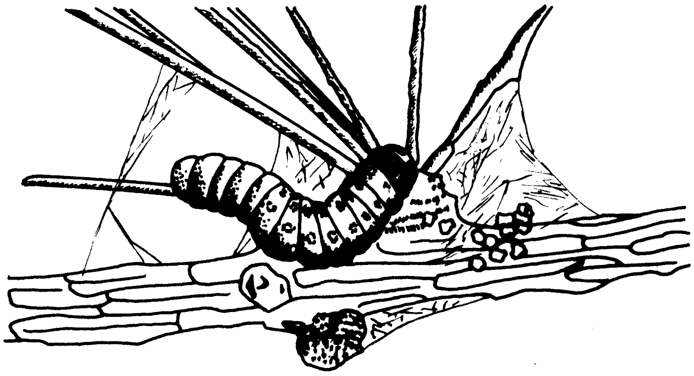
CHAPTER 17

THE LARCH BUDMOTH IN THE ALPS

Werner Baltensweiler and Andreas Fischlin

From: DYNAMICS OF FOREST INSECT POPULATIONS
Edited by Alan Berryman
(Plenum Publishing Corporatin, 1988)



Werner Baltensweiler • Department of Plant Sciences, Swiss Federal Institute of Technology, CH-8092 Zurich, Switzerland. **Andreas Fischlin** • Department of Plant Sciences, Project Centre IDA/Celtia, Swiss Federal Institute of Technology, CH-8092 Zurich, Switzerland.

1. INTRODUCTION

During the late 1940s, immediately after World War II, the lush green forests of the Engadine Valley, high in the Swiss Alps, turned an ugly red-brown in the midst of the tourist season. This was due to a spectacular outbreak of the larch budmoth, *Zeiraphera diniana* Guenée (Lepidoptera: Tortricidae). Preparing for a revival of the tourist industry, and having the new insecticide DDT at hand, it seemed only appropriate that the tourist office urge the forest service to control the pest. This was the beginning of what was to become a 34-year study of the population dynamics of the larch budmoth (Fig. 1).

Zeiraphera diniana is known for its periodic devastation of the subalpine larch–cembran pine forests (*Larici pinetum cembrae*[41]) of the European Alps. The wasteful feeding and subsequent drying of needles, as well as the masses of frass and webbing, change the green forests in midsummer into a dirty red-brown, as if a crown fire had scorched them. This spectacular sight, and the regular reappearance of the phenomenon, has for centuries attracted the attention of laymen and foresters alike.

Larch budmoth outbreaks have occurred at regular 9-year intervals in the Alps as far

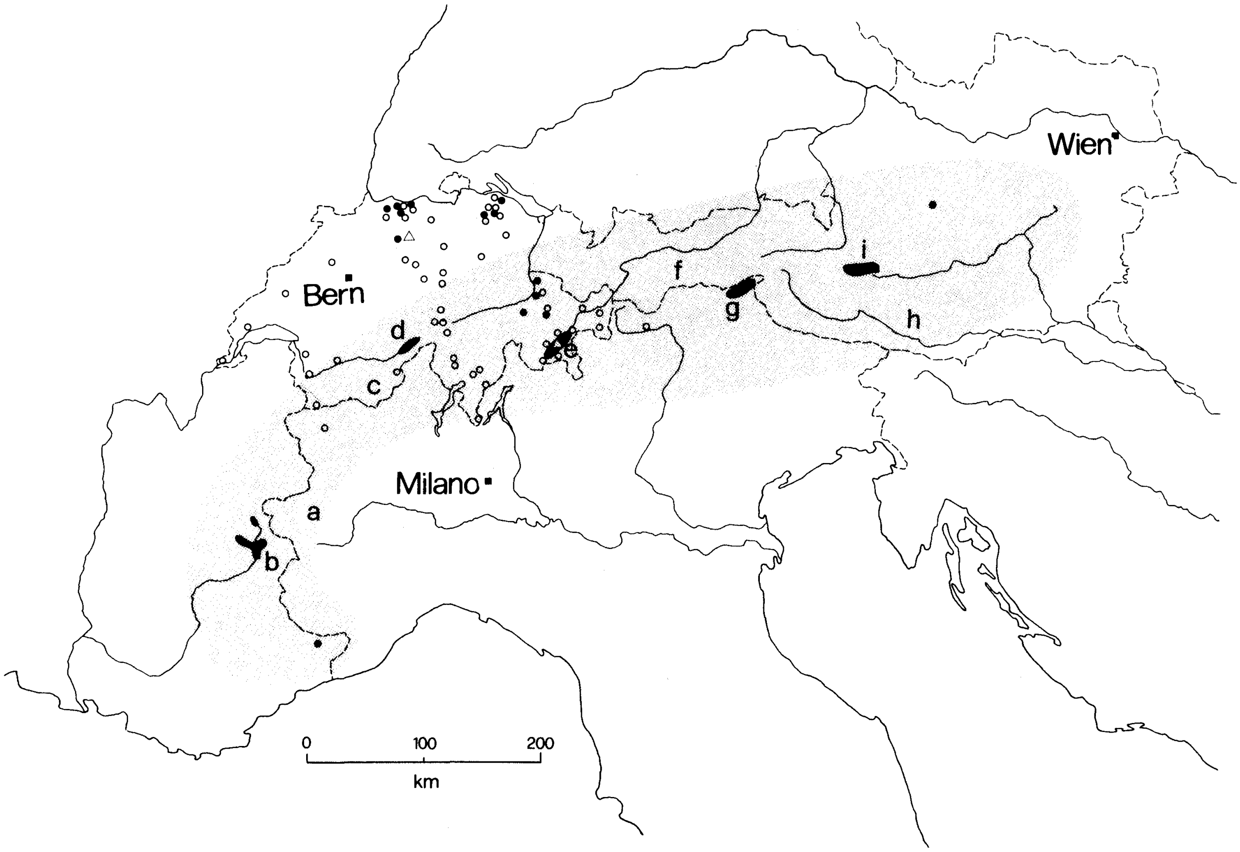


FIGURE 1. Locations of sites at which research on the larch budmoth has been conducted between 1949 and 1986 in the European Alps: large black locations, main study areas >2000 ha; black dots, local sites ~100 ha; open triangles, life-table studies; open circles, light trap or pheromone trap census sites; black squares, major cities. Approximate locations of regions mentioned in Fig. 2: a, = Piemonte; b, Hautes Alpes; c, Vispertäler; d, Goms; e, Oberengadin; f, Tirol; g, Trentino; h, Kärnten; i, Salzburg.

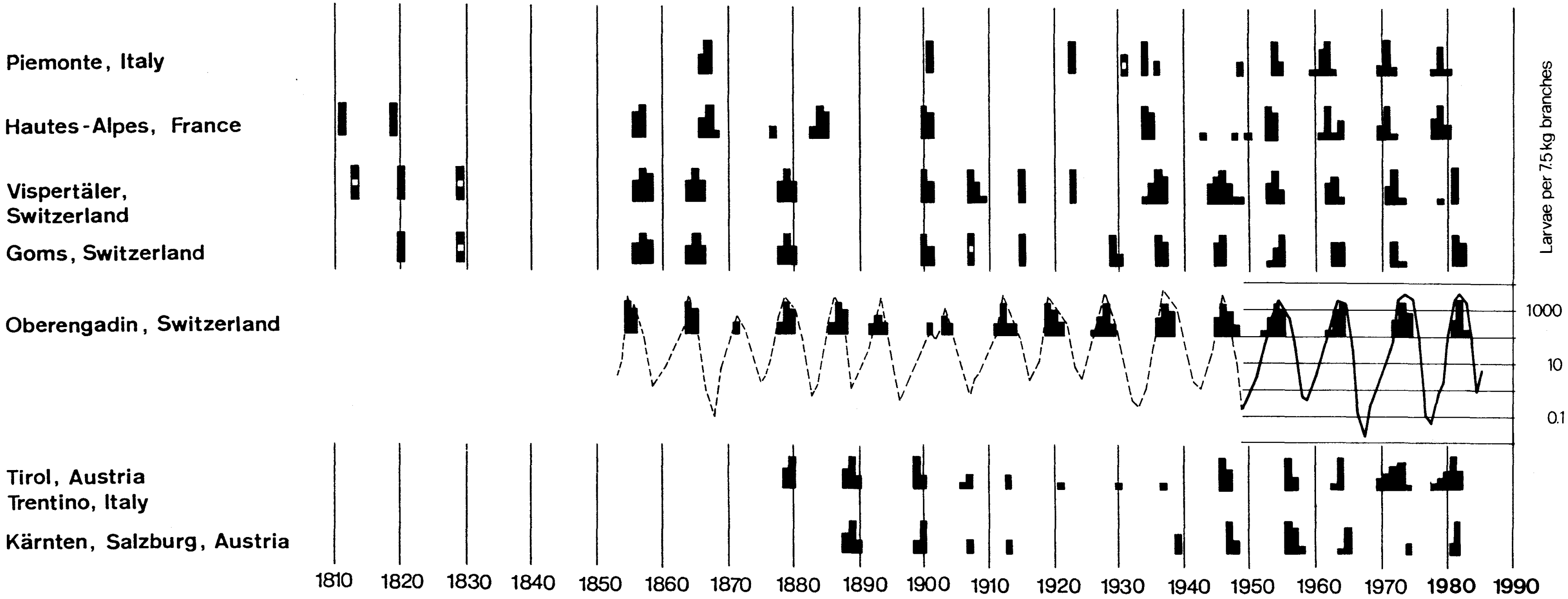


FIGURE 2. Pattern of apparent defoliation by the larch budmoth in seven major regions of the European Alps (see Fig. 1). The height of the columns represents an index of the area affected and columns with a white inset indicate fragmentary information only. The combination of results of the regional population census in the upper Engadine Valley from 1949 until 1986 (see Fig. 4) with the recorded defoliation periods allows us to extrapolate the fluctuations in larval density back to 1853.

