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The potential for using *Larix decidua* ring widths in reconstructions of larch budmoth (*Zeiraphera diniana*) outbreak history: dendrochronological estimates compared with insect surveys

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Abstract In the Alps, larch (*Larix decidua* Mill.) forests show periodic discolouration due to larch budmoth (LBM) outbreaks (*Zeiraphera diniana* Guénéé, Lepidoptera: Tortricidae). Tree defoliation causes severe reductions in radial growth, visible in tree rings. This paper aims at reconstructing LBM outbreak history, and critically examining the potential for using dendrochronological data by comparing tree-ring estimates with insect surveys. The occurrence of LBM outbreaks was investigated using 249 cores from larch growing near the timberline in three regions of the French Alps (Briançonnais, Maurienne, and Tarentaise). Years with an abrupt decrease in radial growth (–40%) were considered as negative pointer years reflecting the potential impact of LBM. The comparison with three non-host conifers (Norway spruce, stone and mountain pines) permitted us to distinguish growth reductions in larch due to climatic effects from those due to defoliation by LBM. The dendrochronological data were matched with information reporting conspicuous discolouration in old forestry reports or recovered from systematic field observations. Twenty-two outbreaks are discernible within the period 1800–1983. A peak reduction in larch growth occurred at intervals of 8.86 ± 1.01 years in the following years: 1801, 1811, 1820, 1830, 1838, 1846, 1857, 1867, 1875, 1884, 1892, 1901, 1909, 1918, 1926, 1936, 1945, 1953, 1963, 1972, 1980, and 1987. Our objective method based on ring measurements and comparison with non-host trees was compared with qualitative techniques based on the visual detection of conspicuous latewood anomalies. Larch in the Briançonnais (which experiences a continental climate) are infested first, whereas the Tarentaise region exhibits a much weaker impact of LBM. Complete tree recovery was observable 3 years after outbreak peaks.

Keywords Dendroecology · European larch · *Picea abies* (L.) Karst · *Pinus uncinata* Mill ex Mirb. · *Pinus cembra* L.

Introduction

The importance of dendrochronological studies for the reconstruction of past insect outbreaks is well documented (Morrow and LaMarche 1987; Schweingruber 1996). The impact of defoliation on tree ring widths is closely related to the type of tree, the timing of defoliation within the growing season, and the prevailing climate (Fritts 1976). For instance, outbreaks of spruce budworm (*Choristoneura fumiferana*) on evergreen hosts (fir and spruce) were reconstructed with the help of dendrochronology by Maclean (1980) and Morin et al. (1993), and those of *Choristoneura occidentalis* by Swetnam and Lynch (1989), and Weber and Schweingruber (1995). Pine defoliation was similarly investigated (Laurent-Hervoüet 1986a, 1986b), and the impact of cockchafer (*Melolontha* sp.) on deciduous oak trees was dated using data on reductions in ring widths (Varley 1978; Christensen 1987; Vogel and Keller 1998).

The periodic impact of the larch budmoth (LBM; *Zeiraphera diniana* Gn.) on European larch growth was evaluated for the first time in the Engadine by Badoux (1952), and later by Geer (1975), Bovey and Grison (1975) and Weber (1997). Röhliberger (1976) reported periodic LBM outbreaks from the Zermatt region (Switzerland) as far back as 1548. Since then, further relevant work was published by Schweingruber (1979), and several LBM time-series were reconstructed for the Engadine and the Grisons (Switzerland) (Pignatelli and Bleuler 1988), as well as for Italy (Piton and Vidano 1989). Several other dendrochronological studies on larch (dealing with dating or climate) might also allow the reconstruction of LBM outbreaks for further regions in the European Alps (Serre 1978; Tessier 1981; Siebenlist-Kerner 1984; Bebbler 1990; Belingard and Tessier 1994; Nola 1994; Hüsken 1994; Urbinati et al. 1996).

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Although the larch plays an important economic role in the French Alps (Fourchy 1952; Pardé 1955), as it covers about 80,000 ha in its natural habitat (Florent 1970), such investigations have not yet been carried out in the French Alps, despite important consequences of defoliation on subalpine forest regeneration (Roques 1993) and the fact that the oldest written evidence concerning LBM outbreaks stems from the Briançonnais (Chaix 1845). Though, at that time, the phenomenon was attributed to spiders as the larch trees were covered entirely with cobwebs, there can be no doubt about the LBM having been the cause. Not only do all the other biological facts mentioned agree with existing knowledge, but the period 1811–1819 fits the 8/9-year periodicity of the outbreak cycle well, when counting back from the 1856 outbreak (Baltensweiler 1964; Baltensweiler and Rubli 1999). Therefore, it seemed worthwhile to analyse the occurrence of LBM outbreaks in the French Alps in the context of the large dendroecological investigation which has been in progress since 1993 by the Laboratoire des Ecosystèmes Alpains, Grenoble (Rolland et al. 1998).

