Larch- and pine-feeding host races of the larch bud moth (Zeiraphera diniana) have cyclic and synchronous population fluctuations

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Population cycles of many forest-defoliating insects often show synchronous fluctuations at both intra-specific (spatial synchrony) and inter-specific levels. However, population dynamics of different host-associated biotypes of the same species, such as those of the larch budmoth (LBM), Zeiraphera diniana (Lepidoptera: Tortricidae), have never been compared. This species causes extensive defoliation of larch forests every 8 to 9 years in the Alps, but it consists of two genetically-differentiated host races, the first one developing on European larch, Larix decidua, and the other one developing on Swiss stone pine, Pinus cembra. The dynamics of Zeiraphera populations have been extensively studied on larch, whereas little is known about larval density and possible population fluctuations on sympatric pines. A larval census on Swiss stone pine was conducted in the Swiss Alps intermittently between 1958 to 2004 and in the French Alps from 1992 to 2004. Population density of Zeiraphera on pine varied up to 5000-fold and showed periodic oscillations, with five peaks in Switzerland and one in France. Because the feeding activity of the pine race is restricted to the elongating shoot of the current year, no conspicuous defoliation of pine trees was noted during years of high larval densities. Zeiraphera populations on pine oscillated in significant synchrony with larch-associated populations, and peak densities were observed either the same year or shifted by ± one year. Our results did not allow any explanation for cyclic fluctuations of LBM on pine, but the synchrony with the larch race’s cycle suggests that studies on genetics as well as on parasitism should be intensified.

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Population dynamics of forest pest insects showing cyclic outbreaks is a fascinating topic for population ecologists. Many studies have emphasized identification of the processes that generate periodic fluctuations of foliage-feeding forest insects, and particularly lepidopteran populations. Several explanations have been proposed, including external forces such as climatic or sunspot cycles, as well as biological mechanisms involving plant quality, maternal effects, predators, pathogens or parasitoids (Ginzburg and Taneyhill 1994, Berryman 1996, Turchin et al. 2003). Spatial synchrony among populations of the same species is a rather common feature exhibited by forest lepidopteran defoliators (Myers 1998, Liebhold and Kamata 2000). More recently, Raimondo et al. (2004a, 2004b) reported synchrony between sympatric populations of different lepidopteran species. Several mechanisms that may cause synchrony have been proposed: dispersal among
populations, exogenous random factors such as weather influences (‘‘Moran effect’’) (Ranta et al. 1995), or trophic interactions with populations of other species (Liebhold et al. 2004). However, population dynamics of host-associated biotypes of the same species have never been compared.

In the Alps, the larch bud moth (LBM) Zeiraphera diniana Guenée (Lepidoptera: Tortricidae) exhibits cyclic population dynamics with regular outbreaks at 8–10 year intervals, and is considered a remarkable model for studies of population cycles (Baltensweiler and Priesner 1988). At peak densities, larval populations are ca 10^5 fold higher than at low density and cause conspicuous defoliation of Alpine larch forests. The processes that produce a subsequent crash have been attributed to various factors: delayed effects of defoliation on the foliage quality of larch, interactions with parasitoids and pathogens, and other factors which could contribute to changes in LBM fecundity and mortality (reviewed by Baltensweiler and Fischlin 1988). A recent model suggests that interactions between LBM and its parasitoids might represent a key factor driving the budmoth cycle (Turchin 2003, Turchin et al. 2003). In addition, dispersal is considered to play an important role in LBM population dynamics throughout the Alps, as outbreaks are accompanied by long-distance mass migrations of moths (Baltensweiler and Rubli 1988). A recent model suggests that interactions between LBM and its parasitoids might represent a key factor driving the budmoth cycle (Turchin 2003, Turchin et al. 2003). In addition, dispersal is considered to play an important role in LBM population dynamics throughout the Alps, as outbreaks are accompanied by long-distance mass migrations of moths (Baltensweiler and Rubli 1988).

