defoliation (Kulman 1971), while emphasizing anew that it concerns more than total ring width.

Earlywood width Following LBM defoliation, earlywood width responded similarly to total ring width in the type and magnitude of change, i.e., with an average decrease of >50%. Conifer tree rings mostly consist of earlywood (Vaganov et al. 2006). Reduced total ring width in European larch therefore led to reduced earlywood width. Earlywood became narrower due to the formation of smaller and less numerous cells (Schweingruber 1979, Vaganov et al. 2006).

As for the duration of change, earlywood width and total ring width were reduced significantly starting in the first year of the outbreak in type 1 outbreaks and in the second year of the outbreak in type 2 outbreaks. In the latter case, maximum growth reduction, synonymous with maximum feeding activity, occurred in the second or third year of the outbreak. Larvae development was possibly delayed due to unfavorable weather conditions in spring, leading to defoliation in late summer (Weber 1997, Rolland et al. 2001) when earlywood formation is already completed (Cuny et al. 2014) and when trees start storing carbon reserves for the next year (Pallardy 2008). In the following spring, diminished carbon reserves due to late-summer

Table 2. Changes in tree-ring parameters in LBM defoliation years.

	Total ring width		Earlywood width		Latewood width		Blue intensity	
	P-value	% Change	*P*-value	% Change	*P*-value	% Change	*P*-value	% Change
1888	ns	−44	ns	−36	0.003	−61	0.002	−32
1889	0.003	−56	0.003	−53	0.002	−58	ns	−25
1890	0.001	−56	0.001	−58	0.006	−56	ns	−28
1908	ns	−50	ns	−45	<0.001	−67	<0.001	−24
1909	<0.001	−69	<0.001	−71	<0.001	−67	0.001	−25
1937	<0.001	−56	<0.001	−55	<0.001	−71	<0.001	−35
1938	<0.001	−57	<0.001	−60	<0.001	−55	<0.001	−21
1939	<0.001	−42	<0.001	−44	0.001	−45	0.001	−19
1945	<0.001	−62	0.007	−57	<0.001	−70	<0.001	−40
1946	0.002	−53	0.004	−58	0.002	−55	ns	−23
1954	ns	−45	ns	−41	ns	−51	ns	−23
1955	ns	−41	ns	−46	ns	−28	ns	−8
1963	ns	−45	ns	−17	<0.001	−58	<0.001	−28
1964	<0.001	−52	<0.001	−45	<0.001	−68	<0.001	−30
1965	<0.001	−71	<0.001	−69	<0.001	−75	<0.001	−36
1966	<0.001	−63	<0.001	−59	<0.001	−65	<0.001	−24
Mean ± SD		−54 ± 10		−51 ± 13		−59 ± 12		−26 ± 8

The Kruskal–Wallis test was run for each tree-ring parameter to quantify differences between individual years of LBM defoliation and the 2 years prior. An individual year had to be significantly different ($P < 0.05$) from both prior years to reject the null hypothesis, otherwise changes were deemed non-significant (ns). For significant changes, the higher of the two *P*-values was reported.

defoliation caused earlywood width to decrease and, thereby, record LBM defoliation 1 year after the start of the outbreak. As a consequence, earlywood width and total ring width may bear a lag of 1–2 years between the initial year of LBM defoliation and the peak of growth reduction. Similarly, several studies on budworm (*Choristoneura* spp.) defoliation report a lag of 1–4 years between the onset of defoliation and the onset of noticeable growth suppression (Alfaro et al. 1982, Swetnam et al. 1995, Mason et al. 1997, Ryerson et al. 2003, Axelson et al. 2014) due to previously stored photosynthates that permit radial growth to continue after defoliation (Alfaro et al. 1982).

