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Journal Article**Author(s):**

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Publication date:

2009

Permanent link:

<https://doi.org/10.3929/ethz-b-000156863>

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Originally published in:

Oecologia 160(2), <https://doi.org/10.1007/s00442-009-1290-4>

Summer temperature dependency of larch budmoth outbreaks revealed by Alpine tree-ring isotope chronologies

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Received: 10 July 2008 / Accepted: 15 January 2009 / Published online: 14 February 2009
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Abstract Larch budmoth (LBM, *Zeiraphera diniana* Gn.) outbreaks cause discernable physical alteration of cell growth in tree rings of host subalpine larch (*Larix decidua* Mill.) in the European Alps. However, it is not clear if these outbreaks also impact isotopic signatures in tree-ring cellulose, thereby masking climatic signals. We compared LBM outbreak events in stable carbon and oxygen isotope chronologies of larch and their corresponding tree-ring widths from two high-elevation sites (1800–2200 m a.s.l.) in the Swiss Alps for the period AD 1900–2004 against isotope data obtained from non-host spruce (*Picea abies*). At each site, two age classes of tree individuals (150–250 and 450–550 years old) were sampled. Inclusion of the latter age class enabled one chronology to be extended back to AD 1650, and a comparison with long-term monthly resolved temperature data. Within the constraints of this local study, we found that: (1) isotopic ratios in tree rings of larch provide a strong and consistent climatic signal of temperature; (2) at all sites the isotope signatures were not disturbed by LBM outbreaks, as shown, for example, by exceptionally high significant correlations between non-host spruce and host larch chronologies; (3)

below-average July to August temperatures and LBM defoliation events have been coupled for more than three centuries. Dampening of Alps-wide LBM cyclicity since the 1980s and the coincidence of recently absent cool summers in the European Alps reinforce the assumption of a strong coherence between summer temperatures and LBM defoliation events. Our results demonstrate that stable isotopes in tree-ring cellulose of larch are an excellent climate proxy enabling the analysis of climate-driven changes of LBM cycles in the long term.

Keywords Climate change · Defoliation · Dendrochronology · European larch · Stable isotopes

Introduction

European larch (*Larix decidua* Mill.) is a species of trees growing at the highest altitudes in the European Alps and also one of the most temperature sensitive in this zone. With a longevity of 850+ years and its widespread utilization as timber (Büntgen et al. 2006a), it is considered to be an ideal archive for summer temperature reconstructions. To date, however, only a few temperature reconstructions have been made from larch, and none of these have been based on stable isotopes. The only long-term temperature reconstructions for the greater Alpine region (GAR) were built from tree-ring width (TRW) and maximum latewood density (MXD) measurements of numerous living and historic larch trees (Büntgen et al. 2005, 2006b). Therefore, this species is vastly under-represented or even absent in tree-ring networks (Frank and Esper 2005; Treydte et al. 2007). One possible factor for this scarcity of studies on larch may be related to earlier research (e.g., Schweingruber 1985) that questioned the

Communicated by Jim Ehleringer.

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suitability of larch for climate reconstructions because of the periodic population waves of the gray larch budmoth (LBM, *Zeiraphera diniana* Gn.). The LBM is a foliage-feeding Lepidopteran insect that is characterized by periodical outbreaks (8- to 10-year intervals), mainly in the interior valleys of the European Alps (Baltensweiler et al. 1977). The feeding of the LBM on larch needles causes massive defoliation that results in reduced tree growth and, thereby, interfere with the climatic signal contained in tree rings. While relatively short time series of these oscillations have been compiled from multi-annual surveys (Baltensweiler and Rubli 1999), century-long series have been reconstructed from tree-ring data (Rolland et al. 2001; Weber 1997) with a recent study spanning the past 1200 years (Esper et al. 2007). The population cycles of LBM are affected by numerous interactions with lower (e.g., host plants, prey) and/or higher trophic levels (e.g., predators, diseases; Berryman 1996). Several mechanisms have been put forward to explain LBM oscillations, including behavioral changes in population quality (Baltensweiler 1993a), budmoth–disease interactions (Anderson and May 1980), induced host defenses (Fischlin 1982), and host–parasitoid interactions (Turchin et al. 2003). However, it remains unclear how these cycles are modulated by climatic influences (Esper et al. 2007).

Periodic oscillations in abundance are one of the most remarkable characteristics of many animal population dynamics that are present in many forest insect species in the groups of Lepidoptera (Leavitt and Long 1986; Simard et al. 2008; Weidner et al. 2006), Thysanoptera (Ellsworth et al. 1994), and Coleoptera (Haavik et al. 2008). At their peak abundance, populations may reach very high densities over large areas, resulting in massive defoliation (Berryman 1996; Kurz et al. 2008; Mattson and Addy 1975). It is unclear whether such events also alter isotopic ratios in tree-ring wood and cellulose.

Stable carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotopes in tree-ring cellulose provide a continuous record of environmental conditions during tree growth (e.g., Anderson et al. 1998; McCarroll and Loader 2004) that is complementary to classical dendrochronological variables such as ring width. Hence, isotopes have the potential to shed light on the relationship between population dynamics and climate variations as embodied in tree-rings. Physical conditions and tree responses are reflected in both isotopes. $\delta^{13}\text{C}$ values depend on factors affecting photosynthetic uptake of CO_2 (such as light, relative humidity, temperature, atmospheric CO_2 concentration). They are therefore modulated by stomatal conductance and the rate of carboxylation during photosynthesis, which are regulated in turn not only by climatic variables but also by other factors, such as nutrient and water availability (Farquhar et al. 1982; Leavitt and Long 1988). $\delta^{18}\text{O}$ values are constrained by the

isotopic ratio of the source water (Roden et al. 2000), the isotopic signature of leaf water, as a consequence of evaporation and the Péclet effect (Barbour et al. 2004), biochemical fractionation during biosynthesis of photosynthetic sugars, and the re-equilibrium exchange between the carbohydrate and xylem water during tree-ring xylem cellulose synthesis (Yakir et al. 1990).