back as recorded history, growth ring reductions with a 9-year frequency having been observed in fossil larch dating from Roman times and in the beams of fifteenth century farm houses. The first written account, in 1815, attributed the outbreak to spiders that covered the larch trees with their silvery webbing.[33] Since then periodic outbreaks have been reported in various parts of the Alps (Fig. 2). Although such historical records can never provide a completely accurate picture, they do illustrate the remarkably constant frequency of defoliation damage in time and space. The best-recorded sequence of outbreaks is from the Engadine valley in southeastern Switzerland, where foresters have observed and documented 16 outbreaks since 1855. Here, the heaviest defoliation occurs at altitudes of 1600–2100 m, lasts 2.93 ± 0.21 (standard error) years, and recurs at intervals of 8.47 ± 0.27 years. In other parts of the Alps, the outbreaks are less regular. Nevertheless, when considering the entire alpine arch, trends in the spatial sequence of outbreaks can be recognized[20]: For example, defoliation occurred first in the eastern parts of the Alps during the 1850s and 1860s; in the western parts during the 1940s, 1950s, and 1960s; and simultaneously in both east and west and last in the central Alps in all other instances. At lower altitudes of 1200–1600 m, defoliation occurs only half as often, and therefore rather irregularly, and also appears 1–4 years later than in the subalpine zone.

The species was once considered the most dangerous pest of larch forests,[29] but the results of our more recent research, as presented in this chapter, led us to develop a quite different appreciation of the larch budmoth problem.

2. BIOLOGY AND ECOLOGICAL RELATIONSHIPS

The larch budmoth was first described in 1845 as *Sphaleroptera diniana* Gueńee from specimens collected from larch trees in the French Alps and 1 year later as *Grapholita pinicolana* Zeller, from Scots pine in the Baltic and as *Poecilochroma occultana* Douglas from fir-trees (?) in England. These have since been synonymized and, after being included in several tortricid genera such as *Steganoptycha, Enarmonia, Semasia,* and *Eucosma,* the species was finally placed in the holarctic genus *Zeiraphera.*[22,30] The species has several ecological equivalents throughout the holarctic region, being described as *Z. diniana* var. *desertana* in Siberia, *Zeiraphera lariciana* in Japan,[55] and *Zeiraphera improbana* in North America.[62] With the exception of *Z. lariciana,* however, no detailed differentiation on taxonomic grounds has yet been provided.

2.1. Life Cycle

Unless explicitly specified, the following description applies to the univoltine larch budmoth living in its optimal habitat at 1700–2000 m (Fig. 3). Moth flight occurs from July to October, with adults living for more than 30 days and egg laying lasting around 20 days. Females lay 20–180 eggs, with a maximum of 350, depending on the nutritional status of the larval food supply. Eggs are deposited by means of a protractile ovipositor underneath the lichen *Parmelia exasperatula,* which covers 3-year-old and older larch branches at altitudes above 700 m. Eggs may also be laid between cone scales or beneath bark scales.

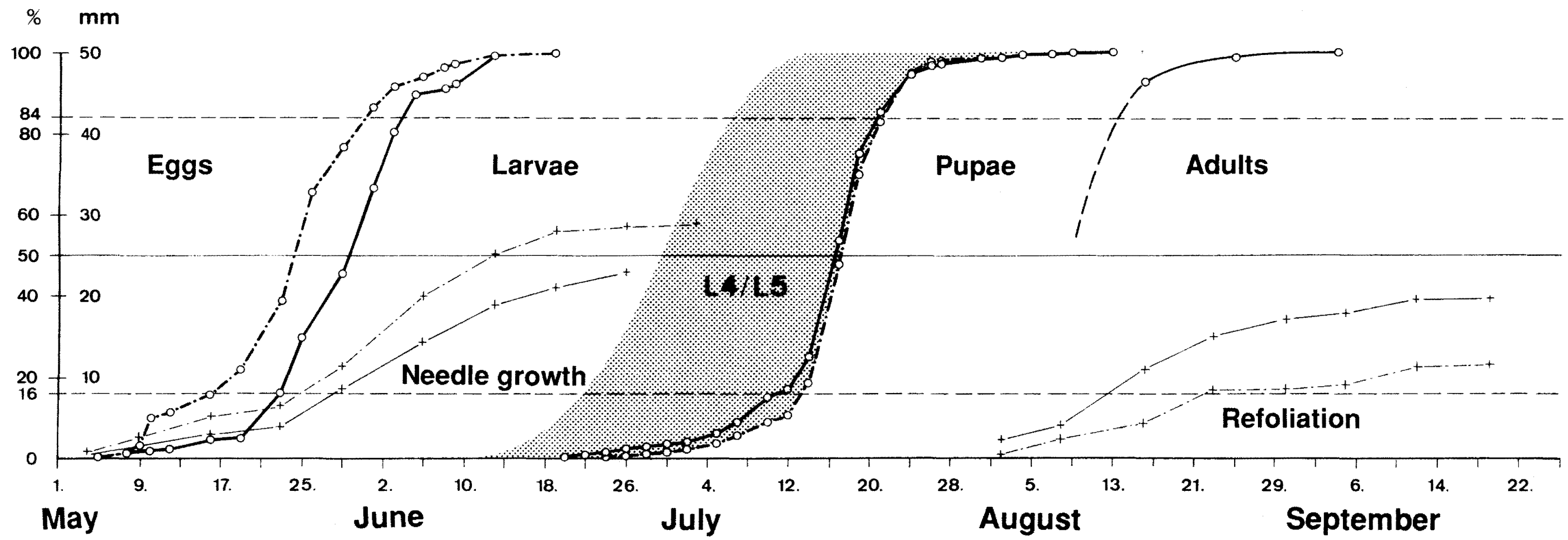


FIGURE 3. Phenological diagram of larch budmoth development and larch foliage growth in the Oberengadin (Upper Engadine); at the lower (1820 m –·–·–·–) and upper (1900 m ——) Sils sites, in 1972.

Eggs overwinter as diapausing embryos in the late gastrula stage, their supercooling point during this state being −51.3°C.[12] Diapause enables the species to synchronize egg development with the phenology of the host plant at altitudes of 500–2200 m. This flexibility is crucial because the coincidence of first instar larval emergence and the sprouting of the larch foliage is essential for the establishment of the population. Depending on weather, altitude, and exposure, the emergence period may take up to 4 weeks during May and June but may also vary by more than a month from one year to the next.

Optimal first-instar survival occurs when needles are 6–18 mm long. Once established, the first and second instars feed within the needle cluster, at the base of the needles, where they are protected from environmental hazards. During the fourth instar, they construct a characteristic needle case and in the fifth they live within webbing along the branch axis. The last larval instar exists for 10–14 days and is the longest and most destructive stage. On maturing, the fifth instar becomes negatively phototactic, leaves the larch tree in full sunshine, and immediately moves into the litter, where it constructs a pupation chamber at the base of the litter horizon. There it pupates, remaining in this stage for 25–36 days.[59]

Moths emerge early in the morning, with the males some days before the females. Flight activity starts at dusk, when temperatures are above 7°C, and lasts until midnight. Late in the season, however, when nights become too cold, flight activity shifts to midday. The female budmoth produces a powerful sex attractant.[23]

2.2. Relationship with the Host Plant

Each new generation of a univoltine herbivore has to cope with a food supply that may vary both quantitatively and qualitatively. The coincidence of first-instar larval emergence with the sprouting of larch foliage is crucial for the establishment of the new generation. This quantitative aspect, in itself rather variable due to site and weather factors, can be drastically modified by variability in food quality.

In the deciduous genus *Larix,* needle growth occurs before shoot elongation. Therefore, the chemical and morphological constitution of the new needles is strongly dependent on nutrient reserves stored during the previous fall and on the prevalent growth conditions, i.e., temperature and moisture in spring. The deciduous growth rhythm of larch probably evolved in regions in which late frosts frequently destroyed the new needles.[32] In response, the plant has evolved the capacity to flush a new set of needles during the same season. However, the second set of needles is unable to mature properly and is susceptible to early killing by fall frosts before the nutrients can be resorbed. The following spring, the needles of these trees, short of starch and nitrogen, grow more slowly and do not reach normal lengths.