Latewood width Similar to earlywood width and total ring width, latewood width exhibited an average decrease of >50% in response to LBM defoliation. The 59% decrease was the highest amongst the four tree-ring parameters, which was not verified in the non-defoliation years tested (42% decrease). Latewood, like earlywood, became narrower due to the formation of smaller and less numerous cells (Schweingruber 1979, Vaganov et al. 2006). More importantly, reduced latewood width following LBM defoliation is associated with the incidence of light rings (Schweingruber 1979, Weber 1997, Nola et al. 2006). A key indicator of insect defoliation in many conifers, light rings are characterized by thin-walled latewood cells that appear lighter under a microscope (Filion et al. 1986, Liang et al. 1997). Light rings have exceptionally low latewood density (Esper et al. 2007), as low cell wall thickness is related to low wood density (Vaganov et al. 2006).

Latewood width was reduced significantly starting in the first year of the outbreak in both type 1 and type 2 outbreaks. Contrary to earlywood width and total ring width, latewood width detected LBM defoliation with no lag between the initial year of LBM defoliation and the peak of growth reduction. By comparison, latewood width reduction in non-defoliation years was mostly non-significant. We therefore stress that latewood width ought to be used alongside total ring width to date LBM outbreaks with more temporal accuracy and help differentiate between defoliation and non-defoliation years. Several studies on larch sawfly (*Pristiphora erichsonii* Hartig) defoliation have emphasized the higher potential of latewood width compared with total ring width to detect defoliation (Harper 1913, Filion and Cournoyer 1995, Liang et al. 1997, Case and MacDonald 2003, Girardin et al. 2005). Similar to LBM type 2 outbreaks, larch sawfly outbreaks provoked a conspicuous decrease in latewood development in the first year of the outbreak, but no significant reduction in total ring width. This difference can be explained by the fact that earlywood formation, supplied from carbon assimilates of the previous year (Pallardy 2008), is completed by mid-August in conifers (Cuny et al. 2014). Earlywood is therefore largely formed when late larvae development postpones defoliation in late summer (Weber 1997, Rolland et al. 2001). Latewood, on the other hand, is produced between late August and late October (Cuny et al. 2014) from carbon assimilates of the current year (Pallardy 2008). Because of defoliation, latewood cells are 'starved in development' and show low cell wall thickening (Harper 1913).

Blue intensity Blue intensity exhibited an average decrease of <50% in response to LBM defoliation. The 26% decrease was the lowest amongst the four tree-ring parameters, which was