There have been very few studies carried out on the impact of phytophagous insects on the stable isotope composition in plant material and, in addition, the results of these are rather controversial. While some insect–isotope studies observed enriched $\delta^{13}\text{C}$ values in the tree rings of host species during infestations (Leavitt and Long 1986; Simard et al. 2008) or hardly any effect (Weidner et al. 2006), others inferred a complete lack of infestation response based on unaltered $\delta^{13}\text{C}$ signatures and unaffected water use efficiency (the ratio between photosynthesis and transpiration) (Ellsworth et al. 1994; Haavik et al. 2008). Investigations of the influence of forest insect outbreaks on $\delta^{18}\text{O}$ values are extremely rare and restricted to Lepidoptera: while Weidner et al. (2006) described a slight decrease, Simard et al. (2008) observed no changes in $\delta^{18}\text{O}$ signatures during outbreak events. By combining enriched $\delta^{13}\text{C}$ and unaffected $\delta^{18}\text{O}$ values in outbreak years, Simard et al. (2008) concluded that there may be an influencing factor other than climate. If factors other than climate dominate the isotopic signatures during insect infestations, climate reconstructions will be biased. Disentangling the role of insect infestations and climate on isotopic signatures in tree-ring cellulose is thus essential to prevent artifacts and, consequently, errors in climate reconstructions.

We have performed a study in which we assessed the relationship between LBM outbreaks and the carbon and oxygen signatures obtained from tree-ring cellulose of larch (*Larix decidua* Mill.). We combined an intra-species comparison of larch from two different valleys within the main crest of the Swiss Alps, canton Valais (northern and southern aspect each; AD 1900–2004), with an inter-species comparison between the LBM host species larch and the LBM non-host species spruce (*Picea abies*) from one of these sites for tree individuals within an age class of 150–250 years. To extend our investigated period and to take into account possible age-dependent effects of tree individuals on isotopic signatures during LBM outbreaks and their response to climate, we built an additional isotope chronology from older individuals (450–550 years) extending back to AD 1660. Thus, our objectives are twofold: (1) to clarify whether LBM-induced defoliation events have an impact on isotopic signatures in tree-ring cellulose, thereby masking climate signals, and (2) to address the long-term relationship between climatic conditions and LBM oscillations.

Materials and methods

Sampling strategy

Larch samples (*Larix decidua* Mill) were collected at two locations situated within the subalpine belt of larch–Swiss Stone pine (*Pinus cembra*) forests: the Lötschental (LOE) and the Simplon (SIM) region, both near the main crest of the Swiss Alps, canton Valais (coordinates of the individual sites are provided in Table 1). The elevation of the sites varies between 1800 and 2200 m a.s.l. Sampling occurred within the framework of the EU project Millennium. In each valley, trees were cored twice at breast height using a 5-mm increment borer. Thereby, care was taken to select trees under similar growth conditions on north-facing (N) and south-facing (S) slopes near the upper tree line. At both sites and both aspects, trees within an age-class of 150–250 years (LOE-S, LOE-N, SIM-S, SIM-N) were sampled. In the Lötschental, additional samples from 450- to 550-year-old individuals (CHRONO-N and CHRONO-S) were collected (Table 2).

Table 2 Long-term chronology of detected LBM events in 450- to 550-year-old individuals in the Lötschental region

LBM events	19th Century	18th Century	17th Century
CHRONO (average of S and N)	1896	1777	1685
	1888	1771	1675
	1880	1758	1668
	1856	1753	1660
	1830	1743	
	1821	1732	
	1813	1720	
	1801	1708	
		1703	

Sample analysis

Tree-ring width was measured with a semi-automated RinnTech system (0.01-mm resolution; Heidelberg, Germany) and cross-dated following standard procedures (Stokes and Smiley 1968) and the program COFECHA (Holmes 1983) to ensure correct dating of each tree ring to

Table 1 Site characteristics and detected gray larch budmoth (*Zeiraphera diniana* Gn.) events for each of the study sites

Site character	Study sites ^a					
	CHRONO-S	CHRONO-N	LOE-S	LOE-N	SIM-S	SIM-N
Latitude °N	46°26'	46°23'	46°26'	46°23'	46°12'	46°11'
Longitude °E	7°48'	7°47'	7°48'	7°47'	8°04'	8°03'
Aspect	140°	345°	14°	345°	220°	20°
Slope	35°	40°	35°	40°	25°	30°
Altitude (m a.s.l.)	2100	2200	2100	2200	1800	1800
Time period	1650–2004	1650–2004	1900–2004	1900–2004	1900–2004	1900–2004
Number of trees	3	2	4	4	4	4
Age class (years)	400–500	400–500	150–250	150–250	150–250	150–250
LBM events (20th century)	1981	1981	1981	1981	1981	1981
		1974		1974		
			1972		1972	1972
			1963	1963	1963	1963
		1954	1954	1954	1954	1954
		1945	1945	1945	1945	1945
		1937		1937		1937
					1925	1925
		1923	1923	1923	1923	
		1915		1915		
			1912		1912	
		1908	1908	1908	1908	1908

LBM, Gray larch budmoth (*Zeiraphera diniana* Gn.)

^a Study sites: CHRONO-S, CHRONO-N, long-term chronology sites (S, south-facing; N, north-facing) in the Lötschental region; LOE-S, LOE-N, younger material from the Lötschental region; SIM-S, SIM-N, younger material from the Simplon region

its calendar year of formation. Four to five dominant trees from each field site were selected for isotope analyses. These trees were split year-by-year using a scalpel; earlywood and latewood were not separated because of the rings being too narrow, and there was therefore insufficient material for isotope measurements. Isotope analysis of 50 sub-samples showed a very strong correlation between latewood and earlywood isotope values, thus justifying whole-ring analysis (data not shown).

