



Tracing the influence of larch-bud-moth insect outbreaks and weather conditions on larch tree-ring growth in Engadine (Switzerland)

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Tree-ring analysis of insect-defoliated trees has so far been used for detecting past insect outbreaks only. We hypothesize that the impact of the larch-bud-moth (LBM) *Zeiraphera diniana* outbreaks on the growth of larch *Larix decidua* in the Engadine (Switzerland) is closely coupled to the spatial development of the outbreak and the ecological characteristics of the respective sites and weather conditions. We tested this hypothesis by reviewing data sets available in the literature and by analysing original data. We monitored LBM population densities and the needle phenology, growth and defoliation of larch over 28 years, i.e. over four outbreak cycles. In addition, information on defoliation patterns covering six earlier outbreaks over 50 years was matched with tree-ring information. Tree-ring chronologies of 18 larch stands were analysed with regard to abrupt growth changes and latewood events. Defoliation induces an immediate reduction in latewood, followed by a reduction in needle length and a significant decrease in radial growth in the subsequent year. We have called this tree-ring pattern the “larch-bud-moth syndrome”. A careful analysis of the various parameters of the LBM syndrome for two specific population cycles enabled us to define different interaction patterns between weather conditions and tree growth. These can then be included in climate change models to help disentangle the impact of insect defoliation from that of adverse climatic conditions.

Insect outbreaks are generally thought to be triggered by deviations from long-term weather conditions. They regionally cause great economic losses, affecting forest management and environmental sustainability. In view of the increased variability of weather as a consequence of climatic changes, unprecedented interactions between insect population dynamics and forest responses may arise. The case of the current outbreaks of mountain pine beetle *Dendroctonus ponderosae* in northwest America (Hicke et al. 2006) may serve as a worrying example. In order to handle such environmental hazards in the future, forest managers require a profound knowledge of not only the climate system and insect biology, but also of the interactions between climate changes, insect population dynamics and forest responses. Long time series of data from meteorological, insect, and forest observations would be useful, but are only very rarely available. However, in many cases tree rings may help. Dendrochronological methods enable the interpretation of tree rings and the reconstruction of the past environmental conditions under which the trees grew. Tree growth is strongly influenced by climate, and climatic conditions can be reconstructed using tree rings (Hughes 2002). Insects may also affect tree growth. For example, dramatic growth changes may be induced by tree defolia-

tion, and tree-growth patterns are therefore strongly affected by insect population dynamics and may be used to reconstruct past defoliation activities.

Outbreaks of the larch bud moth *Zeiraphera diniana* (referred to hereafter as LBM) belong to the most intensively studied cycles in ecology (Coaz 1894, Auer 1977, Baltensweiler and Rubli 1999). They occur very regularly at 8–10 year intervals and cause a striking, reddish brown discolouration of larch *Larix decidua* forests in the European Alps (Baltensweiler and Rubli 1984). Discolouration events have been systematically recorded in Switzerland by the forest service of Canton Grisons since its establishment in 1864 (Auer unpubl. a). The reddish brown discolouration is induced by the wasteful feeding of large numbers of 4th and 5th instar larvae and the subsequent drying out of the nibbled needles in the continental subalpine climate. Thus, outbreaks become noticeable not so much as a consequence of needle consumption, i.e. defoliation, but rather due to the desiccated debris of the inedible foliage. Nevertheless, we use in the following the two terms “defoliation” and “discolouration” synonymously. In the 1950s local tourist organisations in the Engadine requested chemical controlling of the LBM in order to prevent the unaesthetic effects of the recurring

outbreaks. The authorities responded by carrying out a larval census, as a first step to detect the potential foci of the population cycle (Auer 1961). The census covered all the 6000 ha of forest in the Engadine. Thus, long-term records of LBM outbreaks in the Engadine and phenological observations in larch stands are available, which provide a unique source of information for studying population cycles in biology.

Defoliation, as the immediate criterion for assessing LBM impact, was estimated as the proportional loss of green biomass in larch forest at a given site. In order to evaluate the impact of defoliation on growth processes, it is important to know the development of both the larch and the moth. Larch, being deciduous, refoliates after defoliation about 3–4 weeks later, usually early in August. However, refoliation is induced only if the loss of biomass exceeds the proportion of 50%. This second flush grows only short needles, which are often killed in October by early frosts. Defoliated larch trees cannot accumulate assimilates, and, as a result, they are deprived of resources in the following spring, so that again only rather short needles grow. This means that needle length can be used as an indicator of a delayed response to defoliation. Short needles contain much raw fibre and have only a very low nitrogen content, which tends to induce the “crash” of the larval population (Benz 1974).

The larch-LBM system has been very useful for modelling population dynamics (Baltensweiler and Fischlin 1988, Berryman 2002, Björnstad et al. 2002). However, dealing with 8–10 year cycles requires long time series. The dendrochronological analysis of host trees may ideally help to fill this gap (Esper et al. 2007). However, doubts still exist about distinguishing the tree-ring patterns induced by LBM from those caused by climatic anomalies. A clear and straightforward method for identifying LBM-induced tree-ring patterns is still missing. The objective of this paper is to describe tree-ring patterns induced by LBM outbreaks in order to differentiate between them and patterns induced by weather conditions.

In the work described here, we studied the relationships and complex interactions between tree growth, insect outbreaks and climatic conditions in the larch-LBM system in the Engadine (Switzerland) using larch tree rings, meteorological data and insect survey observations. We aim to provide a standardised tool to reconstruct past LBM outbreaks for periods of time prior to instrumental weather observation and systematic forest records.

Data sets and methods

The LBM population cycle in the Upper Engadine

Research on the population dynamics of the LBM began at the end of the 1940s with the ultimate goal of controlling the recurring outbreaks of the LBM (Auer 1961). The study area was the entire Upper Engadine Valley (southeastern Switzerland, 9°50'E, 46°30'N; Fig. 1) with its 6000 ha of forest. The valley bottom rises from 1600 to 1800 m a.s.l. over a distance of 50 km, while the forest limit lies at 2100 m. The optimum area for the bud moth, identified as the zone of first defoliation, is confined to the subalpine forest

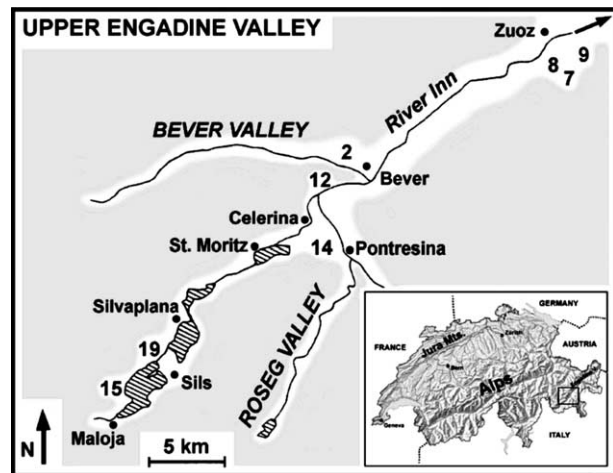


Fig. 1. Study area (Upper Engadine) and sites. Early gradation type area: sites 15, 19, 12, 2. Late gradation type area: sites 14, 7, 8, 9.

at an altitude between 1700–2000 m a.s.l. Larch–cedar pine forests (*Larici-Pinetum cembrae*) (Ellenberg and Klötzli 1972) dominate on the moister northwest (NW)-facing slopes, while the dry southeast (SE)-facing slopes are mainly covered with almost pure and patchy larch stands, often also used as pastures.