LBM has two host races, feeding respectively on European larch (Larix decidua) and Swiss stone pine (Pinus cembra). On larch, LBM exhibits periodic outbreaks resulting in spectacular defoliations, which have triggered extensive studies to find control measures (Auer 1974a, Martouret and Auer 1977, Auer et al. 1981). In contrast, the dynamics of LBM populations on Swiss stone pine have received little attention. High numbers of larvae have been rarely observed and even less often reported (Barbey 1925), since the larvae feed on the growing needles of the current shoot but do not attack the perennial needles. The existence of these two races was first suspected by Coaz (1880) and Thomann (1929), but ascertained only in 1995, when Emelianov et al. (1995) showed that the two LBM forms are clearly genetically differentiated “host races”. The larch and the pine races differ in a number of heritable traits, including colouration of 5th larval instar (Baltensweiler 1977, 1993a), host preference for egg-laying and synchrony with host phenology (Bovey and Maksymov 1959, Day 1984), sexual pheromones (Guerin et al. 1984, Baltensweiler and Priesner 1988), and insect responses to host volatiles (Syed et al. 2003). Several studies of pre- and post-mating isolation between the two sympatric host races have provided evidence for host-induced assortative mating (Emelianov et al. 2001), and allowed estimation of the frequency of hybridization between host races in the wild (about 3%, Drès 2000, Emelianov et al. 2003). Host choice experiments have shown that both LBM host races prefer to alight on their own host tree. However, variation in host preference has been observed within the LBM races, some adults of each race showing a tendency to alight on the host of the other race (Emelianov et al. 2003).

Z. diniana can also develop on other species of genus Pinus. Unlike on P. cembra, outbreaks of Z. diniana have been reported from Kamchatka (Russia) on Pinus pumila Regel (Khomentovskoy et al. 1997), from Scandinavia on Pinus sylvestris L. in mixed pine/spruce forests (Ehnström et al. 1974) and from Scotland in plantations of lodgepole pine (Pinus contorta) (Day et al. 1991). In addition, very destructive outbreaks have been observed on Norway spruce (Picea abies) in the Ore Mountains (Czech Republic) (Kalina et al. 1985, Baltensweiler 1991). Although these outbreaks on evergreen conifers occur rather sporadically, it is noticeable that they were caused by larvae which corresponded in ecological and morphological traits to the pine host race. These observations suggest the interest of studying the population dynamics of LBM developing on Swiss stone pine.

LBM populations developing on this host were regularly surveyed in Engadine during the 1960s and the 1970s along with the survey of LBM density on larch (Auer 1958–1975), but these data were never published. Therefore, the objectives of this study were (1) to measure LBM larval density on Swiss stone pine and assess its annual variation over a consequent time period in the French Alps and in Engadine, taking into account the as yet unpublished data; and (2) to compare the dynamics of LBM populations on Swiss stone pine with that of the LBM populations developing in the surrounding larch forests.

Material and methods

Census of LBM larvae on Pinus cembra

The collection of density data for the pine host race is complex and time consuming because it has to be based on the counting of damaged shoots rather than on a weight basis, as in the case of the larch race.

Newly emerged pine budmoth larvae feed upon the growing needles of the elongating shoots of the current year. Their first appearance is indicated by delicate webs. Later the third and fourth instar larvae attach the small lateral shoots of the outermost whorl to the terminal shoot by webbings. Growing larvae feed also on the parenchyma of the growing shoots and on conelets and male flowers, and gradually accumulate frass and webbings around the tips of the branches. However, this damage is readily visible only on small pines up to 5 m height. Infestation on mature pines cannot be detected reliably from the ground. Thus, we
selected the individual shoots of a branch as the basic sampling unit and expressed the density as number of larvae per 100 shoots. 

