

## Systems analysis of the larch bud moth system. Part 1: the larch - larch bud moth relationship<sup>1,2</sup>

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Several attempts to explain the cyclic fluctuations in the abundance of the larch bud moth, *Zeiraphera diniana* GN. (Lep., Tortricidae), have already been made. This is the first paper out of a program which treats the various hypotheses by means of systems analysis. Based on data from the laboratory and the Upper Engadine valley of Switzerland, we modelled the hypothesis proposing that the gradation cycles are caused by the interaction between the host plant larch and the insect larch bud moth. In simulation studies the model's behaviour was found to be similar to that of the real system. However, sensitivity analysis revealed this behaviour to be sensitive to the recovery rate of the trees after defoliation. Unfortunately, on this recovery process only scanty field data are available. Therefore, despite consistence of simulation results and observations, the hypothetical model can not be accepted nor rejected definitively. Because a cycle of the system lasts about 9 years, it is not possible to gather in due time the needed measurements on the raw fiber content of the larch needles. Nevertheless these first results give hope that by the adopted approach, i.e. modelling all the hypotheses plus comparing the respective models, we will gain a basis to decide unequivocally which hypothesis best explains the real larch bud moth system.

In the past decade several authors started to investigate the population dynamics of forest insects by means of new methods, the techniques of systems analysis (CLARK *et al.*, 1978; CLARK & HOLLING, in press; CLARK *et al.*, in press; McLEOD, in press). Since in the field of systems analysis there exist many approaches, a precisely defined conceptual framework for the analysis of the larch bud moth system is required. Fig. 1 shows the general context in which the modelling work presented here should be considered. As the figure indicates, notions, ideas and thoughts about the real larch bud moth system may be conceived as a so called verbal model. According to our experience an explicit formulation of verbal models, incorporating as many of the dynamic properties of the real system as possible, provides a solid base for further quantitative modelling processes.

The population dynamics of the larch bud moth (*Zeiraphera diniana* GN.; Lep., Tortricidae) has been continuously investigated during 29 years and is well known in its optimum zone, between 1700 and 2000 m a.s.l. in the European Alps (AUER, 1961; AUER, 1977; BALTENSWEILER *et al.*, 1977). In the course of these studies several hypotheses concerning the causes of the cyclic fluctuations of the larch bud moth have been put forward by members of the research group (Diseases: MARTIGNONI, 1957, AUER, 1961; Parasitoids: BALTENSWEILER, 1958; DELUCCHI *et al.*, 1975; DELUCCHI, in prep.; Host plant interaction: BENZ, 1974; Polymorphism: BALTENSWEILER, 1970; BALTENSWEILER, 1977; BALTENSWEILER,

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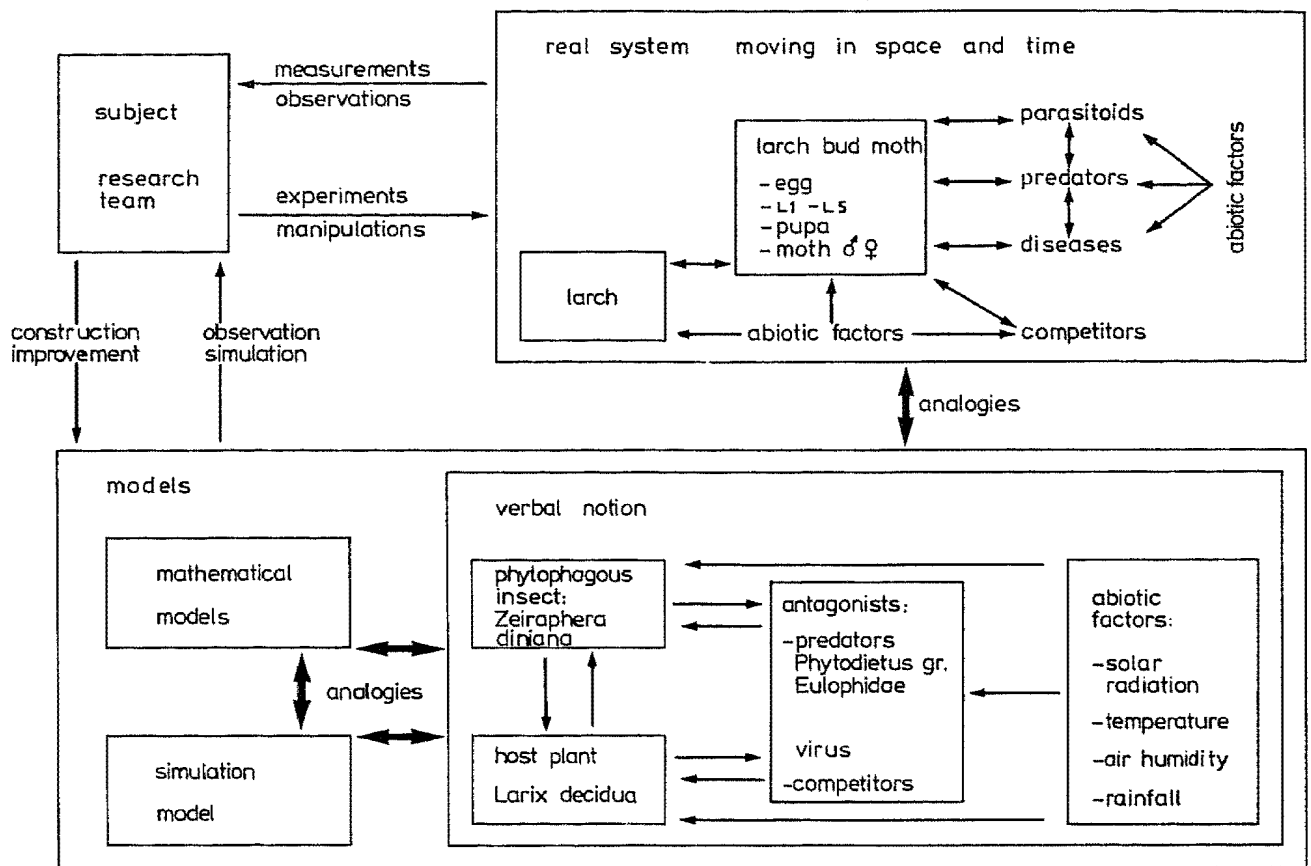