This growth process can be modified to some extent by the prevailing weather conditions. Warm temperatures immediately after snow melt induce rapid needle growth, so that full-grown needles may measure more than 30 mm. Needle growth under these conditions is sigmoid and results in soft, lush needles. Conversely, needle growth during cold springs is slow and linear,[18] with mature needles being stiff and short (<20 mm). During the course of needle growth, the raw fiber content increases from about 8%

needle-fresh-weight to 16%, while the raw protein content falls from about 6% to 4%.[28,64] These values characterize the intrinsic variability of host traits to which budmoth populations are exposed, i.e., the constitutive defense capacities.[57]

Larch trees that have been defoliated to more than 50% refoliate in a similar manner to trees that have suffered from frost. Such trees are also depleted of nutrient reserves in the spring following defoliation and therefore grow short needles (<20 mm) with a raw fiber content of about 18%[28] (see Fig. 3). It may then take 2–7 years for the larch needles to recover their average quality.[46] Although the physiological processes are the same as those following frost damage, this change in foliage quality is induced by insect feeding.[50] As we shall see, this induced change in food quality has important effects on the dynamics of *Z. diniana* populations.

In dense populations, food waste also becomes an important factor. The late fourth- and fifth-instar larvae, living in loose webbing along the branch axis, interfere with each other during their feeding activities. The result is that many needles are only nibbled or partly consumed. In the dry alpine climate, such needles are lost as a nutritional resource within a day. This wasteful feeding is the cause of the ugly red-brown larch forests seen at the height of the outbreak. As a consequence of this destructive feeding, large larvae leave the defoliated trees in search of better food and often feed indiscriminantly on cembran pines, spruces, and firs in the understory. These larvae are robust enough to consume even the perennial needles on these hosts.

In contrast to larch trees, which refoliate within 3–4 weeks, young evergreens stripped of more than 70% of their needles generally die. Larches that have lost more than 50% of their needle biomass sprout quickly and uniformly. If by chance rain is lacking during this crucial refoliation period in July and August, larch trees can also die. However, mortality rarely exceeds 1% of the standing volume in any one outbreak.[26]

2.3. Ecotypes

The original descriptions of *Z. diniana* under three different names are symptomatic of its present status, for even today we are not sure of whether we are dealing with several ecotypes, several host races of one species, or separate species. In most populations, two sympatric color morphs can be distinguished in the fifth instar.[31] A dark morph that lives on larch is called the larch form, and an orange-yellow morph on cembran pine is called the cembran pine form. It has recently been established that these color traits are related to other morphological and ecological characteristics. For instance, the black larch form has a much faster postdiapause development than the cembran pine form, a trait that ensures synchronization of larval emergence with the sprouting of their respective host plants. Rapid development of the larch form usually results in larger adults but also leads to lower fitness on suboptimal foods. Thus, the larch form fails to survive on cembran pine, even when synchronized with foliage flushing, whereas the light cembran pine form thrives on larch but does not reach the size of the larch form. Intermediate color morphs are also found, and these have intermediate postdiapause developmental rates and are superior to the larch form in surviving on suboptimal foliage.[37] Finally, the two forms differ in their sexual communication.[23,49]

By crossing the two color morphs, it was found that the F_1 offspring exhibit the full range of intermediate colors. But even more importantly, the ecological traits are also transferred in a more or less correlated manner.

2.4. Relationship with Natural Enemies

A granulosis virus disease and a diverse parasitoid fauna lead to considerable mortality among larch budmoth larvae, particularly during the peak and subsequent crash of the population. Following a widespread virus epizootic at the end of the 1954–1957 outbreak, this pathogen was considered of great importance.[60] Subsequently, however, widespread virus epizootics have not been observed, yet the amplitude and period of the later cycles have not differed from the earlier one.

A total of 90 obligate primary and 13 obligate secondary parasitoids have been reared from the larch budmoth.[38] They attack all life stages except the adult. The most important parasitoids are the ichneumonid *Phytodietus griseanae* Kerrich and three eulophids, *Sympiesis punctifrons* Thomson, *Dicladocerus westwoodii* Westwood, and *Elachertus argissa* Walker. During the course of a budmoth cycle, a sequence of parasitoid species dominates and this leads to a predictable pattern of mortality. Apparent mortality amounts to about 10% in the population growth phase, rises to 10–20% at population peak, and reaches 70–80% during the collapse. However, the subsequent extremely low density of the budmoth brings about a dissociation between specific parasitoids and their host. Several studies on the most frequent parasitoid species demonstrate that they are regulated by the density of the budmoth and not vice versa.[39,52]

2.5. Flight Behavior and Dispersal

During studies in a 150-year-old larch stand located within a deciduous forest near Lenzburg, Switzerland, a surprising second moth flight was detected about 1 month after all local flights had ceased.[48] Since large masses of budmoths had been observed on many earlier occasions on glaciers, passes, and mountain tops,[42] the most plausible explanation was that the moths had emigrated en masse from areas in defoliated subalpine larch–cembran pine forests. To test this hypothesis, an extensive network of light and pheromone traps was installed on both sides of the Swiss Alps (see Fig. 1). Flight and oviposition behavior were also studied in relation to abiotic factors and defoliation intensity in the Engadine Valley.[25,71]

Regular diurnal breezes, characteristic of mountainous areas, induce moths to fly, by positive anemotactic stimuli, against the downslope and downvalley breezes toward timberline and, given certain weather conditions, even beyond this to the mountain ridges and passes. At these sites, conditions are optimal for airborne insects to be taken up by the gradient winds that can carry them for long distances. Thus, we recognize both local and long-range dispersal patterns. Local upwind dispersal occurs constantly throughout the flight period whenever temperatures exceed 7°C, while weather conditions favoring long-range dispersal are characterized by indifferent barometric pressure over central Europe with airmasses above 10°C at 2500 m.[21] Thus, dispersal on a local scale probably contributes to the regularity of the population cycle, while long-range dispersal, because of its stochastic nature, may be conducive to the conspicuous time sequence of defoliation throughout the Alps. In 1979, for example, masses of moths from the French Alps swamped the southern slope of the Alps and led to defoliation in the following years as far east as the Carinthian Alps in Austria, a distance of approximately 600 km.[17]

In later experiments, we released marked moths in defoliated areas and undamaged forests. The results showed that moths were attracted to green undamaged trees[71] and flew greater distances in defoliated forests. Caged females were found to lay 12.5 ± 8.2 eggs in defoliated stands, as compared with 116 ± 19.1 in green stands.

3. PATTERNS OF NUMERICAL BEHAVIOR

In order to discuss changes in animal numbers, we use the following terms:[69] Oscillation describes numerical changes occurring within a generation; fluctuation describes numerical variations during the course of many generations in sequence. Thus, in its optimum area, the larch budmoth exhibits a regular cyclic fluctuation; i.e., regular cycles of abundance and sparsity follow each other immediately without extended periods of low numbers in between (Fig. 4).

3.1. Oscillation

Although only incomplete life tables have been constructed for budmoth populations in the optimum area, they change dramatically between the growth and decline phases of the cycle. In the growth phase, mortality to the different life stages rarely exceeds 20–30% and total generation mortality is approximately 90%. This low mortality, together with high fecundity, gives rise to a 10-fold increase from one generation to the next. In the decline phase, total mortality rises to 99.98%, egg mortality doubles, small larval instars suffer high mortality, larval parasitism increases 10-fold, and fecundity decreases by a factor of 10.[16]

3.2. Fluctuation

When the forest service of the Canton of Grisons was asked to control the larch budmoth in 1948, it was faced with the problem of predicting when and where defoliation would reach damaging levels. The obvious answer was to design a census method to provide information on the spatial pattern of population fluctuations in successive generations over the 6200 ha of larch–cembran pine forests of the Engadine Valley.[54] This task was facilitated by the forest inventory system, which records the numbers and sizes of trees by species for each stand. Individual larch trees were used as the sample unit, more than 400 of them being selected in a stratified random manner each year. Sample trees are stratified in relationship to topographical features (altitude, exposure) and are weighted