Census of LBM pine race was carried out in the French Alps and in Switzerland. In the northern French Alps, an annual survey was carried out from 1992 to 2004 in the forest of Tuéda, near Méribel-Les-Allues (45°21′N, 6°38′E). The Tuéda forest ranges from 1700 to 2000 m a.s.l., and is considered to be the largest pure stand of *P. cembra* in the northern French Alps. Pines are mixed with Norway spruce (*Picea abies*) at low altitude. Ten mature pine trees were selected at random and then surveyed during the entire study. On each tree, 20 branches were selected in the top third of the crown and on each branch all the shoots were counted. All the shoots were individually examined for larvae, first and second year cones, male flowers and damage inflicted. The census was performed every year from 1992 to 2004, in late June or early July, as soon as 4th-instar larvae were observed. An additional survey was carried out in 1995, this census being extended to the entire tree crown with additional 20 branches in the middle and 20 branches in the lower crown. In 1995 we also counted the total number of branches per tree on 20 trees (including the ten trees used for the larval census and ten additional trees selected at random), in order to obtain an estimate of absolute larval densities per tree.

In Switzerland, a larval census was carried out intermittently in Engadine from 1958 to 2004. Different sampling methods and sites were successively used. During the period 1958–1975, a mature mixed larch-cembran pine forest, occasionally including Norway spruce (*P. abies*), was surveyed at Celerina Staz (forest compartment 18; 46°30′N, 9°53′E; 1800 m a.s.l.), located in the valley bottom of Engadine. Each year, 20 mature pines were randomly selected and one branch of approximately 5 cm diameter was cut in each of the lower, middle and upper third of the crown. On each branch, 150 shoots were examined for larval presence (Auer 1958–1975). During the period 1976–2004, two sites were intermittently monitored, at Pontresina (forest compartment 21; 46°28′N, 9°56′E, 1900 m a.s.l., NW exposure) and Bever (forest compartments 14–15; 46°34′N, 9°52′E; 1750 m a.s.l., S exposure), respectively. Both sites are covered by a mixed larch-cembran pine forest in a patchy structure, with cembran pine regeneration of 3–8 m height on the borders of the gaps. Individual cembran pines were randomly selected by sight at a distance of 10 m and 5–10 terminal shoots examined for larvae. No fewer than 200 shoots were examined per site, and the results of the two sites were pooled per year. However, during the last cycles only the years 1992 and 2002–2004 could be documented by larval numbers (Fig. 2).

**Census of LBM larvae on *Larix decidua***

A larval census of the larch host race was developed by Auer (1961, 1974b, 1977) on a weight basis. It consisted of counting the number of LBM larvae in a sample of one to three kg of twigs (<10 mm diameter) cut out of the top, middle and lower crown of a larch tree, this operation being repeated on a large number (>100) of mature larch trees distributed throughout the Engadine valley. Since this method required the climbing of trees, it was very expensive. Therefore a simpler census was designed to be applied from the ground (Auer and Servais 1976, modified by Roques and Goussard 1982). From each of ten trees per site, five branches from the lower crown (2–3 m above ground) were selected at random, and a sample of 0.40 m length was cut from each branch for counting the number of LBM larvae. To permit comparison of the data from the different sampling periods, we converted density $m^{-1}$ branch length into density kg$^{-1}$ using a magnification by 34, as suggested by Roques and Goussard (1982) for the French Alps. The timing of the collection was defined with respect to the appearance of typical needle fascicles spun by 4th-instar larvae, about two weeks prior to the sampling of the pine host race. As a spatial extension of the larval census, the typical red-brown discolouration of the larch forests induced by larval densities higher than 100 larvae kg$^{-1}$ (Auer 1977), was mapped throughout the Alps (Baltensweiler and Rubli 1999).

In the French Alps, it was not possible for technical reasons to survey continuously any pure larch forest close to the Tuéda pine stand. We therefore decided to consider pure larch stands of the southern French Alps, in Val Guisane, because this valley had served as one of the main sites for a previous monitoring of larch race populations throughout the Alps from 1960 to 1980 (Auer 1977). Since 1980, the survey of Val Guisane has been restricted to only one site, the forest of Les Combes, which is located near Briançon (44°53′N, 6°35′E; 1850 m a.s.l., S exposure) at ca 50 km of Tuéda. Data on LBM populations were collected for this stand from 1978 to 2004 according to the method of Roques and Goussard (1982). In addition, we compiled the annual observations of *Zeiraphera* damage on larch in the northern French Alps which were published by Département Santé des Forêts (French National Forestry Office).