For the 20th century (AD 1900–2004), the CHRONO samples were measured on a single-tree basis (two cores per tree, two and three trees, respectively), while for the period AD 1899–1650, five trees and two cores per tree were pooled prior to analysis for each annual ring. The four trees (two cores per tree) of each additional stand (LOE-N, LOE-S, SIM-N, SIM-S) were treated with the same pooling approach (Tables 1, 2). The pooling of rings of the same year from different cores has been used successfully for climate analysis; this approach retains the annual resolution, but the workload for sample preparation is reduced (Treydte et al. 2007). Alpha cellulose was extracted using standard procedures (Boettger et al. 2007) adapted for larch (1 vol% NaClO₂ solution; only one NaOH step with 17 vol% NaOH at 25°C), homogenized by sonification, and freeze-dried for 24 h. Carbon isotopic ratios were assigned with a reproducibility of 0.1‰ by combustion to CO₂ at 1025°C in an elemental analyzer (EA-1110; Carlo Erba Thermoquest, Milan, Italy) coupled to an isotope ratio mass spectrometer (Delta S or Delta Plus XL; Thermo Finnigan Mat, Bremen, Germany). Oxygen isotopic ratios were determined after pyrolysis to CO at 1080°C, with a reproducibility of 0.3‰ using a continuous flow method similar to that used for carbon and with the same mass spectrometers connected via a variable open-split interface Conflo II (Thermo Finnigan Mat; Saurer and Siegwolf 2004). The isotope values were expressed as a ratio of heavy to light isotope (R_{sample}) in the delta notation as

$$\delta^{13}\text{C} \text{ or } \delta^{18}\text{O} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1,000\text{‰}$$

relative to an international standard (R_{standard} : VPDB for carbon and VSMOW for oxygen). All $\delta^{13}\text{C}$ isotope series were corrected for the decline in $\delta^{13}\text{C}$ of atmospheric CO₂ due to fossil fuel burning since the beginning of industrialization using ice core data supplemented with the isotope measurements of atmospheric CO₂ for recent years (Leuenberger 2007).

To assess the strength of the isotopic signal, we calculated the mean inter-series correlations (RBAR) and the expressed population signal (EPS) for each isotope series. While RBAR is a measure of common variance between single series, EPS is an absolute measure of chronology

variance (threshold usually set to $\text{EPS} > 0.85$; McCarroll and Loader 2004).

Tree-ring width data were standardized using a 150-year cubic smoothing spline filter (Esper et al. 2002) to remove the age-trend while preserving mid-term variations. A single isotope and TRW chronology was developed for the CHRONO samples (AD 1650–2004; for the period AD 1900–2004, each tree separately) and all other sites (AD 1900–2004).

Climatic data

We used two alpine-wide meteorological datasets: (1) the HISTALP database (Auer et al. 2007) of monthly homogenized instrumental temperature (back to AD 1760) and precipitation measurements (back to AD 1800) for the GAR (4–19°E, 43–49°N, 0–3,500 m a.s.l.) and (2) the gridded dataset “European Alps Temperature and Precipitation Reconstructions” (Casty et al. 2005) where instrumental data were combined with documentary proxy evidence at a $0.5^\circ \times 0.5^\circ$ resolution covering the period AD 1500–2000. While the AD 1901–2000 period is based on CRUTS2 data (Mitchell and Jones 2005), the period prior to the 20th century is based on documentary evidence that does not include any tree-ring evidence at any time.

Annual isotopic data of combined N- and S-CHRONO samples (AD 1900–2004) were compared with all existing monthly temperature (19) and precipitation (32) series (averaged prior to calculation) obtained from the Swiss part of the HISTALP database. Correlation analysis was conducted on a monthly basis from March of the previous year to December of the current year as well as on seasonal averages, using bootstrapped correlation analysis for significance testing ($P < 0.05$; Guiot 1991). To quantify temporal changes in the relationship between climate and tree-ring isotopes, we additionally calculated moving correlations over 40-year time windows, thus producing a time series of bootstrapped correlation coefficients on a monthly basis from January to October of the current year (Biondi and Waikul 2004; Reynolds-Henne et al. 2007).

In addition, the monthly temperature reconstructions of Casty et al. (2005) from the grid cell 46.25°N 7.75°E covering the Lötschental were used for the analysis of the climate–isotope–LBM relationship over time (AD 1660–2000).

Gray larch budmoth outbreaks and stable isotopes

To accurately detect LBM outbreaks, all samples were screened for particularly narrow TRW and/or irregular latewood cells (missing, malformed, or lighter brown) following the dendrochronological skeleton plot technique (Schweingruber et al. 1990) and compared to a TRW

dataset of larch samples containing 78 samples from the Simplon region and 330 samples from the Lötschental region (Büntgen et al. 2005). Moreover, a dataset of 180 MXD series from the same sites (Büntgen et al. 2006b) was screened for exceptionally low MXD values caused by LBM outbreaks. The comparison of these data with historical records of LBM outbreaks reaching back to AD 1850 (Baltensweiler and Rubli 1999) and back to AD 832 (Esper et al. 2007) enabled us to identify—on an annual basis—seven to nine LBM outbreaks within the 20th century and 21 over the 1650–1899 period. Some years were only detected on one of the slopes (Tables 1, 2).

Superposed epoch analysis (SEA) and Wilcoxon–Mann–Whitney tests were applied to identify potential isotope responses to outbreak events in the isotope records. The SEA method isolates signals that are difficult to detect against relatively large levels of background noise (Adams et al. 2003). We applied SEA to our LBM events as follows: for each detected defoliation event, an 11-year window was centered on the outbreak year (defined as year 0). This provides a reasonable interval for resolving responses to LBM outbreaks without having to extend from one LBM event into another (8- to 10-year interval). The Wilcoxon–Mann–Whitney test (also called Wilcoxon–Mann–Whitney rank sum test) was used to quantify differences between two independent groups. The P_{wilcox} value indicates whether there is a statistically significant difference between the medians of the two groups (this is the case if $P_{\text{wilcox}} < 0.05$; Stahel 2002).

Isotopic values of host (larch) and non-host (spruce) species during LBM outbreak years were compared. To this end, we used a published carbon isotope (Treydte et al. 2001) and a new oxygen isotope dataset obtained from usually LBM-unaffected spruce (*Picea abies*). The sampled spruces originate from six mid- to high-elevation sites (1400–1950 m a.s.l.) of the northern and southern aspects in the Lötschental, Valais, Switzerland. They are located nearby our larch sampling sites and cover a period of 50 years (AD 1946–1995).

Results

Climate–isotope relationship (AD 1900–2004)

The separate analysis of five trees (two from the N-facing and three from the S-facing slope) from the CHRONO site for AD 1900–2004 showed a highly synchronous carbon and oxygen isotope signal in all trees, as indicated by the mean inter-series correlation (RBAR = 0.76 for carbon and 0.81 for oxygen) and the EPS (0.94 for carbon and 0.96 for oxygen). Both statistics thus suggest a strong climate forcing at this site. Absolute differences between the mean values of

the trees were up to 1.6‰ for $\delta^{13}\text{C}$ and 1.5‰ for $\delta^{18}\text{O}$, but these are not considered further because all analyses were performed with the average site chronologies only.