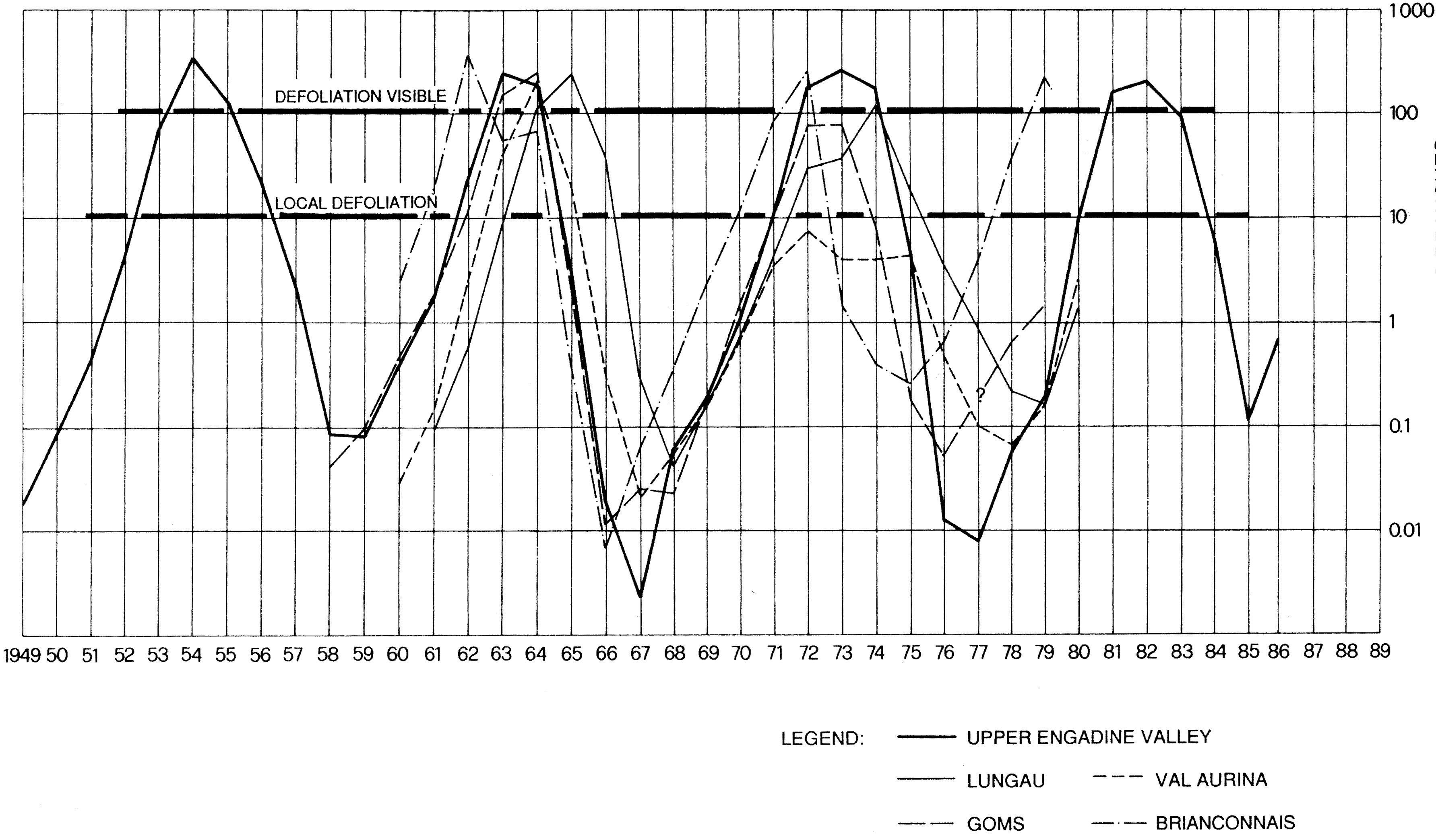


FIGURE 4. The cyclic fluctuation of larch budmoth populations at the five major study areas (see Fig. 1) expressed by the weighted mean of large larvae per 1.0 kg of larch branches (1949–1976 data from Auer,[11] 1977–1981 data from Baltensweiler,[20] 1982–1986, unpublished data).

according to host-tree density per unit area.[6] The sample, 1 kg of twigs and foliage, is extracted from three branches cut at three levels within the crown. This annual census provides an average density estimate for the larval population and can be converted to an absolute population estimate for the entire Engadine Valley.[4,11]

The population census was initiated in the Engadine Valley in 1949 and, with minor modifications, continued until 1976.[4,9,11] From 1977 to 1986 the census was continued on a reduced scale,[20] but from 1959 to 1980 it was extended to four additional outbreak areas spread along the entire alpine arch from the Brianconnais to Salzburg. In addition, 20 sample plots containing 4–20 larch trees were selected systematically along an altitudinal profile from high-elevation areas, characterized by large-amplitude cyclic fluctuations, to low-elevation stands within the deciduous forests of the colline region, where populations fluctuate much less extremely.[10]

This census for the high Alps is summarized in Fig. 4. Budmoth larval densities vary with remarkable regularity and by more than 10,000-fold over four or five generations. Altogether 13 complete cycles have been described, 11 of them causing general defoliation throughout the area, while only one cycle caused no visible damage (Valle Aurina, 1967–1977).[64] By superimposing the density curve of the Engadin on the defoliation records (Fig. 2), it is easy to visualize how populations have fluctuated in this subalpine region for more than 100 years.

At altitudes of 1200–1600 m, populations only occasionally reach densities that cause defoliation, and at altitudes below 1000 m they never do. However, it is interesting to note that these lower populations also exhibit cyclical fluctuations, albeit with a much smaller amplitude, which reach their peaks 1–3 years later than do subalpine populations.[10] Still farther away, along the Rhine River between the Lake of Constance and Basel, the budmoth fluctuates irregularly and, in small larch stands within the deciduous forest, it may become locally extinct.

4. HYPOTHESES FOR THE CAUSES OF OBSERVED POPULATION DYNAMICS

The question of central importance is: What causes larch budmoth populations to cycle so regularly and with such little variation in amplitude and periodicity? Many hypotheses have been erected to explain this rather common phenomenon in animal populations, including weather or sun-spot activity; interactions with parasites, predators, pathogens, and host plants; genetic factors; and finally mass dispersal. The more plausible of these hypotheses are discussed below:

4.1. The Food Quality Hypothesis

Changes in food quality are considered an important factor in regulating larch budmoth populations. The raw-fiber content of needles increases considerably during an outbreak and has a strong negative effect on larval survival and female fecundity.[28,46,63] In addition, increases in raw-fiber content can be induced by budmoth feeding in the previous generation, and it then takes several years for these changes to relax.[28,45] On theoretical grounds alone, this delayed negative feedback mechanism could be sufficient to generate regular population cycles.[28,43]

This hypothesis was tested by constructing a detailed mathematical model of the larch–larch budmoth system (Fig. 5).[43] Simulations of budmoth population dynamics resulting from this model closely mimic the real population cycles (Fig. 6). In addition, *a priori* model predictions of larch needle raw-fiber content correspond closely to later experimental data.[46] These results led us to believe that food quality change induced by previous budmoth feeding is the most plausible explanation for the 9-year population cycle.

4.2. The Self-Regulation Hypothesis

The self-regulation hypothesis proposes that cycles can be induced in populations consisting of several genotypes correlated with ecologically different phenotypes, if mechanisms for density-dependent selection are present.[34,56] The data on larch budmoth ecotypes are consistent with such a hypothesis. Not only have color morphs been observed,[13–15,35–37] but their proportions are correlated with the population cycles.[14] How-

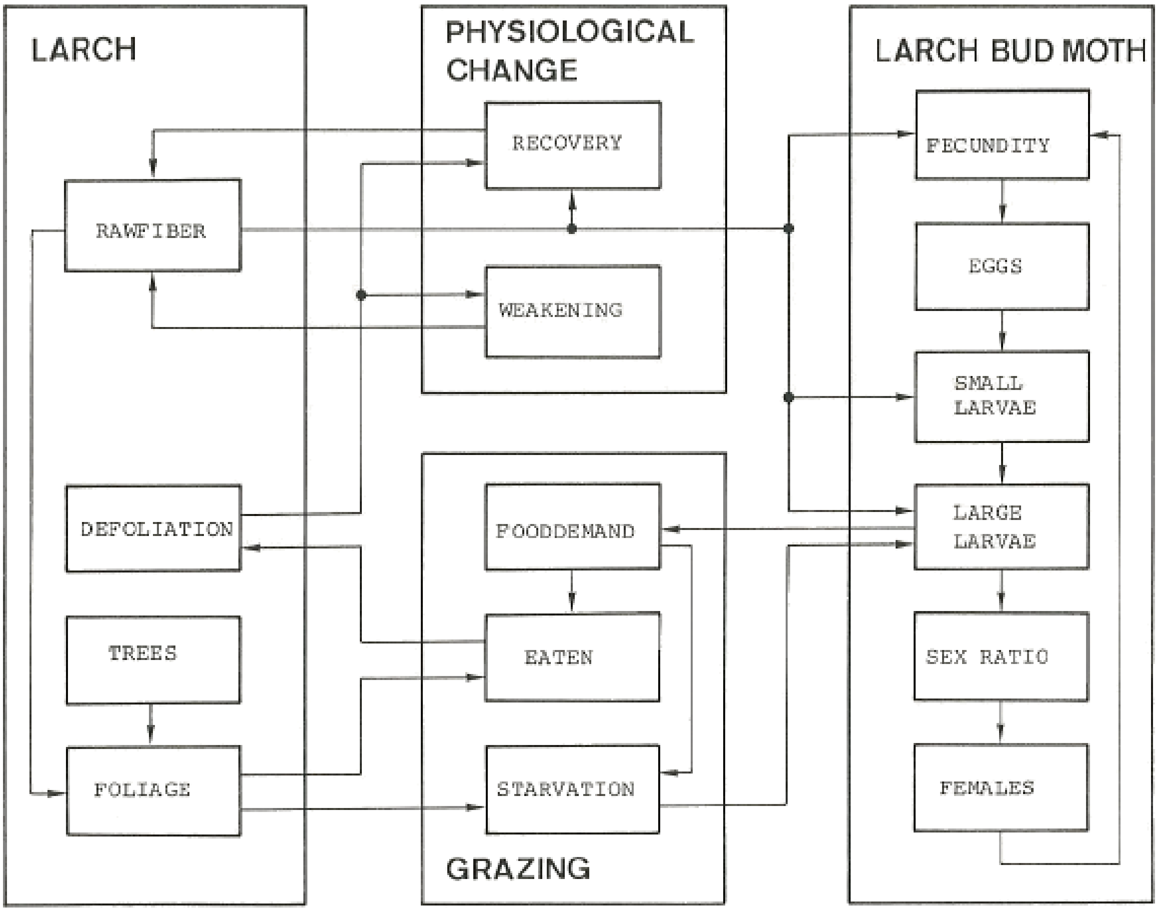


FIGURE 5. Structure of the larch–larch budmoth relationship. The depicted functional dependencies are based on observed and quantified correlations. (From 43).