Auer (1961) designed a larval census to localise large populations for timely pest control operations in the Swiss Alps. Samples of 1–3 kg branches were collected annually during the years 1949–1976 from 500–2100 trees (distributed anew each year at random) throughout the Upper Engadine Valley. The branches were examined for larvae (Auer 1961, 1977) to relate insect numbers in time and space to altitude, topography and forest structure within the Engadine. Between 1949–1985 four complete population cycles were thus numerically quantified (Auer 1961, 1977, Baltensweiler and Rubli 1999) and matched with the appearance of visible discolouration. Light discolouration, but from a distance easily visible, is caused by the density of >100 L5 larvae kg^{-1} branches (Auer 1961). Three classes of discolouration were distinguished:

- light: $<33\%$ of green biomass discoloured (defoliated)
- medium: 33–66% of green biomass discoloured (defoliated)
- heavy: $>66\%$ of green biomass discoloured (defoliated)

However, due to the extraordinary amplitude of population numbers as well as the rather strict periodicity of these outbreaks, each generation exhibits characteristic qualities and quantities which is most easily defined by its position within the ‘gradation’. In this paper we use the term ‘gradation’ in the entomological sense, i.e. the increase in insect numbers from a minimum to a maximum and the subsequent decrease to the following minimum density (Schwerdtfeger 1968). Because of the easy recognition of defoliation in the field and its impact on the following generations we rely on the discolouration pattern for labelling the individual year within the course of a LBM

gradation. We term the first year of visible discolouration as “cycle year 1” and the year just preceding it as “cycle year 0”. Thus, it is possible to account for the variable length of the gradations and provide a calibration of the individual years within the course of a cycle for various local sites but also for the temporal comparison between sites. Please note that this terminology of cycle years does not correspond with density figures. For methodological reasons the exact determination of population minima on the spatial scale of sites is often not possible whereas the first year of defoliation is unambiguous.

During the census period a rather consistent pattern was observed in the sequence of locally site-specific discolouration, which led us to specify the early and late gradation types (Auer 1961). The site Sils, 15 (Fig. 1), represents the proper early gradation type as it is defoliated in all cycles already in the first year of the relevant defoliation period (Table 1), whereas the site Celerina, 14, is the typical late gradation type since it becomes defoliated generally one year later. Optimum weather conditions may cause that defoliation covers rather unusually most of the Engadine valley at the same time and thus synchronise defoliation patterns (Baltensweiler 1964). However, in general, the differentiation in early and late gradation types allows an appropriate description of population dynamics in relation to local ecological characteristics.

Table 2 lists the years of first discolouration for eight sites within the Engadine which are allocated to either the early or the late gradation type, considering the last ten outbreaks between 1900–1985. The comparison of seven ecological characteristics (Table 2) allows to generalise that the early gradation sites are located at the northwestern slope of the valley (aspect SE/SW) whereas the late sites are on the opposite valley side (aspect flat or N/NE/NW). The stand composition also differs between the two gradation types: all early-gradation sites are in pure larch stands, whereas late gradation types are in mixed larch-cembra pine forests. Thus the categorisation into early and late gradation sites reflects implicitly the influence of weather on

the population dynamics of the LBM, the early gradation sites representing then optimum sites.

The identification of the individual years within the course of a LBM gradation for the local sites are defined by applying the prefix ‘cycle’ (Table 1):

- cycle year 0: the year just prior to the year of first visible discolouration;
- cycle year 1: first year with visible discolouration;
- cycle year 2: second year with visible defoliation;
- cycle year 3: third year of an outbreak, occasionally still some light discolouration might occur;
- cycle year 4–9: no visible discolouration.

This terminology also enables us to take into account the differences in spatial development of the various outbreaks by mapping the gradation years.

Monitoring the annual flush of larch

In analysing the development of LBM populations, we studied the coincidence of the hatching of the first instar larvae and the flushing of the larch tree. Because of the widespread use of larch in phenological studies, relevant information concerning the beginning of larch needle growth is available throughout Europe, even for the subalpine region (Defila 1992). Unfortunately, the reported dates of flushing are based on descriptive terms only. The applied criterion ‘greenness’ cannot be related to needle length, as it depends on the spreading out of the needles of the individual fascicles (Volkert and Schnelle 1966). Therefore, the annual flush of larch was monitored by measuring periodically the growth of needles until they reached their final length. At each site we selected and labelled one branch 1.5–2 m above ground from four different trees. Then, we selected six short shoots, i.e. three on the proximal and three on distal side of the third node between the third and fourth long shoots (or possibly also the fourth node) of the labelled branch (Fig. 2). Thus, we recorded 24 measurements at

Table 1. Identification of the defoliation pattern for the early gradation type at site 15 (Sils) for the ten LBM cycles 1901–1989 (Baltensweiler and Rubli 1999). Numerically, a gradation may increase from a minimum density in cycle year 6 between e.g. the second and the third cycle to a peak density in cycle year 1 or 2 and decrease again to a minimum in cycle year 5 or 6 separating cycles 3 and 4.

Status Year	no def. 0	1st.def. 1	2nd.def. 2	spor.def. 3	no def. 4	no def. 5	no def. 6	no def. 7	no def. 8	no def. 9
1902	1903	1904	1905	1906	1907	1908	1909	1910		
1911	1912	1913	1914	1915	1916	1917				
1918	1919	1920	1921	1922	1923	1924				
1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	
1935	1936	1937	1938	1939	1940	1941	1942	1943		
1944	1945	1946	1947	1948	1949	1950	1951			
1952	1953	1954	1955	1956	1957	1958	1959	1960		
1961	1962	1963	1964*	1965	1966	1967	1968	1969	1970	
1971	1972	1973	1974*	1975	1976	1977	1978	1979		
1980	1981	1982	1983	1984	1985	1986	1987			
1988	1989									

- no def.: no discolouration visible from the distance.
- spor.def.: sporadic (*), generally only light discolouration.
- cycle year 0: the year prior to the first year of visible discolouration.
- cycle year 1: first year with visible discolouration = 1st year of outbreak.
- cycle year 2: second year with visible discolouration = 2nd year of outbreak.
- cycle year 3: third year, eventually sporadic light discolouration.
- cycle year 4 to 9: no visible discolouration.