Fig. 1: Context of the systems analysis of the larch bud moth system.

1978; Migration: BALTENSWEILER & FISCHLIN, 1979). In addition its classical population dynamics have been discussed by various other authors (CLARK *et al.*, 1967; VARLEY & GRADWELL, 1970; DEMPSTER, 1975; VAN DEN BOS & RABBINGE, 1976; WAY & BEVAN, 1977).

All these explorations of the larch bud moth population dynamics have one characteristic in common. They all must deal with the large amplitude cycles in the larch bud moth abundance within the optimum zone. Moreover, the analysis of historic forestry reports on defoliation patterns and of dendrochronologic data revealed a strong periodicity of these cycles. From the outbreaks reported since 1854 an average duration of the cycles of 8.6 years was calculated (BALTENSWEILER, 1978). In the Upper Engadine valley data on the abundance of the larch bud moth larvae have been collected for 3 cycles since 1949. In addition the changes in larval numbers were measured for 2 cycles in each of 4 other valleys and in a 5th valley for one cycle. Thus in the optimum zone a total of 12 cycles has been studied quantitatively (AUER, 1977). Each of these cycles has its own characteristics. For instance, there have been cycles with no visible defoliation of the larch trees, as occurred in several alpine valleys in the 19th century (BALTENSWEILER, 1962a; BALTENSWEILER, 1962b; BALTENSWEILER, 1964) or more recently in Val Aurina, in northern Italy (OMLIN & HERREN, 1975). However, one characteristic in the population dynamics of the larch bud moth could be observed consistently: the cyclic change in abundance. Our primary attention is paid to the cyclic behaviour and not to minor differences among the cycles, which may be neglected at first pass. From the data of the 12 cycles mentioned a mean period length of 9.2 years and a mean amplitude of 0.049 to 237.11 larvae/kg branches is obtained.

In analysing the larch bud moth system, the main aim is to explain this «average cycle» by a hypothetical model.

Analysis of weather and its elements showed that the weather variations are uncorrelated with the larch bud moth cycles (AUER, 1961; BALTENSWEILER, 1966). From these facts it was concluded that the «average cycle» is caused by intrinsic properties of the larch bud moth system, not by inputs of abiotic factors like temperature, relative air humidity, rainfall or solar radiation. For instance in the Upper Engadine valley, a typical representative of the optimum zone, the climate of the past 124 years merely provided the necessary environment for the larch bud moth system to cycle.

Recent investigations have emphasized how much migration may contribute to heterogeneous spatial patterns in abundance. It was possible to generate such heterogeneity merely by migration of organisms, even within a homogeneous, but limited environment (FISCHLIN, in prep., a). Thus there is no need for spatially varying forcing functions such as weather factors. Nevertheless migration depends on local dynamics. Hence modelling spatial dynamics adequately demands modelling local dynamics.