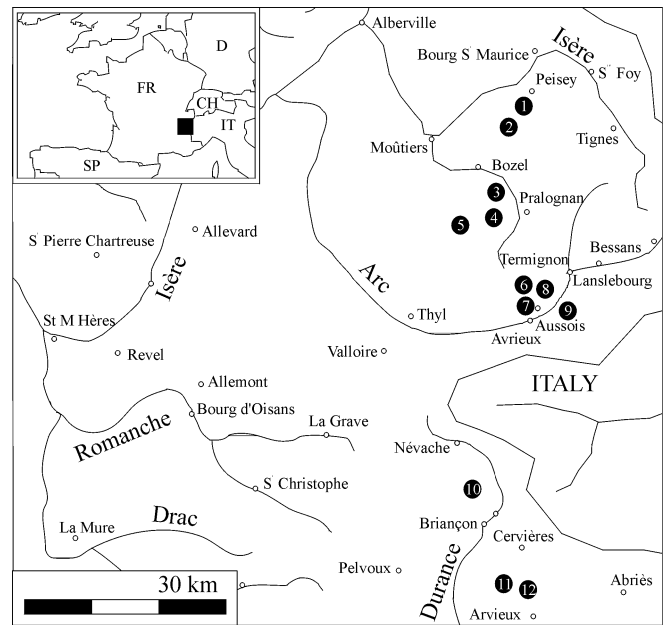
This dendroecological programme endeavours to elucidate the response of four conifer species to the impact of the harsh climate at the alpine timberline along the gradient from the outer to the inner Alps. From the 37 tree populations studied by this programme (Petitcolas et al. 1997), seven larch forests were selected and analysed for their specific growth response to LBM defoliation in order to reconstruct the sequence of outbreaks during a long period.

Moreover, the pattern of LBM outbreaks had been mapped according to their extent and intensity all over the European Alps since 1960 within the research programme Population Dynamics of the Larch Budmoth of the Institute of Entomology, ETH Zürich, in collaboration with the National Forest Service. Furthermore, information about LBM outbreaks had been systematically collected from forestry records and the literature for the entire subalpine distribution area of larch (Baltensweiler and Rubli 1999) as far back in time as available.

In this study, reconstructions of LBM outbreaks are attempted by combining two completely different monitoring techniques: (1) a dendrochronological reconstruction method, and (2) a tree-discolouration survey. We will attempt to answer two questions:

1. When did the main outbreaks of LBM occur during the last 200 years in the French Alps?
2. Are radial-growth reductions in larch consistent with the pattern of observed defoliation derived from the literature, insect surveys and forest archives?

Thus, this paper aims at critically examining the potential for using dendrochronological data in reconstructing the history of LBM outbreaks.



		Spruce	European Larch	Stone pine	Mountain pine
1	St Jacques	TSUE	TSUM	TSUA	
2	Bellecôte		TCUM	TCUA	
3	Chal	Tarentaise	TCAE		TCAP
4	Biol				TCUP
5	Tuédia		TSAE	TSAA	
6	Plan d'Amont			MSUA	MSUP
7	Barbier	Maurienne	MSAE	MSAA	
8	Mont Fleury		MCAE		MCAP
9	Le Jeu		MCUE	MCUM	MCUA
10	Granon	Briançonnais		BSAM BSUM	BSAP BSUP
11	Ayes				BCAA BSAA
12	Izoard		BCAM BCUM	BCUA BSUA	BCAP BCUP

Fig. 1 Map of sites from which dendrochronological data were obtained in south-eastern French Alps, with seven populations of *Larix decidua* (Mill.), nine of *Pinus uncinata*, ten of *Pinus cembra*, and eight of *Picea abies* (32 tree populations in total)

Materials and methods

Dendrochronological sampling

According to Weber and Schweingruber (1995), the reconstruction of LBM outbreaks has to be based on a great deal of chronological data in order to detect missing rings. Thus, seven subalpine populations of *Larix decidua* (Mill.) were sampled in three French alpine regions, from 1,980 to 2,260 m above sea level. They are located in the Briançonnais (four sites), the Haute-Maurienne (one site) and the Moyenne-Tarentaise (two sites) (Figs. 1, 2). In each population, three cores per tree were taken at breast height from 12 dominant trees. All ring widths were measured and cross-dated (Petitcolas 1998; Rolland et al. 1998). Thus, 83 larch trees were sampled with 249 cores covering >40,000 ring widths. The longest period of chronological data for larch covers 1665–1994 (330 years). The heights of the dominant trees sampled were between 9.5 and 26 m (with a mean value of 17 m) (Petitcolas et al. 1997).

LBM attacks are characterized by a great number of trees showing simultaneously a strong reduction in growth. However, according to Schweingruber (1996, p 306): "Narrow ring-widths can also form in climatically poor years", thus "reliable evidence is only possible when comparisons are made with less or unaffected species, e.g., with spruce and stone pine". Consequently, three other subalpine coniferous species were also sampled: Norway