Table 2. Characterization of dendrochronological sampling sites (Weber 1997). Allocation of outbreak year 1 (Baltensweiler and Rubli 1999; Auer, unpubl.).

	Early gradation type				Late gradation type			
	site 15	site 19	site 12	site 2	site 14	site 8	site 9	site 7
Altitude m a.s.l.	1840	1840	1830	1820	1830	1890	2100	2200
Aspect	SE	SE	SE	SW	–	N	NW	NE
Slope angle (°)	20	30–45	20	15	0	5–30	20	40
Stand composition: l larch; p pine	pure l	pure l	pure l	pure l	mixed l-p	mixed l-p	mixed l-p	mixed l-p
Stand age (larch only), years	250–285	85–430	115–140	110–340	230–300	240–270	390–510	165–225
Canopy area (%)	50	70	70	70	60	50	35	50
Hydrological characterisation	dry	dry	dry	dry	medium	medium	dry	medium
No. larch trees sampled	10	20	20	20	10	10	10	10
**	1903	1903*	1904*	1903*	1903*	1903*	1903*	1903*
	1912	1912	1913	1913	1913*	1913	1912	1912
	1919	1919*	1919	1920	1919	1919	1919	1920
	1926	1927	1927	1927	1928	1928	1928	1928
	1936	1936	1936	1936	1937	1936	1937	1937*
	1945	1945	1945	1945	1946	1946	1946	1946
	1953	1953*	1954	1953	1954	1954	1954*	1954*
	1962	1963	1963	1963	1963*	1963*	1963	1963
	1972	1972	1972	1972	1973*	1972	1972*	1972
	1981	1982	1982	1982	1982	1982	1982	1982

* no LE effect, ** outbreak disturbed by weather.

each site and sampling time. These branches were sampled for at least five subsequent years or longer. Short shoots or fascicles are the lateral needle clusters along the branch, whereas the long shoot is defined as the annual elongation or growth of the branch. This test chart was adopted on the basis of extensive measurements throughout the crowns of mature larch trees (Jaccard 1965). The repeated measurement of the same branches on the same trees relativises the measurements and, in addition, sampling at 15 sites located throughout the Engadine valley provides a reliable basis for comparative phenology. In this paper detailed information is presented only for the Sils site as it was studied for the longest uninterrupted period from 1961 to 1989, i.e. three complete gradation periods.

The growth curves of the needles allowed the extrapolation of the phenological dates of 10 mm (T_{10}), 20 mm (T_{20}) and maximum (T_{max}) needle lengths per season, which are expressed in number of days since 1 January. These data provide information about the beginning of the growing season at specific sites during the years 1961–1989 (the year 1985 is missing), and characterise at the same time the phenological status of the sites relative to neighbouring sites. The phenological classification (e: early, n: normal, l:

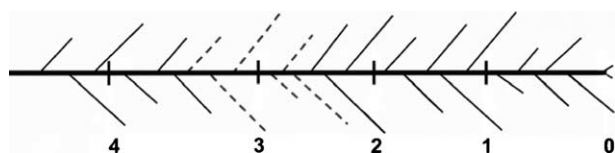


Fig. 2. Method for measuring needle length. The figure shows the model of a shoot. Three fascicles (short shoots) distal and proximal of the 3rd node are bunched together, and the longest needles of each cluster are measured (broken lines).

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late year) is based on the normal distribution of the T_{10} - dates.

Tree-ring analysis

Traditionally, dendrochronological methods have been used for climatic purposes, but in recent decades they have increasingly been applied to answer other ecological questions. Pioneering studies on the effects of defoliating insects on tree growth were conducted by Mott et al. (1957) and Blais (1958, 1965) in North America on the spruce budworm *Choristoneura fumiferana*. Specific studies concerning LBM defoliation were carried out in the Central Alps by Badoux (1952), Geer (1975) and Schweingruber (1979). Since then tree rings have been used to reconstruct past spatiotemporal LBM dynamics for long time series (Pignatelli and Bleuler 1988, Weber 1995, 1997, Rolland et al. 2001, Esper et al. 2007). Weber (1995, 1997) published extensive dendroecological information from 18 larch stands distributed within the Upper Engadine Valley. At each site 10 to 20 larch trees were sampled and evaluated by means of the skeleton plot method (Schweingruber et al. 1990, Weber 1994). Two growth parameters, abrupt growth changes (AGC) and latewood events (LE), were visually assessed and processed to annual time series (master plots), then weighted with respect to the number of trees and the highest possible class of growth change (Weber 1994). Using the skeleton plot method (Schweingruber et al. 1990) so-called “event years” are recorded. Event years are years in which particularly narrow or large rings are formed by a tree. If several trees are showing event years, such years are defined as pointer years. An abrupt growth change (AGC) is defined as a change in growth occurring when the average width of a series of four rings is at least 40% smaller or 160% wider than the average ring width of

the preceding four years (Schweingruber et al. 1990). Thus, positive abrupt growth changes are growth releases, whereas negative values represent growth reductions. Pointer years and abrupt growth changes are the result of a number of complex factors, and therefore, although they reflect the environmental conditions in which trees have been growing, their ecological significance is not diagnostic and difficult to be interpreted. However, at given site conditions, assuming that trees presently react as they reacted in the past (uniformitarianism principle), pointer years and abrupt growth changes, i.e. tree-ring widths, have frequently been used as indicators of stress created by environmental changes (reviewed by Cherubini et al. 1998). The frequencies of abrupt growth changes (AGC) and latewood events (LE) are expressed as percentages of the relevant number of trees per site and year (Weber 1997).

A time series of AGC values derived from the skeleton plot method from Weber's Celerina site was compared with ring-width data from nine larch trees of the same site measured using standard methods (Cherubini unpubl.).

In order to exploit to the full the information from the observations on defoliation patterns since 1864 (Auer unpubl. b), from the insect population census during the years 1949–1980 (Baltensweiler and Rubli 1999) and from the dendrochronological data collected by Weber (1995, 1997), a number of data series were assembled:

- Table 1: early gradation type Sils 15;
- Table 2: early gradation type Sils 15, Sils 19, Samedan 1, Bever 2 and late gradation type Celerina 14, Zuoz 7, Zuoz 8, Zuoz 9;
- Figure 3: Sils 15, Celerina 14;
- Figure 4: Sils 15;
- Figure 5: Celerina 14;
- Figure 6: as in Table 2;
- Figure 7: Bever 2.