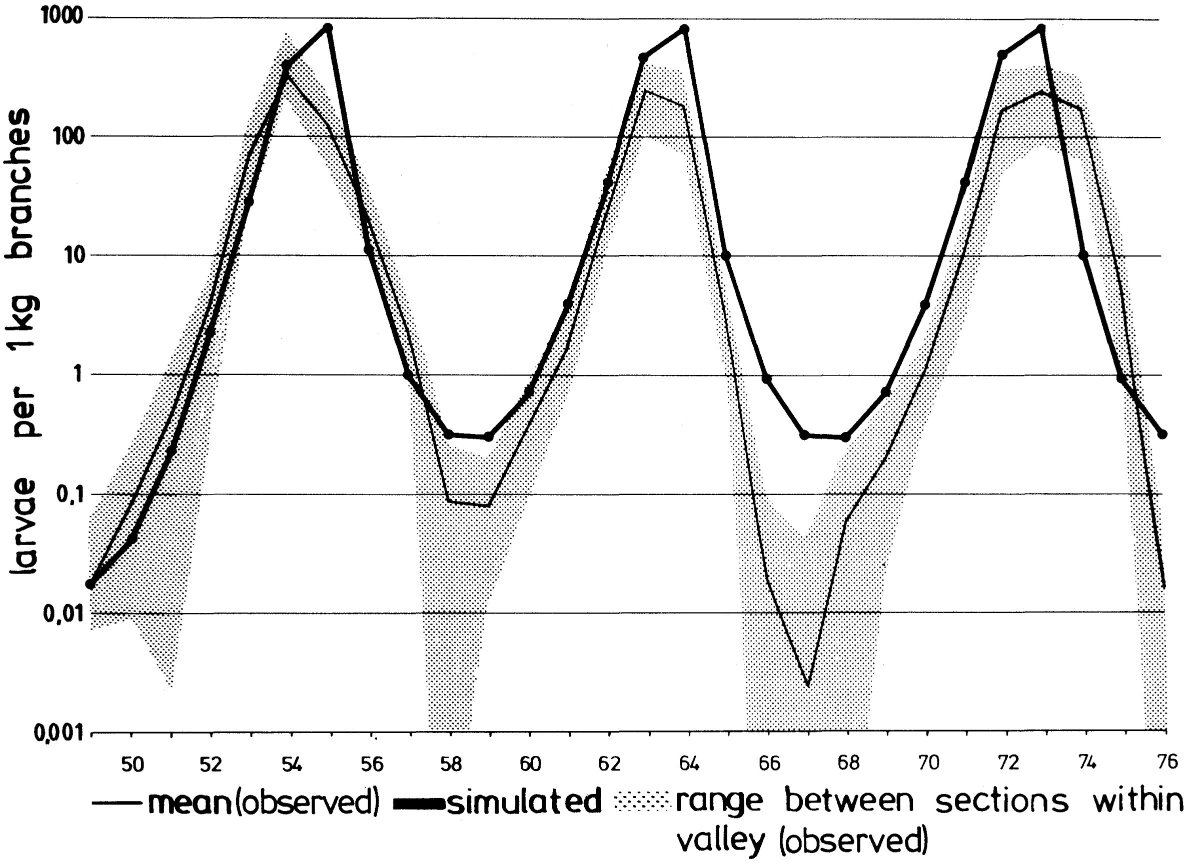


FIGURE 6. Simulated population fluctuations of the larch budmoth in the Upper Engadine Valley. The model is based on the larch–larch budmoth relationship (see Fig. 5) and excludes dispersal. (From 43, 45).

ever, theoretical studies suggest that polymorphism–selection cannot alone induce sustained cycles.[47,70] For this reason, the classical self-regulation hypothesis has to be modified by combining it with the food-quality hypothesis or by including assortive mating. In the first case, changing food quality becomes the selective process that induces varying genotypic frequencies. The different ecological traits then cause populations to increase up to the point where defoliation alters food quality.[19] This is essentially equivalent, however, to the food-quality hypothesis because the mechanism inducing the cycles is a delayed negative feedback between host plant and budmoth populations.

In a second form of this hypothesis, sex-attractant polymorphism is assumed to separate subpopulations temporarily, by means of assortive mating, during the phases of low population density when pheromone communication is essential for reproduction.[19,43,49]

4.3. The Antagonism Hypothesis

On the basis of classical theory, we might expect interactions with antagonists (predators, parasitoids, pathogens) to induce cyclic population dynamics.[3,5,7,53,58,72,73] In 1957, immediately after the first cycle we had studied intensively, it seemed obvious to everybody that the granulosis virus disease played a crucial role in suppressing the outbreak.[27] But since substantial numbers of diseased larvae could not be found in subsequent outbreaks, this idea had to be abandoned. It is unfortunate that this fact was not taken into account in recent theoretical papers that revive the pathogen–host relationship hypothesis for budmoth cycles.[3] It is worth noting that if the larch budmoth project had been terminated after the first 10 years of research, we would not have discovered that disease epizootics were not a regular phenomenon,[27] and most scientists would now be convinced that the cycles were caused by the interaction between virus and budmoth.

The impact of several species of parasitoids was studied carefully in an attempt to determine their roles in budmoth population dynamics.[1,38,52,66] These studies generally indicate that parasitism merely tracks the larch budmoth population; i.e., budmoth population fluctuations regulate the numbers of parasitoids and not vice versa.

4.4. The Dispersal Hypothesis

The dispersal hypothesis cannot be considered independently from the other hypotheses because budmoth population dynamics are determined by a combination of local factors as well as dispersal processes. The influence of dispersal has been postulated in the form of four hypotheses: the *Herdtheorie,* the conglobation hypothesis, the translocation hypothesis, and the cycle synchronization hypothesis.[43,44]

Forest pest fluctuations cause defoliation to appear and disappear in distinct patterns in time and space. This observation led to the formulation of the *Herdtheorie* during the 1930s.[40] This theory proposes that populations spread out from hot spots (*Herd*), or epicenters, and swamp other unpopulated areas. In the case of the larch budmoth, this theory was abandoned, however, when the annual census demonstrated that budmoth larvae were everywhere all the time.[4] Another observation that went against the *Herdtheorie* was that budmoth populations grew at similar rates in all alpine valleys, a fact that is most consistent with autochthonous population growth.

The conglobation hypothesis proposes that locally high budmoth populations occur because they tend to aggregate in preferred habitats.[68] This is based on the observation that budmoths tend to fly from suboptimal montane levels (1000–1700 m) to optimal subalpine levels (1700–2000 m).[25,38] This behavioral characteristics of flying moths, together with the topology of the European Alps, are assumed to be responsible for the observed conglobation.[25,43] According to this hypothesis, budmoth populations are exposed to a regular and more or less constant aggregated influx of moths that replenishes subpopulations that have become locally extinct following severe outbreaks.