Species	Code	Valley	Site conditions					Location		Sampling		Years		Age	
			Place	Soil	Aspect	elevation (m)		Lat N	Lon E	Cores	Rings	First	Last	Min	Max
Larix decidua (7)	BCAM	Briançonnais	Izoard 1	Calcareous	South	W/SW	2250	44°49'	6°44'	36	1851	1931	1993	33	63
	BSAM		Granon 1	Siliceous		SW	2250	44°48'	6°38'	36	7823	1710	1993	100	284
	BCUM		Izoard 2	Calcareous		N/NE	2150	44°50'	6°44'	36	7866	1734	1993	160	260
	BSUM		Granon 3	Siliceous		N	2250	44°48'	6°38'	33	6876	1734	1993	92	260
	MCUM	Maurienne	Le Jeu	Calcareous	North	NW	2100	45°14'	6°48'	36	6515	1665	1994	49	330
	TCUM	Tarentaise	Bellecôte 2	Calcareous		N/NE	2050	45°29'	6°42'	36	3097	1812	1993	55	182
	TSUM		St Jacques	Siliceous		N/NW	2000	45°30'	6°42'	36	6070	1737	1993	118	257
Pinus uncinata (9)	BCAP	Briançonnais	Izoard 1	Calcareous	South	W/SW	2250	44°49'	6°44'	36	2760	1819	1993	48	175
	BSAP		Granon 2	Siliceous		S	2300	44°57'	6°36'	36	3977	1758	1993	68	236
	BCUP		Izoard 2	Calcareous	North	N/NE	2150	44°50'	6°44'	35	6626	1749	1993	98	245
	BSUP		Granon 4	Siliceous		N/NW	2250	44°57'	6°36'	36	6667	1763	1993	114	231
	MCAP	Maurienne	M Fleury 2	Calcareous	South	S	2150	45°15'	6°45'50"	36	7833	1718	1993	116	276
	MCUP		Le Jeu	Calcareous	North	NW	2100	45°14'	6°48'	36	7160	1673	1994	99	322
	MSUP		P. d'Amont 2	Siliceous		N/NE	2100	45°15'	6°43'	36	3233	1770	1993	40	224
	TCAP	Tarentaise	Chal	Calcareous	South	S/SW	2050	45°25'	6°41'	36	4077	1757	1993	56	237
	TCUP		Biol	Calcareous	North	N	1950	45°23'	6°40'	36	2490	1885	1993	29	109
	Pinus cembra (10)	BCAA	Briançonnais	Ayes 1	Calcareous	South	SW	2300	44°50'	6°41'	36	3104	1862	1993	54
BSAA		Ayes 2		Siliceous		W/SW	2200	44°50'	6°41'	36	6253	1774	1993	105	220
BCUA		Izoard 2		Calcareous	North	N/NE	2150	44°50'	6°44'	36	7609	1711	1993	151	283
BSUA			Ayes 3	Siliceous		N	2300	44°49'	6°40'	36	5282	1710	1993	51	284
MSAA		Maurienne	Barbier	Siliceous	South	S	2000	45°14'	6°43'	36	3580	1862	1993	64	132
MCUA			Le Jeu	Calcareous	North	NW	2100	45°14'	6°48'	28	5739	1744	1994	123	251
MSUA			P. d'Amont 1	Siliceous		NE	2150	45°15'	6°43'	36	4261	1802	1993	49	192
TSAA		Tarentaise	Tuéda 2	Siliceous	South	S	2000	45°22'	6°36'	36	2726	1903	1993	39	91
TCUA			Bellecôte 1	Calcareous	North	N/NE	2050	45°29'	6°42'	39	3631	1783	1993	57	211
TSUA			St Jacques	Siliceous		N/NW	2000	45°30'	6°42'	36	3786	1855	1993	73	139
Picea abies (6)	MCAE	Maurienne	M Fleury 1	Calcareous	South	S	2050	45°15'	6°45'50"	36	5570	1729	1993	86	265
	MSAE		Barbier	Siliceous		S/SW	2000	45°14'	6°43'	36	3521	1877	1993	74	117
	MCUE		Le Jeu	Calcareous	North	NW	2100	45°14'	6°48'	36	8278	1546	1994	107	449
	TCAE	Tarentaise	Chal	Calcareous	South	SW	2050	45°25'	6°41'	36	5654	1743	1993	65	251
	TSAE		Tuéda 1	Siliceous		S/SW	2000	45°22'	6°36'	36	3488	1823	1993	57	171
	TSUE		St Jacques	Siliceous	North	N	2000	45°30'	6°42'	36	4793	1792	1993	72	202

Fig. 2 Site description of the 32 sampled tree populations, with forest name and code, kind of bedrock, aspect and elevation (altitude above sea level, in metres), number of cores and total number of ring widths, periods of master chronologies, and minimum/maximum tree ages

spruce [*Picea abies* (L.) Karst] (PA), stone pine (*Pinus cembra* L.) (PC) and mountain pine (*Pinus uncinata* Mill. ex. Mirb.) (PU). They are non-host species for the black monophagous form of the LBM (Baltensweiler 1993), so they can be used for relative comparisons. Similar comparative techniques were used by Eckstein et al. (1991), Morin et al. (1993), Jardon et al. (1993) and Weber (1997) to distinguish between climatic and biotic influences on ring widths.

Non-host trees were sampled similarly to larch stands (12 trees×3 cores in each population), with a total of six PA, ten PC and nine PU populations. Altitude and aspect of the 32 sampled sites are given in Fig. 2. They are all located at the subalpine level near the treeline, either in the same sites or in different locations. Note that there are no spruce forests in the Briançonnais region, which is excessively dry for that species. Non-host species stands without larch were included in the analysis to avoid indirect effects of insect activity on tree growth (Jardon et al. 1993), such as a reduced inter-specific competition during insect outbreaks.

Pointer years

Dendroecological pointer years (PY) are defined as years with extreme ring widths (Schweingruber 1990). For each ring measurement, the relative width reduction was calculated by comparison with the mean value of the 4 previous years. Here, negative PY (extremely narrow rings) were defined according to three threshold values: -40%, -55% and -70% of abrupt decreases in growth, simultaneously observed on trees of the same population. These values are often used in dendroecology (Schweingruber et al. 1991), thus allowing for comparison with the results of other work. The percentage of trees with such growth changes was calculated for each population and year, and the year was considered a PY when the percentage exceeded 8%.

In this paper, this method is improved by a differential calculation method involving non-host species (Eckstein et al. 1991). First, the percentage of trees showing a 40% reduction in growth are calculated on a yearly basis for the four species. Then, the mean value for the three non-host trees (PU, PC, and PA) is obtained, and subtracted from *L. decidua* results to provide an index (I) of the biotic impact:

$$I = \text{host } (L. \text{ decidua}) - \text{non host } (PU + PC + PA) / 3 \text{ (in \%)} \quad (1)$$

These *I*s are computed for each of the three regions (see below).