The proximity of a meteorological station, i.e. in Bever (MeteoSwiss, Zurich, Switzerland), to the dendrochronological site Bever 2 provided perfect conditions for testing the influence of weather on larch growth. We compared monthly mean temperatures in years without defoliation impact, i.e. cycle years 0, 6–9, exhibiting either positive and negative AGC deviations (Fig. 7, 8). We did not take precipitation into consideration as soil water is not a limiting factor in the subalpine zone (Zweifel 1999, Hughes 2002), whereas several studies (Schweingruber et al. 1978, Rolland et al. 2001) have shown that summer temperature is the main factor limiting tree growth at these altitudes where larches grow.

Results

The LBM population cycle

The spatial development of a LBM outbreak can be mapped by recording the spread of discoloured larch stands as the forest services did in the Engadine in the course of the last century (Auer unpubl. b) as well as by doing a larval census like that of 1949–1985 (Auer 1961, 1977, unpubl. a). We observed that the spread of an outbreak generally follows a

regular progression, and this led us to define the early and the late gradation types. Obviously, fastest population growth will occur in areas where all the local site factors favour such growth. The areas of the early gradation type reflect the optimum sites for insect development and therefore represent the space where local dynamics dominate. The late gradation type, in contrast, often benefits from the immigration of moths which arrive from optimum sites.

The larval census revealed that the average population in the 6000 ha of forest of the Engadine reaches a maximum of 258 larvae kg^{-1} ($n=4$) in regular periods of 8–9 years (Auer 1961, 1977, Baltensweiler and Rubli 1999). The maximum density of 1248 larvae kg^{-1} was recorded at the late gradation site Celerina in 1954. Figure 3 depicts the population densities at the Sils and the Celerina sites during the 1970–1977 cycle (Auer unpubl. a). The early gradation type is characterised by a remarkable 20-fold increase from 1971 to 1972 and reached its peak density in 1972 with 798 larvae kg^{-1} , whereas the late gradation type in Celerina peaked at 346 larvae kg^{-1} only in 1973.

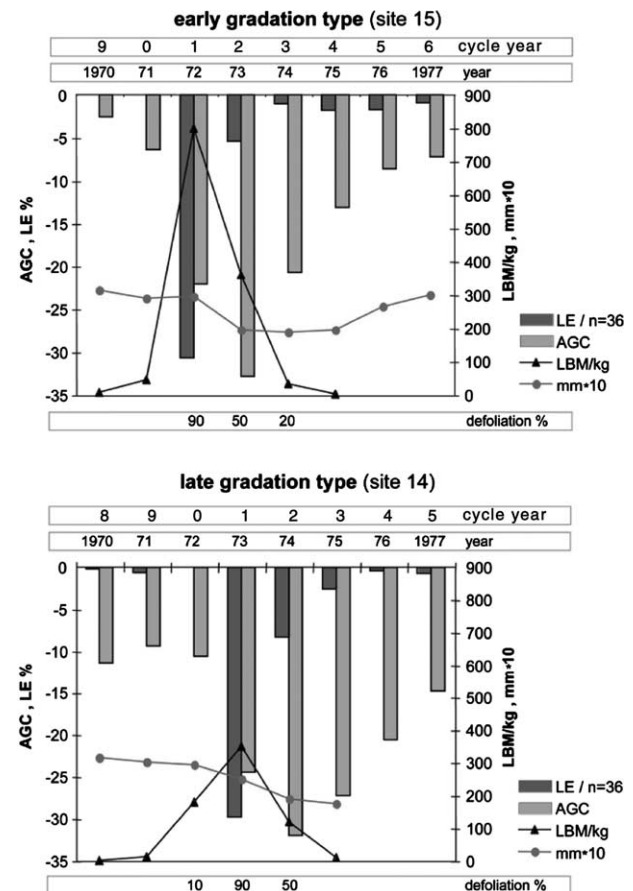


Fig. 3. Synopsis of LBM impact on larch during the 1970–1977 outbreak for two sites representing the early (site 15) and the late gradation type (site 14) in the Engadine. Treering criteria: LE: latewood events (% of trees weighted); AGC: abrupt growth changes (% of trees, weighted). Population density: LBM kg^{-1} : number of larch bud moth larvae per kg larch branches. Larch criteria: mm \times 10: maximum needle length \times 10. Defoliation%: proportion of biomass discoloured.

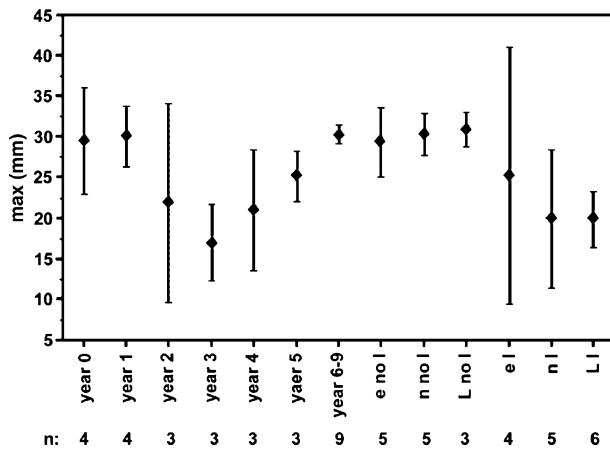


Fig. 4. Maximum needle lengths in the course of an outbreak (cycle years 0 to 9) on site 15 (Sils); means for three outbreaks within the period 1961–1989 (data see Table 3). Error bars: 95% confidence interval. No impact (no I): years 0 and 6 to 9. Impact (I): years 1 to 5. Phenology: e = early year, n = normal year, L = late year. n: no. of values per category.

The flush of larch

The most obvious impact of larval feeding on its host is, apart from the spectacular discolouration, the change in maximum needle length. Figure 4 shows this parameter for

the Sils site, based on the average of three cycles, for each year of the gradation. It is striking that the needle length in cycle year 1, the first year with visible damage, was 30 mm, which equals that of years without defoliation (cycle years 0 and 6–9). The greatest significant decrease to a minimum of 16.9 mm was observed in cycle year 3 only, followed by a slow recovery in cycle years 4 and 5. It is also noteworthy that the maximum needle length in cycle years without defoliation impact (years 0 and 6–9) is not influenced by the onset of needle growth, i.e. the phenological phase.