Modelling spatial dynamics does not mean just adding a new model to the already existing set of models defining only local dynamics. Rather this means adding spatial dynamics to each local model, like adding the third dimension to each point of a plane and by that stretching up the three-dimensional space. In fact, the real forest systems move in a four-dimensional «space» defined by the three dimensions of space plus time, not in a one-dimensional «space» defined by time only as has too often been assumed in classical systems ecology.

Having considered all these arguments the following framework may be proposed. Analysing the larch bud moth system, eight models are worth exploring. Models *a*, *b*, *c* and *d* describe the local dynamics only, whereas the models *a'*, *b'*, *c'* and *d'* include migration as well (table 1).

The problem arises of how to select the «best» model among several of similar plausibility. This task is best reduced to an optimization problem, depending upon the criterion function chosen. However we like to emphasize that the criterion used throughout this work was not merely a performance index calculated by comparing measurements with model behaviour. Rather it was attempted as well to minimize the contradictions between well known ecological properties

Table 1: Framework of the systems analysis of the larch bud moth system proposing the eight models *a*, *b*, *c*, *d* and *a'*, *b'*, *c'*, *d'* respectively.

local dynamics only		local dynamics plus migration	
<i>a</i>	plant-insect relationship		<i>a'</i>
<i>b</i>	model <i>a</i> plus polymorphism		<i>b'</i>
<i>c</i>	epitism and parasitism		<i>c'</i>
<i>d</i>	combinations of <i>a</i> , <i>b</i> , <i>c</i>		<i>d'</i>

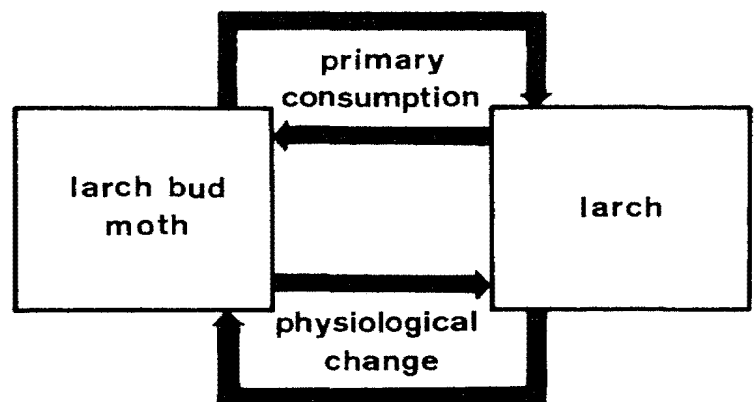
of the real system and the model structure. Unfortunately, in many recent ecological studies, the importance of this latter aspect is not sufficiently appreciated, perhaps due to the difficulty of quantifying structural differences. Fits to observed behaviour may be obtained by many models which even conflict with each other structurally.

The current paper deals with the model *a* (table 1) which describes only the local host plant-phytophagous insect relationship. It should be stressed that this relationship is modelled independently of the role of other structural elements which are present in the real system, such as the polymorphisms in colour and sex attractant (BALTENSWEILER, 1970; BALTENSWEILER, 1977; BALTENSWEILER *et al.*, 1978), the parasitoids, predators (BALTENSWEILER, 1958; DELUCCHI *et al.*, 1975; DELUCCHI & RENFER, 1977) and diseases (MARTIGNONI, 1957; AUER, 1961; SCHMID, 1974). These aspects of the larch bud moth system will be included in the models *b*, *c*, *d* and *b'*, *c'*, *d'* respectively (table 1) and will be discussed elsewhere (FISCHLIN, in prep. [b]).

## THE MODEL

The main host plant of the larch-form of *Z. diniana* is the larch *Larix decidua*. The modelled relationship therefore considers these two components of the real system, henceforth called larch and larch bud moth, only (fig. 2). Abun-

Fig. 2: The larch bud moth system conceived to be composed of the processes physiological change and primary consumption, plus of the elements larch and larch bud moth.



dance and various characteristics of the larch bud moth were found to change in accordance with needle quality (BENZ, 1974). Furthermore, chemical analysis pointed out that the raw fiber content of larch needles might serve as an indicator of needle quality as perceived by larch bud moth larvae (BENZ, 1974; OMLIN, 1977). Hence it was suggested that the cycles of the larch bud moth could be regarded as an undamped oscillation, due to a negative feedback loop consisting of the larch and the larch bud moth larvae (BENZ, 1974). Thus the larch and the larch bud moth should both act in two ways: first as active control elements, controlling the other system components and secondly as controlled processes (WILBERT, 1970). This hypothesis is based on the assumption that the larch bud moth system is a system with two elements, i.e. two populations belonging to different neighboring trophic levels, and with two reflexive relations between these elements: the processes of primary consumption or grazing and of the change in the physiology of the primary producer with its implications (incoincidence, physiological weakening, limited food quantity) for the herbivorous consumer (fig. 2).