Defoliation pattern

Information about LBM outbreaks has been systematically collected from forestry records and the literature for the entire subalpine distribution area of larch (Baltensweiler and Rubli 1999). For the period 1960–1990, discolouration patterns were monitored within the research programme Population Dynamics of the Larch Budmoth in collaboration with the National Forest Service. The Centre National des Eaux et Forêts (St-Martin-d'Hères) organized the survey in the French Alps with the District Forest Service. Discolouration was mapped at a scale of 1:200,000 and allocated to three classes of intensity: (1) light (0–33% of biomass affected), (2) medium (34–65% of biomass affected), and (3) heavy (>66% of biomass affected). Whenever a dendroecological plot was defoliated during a given year, a black square indicates this qualitative information on the relevant figure (see below), regardless of the discolouration intensity. Prior to 1960, the archives are less precise and only indicate a very general association by combining indicators concerning the extent and/or intensity of discolouration. In earlier days, spatial information about sites of discolouration was given in the literature only rather rarely, and in a general manner, e.g. the location was described as “Val Guisane”, or even less precisely, as “Briançonnais”, “Queyras” or “Ubaye”. Thus, mapping based on records from the older literature provides valuable information about periodicity on a large spatial scale but not much local information.

Results and discussion

Periodicity in larch ring-width chronologies

The first 30 autocorrelation coefficients were calculated for the four tree species (Fig. 3) for all the cores for which there was raw data, before calculating mean values (Fritts 1976). The correlations are higher for the two pine species compared to spruce or larch. Only larch shows cyclical autocorrelation, demonstrating a periodicity of around 9 years' duration (and its multiples: 18 and 27 years), in contrast to non-host species (Fig. 3a), as formerly observed by Tessier (1981) in the Vanoise (France). This result coincides with the effects of LBM outbreaks on larch, that recur at intervals of 7–9 years (Auer 1977). Similarly, a Fourier analysis (data not shown here) computed with the same time series revealed two significant cycles (peaks near 9 and 18 years) for the larch only.

The same autocorrelation method was also performed for the seven individual larch populations (described in Fig. 2). The most conspicuous cycles are observed in the three populations, Bcum, Bsam, Bsum, all located in the Briançonnais region (Fig. 3b), the site with the most characteristic continental climate and highest timberline (Cadel and Gilot 1963). Conversely, weaker periodicity is found in the Tarentaise (Tcum, Tsum) and Maurienne (Mcum) sites (in the Savoie), that is consistent with the data of Bachasson (1982) who did not observe a strong impact of LBM in the Valorcine (Haute-Savoie).

Although few populations were compared, local site conditions do not seem to account clearly for these differences, since Bcum, Mcum, and Tcum have the same kind of site characteristics (calcareous bedrock on north-facing slopes). The youngest population of this study (Bcam) is obviously too young to support optimal LBM population growth. Nevertheless, most outbreaks were recorded there, but with a weaker intensity. Several hy-

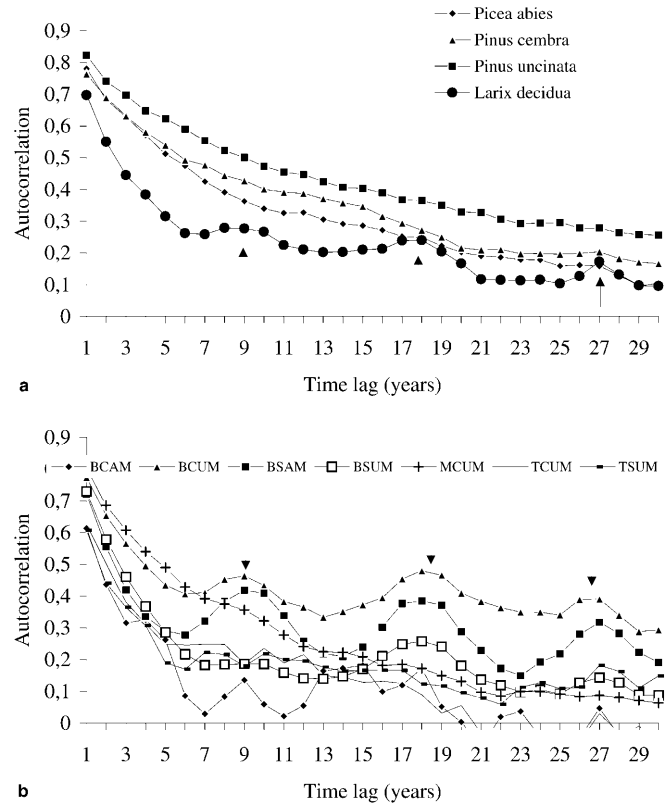


Fig. 3 Thirty first-order autocorrelation coefficients **a** for the four coniferous species, demonstrating 9-year cycles of larch radial growth; and **b** for the seven larch stands

potheses may be proposed to explain why young trees are less susceptible to LBM defoliation compared to older larches. Young trees can be assumed to recover more easily after an outbreak, leading to a less visible pattern in their ring widths due to defoliation. It can also be hypothesized that their needles are less suitable for LBM feeding, for instance due to a lower nitrogen content. Unfortunately, at present only little is known about physiological differences in larches according to their age.