Hence, we calculated correlations between the average $\delta^{13}\text{C}$ - and $\delta^{18}\text{O}$ -isotope series of old trees CHRONO (corrected for the decline in $\delta^{13}\text{C}$ of atmospheric CO_2) and monthly averaged temperature values (Fig. 1). Figure 1a shows the significant positive correlations between both isotope series and summer temperature ($P < 0.05$). The highest correlations were achieved when the July to August temperatures were averaged prior to the calculation: correlation coefficients between temperature and $\delta^{13}\text{C}$ are clearly higher ($r = 0.68$) than those between temperature and $\delta^{18}\text{O}$ ($r = 0.49$). Previous year conditions do not have a significant effect on either carbon or oxygen values, as there are no significant correlations between the isotope series and the months of the previous year (not shown in Fig. 1). In addition to finding high positive correlations with temperature, we also found negative correlations with precipitation (not shown in Fig. 1). This result was expected, as temperature and precipitation are anti-correlated climate parameters in this region.

To test the temporal stability of the climate–isotope relationship, we calculated 40-year running correlations between the monthly temperature records and both isotope series (Fig. 1b). In general, we found positive correlations with temperature for the entire century, which is consistent with the finding above. The temperature signal in both isotope series is mainly restricted to July and August of the current year. Although the correlation coefficients are slightly higher between $\delta^{13}\text{C}$ and temperature than between $\delta^{18}\text{O}$ and temperature, temporal stability is given. Nevertheless, no distinct temporal shifts in the climate–isotope relationship are indicated.

Tree growth, LBM outbreaks, and climate

To determine the influence of LBM outbreaks on various tree-ring parameters without a climatic bias, we calculated the residuals between TRW, $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of the CHRONO samples and the July to August temperature for the period AD 1900–2004 by plotting the tree-ring parameters against climate variables and fitting a regression line (Fig. 2). The LBM event years are highlighted on Fig. 2 to characterize their distribution within all sample years. While for TRW the LBM outbreaks are obviously outliers compared to all years, the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of the LBM event years do not show a significantly different distribution compared to the entire data set. The P_{wilcox} value for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ is higher by a factor of 10–12 compared to the threshold ($P_{\text{wilcox}} < 0.05$), but the TRW–temperature relationship is noticeably lower (compare P_{wilcox} values in Fig. 2), indicating a significant difference

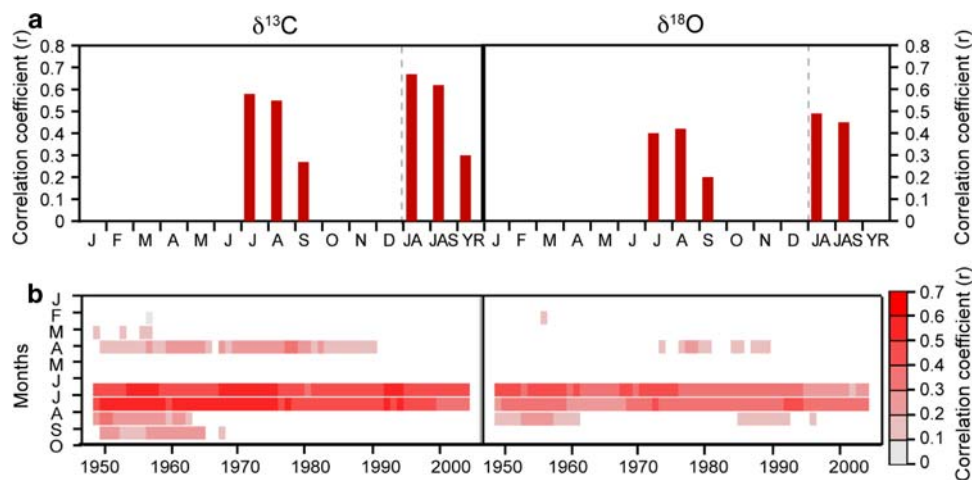


Fig. 1 **a** Bootstrapped significant correlation coefficients ($P < 0.05$) calculated for the stable carbon isotope ($\delta^{13}\text{C}$; left) and stable oxygen isotope ($\delta^{18}\text{O}$; right), averaged monthly temperature for January (J) to December (D) of the current year, averaged for July/August (JA), July/August/September (JAS) and for the entire year (YR) for AD 1900–2004 using the HISTALP dataset. **b** Forty-year running mean values of significant bootstrapped correlation coefficients ($P < 0.05$;

insignificant correlations set to 0) for $\delta^{13}\text{C}$ (left) and $\delta^{18}\text{O}$ (right) and monthly temperature. As indicated on the y-axis, the calculation was performed for individual months January (J) to October (O) of the current year for AD 1900–2004 (40-year window determines 1940 as the first year in the graph). The scale indicates the sign and strength of the correlations

between the LBM event years and non-affected years for TRW, but not for both isotopic ratios.

Site-specific aspects of LBM dynamics (AD 1900–2004)

Results of the SEA (Fig. 3) showed a significant decrease of TRW during the outbreak year, which was even more distinct in the year thereafter for all stands (CHRONO, LOE, SIM). Despite this obvious effect on TRW, hardly any effect was evident from the isotope parameters. The SIM site, in particular, does not show any response of stable isotope signatures during LBM outbreaks. The $\delta^{13}\text{C}$ decrease during LBM outbreaks at the CHRONO and LOE sites is scarcely visible and within the error margins, and the minor effect in the case of $\delta^{18}\text{O}$ does not exceed the overall amplitude of the signal.

Although some outbreak events were detected on only one of the slopes, the response was identical to those that occurred on all slopes. Comparisons of the northern versus southern aspects of the stands revealed no difference in terms of LBM outbreaks for any of the three parameters. The larger variability within the LOE and SIM sites compared to the CHRONO site may be due to a more individualistic response of younger trees to LBM outbreaks (Esper et al. 2007).