In Switzerland, LBM larval density on larch was monitored from 1958–2004 at various spatial scales over the Engadine valley (6280 ha of forest). Previously published papers supplied data based on the annual sampling of 100 to 200 larch trees during the period 1949–1980 (Auer 1977, Baltensweiler and Rubli 1999). However, in the interest of a direct comparison of the two host races, the period 1958–1975 was additionally documented by the estimation of larch host race densities on 20 trees at the site of Celerina Staz (Switzerland), close to the Swiss stone pine site. Since
1990, larval density has been monitored by the method of Roques and Goussard (1982) only intermittently, i.e. in the years 1992 and 2002–2004.

Data analyses

To compare larval density at the different tree crown levels on pine (French Alps), the mean number of larvae observed at the upper third, at the middle and at the lower part of the crown was compared using the non-parametric Kruskal-Wallis test (Statistica 6.0 Microsoft) \((p < 0.05)\). We evaluated synchrony among the two host races by using the cross-correlation of ln-transformed abundance of the two races at each of the two areas, France and Switzerland. The procedure first involved fitting autoregressive (AR) models to each time series using the library ARfit with MATLAB (Neumaier and Schneider 2001), and correlating residuals from these models. The statistical significance of the correlation between the two residuals was then scored by applying two successive tests: a standard test for zero correlation on the residuals (“residual test”), and a bootstrap approach by re-sampling the residual under the null hypothesis and independence among the series (1000 iterations) (Buonaccorsi et al. 2001). Cross-correlation analyses were conducted for lags between \(-2\) to \(+2\) years. These measures and tests for synchrony were applied to the periods 1992–2004 (French Alps) and 1958–1984 (Swiss Alps).

Results

LBM dynamics on pine and larch in the French Alps

The densities of LBM on cembran pine in the forest of Tuéda increased continuously from 1992 to peak in 1995 (Fig. 1). The population then declined for five years to increase again from 2001 on. At the 1995 peak, the larval population was ca 46 times larger than in 2000 (mean number of larvae per shoot \((\pm SE): 0.92 \pm 0.28 \text{ vs } 0.02 \pm 0.01)\). From 1994 to 1996, more than three larvae per shoot were observed in 17.1% of the sampled shoots whereas only 3.3% of shoots contained more than three larvae in the other years. These densely populated shoots were covered with webbings and great amounts of frass, whilst feeding damage was also noticed on bark and on the needles of the elongating shoots. In 1995, 11.8% of the conelets (first-year cones) were also damaged by LBM larvae, whereas only 1.3% of the conelets were attacked in 1992. Similarly, the number of male flowers damaged was greater in 1995 (14.5% of the sampled units damaged) than in 1992 (2.8% of attacks). No damage to second-year cones was observed. No LBM attack was recorded on sympatric spruce trees during the period 1992–2004.

The 1995 census, which embraced the entire tree crown, revealed a significantly higher LBM density in the top third of the crown \((0.92 \pm 0.28 \text{ larvae shoot}^{-1})\) than in the middle and lower thirds of the crown \((0.69 \pm 0.12 \text{ and } 0.77 \pm 0.12 \text{ larvae shoot}^{-1})\), respectively; \(\chi^2 = 16.1; \text{DF} = 2, \text{ p < 0.001})\). The mean number of shoots per branch was \(74 \pm 18\) (mean \(\pm SE\); \(n = 60\) branches per tree on ten trees) and the mean number of branches per tree was \(211 \pm 22\) (\(n = 20\) trees). The mean larval density in 1995 was thus extrapolated to 12 335 larvae per tree in 1995, compared to only 268 larvae in 2000.