Dating of the LBM outbreaks

Low-frequency curves of larch master chronologies (obtained with 3-year weighted moving averages after removing the age trend) in the seven sites (Fig. 4) underline a high level of synchronicity among populations. Major reductions in growth are followed by the rapid recovery of tree growth. On a yearly scale, PY were calculated for each species to date these abrupt decreases in growth. They show many negative anomalies (Fig. 5) (data before 1750 are not shown because of a lower number of cores). Most of the growth crises appear to be periodical, which suggests that they reflect the impact of LBM outbreaks. However, some negative PY might also be attributed to extreme climatic events. The relative method based on comparison with non-host species (Eckstein et al. 1991)

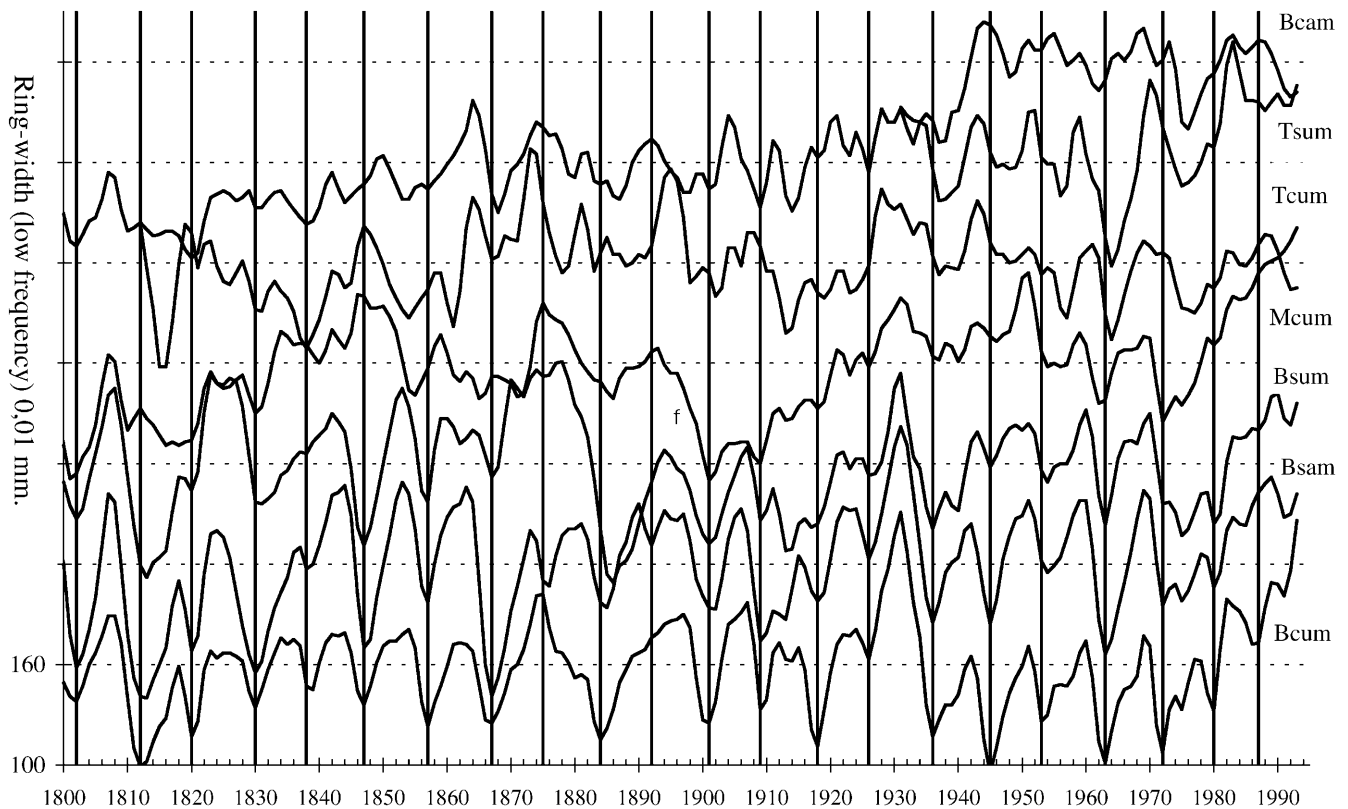


Fig. 4 Low frequencies (obtained with 3-year weighted moving averages, without age trend) of larch chronologies in seven sites since 1800

serves to distinguish reductions in growth due to the weather from those attributed to LBM defoliation. This comparison assumes that different coniferous species near the timberline are sensitive to similar climatic variables, especially summer temperatures (Schweingruber et al. 1977). Some negative PY with a high level of synchronized data among the four species support this hypothesis (Petitcolas 1998). Thus, most species reacted in a synchronized manner during years such as 1813, 1815, 1818, 1849, 1880, 1886, 1888, 1906/1907, 1940, 1948, 1962, 1975, 1984, and 1992. They are the main negative PY found during the last two centuries in the French sub-alpine area. However, in some cases it is difficult to distinguish between climatic or biotic events for years such as 1923 or 1913/1914, because the three non-host species did not react strongly, and larch PY did not occur during the peak phase of the LBM cycle. Unfortunately, the assumption of a similar response to climate among different coniferous species at the timberline is sometimes an invalid approximation (Petitcolas and Rolland 1998).

Using the relative PY method (I %), 22 cycles were dated during the period 1800–1993 (Fig. 6). Beginning with 1801, the outbreaks are numbered successively from the first year of observed defoliation and/or using large values of I from 1 to 22. Eight outbreaks in the time interval 1920–1990 are well documented by their defoliation pattern (type A); for seven more outbreaks information

about defoliation is only fragmentary (type B), and seven outbreaks, for which no information at all was available, were inferred from the occurrence of PY and with regard to the periodicity of their occurrence (type C).