Species-specific response

For the period AD 1946–1995, we compared isotopic data of LBM non-host spruce (*Picea abies*; compare Treydte

et al. 2001) with our LBM host data from the Löttschental (CHRONO, LOE-S, LOE-N; Table 3). The spruce samples are about the same age as the LOE-S and LOE-N stands (150–250 years), whereas the CHRONO samples are older (450–550 years). Surprisingly, spruce correlated with larch for $\delta^{13}\text{C}$ in the same range ($r_{\text{CHRONOLOGY}} = 0.82$, $r_{\text{LOE-S}} = 0.72$, $r_{\text{LOE-N}} = 0.69$) as the larch sites were correlating among each other (between $r = 0.87$ and 0.69). This indicates that inter-species relationships were as strong as intra-species relationships at the same site. Oxygen isotopes provided slightly weaker correlation coefficients between spruce and larch than among the larch sites; nevertheless, the oxygen correlations between spruce and larch were still highly significant ($P < 0.001$), indicating a strong relationship between larch (host) and spruce (non-host). Beyond these findings, we evaluated the host/non-host behavior of the carbon and oxygen isotopes (Fig. 4) during LBM event years by plotting spruce and larch isotope time series with normalized ordinates to account for the natural inter-species isotopic offset. During LBM outbreak years (1954, 1963, 1972 and 1981), host and non-host data revealed the same trend for carbon as well as for oxygen isotopes, showing again that isotopic signatures were not affected by LBM.

Long-term climate forcing and LBM outbreaks

Figure 5 shows all of the LBM event years ($n = 26$) of the period AD 1660–2000 for the TRW (Fig. 5b), $\delta^{13}\text{C}$ (Fig. 5c), and $\delta^{18}\text{O}$ (Fig. 5d) values of the chronology samples and compares these to the averaged July to August

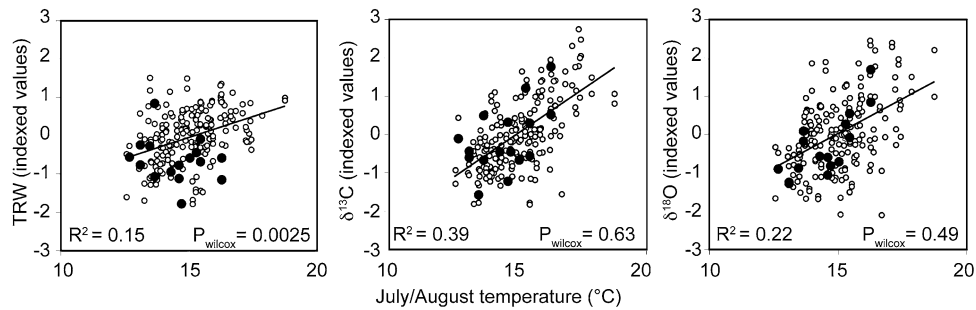


Fig. 2 Analysis of residuals of tree-ring width (*TRW*, *left*), $\delta^{13}\text{C}$ (*middle*) and $\delta^{18}\text{O}$ (*right*) of the chronology [averaged over south-facing (S) and north-facing (N) sites] with July/August temperature for the period AD 1900–2004. All values were standardized to the

same mean (=0) and standard deviation (=1). *Closed circles* Gray larch budmoth (LBM: *Zeiraphera diniana* Gn.) events ($n = 16$). P_{wilcox} values of the Wilcoxon–Mann–Whitney rank sum test indicate significant differences between groups if $P_{\text{wilcox}} < 0.05$.

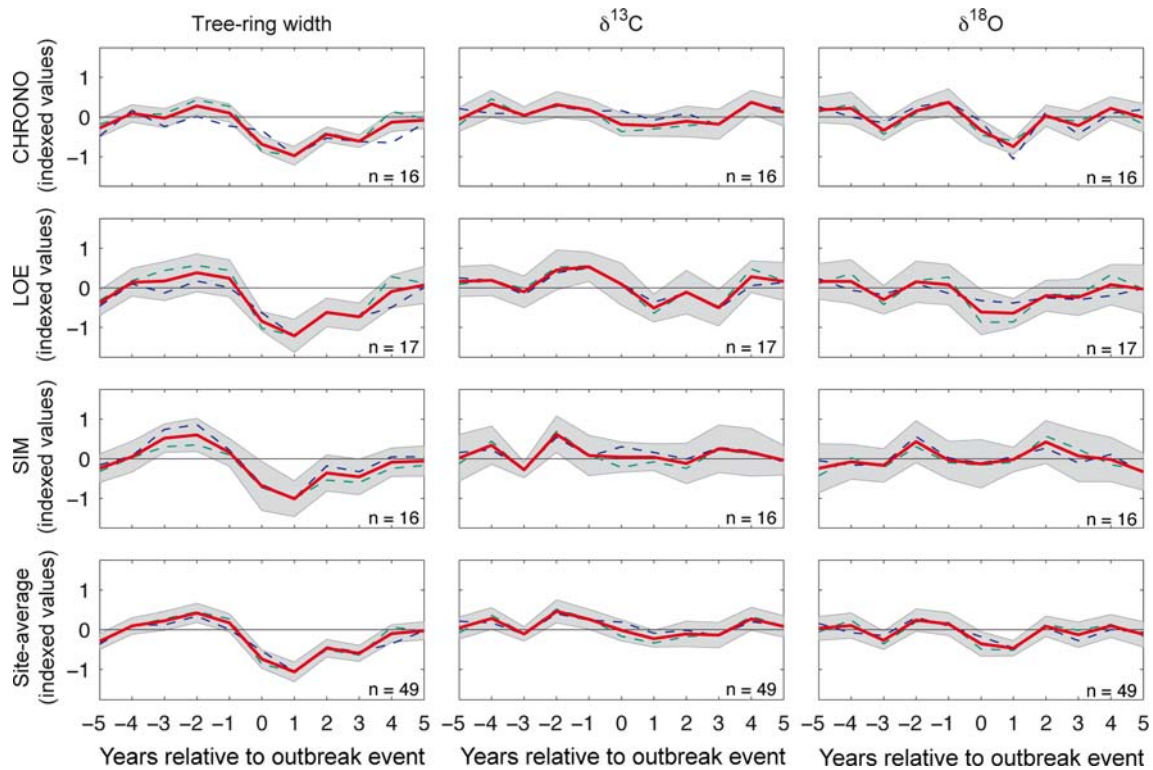


Fig. 3 Outbreak patterns in tree-ring data (tree-ring width, $\delta^{13}\text{C}$, $\delta^{18}\text{O}$) of the three sites (*CHRONO*, long-term chronology sites in the Löttschental region; *LOE*, younger material from the Löttschental region; *SIM*, younger material from the Simplon region) and the average of all sites for AD 1900–2004. All values were standardized to the same mean (=0) and standard deviation (=1). They are centered