The dates of bud burst, defined by a needle length of 10 mm (T_{10}), are generally rather variable. Bud burst at the Sils site varied between 14 May ($d=134$) and 13 June ($d=164$) (Table 3). The classification of the years according to their phenological status resulted in nine early, ten normal and nine late years. In the early years the status T_{10} was reached on average on 18 May ($d=138$), whereas in late years it occurred 19 days later, on 6 June ($d=157$) (Table 3). The end of needle growth, as indicated by T_{max} , sets in on 15 June ($d=166$) in early years and on 28 June ($d=177$) in late years, i.e. the development of needles in late years is eight days shorter (only 22 days). Unfortunately, the amount of data does not allow to draw significant conclusions about the influence of defoliation on the time of sprouting of larch in the following year.

Information about the second flush in Sils is available for the years 1972–1974 (Baltensweiler and Rubli 1984). The

Table 3. Phenology of needle growth 1901–1989, site 19 (Sils).

Year	d T_{10}	d T_{20}	d T_{max}	D P1	D P2	Max. mm	Pheno.	Cycle year
1961	134	163	171	29	37	24.0	e	0
1962	162	170	182	8	20	27.0	L	1
1963	153		168		15	18.5	n	2
1964	146		165		19	15.0	n	3
1965	155		177		22	19.0	L	4
1966	136	151	157	15	21	24.0	e	5
1967	149	161	175	12	26	28.0	n	6
1968	147	155	170	8	23	31.0	n	7
1969	138	150	167	12	29	30.0	e	8
1970	156	165	175	9	19	31.5	L	9
1971	137	151	165	14	28	29.0	e	0
1972	150	162	184	12	34	29.5	n	1
1973	155		175		20	19.5	L	2
1974	151		169		18	18.8	n	3
1975	155		173		18	19.5	L	4
1976	137	153	161	16	24	26.5	e	5
1977	150	162	174	12	24	30.0	n	6
1978	154	162	176	8	22	30.0	L	7
1979	149	156	164	7	15	29.0	n	8
1980	157	165	183	8	26	31.5	L	0
1981	141	156	172	15	31	31.0	e	1
1982	149	160	166	11	17	27.5	n	2
1983	158		173		15	17.0	L	3
1984	164	176	180	12	16	24.5	L	4
1985						25.2		5
1986	141	149	165	8	24	30.0	e	6
1987	150	161	180	11	30	33.5	n	7
1988	140	150	170	10	30	33.7	e	0
1989	138	147	166	9	28	32.5	e	1

d T_{10} : date 10 mm needle length.
d T_{20} : date 20 mm needle length.
d T_{max} : date maximum needle length.
D P1: duration period $dT_{10}-dT_{20}$ in d.
D P2: duration period $dT_{10}-dT_{max}$ in d.
Max. mm: Maximum length in mm.
Pheno.: e early year, n normal year, L late year.

onset of refoliation varied between mid-July and 10 August, reaching a maximum length between 12 and 20 mm. In 1972 no refoliation occurred in the central part of the Upper Engadine, which subsequently led, as a rare event, to considerable larch mortality (Geer 1975, Baltensweiler and Rubli 1984).

Tree-ring analysis

The comparison of the results obtained by using the skeleton plot method (Weber 1997), with the standard ring-width measurements taken at the same site in Celerina (Cherubini unpubl.), shown in Fig. 5, exhibits an overall, good agreement between the two methods. Of particular interest is the analysis of the AGC- and LE-patterns in the course of the cycle (Fig. 6a-b). The LE-values of both gradation types fall immediately in the first year of the outbreak (cycle year 1) to their minimum of -30% , whereas the AGC-values decrease in cycle year 2 only to their minimum of approximately -30% and recover much slower than the LE criterion in cycle year 6 only to their pre-outbreak level of -5 – -10% . Furthermore, AGC-values recover faster in the early gradation type sites, i.e. on slopes with a SE aspect.

The impact of weather on larch growth

The dendrochronological site 2, Val Bever (Weber 1997), was selected not only for its closeness to the meteorological station at Bever (Schuepp 1960), but also for the relatively large number of positive AGC values deviations in years showing no defoliation impact, i.e. cycle years 0, 6–9. Figure 7 exhibits the added annual deviations of AGC and LE at this site. Within the period 1901–1981 there are 10 positive and 25 negative AGC deviations whereas LE exhibits only negative deviations. The monthly mean temperatures in years of positive AGC deviations were 1.2°C in May (p-value = 0.02; unpaired t-test; 95% confidence interval) and 1.6°C in June (p-value = 0.001; unpaired t-test; 95%

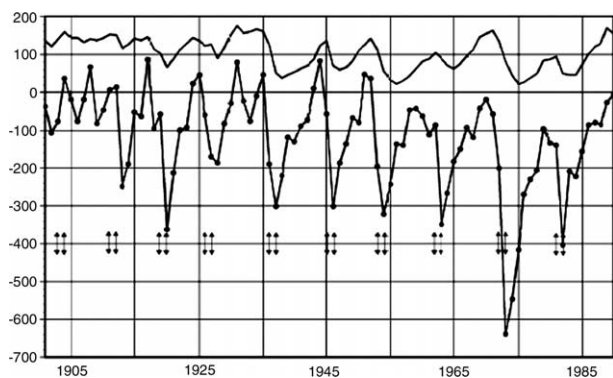


Fig. 5. Celerina, site 14: comparison of ring-width measurements 1901–1990 (Cherubini unpubl.) with AGC-values according to the skeleton plot method (Weber 1995).

— ring width ($\text{mm} \times 10^{-2}$).
 - - - AGC values, for graphical reasons multiplied by 10.
 ↑ outbreak year 1 and 2 (defoliation).
 ↓

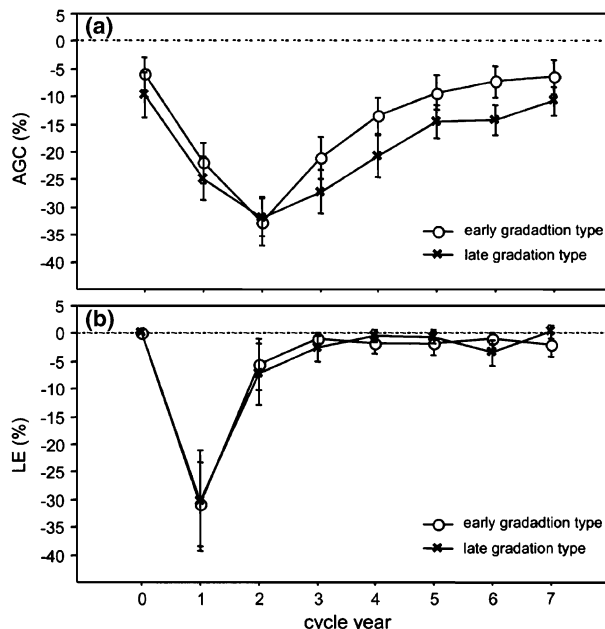


Fig. 6. Variation of AGC and LE values in the course of a gradation in the early and late gradation type areas (Table 4). Error bars: 95% confidence interval. Early gradation type: sites 15, 19, 12, 2. Late gradation type: sites 14, 8, 9, 7. 9 cycles between 1911 and 1981: $n = 36$.

confidence interval) (Fig. 8), which is significantly warmer than in years of negative AGC deviations.