The fluctuations in density of LBM on larch during the period 1960–2004 in the Valley of Guisane were characterized by four full cycles, with peak densities in 1962, 1972, 1979 and 1996. Data are lacking for the 1986–1987 period, which theoretically corresponded to a period of maximum larval density. However, the peak density expected for this period failed due to unusual
weather conditions (Baltensweiler 1993b). In 2003, the larval survey could be carried out on only one larch tree, and moreover was performed very late in the season. Therefore, LBM population level on larch was probably underestimated that year. In 1996, LBM populations peaked with ca 13.5/1.6 larvae m^-2 (mean/SE; or approx. 467.5 larvae kg^-1). However, light defoliation was already observed in 1995 and persisted in 1997, the larval density being higher in both years than the 10% defoliation threshold of seven larvae as postulated by Roques and Goussard (1982) (Fig. 1). When applying the dendromorphological criteria proposed by Auer (1974b) following the analysis of 100 larch trees in the Engadine, such as length and weight of branches in relation to the breast height diameter of the tree (DBH), we extrapolated the absolute number of larvae per larch tree of 40 cm DBH in 1992 to 48 500 larvae, i.e. four times as high as mean density per tree on cembran pines. Thus, the two host races fluctuated synchronously in this site during this period, although peak numbers of larvae were offset by one year. A significant cross-correlation was found for lag zero between the LBM cycles on pine and on larch, when using different AR models and two different tests (Table 1). For lag different from zero, the hypothesis of no synchrony was accepted, confirming that log-abundance fluctuations were clearly simultaneous in the two host races (i.e. for lag zero).

### Table 1. Cross-correlation coefficients (r) of ln-transformed abundance of the two host races, and P values resulting from tests of “no synchrony” among the residuals: residual test [P(r)] and bootstrap test [P(B(r))]. The correlation on residuals was calculated after fitting autoregressive [AR(q)] models to each time series with different orders q. The table presents the results for lag zero. For all other lags (−2, −1, +1, +2), the hypothesis of “no synchrony” was accepted, suggesting that populations of the two host races oscillate in a similar manner and at the same time (lag zero).

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LBM dynamics on pine and larch in the Swiss Alps

In the Engadine, the populations on pine passed through three full cycles between 1958 and 1984, with a mean of 32.7 larvae per 100 shoots at peak density (Fig. 2). The minimum density was defined by two values, >0.01 in 1967 and 0.42 larvae per 100 shoots in 1977. Because of the intermittent census no further peak densities were recorded after 1985. The fragmentary data, however, suggest by their sequence a peak in 1989 and a fifth peak during the period 1998–2000.

The evolution of larval densities on larch for the period 1949–1989 exhibited four cycles at regular intervals and the beginning of the rise phase of the 5th cycle. In 1989 slight defoliation was observed at the Sils site only, but then no further defoliation damage occurred throughout the Engadine. In 1992 population density was as low as 0.28 larvae kg^-1. Ten years later, in 2002, the larch race was again at a similar low density of 0.45 larvae kg^-1 and dropped the following year to a minimum of 0.02 larvae kg^-1. Fragmentary as these data may be, they also suggested two peaks for the larch race in 1989 and in 1999 or 2000. This reasoning was supported not only for 1989 by the observed defoliation damage in the Sils area but also for 1998 (Baltensweiler 1993a, Baltensweiler and Rubli 1999). In 2000, defoliation was even more general throughout the Engadine, a level of damage representative for a density >100 larvae kg^-1 (Auer 1977).

Fig. 2. Comparative annual fluctuations in the mean larval density of *Zeiraphera diniana* on *Pinus cembra* and on *Larix decidua* during 1949–2003 in the Engadine, Swiss Alps. Census methods differed according to year and host tree.
Comparison of fluctuation of larval numbers on larch and pine showed that Swiss populations oscillated in a similar manner and at the same time. Peak densities were observed at one year’s interval on the two tree hosts, populations on larch reaching the peak one year before (1973, 1982) or after (1964) pine populations. For the last cycle, the minimum density was observed the same year on both tree hosts, in 2003. As in the French Alps, all the measures and tests for synchrony indicated that the LBM cycles on pine and on larch developed in significant synchrony for a lag zero (Table 1).