on the outbreak event (*year 0*) and show values up to 5 years before and after these events. The *red curve* is an average of all outbreaks within one stand ($n =$ number of events averaged), combining data on the southern slopes (*green curve*) and northern slopes (*blue curve*). *Gray shadings* indicate ± 2 SE of the averaged *red curve*. The *horizontal black line* denotes the average over the 11-year window

temperature reconstruction of the corresponding grid cell (Casty et al. 2005; Fig. 5a) of these outbreak years. As noted above for the 20th century, TRW in the outbreak years is significantly below average, with only one exception (1896), whereas this is not the case for both isotope ratios. Interestingly, we observed that the July to August temperature in LBM event years was significantly lower than the long-term average value ($P_{\text{wilcox}} = 0.004$),

indicating that cool summers are conducive to LBM outbreaks. Such an anomaly in weather conditions during LBM event years was found only for the July to August temperature, while the temperature data of the other months were not found to be much different from long-term averages (data not shown). Apparently, the isotope ratios still respond to deviations in summer temperature during LBM years; in particular, the cold summer of 1758

Table 3 Correlation matrices between larch (CHRONO, LOE-S, LOE-N) and spruce for carbon isotopes and oxygen isotopes

	CHRONO (N and S averaged)	LOE-S	LOE-N
$\delta^{13}\text{C}$			
LOE-S	0.87***		
LOE-N	0.80***	0.69***	
Spruce	0.82***	0.72***	0.69***
$\delta^{18}\text{O}$			
LOE-S	0.89***		
LOE-N	0.77***	0.73***	
Spruce	0.68***	0.63***	0.54***

All correlation coefficients are highly significant (*** $P < 0.001$)

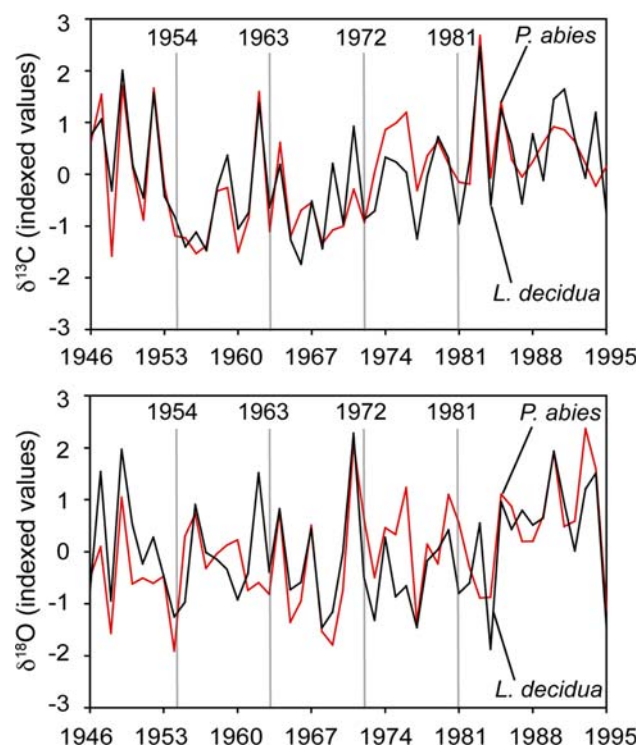


Fig. 4 A comparison of larch (black line; *Larix decidua* Mill.) and spruce (red line; *Picea abies*) $\delta^{13}\text{C}$ (upper panel) and $\delta^{18}\text{O}$ (lower panel) data in the Löttschental for the period AD 1995–1946 (maximum length of spruce data). All isotope values were standardized to the same mean (=0) and standard deviation (=1). Vertical bars specify LBM event years ($n = 4$)

is evidently reproduced in the signature of both isotopes. The correlation between isotope values and July to August temperature for these outbreak years is significant ($P < 0.05$) for $\delta^{13}\text{C}$ as well as for $\delta^{18}\text{O}$, similar to the results found for the calibration period for all years (see above). Interestingly, the correlation coefficient between TRW and temperature, when only LBM outbreak years are used, turned out to be slightly negative (not significant),

whereas one would expect a positive correlation between the two variables. This shows that the relationship between TRW and temperature is disturbed during years of LBM defoliation whereas the isotope–temperature relationship remains distinct.

Discussion

We have provided several lines of evidence that LBM events do not affect the isotope ratios in tree rings of larch, neither during nor after an outbreak year:

- The climate–isotope relationship of the calibration period (AD 1900–2004) reveals the expected results despite several strong outbreaks during this period: correlations are restricted to the vegetation period with robust, consistently positive correlations for temperature (in agreement with theoretical expectations; see McCarroll and Loader 2004). The magnitude of the correlation coefficients is amongst the highest yet reported. They are somewhat higher for carbon than for oxygen isotopes, with relationships being stable over the 20th century.
- When climate variations are removed by calculating residuals, there is no statistically significant difference in isotope values between years affected by LBM outbreaks and other years, whereas for TRW the differences are significant.
- SEA (reflecting an average response of all outbreaks) shows distinct decreases of TRW during LBM events (and the following years); the amplitudes of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ do not provide such a distinct deviation. This result is confirmed by trees of two different age classes and several sites that cover two different aspects (N vs. S) and located up to 50 km apart. The similar behavior of trees on north- and south-facing slopes is to be expected, as exposure has little effect on temperatures that are relevant for trees at such elevations (Körner and Paulsen 2004).
- Further evidence is provided by the high correlation coefficients between larch (host) and spruce (non-host) for both isotope series as well as by the similar curve patterns of the chronologies of different species from the same site in the absence of insect impacts. This similar behavior is not self-evident because the species may differ in their sensitivity to climate (Saurer et al., 2008; Treydte et al. 2007). The strong climatic limitation of tree growth at our high-altitude study sites may have a similar limitation effect on the isotope variations and thus result in the strong correlation between larch and spruce, even during LBM defoliation events.