Discussion

The research team of the Institute of Entomology at the Swiss Federal Institute of Technology (ETH) Zürich (1949 to 1989) benefited from being able to study an exemplary array of four classic LBM outbreaks during the 40-year period of LBM monitoring from 1949–1989 (Baltensweiler and Rubli 1999). This allowed the extrapolation of the course of the LBM cycle in combination with related time series to the entire 20th century (Table 1).

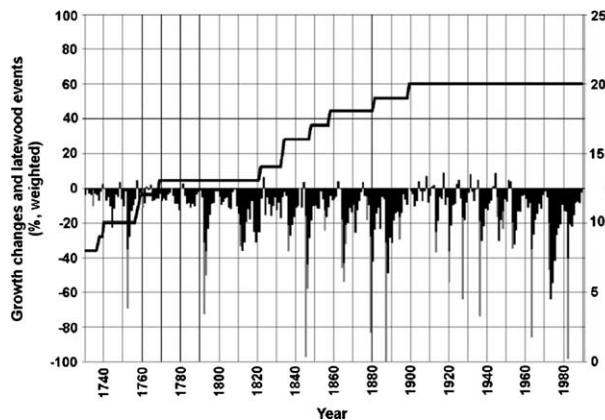


Fig. 7. AGC/LE-master plot (Weber 1994) for site 2 (Val Bever), a pure larch stand. Black columns: AGC values. Grey columns: latewood event values. Black line: no. of sampled trees (n).

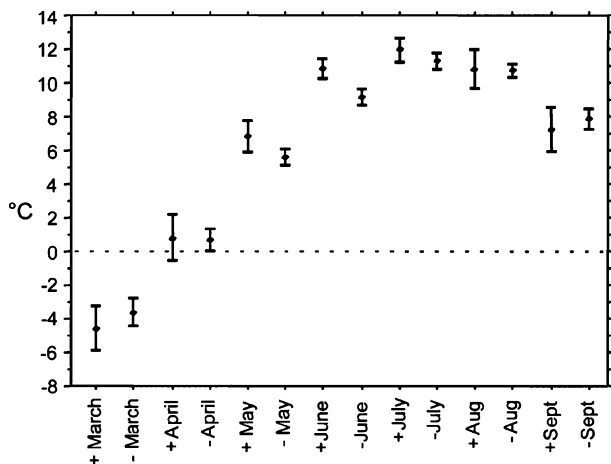


Fig. 8. Monthly mean temperatures (meteo station Bever, 1712 m) in years with either positive ($n = 10$) or negative ($n = 25$) deviations of AGC-values as observed at site 2, Val Bever (Fig. 7) for the time period 1901–1981. Only years with no LBM impact are considered (years 0 and 6 to 9). Mean monthly temperatures: °C, 95% confidence interval.

Larch growth and weather

In order to evaluate the growth response of larch to external impacts, especially to weather, its special deciduous growth pattern has to be considered. Obviously, specific ecophysiological characteristics must have evolved in order to provide the larch with advantages in competing with the evergreens in the harsh environment of boreal or upper montane and subalpine forests (Gower and Richards 1990). Burger (1926) postulated that the deciduous growth rhythm might have evolved in regions where late frosts in spring frequently endanger vegetative growth. Since annual needle growth occurs before shoot growth, needles are able to flush a second time at the expense of shoot growth (Baltensweiler and Rubli 1984). This also enables the trees to make efficient use of nutrients, which should improve their net carbon gain.

Nitrogen nutrition is of particular interest because it positively correlates with a plant's photosynthetic capacity and because its availability is generally rather low in cold-temperate ecosystems (Gower and Richards 1990). Larches are very efficient in retranslocating nitrogen from their senescing needles to their branches and stem (Gower and Richards 1990), from where it can be reinvested into new foliage in the following spring during early flushing. It was this rather specific physiological feature that led us to compare the weather patterns in spring during the years when there was either conspicuously increased or reduced growth. It was expected that an early and warm spring would induce increased growth, whereas a late and cool spring would cause reduced growth.

The positive and negative deviations of AGC values in years without defoliation impact (cycle years 0, 6–9) provided valuable data to test the influence of the prevailing weather on the growth of larch. Unpaired tests between positive and negative AGC deviations (Val Bever site, Fig. 8) and the mean monthly temperatures (at Bever) in the relevant years confirmed this hypothesis. Comparable results (not displayed here) were obtained for site 19, Sils Baselgia, using the meteorological station Sils

Maria. Thus, positive AGC values clearly reflect the extension of the growth period by early springs without any cold spells such as the "Eisheilige" (12–15 May) or the "Schafskälte" (10–20 June). These are two well-known Central European climatic singularities, i.e. characteristic weather conditions, which tend to occur regularly in a particular location at an almost fixed calendar date.

LBM development and the phenology of larch

The LBM monitored in Sils 15 from 1961 to 1988 had to cope with a host which has a very early, but also very variable, flush. The important temporal coincidence of egg hatch and needle-flush is well buffered at subalpine altitudes by the radiation climate. Eggs hibernating underneath the black lichens on branches exposed to direct solar radiation hatch 14 to 20 days before eggs exposed on the north side of the trees (Bovey 1966, Baltensweiler 1984, 1993). First instar larvae install themselves successfully within the closed fascicles of needles 5–8 mm in length.

The period of needle growth coincides with the growth phase of the small first and second instar larvae, which very characteristically feed head down at the base of the needles, i.e. on the tissue most rich in nitrogen (Omlin and Herren 1976, Matyssek 1985), where they are well protected within the fascicle. By the time the needles reach their maximum length (T_{max}) and the long shoots begin to grow, the LBM is in its third instar and starts to feed at the tip of the needles, which by then are spun together into a tube-like shelter. The growth period of needles varies between 31 days in early years and 22 days in late years. The coordination of the two growth phases is of prime importance as the protein content of larch needles falls from its maximum content of about 35 mg g^{-1} at the beginning of growth to 25 mg g^{-1} a month later (Omlin and Herren 1976, Matyssek 1985). Thus, the LBM exploits the most optimal food resource in the subalpine larch-cembra pine forests before other tree-feeding Lepidoptera begin to develop (Delucchi et al. 1974).