The translocation hypothesis refers to the emigration of a substantial proportion of the population to new, less hostile habitats.[69] Since subpopulations of the larch budmoth regularly deplete their food resource, they are forced to lead a nomadic life. The increased mobility of moths in defoliated stands, their attraction to green larch foliage,[71] the conspicuous mass flights on mountain passes and mountain tops,[21,42,59] and defoliation patterns in neighboring valleys[13] support this hypothesis. According to the translocation hypothesis, outbreaks collapse because of overexploitation of the food resources and mass exodus of the adult population.[43]

Finally, the synchronization hypothesis attempts to explain the synchronous pattern of conspicuous defoliation along the alpine arch (Fig. 2). Population cycles are sometimes

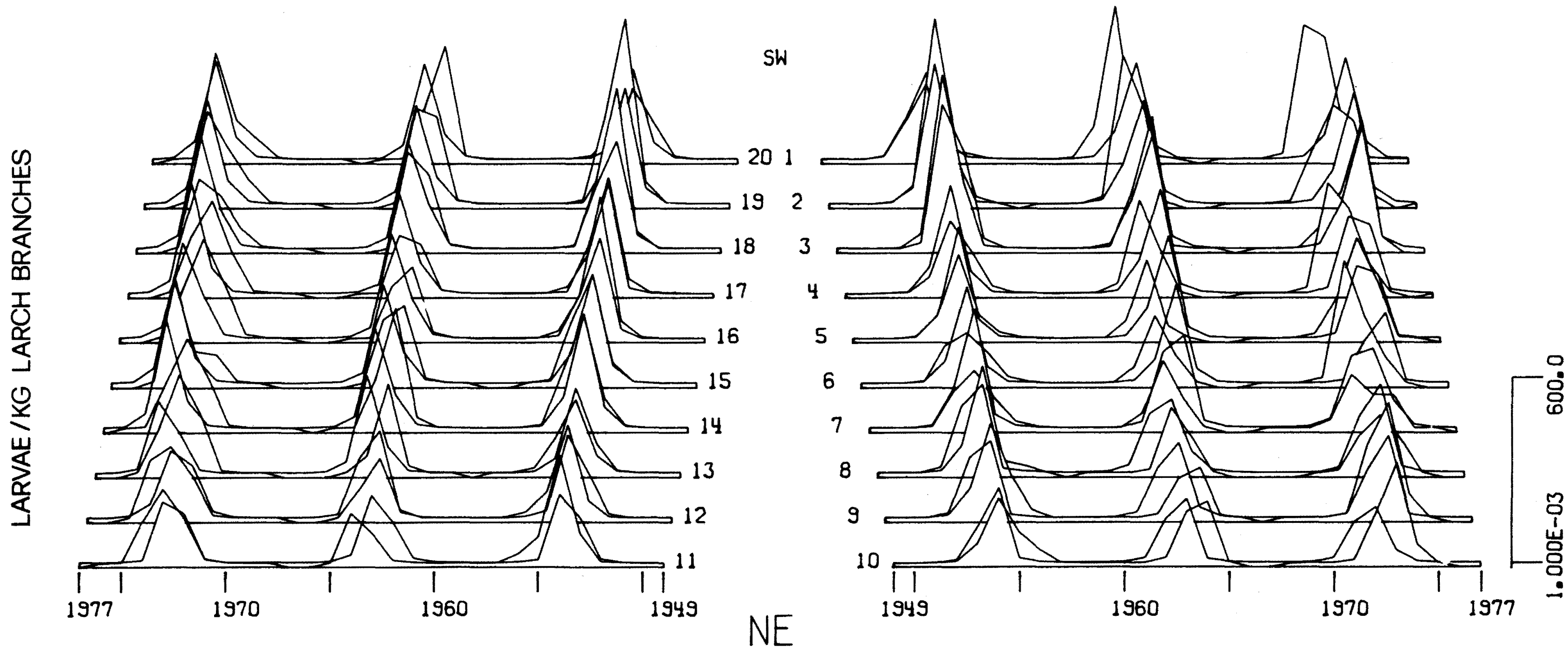


FIGURE 7. Simulated population fluctuations of the larch budmoth in the Upper Engadine Valley based on a model of the larch–larch budmoth relationship (see Fig. 5) that includes dispersal processes (translocation as well as conglobation). The simulated and observed larval densities (linear scale) are shown for each of the 20 sites within the Engadine Valley (From 43).

slightly out of synchrony, e.g., the delayed defoliation sequence from the western to eastern Alps during the 1960s (Fig. 4). However, these delays are usually small and follow a distinct pattern. Otherwise, the cycles show remarkable synchrony, even from one end of the Alps to the other, and the closer the valleys the greater their synchrony. The synchronization hypothesis explains these patterns by the exchange of relatively small numbers of moths between neighboring valleys that would otherwise be fluctuating independently of each other. Cycles initially out of synchrony can be synchronized in our model by the exchange of surprisingly few moths, provided the valleys are arranged in a line, as is the case in the alpine arch.[44]

The various dispersal hypotheses (except for the *Herdtheorie*) have been studied by means of simulation. Their inclusion generally increases the realism of the simulation (Fig. 7) but does not substantially alter the general cyclic behavior and therefore does not refute the food quality hypothesis. By contrast, migration is critical in stabilizing the system, guaranting re-establishment of the cycle after local extinctions[43] and synchronizing population fluctuations over large geographical regions.

As a result, our studies generally support the food-quality hypothesis. We should note, however, that our model of induced host responses to defoliation is based on rather limited data, and new information could change our conclusions. If additional mechanisms need to be included in our explanation of larch budmoth population cycles, we suspect that parasitism or genetic polymorphism are the most likely candidates. By contrast, dispersal is responsible for the stability of the cycles, the resilience of the larch budmoth system, and the synchronization of fluctuations between alpine valleys.

5. IMPLICATIONS FOR DEVELOPING MANAGEMENT STRATEGIES

A diverse palette of techniques has been developed for controlling larch budmoth populations, including chemical[8] and microbiological[61] insecticides, mating disruption by means of sex attractants,[24] biological control by releasing parasitoids,[2] releasing budmoths in order to enrich the parasitoid potential at low population densities,[51] and silvicultural measures such as the afforestation with less susceptible tree species or various stand-management practices.[26]

5.1. Feasibility of Management Strategies

Spraying chemical insecticides or *Bacillus thuringiensis* with helicopters in alpine areas is technically feasible but expensive. Simulations on our model indicate that this strategy may fail, however, since the protection of larch foliage is equivalent to eliminating the key regulating mechanism in the system. Without the negative feedback between foliage and insect, the budmoth population would remain high, and the application of insecticides might have to be repeated at frequent intervals.[43] It is also feared that spraying would result in high tree mortality due to continuous stress from high populations near the threshold of defoliation.

Biological control by inundative releases of parasites is extremely expensive and poses some almost insurmountable difficulties. Rearing parasites is even more difficult than rearing the budmoth. Mating disruption using sex pheromones seems to offer some potential. Model simulations over large units (e.g., a whole alpine valley such as the Upper Engadine) suggest that this technique could succeed.[43] However, it would again become necessary to repeat the treatment almost on a continuous basis, rendering the method very expensive. In addition, immigration due to conglobation or long-range dispersal might soon devaluate the control effort.[43]

Changes in forest management practices take a long time to have an impact on subalpine forests. Not only are growing conditions poor, but few other tree species are available or can compete with larch. Within the Engadine Valley, for example, native inhabitants favor larch because of its rapid growth, its capability to reproduce naturally, and its aesthetic properties.

5.2. Economic Aspects of Population Management

Only recently has it become possible to make a realistic estimate of the diverse impacts of larch budmoth outbreaks on the forest ecosystem and forestry economy. Proponents of tourism have often claimed that budmoth outbreaks cause tourists to leave or avoid the area. However, no data have been gathered to support this view. It could well be that tourism is less affected than has been feared, since visible defoliation rarely affects a whole valley during the same season. Also, not all outbreaks coincide with dry weather, so the conspicuous defoliation patterns are not always visible.

Tree mortality due to budmoth defoliation is negligible ($<1\%$ of the total volume).[26] However, local impacts may be significant; e.g., salvage operations often disrupt the management and cutting plans of the district. Within the realm of a single community, therefore, large numbers of dead larch trees can cause severe economic hardship by disrupting sustained harvesting.

Natural reproduction of host trees is not directly affected by the larch budmoth outbreaks and, although trees are weakened by defoliation, this has never been observed to reduce reproductive output.

Larch budmoth outbreaks do not threaten either the existence or composition of the subalpine larch–cembran pine forest. On the contrary, the components of this forest ecosystem seem to be well adapted to each other. Dendrochronological data show that larch and budmoth coexisted at least since Roman times. A hypothesis could even be proposed that without the larch budmoth the subalpine larch–cembran pine forest would change to a less desirable state. For example, the consumption of 50–100% of the larch needle biomass every 9 years over large areas probably accelerates nutrient cycling, and the defoliation of vulnerable cembran pine in the understory can cause considerable mortality and postpone the succession to the climax community, i.e., a subalpine larch–cembran pine forest with a much higher percentage of pines.[26] Larch does not reproduce well under a tight pine canopy and survives only in relatively open stands. Thus, the interaction between the larch budmoth and its host, the larch, may even be considered mutualistic.

5.3. Conclusions

Since control would have to be applied almost continuously to entire alpine valleys, even in the case of the most promising pheromone disruption technique, and since economic losses due to the budmoth turn out to be rather minor, we no longer consider the larch budmoth a pest worth controlling. The decision to abolish control measures is made even easier when the risks of increasing larch tree mortality are considered. The larch budmoth research project not only exemplifies how easily wrong decisions can be made, but that long-term research on a scale appropriate to the organism is necessary to provide the basis for correct management decisions. Close scrutiny has shown that this forest defoliator is, in fact, not a pest. In this respect, the story of the larch budmoth provides a lesson for the administration of future ecological research.[27]

ACKNOWLEDGMENTS. We thank Dr. D. Rubli for drawing and preparing the figures and the innumerable scientists who have made possible this review by their research or who have contributed with their stimulating ideas during many discussions. All this has helped us tremendously to clarify our own ideas.

This chapter represents contribution no. 120 of the Working Group for the Study of the Population Dynamics of the Larch Budmoth of the Swiss Federal Institute of Technology, Zürich, Switzerland.