Discussion

This paper summarises various, unrelated research efforts concerning the fluctuation of larch bud moth host races in the Alps. In spite of shortcomings in methodology and incompleteness of census data, the results are surprising enough that they should stimulate well-concerted research efforts designed to tackle evolutionary aspects of the phenomenon. Thus, for the first time, annual fluctuations of LBM larval populations on Swiss stone pine could be compared to the simultaneous fluctuations observed on larch. Two important results emerged from this census: (1) larval populations on pine were not stable but cycled at more or less regular intervals of 8–10 years with a 5000-fold change in abundance, and (2) larval populations on pine and larch fluctuated synchronously, peak densities being offset by about one year.

Although it might be argued that the different sampling methods and missing values preclude a reliable comparison, we found that few grave quantitative discrepancies occurred. We assume that the course of the most recent cycle of LBM on pine in the Engadine was estimated with great reliability, using values of minimum and maximum densities. Similarly, the fluctuations of LBM populations on larch since 1992 were estimated in relation to the maxima and minima of the four previous cycles from 1949 to 1985 and the defoliation patterns observed during the years 1998–2000, that had been mapped throughout the Engadine. Thus, enough reference points are available to arrive at a reasonably accurate estimate of the density curve on larch, allowing us to confirm synchrony between the cycles of the populations developing on the two hosts in the Engadine. The enormous amplitude of the cycles of both pine and larch populations to some extent overrules the more minor deviations due to differences in sampling methodology, i.e. sampling within the tree crown and/or sampling mature vs small pines. However, in view of future studies some concern is justified concerning a) the basic sampling unit on pine and b) comparison of results with those obtained using the classic sampling method on larch on a weight basis (Auer 1961) with the method of Roques and Goussard (1982) using branch length.

a) the feeding behaviour of larvae on pine led us to adopt the shoot as basic sampling unit. However, an earlier analysis of the branching patterns of young stone pines in Celerina in 1963 showed that of terminal shoots (32% of all shoots), 40% were attacked by larvae whereas of lateral shoots (68% of all shoots), only 11% were infested (Baltensweiler 1963). Thus, a future sampling design should take into account the difference in attack probability of the “shoot” sampling unit.

b) the mean length of larch branches corresponding to a weight of 1 kg increases from 41 to 68 m from west to east of the Alpine arch (Auer 1977), whereas Roques and Goussard (1982) estimated that this length may vary from 30 to 40 m between sites within the Briançonais area. Therefore, instead of applying the commonly used conversion factor of 1 kg for 50 m branch length, we employed a conversion factor of 34 for the site of Les Combes (Roques and Goussard 1982).

The two main questions emerging from our results were: (1) why do LBM populations on pine show regular fluctuations? And (2) why do they oscillate in apparent synchrony with larch populations?

In other cyclic forest Lepidoptera, several mortality and reproductive factors were tentatively correlated with changes in population density (Turchin 1990, Berryman 1996, Hunter and Price 1998). Various models, including multiple regulatory factors, have been proposed to explain regular insect outbreaks (Wildl 1999, Umbanhowar and Hastings 2002, Dwyer et al. 2004). However, the relative importance of specific mechanisms that cause cyclic dynamics is likely to vary among insect species, and mechanisms remain undetermined for most forest insects.

For the larch race of the LBM, the cycle is determined by immediate density-dependent processes, such as destruction of larval habitat, lack of food, or moth dispersal, which induce the crash of peak densities. These are followed by delayed density-dependent processes, such as food deterioration and buildup of parasitoids during the decline phase of the cycle (Benz 1974, Delucchi 1982, Baltensweiler and Fischlin 1988, Baltensweiler and Rubli 1999). However, none of these processes has been studied in a consistent manner in the pine race. In particular, it is still unknown whether feeding activity of the pine race, which is basically restricted to the elongating shoot, has any physiological or morphological impact on the mature pine, effects which might deter moths from oviposition or deter survival of subsequent larval generations.