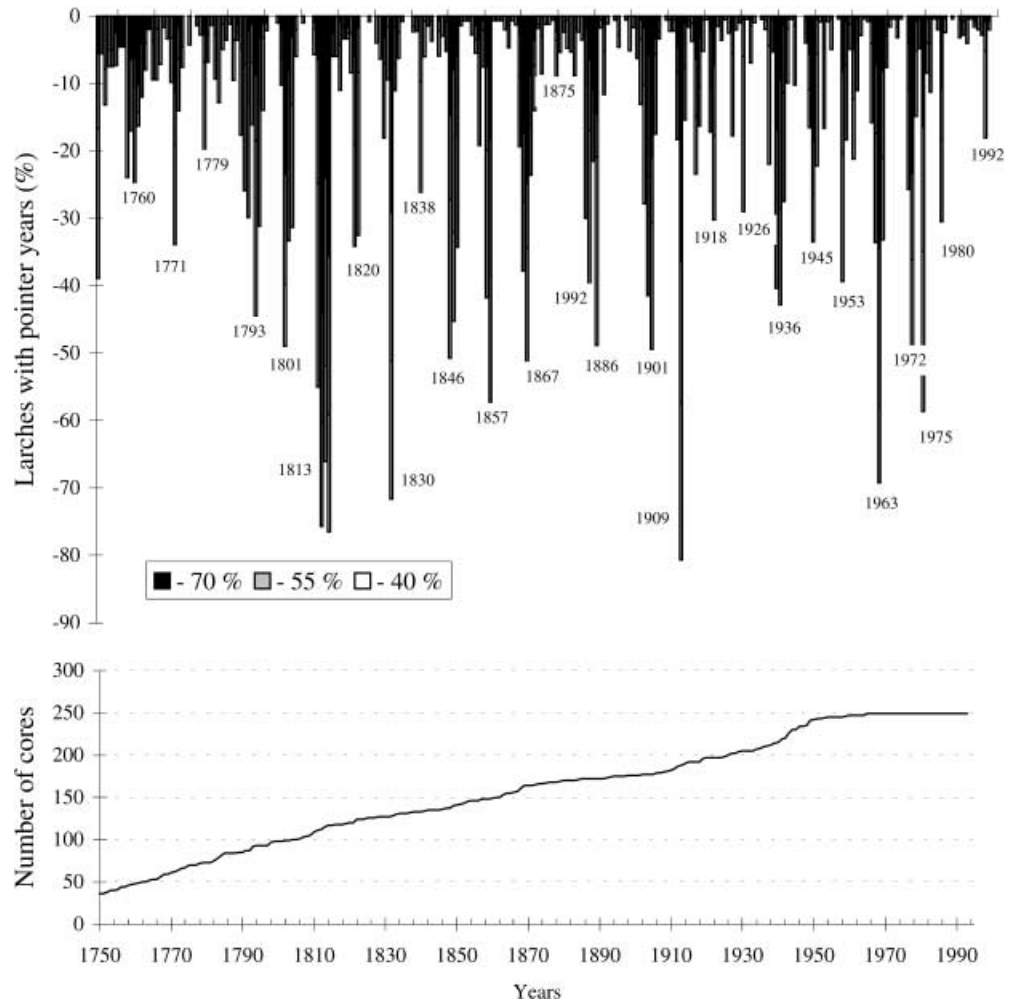
Successive outbreaks are separated by 7–10 years, with a mean interval of 8.86 ± 1.01 years ($n=21$, 1800–1993). This is comparable to the result of Weber (1997), who found a mean interval of 8.58 ± 1.66 years in the optimal (for LBM) Upper Engadine valley and 8.59 ± 2.13 years in the suboptimal Goms valley (since 1740; with 57 cycles since 1503 and 59 since 1472). Similarly, Baltensweiler and Fischlin (1988) found a mean interval of 8.5 ± 0.26 years in the upper Engadine (16 cycles since 1850).

Many missing rings occurred during the defoliating periods, as already observed by Jardon et al. (1993) for *Larix laricina* [(Du Roi) K. Koch] infested by *Pristiphora erichsonii* (Htg.) in Québec. Similarly, Weber (1995) suggested that: “The amount of *Larix decidua* missing rings may be a valuable indicator to estimate the intensity of an outbreak, since all of them (...) are found within periods of defoliation”. Since 1800, the larch cores showed 237 missing rings, versus nine and 12 for stone and mountain pines, respectively, especially in 1975, 1972, 1963, 1945, 1909, 1901, 1886, 1867 and 1811.

Observed defoliation pattern and growth reduction

At the outset of this section, it should be remembered that the sites of the seven larch stands were selected for a study of the comparative tree growth of conifers at the alpine

Fig. 5 Chronology of pointer years with abrupt reduction in growth calculated for three different thresholds (–40%, –55% and –70% for all populations of *L. decidua* since 1750)



timberline (Petitcolas et al. 1997) and not for the recording of LBM outbreaks. Thus the sites might either not be optimal for LBM outbreaks, nor suitable for the easy observation of defoliation. Furthermore, the restricted extent of the dendroecological sites adds to the study's limitation that the quality of information suffers from many shortcomings. LBM outbreaks as defined by discolouration pattern may vary considerably in extent, intensity and duration (Fig. 6). Based on extensive studies of population dynamics, an outbreak is characterized by its occurrence during 4 consecutive years (Baltensweiler and Rubli 1999), except for the 1917–1919 outbreak (3 years).

Our dendrochronological results are consistent with defoliation-pattern observations, since Pardé (1955) observed a strong growth reduction in a permanent larch plot in Montgenèvre (1,850–1,900 m, northern exposure, near our sites in the Briançonnais), from 1950 to 1954, due to a LBM outbreak peaking in 1953 (no. 18). Similarly, peaks in 1962, and 1970/1971 were reported by Auer et al. (1981) (nos. 19 and 20), and in an extensive study of LBM defoliation in the French Alps since 1811, published by Baltensweiler and Rubli (1999).