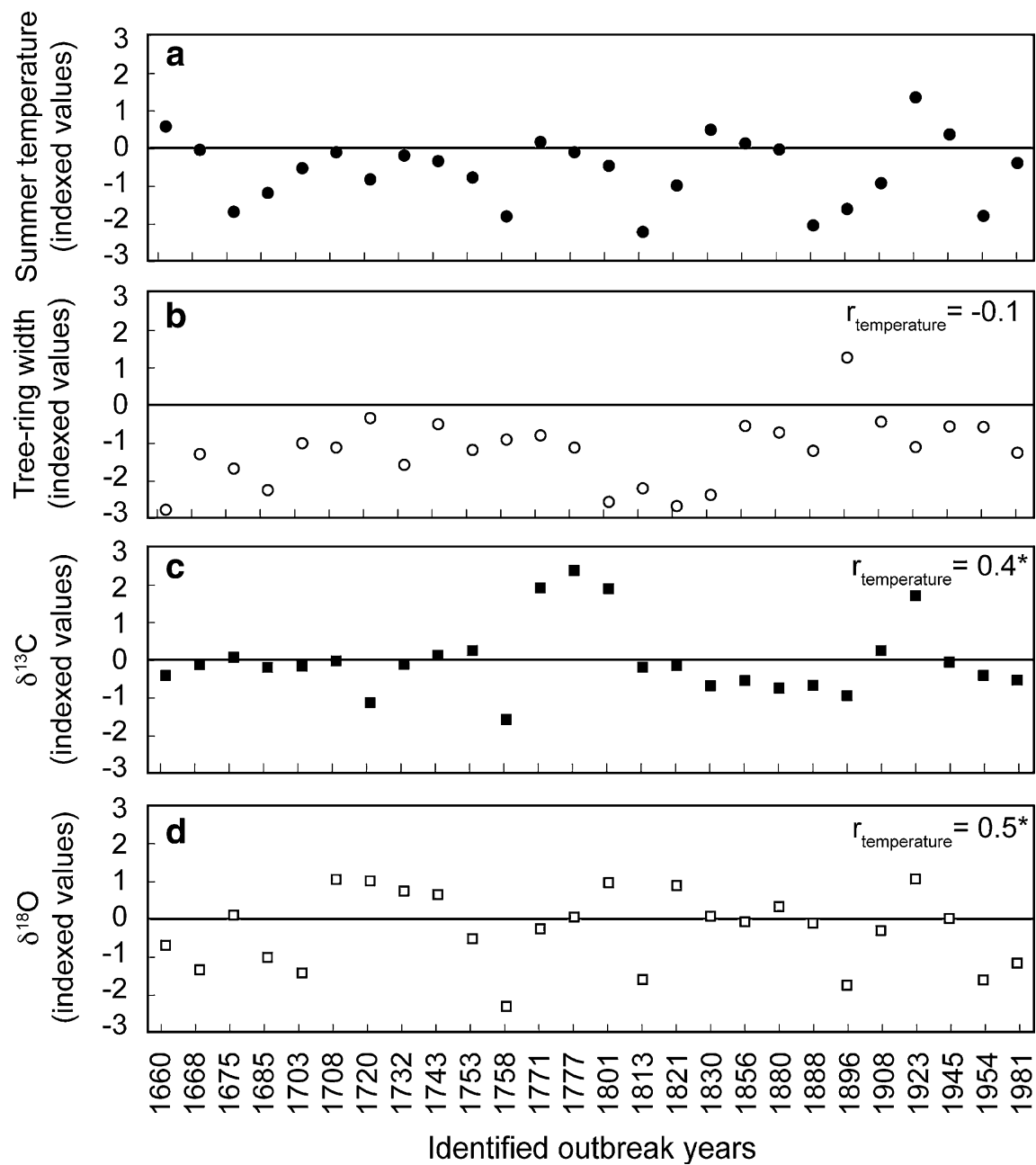


Fig. 5 All 26 outbreak years and tree-ring parameters for AD 1660–2000: **a** July to August temperature according to Casty et al. (2005), **b** tree-ring width, **c** $\delta^{13}\text{C}$, **d** $\delta^{18}\text{O}$. All values were standardized to the same mean ($=0$) and standard deviation ($=1$). Correlation coefficients

represent the relationship between tree-ring variables and reconstructed temperature ($*P < 0.05$). The horizontal black lines indicate the average over the 340-year period

The negligible effect of LBM infestations on tree-ring isotope ratios in larch, as shown above, is rather surprising, as even subtle changes in leaf physiology, such as stomatal closure (e.g., during water shortage), are known to strongly affect both carbon and oxygen isotopes (Barbour et al. 2004; Leavitt and Long 1988). The physiological response of conifers to insect-related defoliation could therefore significantly impact the rate of photosynthetic assimilation. Based on the hypothesis of an increased photosynthetic rate

as a compensatory mechanism for defoliation, this would trigger a $\delta^{13}\text{C}$ enrichment in tree-ring cellulose. The synchronous behavior of carbon and oxygen isotopes during LBM defoliation events suggests that isotope composition depends directly on climatic conditions. This synchronicity is present not only within species at different sites but also between host (larch) and non-host (spruce) species, thereby confirming that regional climate variations are primarily responsible for the isotopic composition.

We assume that during the main defoliation event itself, hardly any photosynthesis takes place due to either a lack of needles or desiccated or dysfunctional (brown) needles. Accordingly, very little photosynthates are produced and, thus, hardly any tree-ring cellulose is built in which a climatic signal could be incorporated. Consequently, the tree-ring cellulose of LBM outbreak years is formed either before the heavy feeding occurs or shortly thereafter, i.e., when larch trees re-leaf 3–4 weeks after defoliation (Baltensweiler et al. 2008). The re-leafing could explain the apparent phase shift between the main production of wood during outbreak years and the observed high correlations with July to August climate conditions, although it is difficult to establish a causal link. This theory is in agreement with results from previous studies on the impact of phytophagous insects on the carbon isotope composition of plant material showing a lack of infestation response on photosynthetic discrimination and carbon isotopic composition of the remaining leaf material and tree-ring cellulose (Ellsworth et al. 1994; Haavik et al. 2008).

Our unaffected isotopic signatures in tree rings during LBM outbreak events seem to be contrary to findings by Simard et al. (2008) who investigated another Lepidopteran species, the eastern spruce budworm (ESB, *Choristoneura fumiferana* Clem.). Their comparison of host species (*Abies balsamea* and *Picea mariana*) and non-host species (*Pinus banksiana*) revealed carbon isotope enrichments during two outbreak episodes, while oxygen isotopes remained unaffected. Although species of the same order, LBM and ESB have different life cycles: while LBM defoliation events are strongly coupled with one vegetation period and reoccur with a periodicity of 8- to 10-year intervals, ESB events appear in decadal scale frequency (32- to 34-year intervals) and last for 5 years and more. If trees are affected for several following years, they need to mobilize reserves to maintain functionality. Carbon allocation, however, can alter the isotopic signatures in tree rings in a characteristic manner (Keel et al. 2006). Thus, it may well be that ESB events influence the isotope signal while LBM outbreaks do not.