Recently developed mathematical models for analyzing and simulating the annual fluctuations in population density of several forest Lepidopteran species have suggested that these fluctuations may be driven by parasitoids (Berryman 1996) or by the combined effects
of several kinds of enemies, including pathogens and predators (Dwyer et al. 2004). Such a model was proposed by Turchin et al. (2003) for LBM, based on the annual mean density of LBM larvae for the entire Engadine valley. The model’s results led the authors to conclude that LBM–parasitoid interactions are the dominant factor governing the LBM cycle on larch. However, these conclusions appear rather contradictory to those of previous field studies conducted by Delucchi (1982) and Baltensweiler and Fischlin (1988), which both stated that parasitism exerts only a limited impact in comparison to the effect of food deterioration (Benz 1974) and dispersal triggered by defoliation (Baltensweiler and Rubli 1999).

Another surprising aspect emerging from our results is the synchrony of the population cycles on the two conifer hosts. In contrast to the many examples describing synchrony of forest lepidopteran outbreaks over a large spatial scale (Myers 1998, Liebhold and Kamata 2000, Liebhold et al. 2004), LBM populations on larch and pine cycle concertedly in the western Alps as well as in the Engadine, but both races show temporal lags in synchrony between distinct geographical sites. Such moving outbreaks have been described as “traveling waves” (Bjornstad et al. 2002). Simultaneous fluctuations of LBM populations on larch and on pine suggested some kind of inherent linkage between cycles of the two host races on local or regional grounds. Synchrony between sympatric populations of different species of forest Lepidoptera, including tortricid leaf rollers and some polyphagous Geometridae and Noctuidae, has also been observed. Weather (Raimondo et al. 2004a) as well as generalist predators (Raimondo et al. 2004b) have been suggested to be synchronizing agents. Little is known about the effect of parasitoids on LBM fluctuations on pine. Sporadic information about high parasitism rates (63% and 54% in declining LBM populations on pine at Pontresina in 1975 and 1976, respectively [Herren, in litt]) (Fig. 2) suggests that generalist ecto-parasitoids occurring on both host races may exacerbate the crash of the pine race. This could be due to the switch-over of generalist parasitoids from the LBM populations developing on larch to those developing on pine in the course of the declining cycle on larch (Baltensweiler 1958, unpubl.). Thus parasitoids could make up for the absent insect–host plant interaction and therefore account to some extent for the synchrony between the cycles observed on the two hosts.

In view of the many competing theories and models to explain the LBM cycle on larch (Baltensweiler and Fischlin 1988, Baltensweiler 1993a, Ginzburg and Taneyhill 1994, Berryman 1996, Baltensweiler and Rubli 1999, Turchin et al. 2003), it would be mere speculation to search for an explanation of the cycle on pine with the current knowledge. Nevertheless, it is tempting to associate the synchrony of the two cycles with a genetic interaction of the two host races. The probability that moths of the larch race alight on pine has been estimated at 13% (Emelianov et al. 2003), and females from both pine and larch races that have alighted on pine trees have been shown to attract larch race males (Emelianov et al. 2001). Though gene flow between the host races has been estimated to be very low (Drès 2000, Emelianov et al. 2004), the similarity of some of the larch race larval morphs to those of hybrids between larch and pine races (Baltensweiler 1993a, unpubl.) suggests the interest of further genetic studies.

Whether or not synchrony occurs in other host-associated biotypes that show population cycles remains under question; no other study is available from the literature. Even for identified “host races” (sensu Drès and Mallet 2000) that show regular population fluctuations, like LBM or the European corn borer Ostrinia nubilalis, previous research has focused on the genetic differences between forms, the rate of hybridization or gene flow, host-plant preferences for oviposition, assortative mating, or pheromone-mediated cross attraction (Guerin et al. 1984, Emelianov et al. 1995, 2001, 2003, 2004, Martel et al. 2003, Thomas et al. 2003, Bethenod et al. 2005). This study therefore represents a first comparison of population dynamics between two genetically differentiated host races.

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