REFERENCES

1. Aeschlimann, J.-P., 1969, Contribution à l'étude de trois espèces d'eulophides (Hymenoptera: Chalcidoidea) parasites de la tordeuse grise du mélèze, *Zeiraphera diniana* GUENÉE (Lepidoptera: Tortricidae) en Haute-Engadine, *Entomophaga* **14:**261–320.
2. Aeschlimann, J.-P., 1975, Biologie, comportement et lacher expérimental de *Triclistus pygmaeus* Cresson (Hym, Ichn.), *Mitt. Schweiz. Entomol. Ges.* **48:**165–171.
3. Anderson, R. M., and May, R. M., 1980, Infectious diseases and population cycles of forest insects, *Science* **210:**658–661.
4. Auer, C., 1961, Ergebnisse zwölfjähriger quantitativer Untersuchungen der Populationsbewegung des Grauen Lärchenwicklers *Zeiraphera griseana* Hübner (=diniana GUENÉE) im Oberengadin (1949/1960), *Eidg. Anst. Forstl. Versuchswes. Mitt.* **37:**173–263.
5. Auer, C., 1968, Erste Ergebnisse einfacher stochastischer Modelluntersuchungen über die Ursachen der Populationsbewegung des grauen Lärchenwicklers *Zeiraphera diniana* Gn. (= *griseana* Hb.) im Oberengadin, 1949/66, *Z. Angew. Entomol.* **62:**202–235.
6. Auer, C., 1971, Some analyses of the quantitative structure in populations and dynamics of larch bud moth 1949/1968, in: *Statistical Ecology* (G. P. Patil, ed.), Vol. 2, pp. 151–173, Pennsylvania State University Press, University Park, Pennsylvania.
7. Auer, C., 1971, A simple mathematical model for "key-factor" analysis and comparison in population research, in: *Statistical Ecology* (G. P. Patil, ed.), Vol. 2, pp. 33–48, Pennsylvania State University Press, University Park, Pennsylvania.
8. Auer, C., 1974, Ein Feldversuch zur gezielten Veränderung zyklischer Insektenpopulationsbewegungen, *Schweiz. Z. Forstwes.* **125:**333–358.
9. Auer, C., 1975, Dendrometrische Grundlagen und Verfahren zur Schätzung absoluter Insektenpopulationen, *Eidg. Anst. Forstl. Versuchswes. Mitt.* **50:**88–131.
10. Auer, C., 1975, Jährliche und langfristige Dichteveränderungen bei Lärchenwicklerpopulationen (*Zeiraphera diniana* Gn.) ausserhalb des Optimumgebietes, *Mitt. Schweiz. Entomol. Ges.* **48:**47–58.
11. Auer, C., 1977, Dynamik von Lärchenwicklerpopulationen längs des Alpenbogens, *Eidg. Anst. Forstl. Versuchswes. Mitt.* **53:**71–105.

12. Bakke, A., 1969, Extremely low supercooling point in eggs of *Zeiraphera diniana* (GUENÉE), *Norsk. Entomol. Tidsskr.* **3**:81–83.
13. Baltensweiler, W., 1964, *Zeiraphera griseana* HÜBNER (Lepidoptera: Tortricidae) in the European Alps. A contribution to the problem of cycles, *Can. Entomol.* **96**:792–800.
14. Baltensweiler, W., 1971, The relevance of changes in the composition of larch bud moth populations for the dynamics of its numbers, in: *Dynamics of Populations.* Proceedings of the Advanced Study Institute of Dynamics Numbers Popul. Oosterbeek. (P. S. DenBoer and G. R. Gradwell, eds.), pp. 208–219, Pudoc, Wageningen.
15. Baltensweiler, W., 1977, Colour-polymorphism and dynamics of larch bud moth populations (*Zeiraphera diniana* Gn., Lep. Tortricidae), *Mitt. Schweiz. Entomol. Ges.* **50**:15–23.
16. Baltensweiler, W., 1978, Insect Population Dynamics, pp. 381–394 in Proc. XVI IUFRO World Congress, Norway 1976, Div. 2.
17. Baltensweiler, W., 1982, Zur Entwicklung der gegenwärtigen Massenvermehrung des Grauen Lärchenwicklers (*Zeiraphera diniana* Gn.). Inst. Phytomedizin, ETH Zürich, unpublished report 91.
18. Baltensweiler, W., 1983, The impact of weather on the life system larch–larch bud moth in the European Alps. in: *The role of insect–plant relationship in the population dynamics of forest pests,* (A. S. Isaev, ed.), pp. 73–83, Proc. Symp. IUFRO/MAB, Irkutsk 1981.
19. Baltensweiler, W., 1984, The role of environment and reproduction in the population dynamics of the larch bud moth, *Zeiraphera diniana* Gn. (Lepidoptera, Tortricidae), in: *Advances in Invertebrate Reproduction* (W. Engels, W. H. Clark, Jr., A. Fischer, P. J. W. Olive, and D. F. Went, eds.), Vol. 3, pp. 291–302, Elsevier, Amsterdam.
20. Baltensweiler, W., 1985, On the extent and the mechanisms of the outbreaks of the Larch Bud Moth (*Zeiraphera diniana* Gn., Lepidoptera, Tortricidae) and its impact on the subalpine Larch-cembran pine Forest ecosystem, in: *Establishment and Tending of Subalpine Forest: Research and Management,* Proc. 3rd IUFRO Workshop P 1.07-00, 1984, *Eidg. Anst. Forst. Versuchswes., Ber.* 270 (H. Turner and W. Tranquillini, eds.), pp. 215—219.
21. Baltensweiler, W., and G. von Salis, 1975, Zur Dispersionsdynamik der Falter des Grauen Lärchenwicklers (*Zeiraphera diniana* Gn., Tortricidae). *Z. angew. Entomol.* **77**:251–257.
22. Baltensweiler, W., Benz, G., Bovey, P., and Delucchi, V., 1977, Dynamics of larch bud moth populations, *Annu. Rev. Entomol.* **22**:79–100.
23. Baltensweiler, W., Priesner, E., Arn, H., and Delucchi, V., 1978, Unterschiedliche Sexuallockstoffe bei Lärchen- und Arvenform des Grauen Lärchenwicklers (*Zeiraphera diniana* Gn., Lep., Tortricidae), *Mitt. Schweiz. Entomol. Ges.* **51**:133–142.
24. Baltensweiler, W., and Delucchi, V., 1979, The study of larch bud moth migration in the Engadine valley by means of a parapheromone, *Mitt. Schweiz. Entomol. Ges.* **52**:291–296.
25. Baltensweiler, W., and Fischlin, A., 1979, The role of migration for the population dynamics of the larch bud moth *Zeiraphera diniana* Gn. (Lep., Tortricidae), *Mitt. Schweiz. Entomol. Ges.* **52**:259–271.
26. Baltensweiler, W., and Rubli, D., 1984, Forstliche Aspekte der Populationszyklen von *Zeiraphera diniana* Gn. (Lep., Tortricidae), *Eidg. Anst. forstl. Versuchswes., Mitt.* **60**:1–148.
27. Baltensweiler, W., and Fischlin, A., 1987. On methods to analyze ecosystems: lessons from the analysis of forest-insect systems, in: *Potentials and limitations of ecosystem analysis* (E. D. Schulze and H. Zwölfer, eds.), pp. 401–415, Springer, Berlin.
28. Benz, G., 1974, Negative Rückkoppelung durch Raum- und Nahrungskonkurrenz sowie zyklische Veränderung der Nahrungsgrundlage als Regelprinzip in der Populationsdynamik des Grauen Lärchenwicklers, *Zeiraphera diniana* (GUENÉE) (Lep., Tortricidae), *Z. angew. Entomol.* **76**:31–49.
29. Bovey, P., 1958, Le problème de la tordeuse grise du mélèze *Eucosmu griseana* (Hübner) (Lepidoptera: Tortricidae) dans les forêts alpines, Proc. 10. Congr. Internat. Entomology, 1956, **4**:123–131.
30. Bovey, P., 1978, *Spilonota* und *Zeiraphera,* in: *Die Forstschädlinge Europas.* Band 3: Schmetterlinge (W. Schwenke, ed.), pp. 153–177, Verlag Paul Parey, Hamburg.
31. Bovey, P., and Maksymov, J. K., 1959, Le problème des races biologiques chez la tordeuse grise du mélèze *Zeiraphera griseana* (HB), *Vierteljahrsschrift d. Naturforsch. Ges. Zürich* **104**:264–274.
32. Burger, H., 1926, Untersuchungen über das Höhenwachstum verschiedener Baumarten, *Eidg. Anst. Forstl. Versuchsw., Mitt.* **14**:29–158.
33. Chaix, B., 1845, *Préoccupations statistiques, géographiques, pittoresques et synoptiques du Département des Hautes Alpes,* Allier, Grenoble.