The absence of an isotope effect during LBM defoliation events is in contrast to the TRW response patterns. A narrow ring is formed not only during the outbreak year itself, but often—even more pronounced—in subsequent years (up to 6 years). Accordingly, the LBM effect dominates TRW relative to the climatic influence during these periods. Detecting a climate signal in TRW during LBM event years is still possible, but corrections are needed, such as a replacement of LBM-induced negative growth depressions with information derived from non-affected trees (Büntgen et al. 2006b; Esper et al. 2007).

When a long climate record covering more than three centuries is considered (Casty et al. 2005), cold summers

are often related to severe LBM outbreaks, and the isotope ratios reliably mirror these relatively cool conditions. Based on TRW only, this assumption would lead to circular reasoning because LBM detection is predicated on the identification of narrow TRW, which may, alternatively, be caused by cold summers. For further validation, we additionally calculated July to August temperatures (Casty et al. 2005) of the LBM outbreak events determined by Baltensweiler and Rubli (1999) for the Valais and Engadin regions for the period AD 1850–1990 and compared these to average July to August temperatures of AD 1660–2000. Although the number of identified outbreak events is, compared to our dataset, lower (according to the terminology by Baltensweiler and Rubli 1999 medium and heavy discoloration events were considered), we demonstrate significantly lower ($P < 0.05$) July to August temperatures during LBM event years compared to the long-term average for the Engadin ($P_{\text{wilcox}} = 0.011$) and the Valais regions ($P_{\text{wilcox}} = 0.024$), thus confirming our discovery.

This highly significant finding over a period of 340 years indicates that cool July to August temperatures promote LBM outbreaks—even if the latter are occurring at highly regular intervals. This is rather surprising as outbreaks are usually triggered earlier in the vegetation period and are likely to be linked to subcontinental climate dependencies of LBM population cycles: one dominating factor for an optimal development of LBM population cycles is the duration of the winter diapause, which is highly conditioned by annual temperature profiles. Two aspects are crucial for the survival of the 2-mm-long first instar larvae: the fixed amount of energy for egg development and hatching provided at the time of oviposition (usually in August) and the hatching of the larvae 9–11 months later simultaneously with the flushing of the larch trees. Ideal requirements to fulfill these criteria are long, cold winters with more than 120 days below 2°C. If spring and summer temperatures are high, the ontogenetic development from egg to moth is terminated soon, leading to an early diapause with fewer frost days, resulting in an elevated egg mortality (Baltensweiler 1993b; Baltensweiler et al. 1977). This finding is consistent with our discovery that devastating LBM events are coupled with low late-summer temperatures.

Another potential explanation for the ecological significance of low summer temperatures is the link between needle quality and summer temperatures. One basic regulatory mechanism of the LBM cycle is the induced change in food quality for two or more subsequent larval generations (Baltensweiler 1993b). Larch as a deciduous species re-grows its needles every year. Therefore, the LBM has to adapt its development to needle maturation and has to cope with large changes in food quality (e.g., raw fiber and

protein content). Synchronization of larvae evolution and needle maturation is a prerequisite for outbreak events (Asshoff and Hattenschwiler 2006; Baltensweiler et al. 1977). Slight asynchrony of these fine-tuned events may result in serious consequences for species interaction. If summer temperatures are a driving force for needle maturation, they indirectly have an impact on the LBM cycle as an LBM outbreak can occur only if needle maturation is in optimal agreement with LBM larvae development. Poor food quality, induced by above-average summer temperatures, leads to heavy larval and pupal mortality and reduced fertility, as observed by Baltensweiler et al. (1977) and Fischlin (1982). However, it has recently been suggested that LBM population cycles may be driven by parasitoids rather than changes in needle quality (Berryman 1996; Turchin et al. 2003). Therefore, an interaction between late-summer temperatures and parasitoids with an indirect effect on LBM populations cannot be ruled out completely.

The reconstructed persistence and regularity of LBM reoccurrence over the past 1200 years is remarkable (Esper et al. 2007). However, since the early 1980s no alpine-wide synchronized LBM outbreak event has occurred. Locally, LBM populations have attained sub-defoliating peak densities only, suggesting a diminishment of the oscillation amplitude, but not necessarily an alteration of the period. This absence of massive outbreaks is the longest detected within the last 1200 years. Simultaneously, temperature reconstructions from the European Alps reveal that conditions during the late 20th century represent the warmest period of the past millennium (Büntgen et al. 2006b; IPCC 2007). This coincidence together with our finding of July to August temperature dependencies of LBM outbreaks leads us to conclude that high summer temperatures can dramatically impair LBM dynamics. Similar observations have been made for oak–winter moth phenology (another Lepidopteran species), which has been significantly disturbed by recently higher spring temperatures (Visser and Holleman 2001). It remains to be seen how this recent warming trend will influence the prominent forest disturbance phenomenon of LBM infestations and how it will alter ecosystem processes in subalpine larch forests. We suggest that stable isotopes in tree rings in combination with TRW are a powerful tool to study the impact of climate on insect infestations over centuries to millennia, provided that isotope ratios are not affected by the outbreaks but by climate only, as was shown for the LBM in this study.

In conclusion, we would like to emphasize that besides our discovery of late-summer dependencies of LBM cycles, the preservation of a climatic signal in the isotopic signature of tree rings during LBM outbreak events is striking. While larch TRW and density contain a strong climatic signal after appropriate corrections for LBM

infestations, a more complete retrieval of information from this unique long-living archive is provided by the additional consideration of stable isotope ratios.

Acknowledgments This work was funded by the EU project FP6-2004-GLOBAL-017008-2 (MILLENNIUM). Thanks to A. Verstege and D. Nievergelt for support in the Dendro-LAB, to M. Tröndle and L. Läubli for assistance with sample preparation and to G. Helle for the oxygen measurements of the spruce samples. Many thanks also to U. Baltensperger and D. McCarroll for the valuable discussions and helpful comments. The experiments comply with the current laws in Switzerland.

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