The impact of defoliation on needle growth

The reduced maximum needle length in cycle years 2–5 clearly reflects a delayed impact of defoliation in cycle year 1, with the most significant decrease (43% of normal needle length) occurring in cycle year 3. What was rather unexpected was to find that the maximum needle length is not affected by the phenological date of the beginning of the growth phase, i.e. whether it starts early or late in the season (cycle years 0, 6–9).

The impact of defoliation on tree-ring patterns

Figure 5 shows the comparison of the AGC values with standard ring-width measurements taken at the identical site in Celerina (Auer unpubl. c). Although the skeleton plot method involves a qualitative and not a quantitative analysis, it provides exact information on tree-ring growth responses to environmental conditions with annual resolution. Furthermore, the skeleton plot method, which is a

quick assessment tool, provides a synoptic view of large samples of cores on a long-time scale by comparing the two criteria AGC and LE, either between sites or between negative and positive values within a site.

In contrast to maximum needle length, radial growth, which is indicated by abrupt growth changes (AGC), reacts to defoliation already in cycle year 1 by a significant drop from -6% to -22% (AGC early sites, paired t-test) (Fig. 6a). The largest impact (-32.5%) occurs in cycle year 3. The general threshold of negative AGC percentages in years without the LBM impact is interpreted as being due to the large variety of sites ranging from 1700 to 2200 m a.s.l. and various other aspects.

The criterion LE responds more immediately and intensely to defoliation than AGC. It decreases from 0% to -31% (Fig. 6b) already in cycle year 1 and rebounds in cycle year 2 to -5% . The following cycle years 3–7 reflect a general threshold of -1 to -2% . The immediate decrease in LE in cycle year 1, after the loss of $>50\%$ of assimilating biomass, is clearly due to the investment of all the nutrient resources, whether stored from the previous year or currently being produced, in the reflush. In 1972, however, defoliated larches in the central part of the Upper Engadine did not have a chance to reflush properly because, after a winter of sparse snow cover, there was no rain in August. As a consequence, widespread larch mortality, amounting to a three fold loss as in normal years, occurred as a rather rare event.

Interpretation of an impeded outbreak by means of tree-ring patterns

Figure 5 shows a rather regular periodic course of ring-width and AGC values at the site Celerina 14, the exemplary late gradation type site, throughout the 20th century except for the first 10 years 1901–1910. A similar anomaly can be seen in Fig. 7, the masterplot of AGC and LE values for the early gradation type at site Bever 2. A detailed analysis of the relevant forestry reports and weather data revealed that an incipient outbreak had caused light defoliation along the Lake of Sils in 1901, no defoliation anywhere in 1902, but again defoliation in 1903 and 1904. In both these latter years, patchy and light discolouration was restricted to the lower mountain slopes on the sunny side of the Engadine valley between Sils and Samedan.

More recent analyses (Baltensweiler 1993) suggest this pattern was probably due to the alternating sequence of favourable and unfavourable late winter and spring weather. Such weather either increases egg survival or induces catastrophic egg mortality, and may also influence larch growth selectively, depending on the site location. Thus, an extremely warm April in 1902 (mean monthly temperature: 2.4°C ; standard 1901–1910: 0.3°C ; Auer unpubl. b), followed by an extremely cold May (mean monthly temperature: 2.3°C ; standard 1901–1910: 5.3°C) induced high egg mortality and delayed the flush of the larch, so that no defoliation occurred. The weather continued to be extremely variable. Spring 1903 was cool (mean temperature March–May = -0.3°C ; standard 1901–1910: $+0.26^{\circ}\text{C}$), combined with a high snow cover. The meteorological station Bever (1712 m a.s.l.) reported a snow depth of

0.47 m at the end of April and the snow cover lasted until 18 May. Therefore, the growing season began late, especially in forests with northwestern and northern aspects at higher altitudes. In contrast, spring 1904 was extremely warm (mean temperature March–May 1.6°C), and defoliation promptly occurred in the sunny forests along the Lake of Sils and above Samedan.

These climatic extremes are clearly reflected in the tree-ring parameters of the corresponding sites, grouped according to aspect and altitude (Table 4), i.e. the late spring 1903 caused the lowest AGC values (means -8.8 to -13.0% , respectively), while the warm spring 1904 left barely any trace (means -1.2 and -1.8% , respectively). The conspicuous LE values in the late gradation type areas (sites 7, 8, 9) in 1903 can be ascribed to the short vegetation periods at these high altitude locations, whereas the LE values in 1904 at the optimum sites 12 and 15 are due to defoliation. Considering the very adverse weather conditions in 1903 it is, admittedly, difficult to ascribe the LE value of -30% at site 15 to either defoliation or weather. However, since defoliation was reported to have occurred in the area, and since the surviving populations from the outbreak 1901 probably recovered at this optimum site earlier than anywhere else, the most likely cause is defoliation.

The course of the 1972 outbreak

Figure 3 gives a synopsis of the LBM impact on larch, exemplified by the unusually devastating population cycle from 1970–1979. The actual outbreak period, characterised by discoloured forests, lasted from 1972 to 1974. Discolouration appeared at the site Sils 15 very conspicuously at the beginning of July 1972 (Baltensweiler and Rubli 1984). The intensity of the defoliation was very patchy, but was most intense at the sites of the early gradation type on the lower slopes with southeastern aspect. Refoliation set in at the beginning of August 1972, with the new needles reaching lengths up to 18 mm, but generally less than 12 mm. In the forests of Bever, Celerina and Pontresina, i.e. the central part of the Upper Engadine, there was no precipitation for almost five weeks after defoliation and no refoliation at all took place. As a very rare event, extensive tree mortality occurred in this area in the course of the following years. In 1973 the entire Upper Engadine was again defoliated at an even greater intensity. Rather exceptionally, discolouration also reappeared on a more local scale even in 1974.

The population courses at site 15, the early gradation type, and at site 14, the late gradation type, during the population cycle 1970–1977 are shown in Fig. 3. Their impact on larch is also indicated in terms of the intensity of defoliation in percentage, the relevant maximum needle lengths as well as the two criteria AGC and LE at these sites. It is striking that the latewood width (LE) responded immediately in both gradation type areas in the summer of cycle year 1, which generally occurs at densities ≥ 200 larvae kg^{-1} or subsequent to defoliation of at least $>50\%$. Thus, the coincidence of peak populations and LE minima in cycle year 1, combined with the AGC minimum in

Table 4. LBM outbreak 1903/1904. AGC and LE data for two groups of sites (Weber 1995) representative for the early and late outbreak types.