During the period 1923–1989, the eight “well-documented” outbreaks (type A, Fig. 6) reveal that the sites in

the Briançonnais were twice as often defoliated as sites in the Maurienne and Tarentaise regions. Moreover, periods of outbreak show significantly more reduction in growth than years between outbreaks ($c^2=14.9$; $df=1$, $P=0.001$).

The graphic comparison of I versus the three groups of outbreaks described as “well-documented defoliation” (type A, Fig. 6), “fragmentarily documented” (type B), and “undocumented” (type C) in the three regions, Briançonnais, Maurienne and Tarentaise, is presented in Fig. 7. Obviously, the Briançonnais region exhibits not only the highest proportion of negative PY, it shows also the most consistent pattern when comparing the three groups (A, B, C): negative PY are almost nonexistent during the 3 years before an outbreak (from y_{-4} to y_{-2}), but are followed by a steady increase in I up to a maximum of 40% at an outbreak peak (y_0), and a lower value again in the following year (y_1). This same pattern is also observed for the well-documented outbreaks in the Maurienne and Tarentaise regions. Furthermore, tree recovery is complete 3 years after an outbreak peak (y_3 – y_5). Since I excludes the impact of unfavourable weather on growth by taking into account PY in non-host species, the index represents the reduction in growth due to the feeding of the LBM only. Thus outbreaks must have

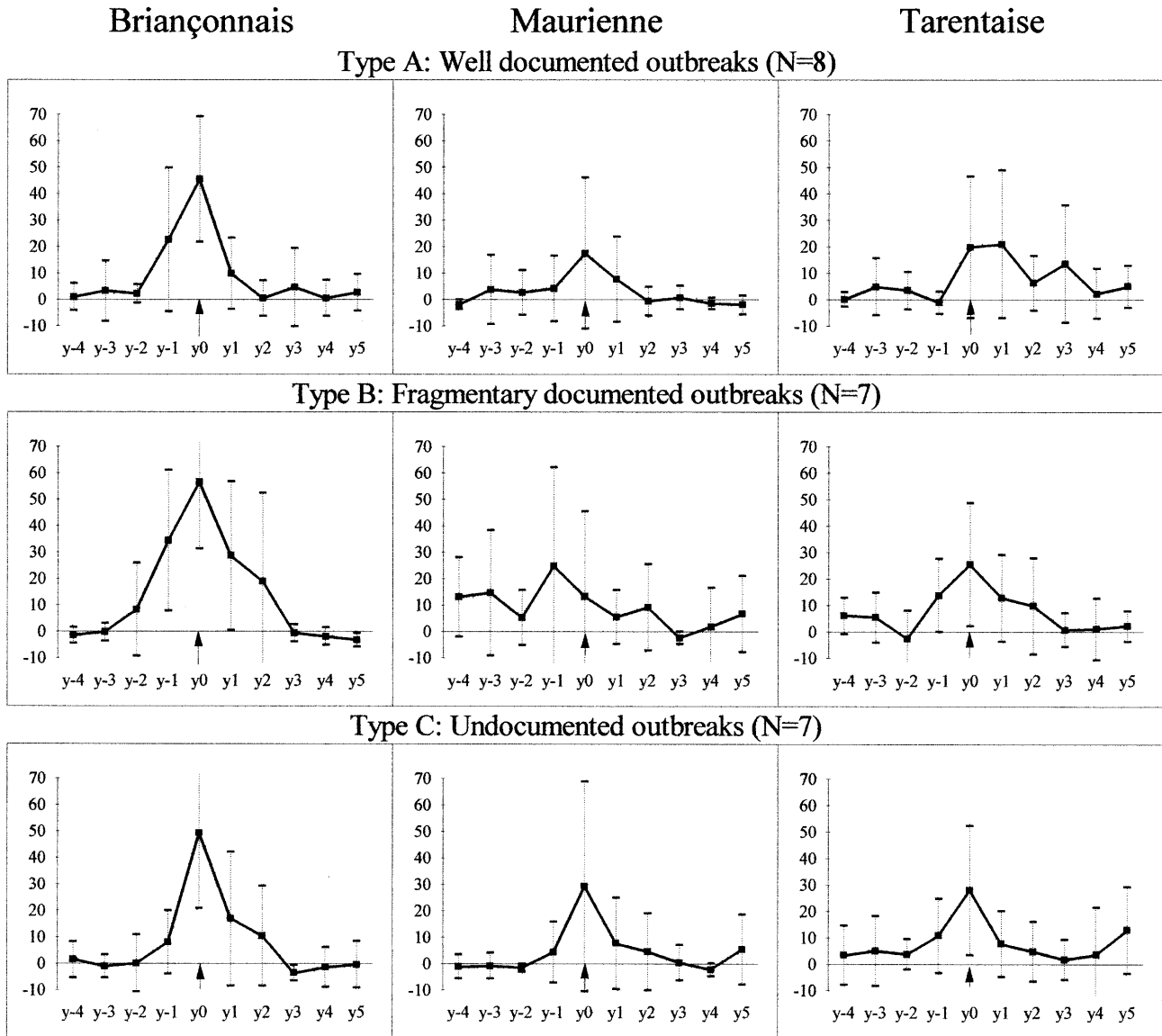


Fig. 7 Tree-ring index of biotic impact (I %) calculated for the three types of outbreaks (A–C) and three regions, from 4 years preceding (y_{-4}) an outbreak peak (y_0) to 5 years after (y_5)

situations, the amount of newly formed wood is sharply reduced. When an LBM outbreak is prolonged for successive years, it leads to a series of extremely narrow rings, or even some missing rings. The 1-year interval between an LBM outbreak and an effect observed in terms of tree ring width reported here may be explained physiologically by incomplete larch refoliation in late summer after LBM defoliation in spring. Such a situation reduces the assimilation of larch, hence nutrient storage is reduced for the formation of subsequent rings.