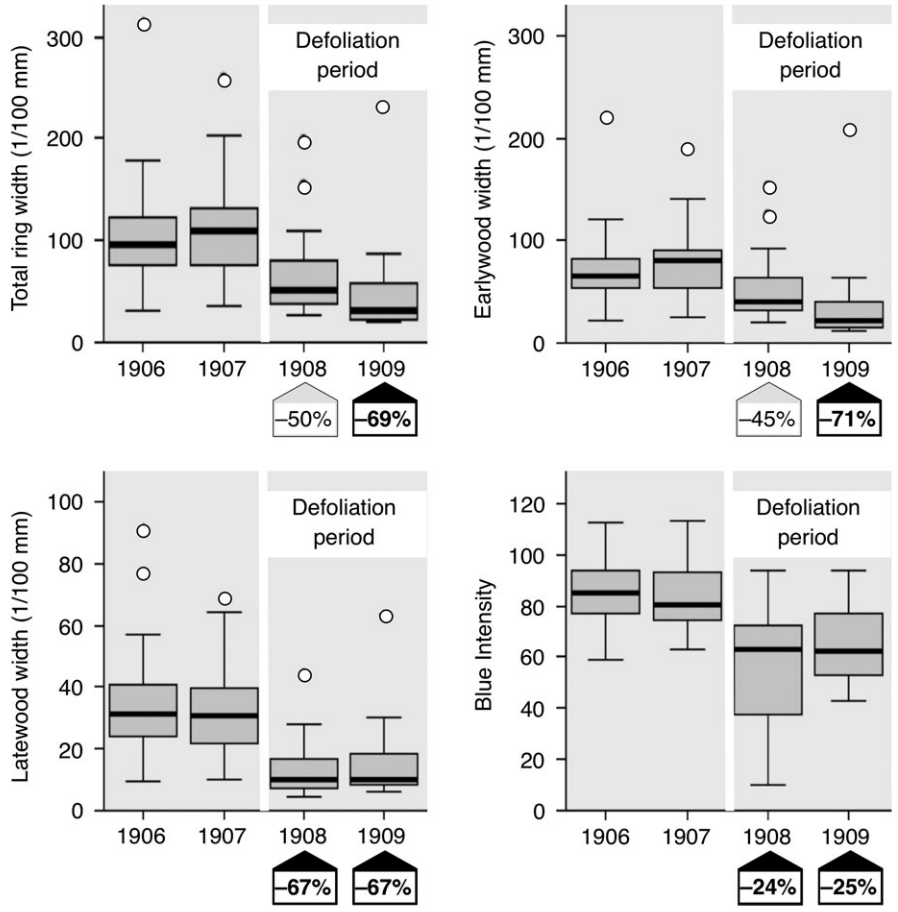


Figure 4. Changes in tree-ring parameters caused by the 1908 outbreak. Boxplots present the 2 years prior to defoliation (1906 and 1907) and the 2 years of defoliation (1908 and 1909). Growth suppression induced by LBM is given as percentages. Significant results appear in black.

Table 3. Changes in tree-ring parameters in non-defoliation years.

	Total ring width		Earlywood width		Latewood width		Blue intensity	
	P-value	% Change	*P*-value	% Change	*P*-value	% Change	*P*-value	% Change
1868	ns	–39	ns	–40	ns	–45	ns	–1
1884	ns	–60	ns	–60	0.020	–52	ns	–6
1933	0.006	–47	0.009	–53	ns	–29	ns	–10
Mean ± SD		–49 ± 11		–51 ± 10		–42 ± 12		–6 ± 5

The Kruskal–Wallis test was run for each tree-ring parameter to quantify differences between individual years of non-defoliation and the 2 years prior. An individual year had to be significantly different ($P < 0.05$) from both prior years to reject the null hypothesis, otherwise changes were deemed non-significant (ns). For significant changes, the higher of the two *P*-values was reported.

verified in the non-defoliation years tested (6% decrease). It is important to recall that, in this study, raw blue intensity data were inverted to facilitate comparison with the other tree-ring parameters. Poorly developed latewood, showing reduced width and lower density, normally translates to higher blue intensity (McCarroll et al. 2002, Campbell et al. 2007, 2011).

Blue intensity was reduced significantly starting in the first year of the outbreak in both type 1 and type 2 outbreaks. Similar to latewood width, blue intensity detected LBM defoliation with no lag between the initial year of LBM defoliation and the peak of growth reduction. By comparison, blue intensity reduction in non-defoliation years was always non-significant. As a consequence, even though we find that blue intensity is the weakest proxy of LBM defoliation we demonstrate its value as a complementary proxy to latewood width to date LBM outbreaks with more temporal accuracy and help differentiate between defoliation and non-defoliation years. Blue intensity, which is derived directly from latewood, and latewood width can be measured simultaneously in CooRecorder software (Larsson 2011), limiting the effort required to obtain the new line of evidence provided by blue intensity.

Conclusion

We show that latewood width and blue intensity can improve the temporal accuracy of LBM outbreak reconstructions, as both proxies systematically detected LBM defoliation in the first year it occurred, as well as the differentiation between defoliation and non-defoliation years. Developing precise tree-ring estimates of insect outbreaks increases our understanding of outbreak patterns over temporal and spatial scales, which is essential knowledge to adequately manage forests in the face of climate change. This study introduces blue intensity as a promising new proxy of insect defoliation and encourages its use in conjunction with latewood width. Nevertheless, more research is needed to test blue intensity in other defoliator systems.

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Conflict of interest

None declared.

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