34. Chitty, D., 1977, Natural selection and the regulation of density in cyclic and non-cyclic populations, in: *Evolutionary Ecology* (B. Stonehouse and C. Perrins, eds.), pp. 27–31. MacMillan Press Ltd., London.
35. Day, K. R., 1976, An ecological study of *Zeiraphera diniana* GN. (=griseana HB.) on conifers in Britain, Ph.D. thesis, University of London, London.
36. Day, K., 1984, Phenology, polymorphism and insect-plant relationships of the larch budmoth, *Zeiraphera diniana* (Guenée) (Lepidoptera: Tortricidae), on alternative conifer hosts in Britain, *Bull. Entomol. Res.* **74**:47–64.
37. Day, K. R., and Baltensweiler, W., 1972, Change in the proportion of the larval colourtypes of the larchform *Zeiraphera diniana* when reared on two media, *Entomol. Exp. Appl.* **15**:287–298.
38. Delucchi, V., 1982, Parasitoids and hyperparasitoids of *Zeiraphera diniana* GN. (Lep., Tortricidae) and their rôle in population control in outbreak areas, *Entomophaga* **27**:77–92.
39. Delucchi, V., and Renfer, A., 1977, The level of abundance of *Phytodietus griseanae* Kerrich (Hym. Ichneumonidae) determined by its host *Zeiraphera diniana* Guenée (Lep., Tortricidae) at high altitude, *Mitt. Schweiz. Entomol. Ges.* **50**:233–248.
40. Eidmann, H., 1934, Untersuchungen über Herdtheorie und Überflug, in: *Die Forleule in Preussen im Jahre 1933* (H. Eidmann, ed.), pp. 28–34. Sonderheft, Verlag M. und H. Schaper, Hannover.
41. Ellenberg, H., and Klötzli, F., 1972, Waldgesellschaften und Waldstandorte der Schweiz, *Eidg. Anst. forstl. Versuchswes., Mitt.* **48**:589–930.
42. Escherich, K., and Bär, W., 1909, Einiges über den grauen Lärchenwickler, *Naturw. Z. Land- u. Forstw.* **7**:188–194.
43. Fischlin, A., 1982, Analyse eines Wald-Insekten-Systems: Der subalpine Lärchen-Arvenwald und der graue Lärchenwickler *Zeiraphera diniana* GN. (Lep., Tortricidae), Ph.D. Diss ETHZ Nr. 6977.
44. Fischlin, A., 1983, Modelling of alpine valleys, defoliated forests, and larch bud moth cycles: The rôle of moth migration, in: *Mathematical models of renewable resources* (R. Lamberson, ed.), Vol. II, pp. 102–104. Proceedings of the 2nd Pacific Coast Conference on Mathematical Modeling of Renewable Resources, University of Victoria, Victoria, B.C., Canada.
45. Fischlin, A., and Baltensweiler, W., 1979, Systems analysis of the larch bud moth system. Part I: the larch-larch bud moth relationship, *Mitt. Schweiz. Entomol. Ges.* **52**:273–289.
46. Fischlin, A., Baltensweiler, W., Delucchi, V., Francesci, G., and Seiffert, F., Is the rawfiber content really correlated with the population cycles of larch bud moth? Some results from chemical analysis of larch needles from the Upper Engadine Valley, unpublished.
47. Fischlin, A., Chitty, D., and Krebs, C. J., *Modelling the real Chitty Hypothesis,* Institute of Animal Resource Ecology, University of British Columbia, Vancouver, B.C., Canada, unpublished.
48. Graf, E., 1974, Zur Biologie und Gradologie des Grauen Lärchenwicklers, *Zeiraphera diniana* Gn. (Lep., Tortricidae) im schweizerischen Mittelland, *Z. angew. Entomol.* **76**:233–251, 347–379.
49. Guerin, P. M., Baltensweiler, W., Arn, H., and Buser, H.-R., 1984, Host race pheromone polymorphism in the larch budmoth, *Experientia* **40**:892–894.
50. Haukioja, E., 1980, On the role of plant defenses in the fluctuation of herbivore populations, *Oikos* **35**:202–213.
51. Herren, H. R., 1976, Manipulation d'une population de la tordeuse grise du Mélèze en vue d'augmenter l'efficacité de ses parasitoides, *Mitt. Schweiz. Entomol. Ges.* **49**:307–308.
52. Herren, H. R., 1977, Le rôle des eulophides dans la gradation de la tordeuse grise du mélèze, *Zeiraphera diniana* GUENÉE (Lep., Tortricidae) en Haute-Engadine, Ph.D. Thèse, ETHZ No. 6037.
53. Howard, L. O., and Fiske, W. F., 1911, The importation into the United States of the parasites of the Gipsy Moth and Brown-Tail Moth: A report of progress with some considerations of previous and concurrent efforts of this kind, *U.S. Dept. Bur. Ent. Bull.* **91**:105–109.
54. Kälin, A., and Auer, C., 1954, Statistische Methoden zur Untersuchung von Insektenpopulationen, *Z. angew. Entomol.* **36**:241–282, 423–461.
55. Kawabe, A., 1980, Descriptions of fourteen new species of the micro moths of Japan, *Tinea* **11**:17–31.
56. Krebs, C. J., 1978, A review of the Chitty Hypothesis of population regulation, *Can. J. Zool.* **56**:2463–2480.
57. Levin, D. A., 1976, The chemical defences of plants to pathogens and herbivores, *Ann. Rev. Ecol. Syst.* **7**:121–159.
58. Lotka, A. J., 1925, *Elements of physical biology,* Williams and Wilkins, Baltimore.
59. Maksymov, J. K., 1959, Beitrag zur Biologie und Oekologie des Grauen Lärchenwicklers *Zeiraphera*

griseana (Hübner) (Lepidoptera, Tortricidae) im Engadin, *Mitt. schweiz. Anst. forstl. Versuchsw.* **35:**277–315.

60. Martignoni, M. E., 1957, Contributo alla conoscenza di una granulosi di *Eucosma griseana* (Hübner) (Tortricidae, Lepidoptera) quale fattore limitante il pullulamento dell'insetto nella Engadina alta, *Mitt. schweiz. Anst. forstl. Versuchsw.* **32:**371–418.
61. Martouret, D., and Auer, C., 1977, Effets de *Bacillus thuringiensis* chez une population de tordeuse grise du mélèze, *Zeiraphera diniana* (Lep.: Tortricidae) en culmination gradologique, *Entomophaga* **22:**37–44.
62. Mutuura, A., and Freeman, T. N., 1966, The North American species of the genus *Zeiraphera. J. Res. Lepid.* **5:**153–176.
63. Omlin, F. X., 1977, Zur populationsdynamischen Wirkung der durch Raupenfrass und Düngung veränderten Nahrungsbasis auf den Grauen Lärchenwickler *Zeiraphera diniana* Gn. (Lep.: Tortricidae), Ph.D. Diss. ETHZ Nr. 6054.
64. Omlin, F. X., and Herren, H. R., 1976, Zur Populationsdynamik des Grauen Lärchenwicklers, *Zeiraphera diniana* Guenée (Lep., Tortricidae), im Ahrntal (Südtirol, Italien): Lebenstafeluntersuchungen und Nahrungsverhältnisse während der Vegetationsperiode 1975, *Mitt. Schweiz. Entomol. Ges.* **49:**203–228.
65. Priesner, E., 1979, Specificity studies on pheromone receptors of noctuid and tortricid Lepidoptera, in: *Chemical Ecology: Odour Communication in Animals* (F. J. Ritter, ed.), pp. 57–71, Elsevier, Amsterdam.
66. Renfer, A., 1974, Caractéristique biologiques et efficacité de *Phytodietus griseanae* Kerrich (Hym., Ichneumonidae) parasitoide de *Zeiraphera diniana* Guenée (Lep., Tortricidae) en haute montagne, Ph.D. Thèse, ETHZ No. 5278.
67. Schweingruber, F. H., 1979, Auswirkungen des Lärchenwicklerbefalls auf die Jahrringstruktur der Lärche, *Schweiz. Z. Forstwes.* **130:**1071–1093.
68. Schwerdtfeger, F., 1963, *Ökologie der Tiere. I. Autökologie,* Paul Parey, Hamburg.
69. Schwerdtfeger, F., 1968, *Ökologie der Tiere. II. Demökologie,* Paul Parey, Hamburg.
70. Stenseth, N. C., 1981, On Chitty's theory for fluctuating populations: the importance of genetic polymorphism in the generation of regular density cycles, *J. Theor. Biol.* **90:**9–36.
71. Vaclena, K., and Baltensweiler, W., 1978, Untersuchungen zur Dispersionsdynamik des Grauen Lärchenwicklers, *Zeiraphera diniana* Gn. (Lep., Tortricidae): 2. Das Flugverhalten der Falter im Freiland, *Mitt. Schweiz. Entomol. Ges.* **51:**59–88.
72. Van den Bos, J., and Rabbinge, R., 1976, *Simulation of the fluctuations of the grey larch bud moth,* Simulation monographs, Centre for Agricultural Publishing and Documentation, Wageningen.
73. Volterra, V., 1926, Variazioni e fluttuazioni del numero d'individui in specie animali conviventi, *Memorie della R. Accademia dei Lincei* **2:**31–113.