Comparison of different methods

Several techniques based on ring widths have been proposed for the reconstruction of LBM outbreaks, with dif-

ferent advantages and drawbacks. The simplest methods (Schweingruber 1979; Pignatelli and Bleuler 1988) used only one species (the larch itself), and therefore they did not clearly isolate the LBM effect from climatic influences on ring widths. In contrast, our technique, as well as Weber's method (1997), is based on a comparison between host and non-host species. Weber (1997) combined spruce and stone pine as non-hosts, whereas we also used mountain pine. Unfortunately, all these conifers proved to be slightly susceptible to LBM defoliation, and hence were not real non-host species. Moreover, it was demonstrated that their responses to climate are sometimes quite different from those of larch, even when they grow in the same forest (Petitcolas and Rolland 1998). Therefore, it seems impossible to find "true" non-host species, i.e. conifers that are both not infected at all by LBM, and have exactly the same ecological requirements as larch. Unfortunately, the choice of "non-host" species is restricted, because only few conifers in Europe are able to grow with larch at high elevations. However, the addition of non-host trees

for calculating relative indices obviously leads to more objective results. Thus, some particular years (such as 1948) associated with extreme climatic events were recorded for both host and non-host trees. Our technique permitted us to remove them from the LBM PY list.

Instead of measuring ring widths to compute PY, some authors have analysed larch cores with a stereo-microscope to examine some intra-ring features (Schweingruber 1979; Weber 1997). For instance, Weber's (1997) method was based on abrupt growth changes, event years, and latewood events (conspicuously low or high percentage of latewood) that were manually coded on skeleton plots. Such visual detection is less objective, but the use of more wood features was shown to be very efficient, especially when latewood events were combined with PY.

The "optimal" dendroecological technique to record LBM events may be based on wood X-ray densitometry, with quantitative measurements made on intra-ring density. As already observed by Schweingruber (1979), an abrupt decrease in latewood density is probably the best criterion for detecting a LBM outbreak. The peak of the outbreaks may be dated precisely by taking into account the reduction of the latewood growth.

Conclusions

This reconstruction of LBM outbreaks based on the combination of both dendroecological data and documented larch discolouration patterns is, to our knowledge, the first one carried out for the French Alps. The growth of larch was investigated in three different regions in the south-eastern French Alps, the Briançonnais, the Maurienne and the Tarentaise. The large sampling programme (32 sites, 1,143 cores) comprised seven larch populations (249 cores) and was compared to 25 populations of the three non-host species (894 cores) which occur in the subalpine region (i.e. PA, PC, PU). This procedure allows one to distinguish between the impact of the LBM on larch and general climatic effects on tree growth. The ring-width data were evaluated by several different methods, such as the PY technique, Fourier analysis, or by the calculation of autocorrelation coefficients and low-frequency ring-width curves. Information about the discolouration of larch stands as an indicator of peak populations was recovered from forestry archives and the literature as far back as 1811, and was systematically recorded and mapped with the help of the Centre National des Eaux et Forêts from 1961 to 1998.

In the course of the last 200 years, 22 outbreaks were dated; for eight of them defoliation was well documented with respect to its extent and intensity (1923–1926, 1934–1937, 1943–1946, 1952–1955, 1961–1964, 1970–1973, 1978–1981, 1986–1989), seven outbreaks were only fragmentarily documented (1810–1813, 1819–1822, 1854–1857, 1865–1868, 1875–1878, 1883–1886, 1900–1930), and seven outbreaks were deduced from data showing a reduction in growth occurring at approximately 9-year intervals (1801–1804, 1828–1831, 1837–1840, 1846–1849,

1907–1910, 1917–1919). It is doubtful that cycle no. 11 (1892–1895) shows an outbreak of weak intensity, and the possible occurrence of an outbreak was primarily justified by the 9-year interval from the previous outbreak. In most cases the identification of an outbreak from the occurrence of negative PY in successive years proved to be very reliable. Thus this dendrochronological method is also efficient and sensitive enough for dating LBM outbreaks for periods where additional information is not available.

I (i.e. the percentage of negative PY for larch not recorded for non-host species) (Fig. 6), is appropriate for the description of the course of LBM population growth and the resulting impact of defoliation on larch growth; it also shows that the Briançonnais is more exposed to LBM outbreaks than either the Maurienne or Tarentaise regions. Furthermore, the delayed maximum *I* in the Tarentaise for the well-documented outbreaks (y_t) reflects that outbreaks in this region depend on the immigration of budmoths from the more optimal Briançonnais (Baltensweiler and Rubli 1999). The time-course of the first 30 autocorrelation coefficients (Fig. 3) clearly demonstrates the intrinsic consistency of the periodic impact of defoliation for the sites in the Briançonnais region. Outbreaks occurred earlier in the Briançonnais, with a periodicity of 8.86 ± 1.01 years (with 21 intervals, and taking into account the weak cycle in 1992).

For future investigations, a visual examination of some intra-ring features such as latewood events, and wood density measurements may provide better information on ring disturbance (Schweingruber 1979), since defoliation affects latewood density and earlywood anatomy differently (Filion and Cournoyer 1995; Liang et al. 1997), as demonstrated by experimental defoliation of larch and pine (Craighead 1940; Polge et al. 1971). Since methods described in this paper are applicable to both single tree data as well as master chronologies, a reinvestigation of previously published data on ring widths and densitometric master chronologies might be of general interest in view of the reconstruction of LBM outbreaks throughout the Alps (Baltensweiler and Rubli 1999).

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