Early gradation type: SE exposure										
Altitude	Sils site 15	Sils site 19	Samedan site 12	Bever site 2	mean	Sils site 15	Sils site 19	Samedan site 12	Bever site 2	mean
	1840	1840	1830	1820		1840	1840	1830	1820	
Year	AGC	AGC	AGC	AGC		LE	LE	LE	LE	
1900	-6.0	-0.4	-7.7	-2.0	-4.0	0.0	0.0	0.0	0.0	0.0
1901	-10.7	3.1	11.3	-3.7	0.0	0.0	0.0	0.0	0.0	0.0
1902	-16.0	-5.8	1.7	-10.7	-7.7	0.0	0.0	0.0	0.0	0.0
1903	-16.7	-6.2	-4.7	-7.7	-8.8	-30.0	0.0	0.0	0.0	-7.5
1904	-12.7	0.0	4.3	3.7	-1.2	-12.0	0.0	-16.0	0.0	-7.0
1905	-11.3	-2.8	-3.7	-2.0	-4.9	0.0	0.0	0.0	0.0	0.0

Late gradation type: NW exposure										
Altitude	Celerina site 14	Zuoz site 8	Zuoz site 9	Zuoz site 7	mean	Celerina site 14	Zuoz site 8	Zuoz site 9	Zuoz site 7	mean
	1830	1890	2100	2200		1830	1890	2100	2200	
Year	AGC	AGC	AGC	AGC		LE	LE	LE	LE	
1900	-8.0	-5.3	-15.3	2.0	-6.6	0.0	0.0	0.0	0.0	0.0
1901	-8.7	-4.0	-13.3	4.0	-5.5	0.0	0.0	0.0	0.0	0.0
1902	-12.7	-9.3	-16.7	-4.0	-10.7	0.0	0.0	0.0	0.0	0.0
1903	-11.3	-12.0	-22.7	-6.0	-13.0	0.0	-12.0	-16.0	-10.0	-9.5
1904	-4.0	-4.0	-4.7	5.3	-1.8	0.0	0.0	0.0	0.0	0.0
1905	-4.0	-6.0	-13.3	-2.0	-6.3	0.0	0.0	0.0	0.0	0.0

cycle year 2, are typical for a normal sequence of events characterising a LBM outbreak.

The typical sequential spread of defoliation in space during most of the outbreaks prompted detailed investigations of the dispersal of LBM moths (Baltensweiler and von Salis 1975, Vaclena and Baltensweiler 1978, Baltensweiler and Rubli 1999). Two factors were found to be of prime importance for the formation of the early and late gradation types: the exodus of moths from defoliated stands and the avoidance of oviposition in such stands. Both these factors contribute to the delayed colonisation of less optimal sites. These findings support those of Ranta et al. (1997), who maintain that the local dynamics of populations cannot be fully understood unless the significance of the spatial linkage of subpopulations via dispersal is taken into account.

General reflections

In an earlier paper on the recorded defoliation pattern of LBM outbreaks since 1864 in the Grisons, Baltensweiler (1964) distinguished between accelerated, normal and impeded outbreaks. A rare accelerated gradation was found to occur after 2–3 years of early spring or warm summer weather, and was characterised by general defoliation of the entire Engadine valley in cycle year 1. Obviously such weather conditions override the site-specific characteristics imposed by topography and enable synchronous population growth throughout the valley. In contrast, the 1972 outbreak, where there were early and late courses of larval densities on local scales, was the result of the interaction of topography and standard weather, which led to site-specific asynchronous population growth and, accordingly, a patchy distribution of defoliation. This configuration is basic for

the inherent functioning of the cycle since the relocation of large quantities of moths after defoliation from the early optimum site to the late site buffers the immediate negative feedback of food deterioration on the subsequent early type generation and reinforces thus the stability of the cycle at the same time also against adverse weather effects. Thus, the extraordinary periodicity of the LBM cycle relies very much on the diverse local topography and the compensatory effect of moth migration on a regional scale.

The response of moths to defoliation by dispersal is also determined by topographic features and the prevailing weather. However, these two factors influence the dispersal behaviour of moths in very different ways and lead to dispersal on either the regional scale, i.e. within the Engadine only or on a much larger scale through long-range dispersal. Due to their odour-mediated navigation system, the moths either move upward within the katabatic windfield and aggregate at the subalpine level or, if these sites are defoliated, they reach the tops of mountains and embark on geostrophic winds in a long-range dispersal.

Provided that the selection of dendrochronological sampling sites specifically takes into consideration the standard course of the LBM outbreak, the dominant impact of defoliation as expressed by the LE criterion (Fig. 6) offers conclusive evidence to differentiate between the impacts of LBM outbreaks, and purely random weather events.

Conclusions

The tree-ring pattern, which we describe in this paper as the “larch-bud-moth syndrome”, arises from the conspicuously negative LE in cycle year 1 of an outbreak, followed by a negative AGC in cycle year 2 or even year 3, and the

recurrence of this pattern at 8–10 year intervals. The existence of this pattern is supported by the observed delay in the appearance of the pattern in tree-ring samples from ecologically diverse outbreak sites within the region.

The LBM fluctuation is spatially asynchronous, due to the interaction of site factors and weather as well as the way the LBM's interaction with the host plant depends on the population density. This confirms the hypothesis proposed by Peltonen et al. (2002) that there is a spatially dependent variation in density dependent dynamics. The claim that there is a difference in the decay of synchrony in space should, however, be restricted to situations where both the extension of landscape topography and the scales of dispersal are similar.

We plan to search for the "larch bud-moth syndrome" in long tree-ring chronologies, such as that published by Esper et al. (2007), but collected from all the main areas of LBM outbreaks in the European Alps (Baltensweiler and Rubli 1999). Preliminary analyses of a fossil larch tree from the first millennium excavated in the flood plain of the Engadine provide encouraging results showing the presence of the "larch bud-moth syndrome" between 100 BC and around 200 AD (Cherubini 2007). Such tree-ring chronologies exhibiting the LBM syndrome and spanning several centuries allow us to evaluate some of the many different models of LBM cycles (Berryman 2002, Björnstad et al. 2002, Turchin et al. 2003, Johnson et al. 2004) on a long time scale.

Our results suggest that it would be worthwhile to re-examine the tri-trophic model of Turchin et al. (2003), which, unfortunately, is based on the mean LBM population for the entire Engadine and therefore strongly falsified. The model needs reconsideration in the light of the importance of the local dynamics and dispersal, as stressed by Ranta et al. (1997).

In contrast to barkbeetle outbreaks which generally cause extensive forest stand mortality and to which we referred to in the Introduction, the LBM leaves in behind the "Larch Bud Moth Syndrome" for centuries as a trace of its cyclic outbreaks in the same forest stands. The detection of the functioning of the complex LBM system in earlier periods will be of utmost importance for helping to understand the impact of future climate changes on insect populations and forest ecosystems.

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