Since this model deals with local dynamics only, a valley, e.g. the whole Upper Engadine valley, is treated as a homogeneous biotope with no spatial structure. Whenever possible the limits of the model system were chosen along natural borders of the real valley (fig. 3). Such an area is called a site.

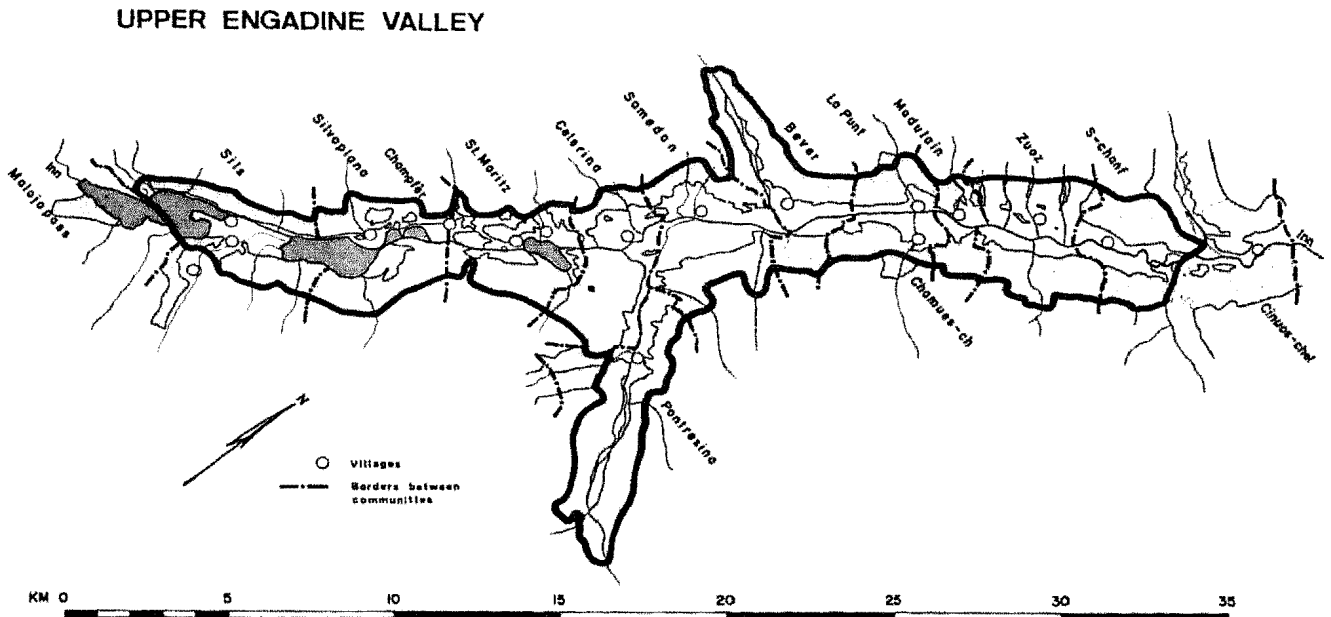


Fig. 3: The limits of the larch bud moth model for the Upper Engadine valley following natural borders whenever possible.

The model consists of variables and mathematical functions. The variables are divided into four sections. The first two, the larch and the larch bud moth, characterize the state of the system. The third and the fourth section correspond to the processes physiological change and grazing. The block diagram in fig. 4 represents this structure. Two state variables are sufficient to determine completely the dynamics of the model system. These were defined for the larch as the raw fiber content indicating needle quality, and for the bud moth as the number of eggs in terms of an absolute population. According to the structural relationships among the variables, the mathematical functions define how the variables depend on each other during a generation of the univoltine larch bud moth.

The yearly iteration starts in autumn. The initial value for the larch bud moth population is the number of freshly deposited eggs ready for embryonic diapause ( $eggs_k$ ). The average egg mortality  $m_{eggs}$  is considered to be constant ( $c_1$ ). Therefore, without conflicting with the basic question, dependent on modeling the plant-insect relationship only, this winter mortality may be viewed as an overall mortality summarizing the effect of various mortality factors such as predation, weather conditions, intrinsic developmental mortality (embryogenesis) and mechanical damage. Its value was estimated from field data (DELUCCHI *et al.*, 1975). The number of eggs having survived the winter is calculated in the following way:

$$eggs := (1 - m_{eggs}) * eggs_k \quad (1)$$

# LARCH BUD MOTH SYSTEM

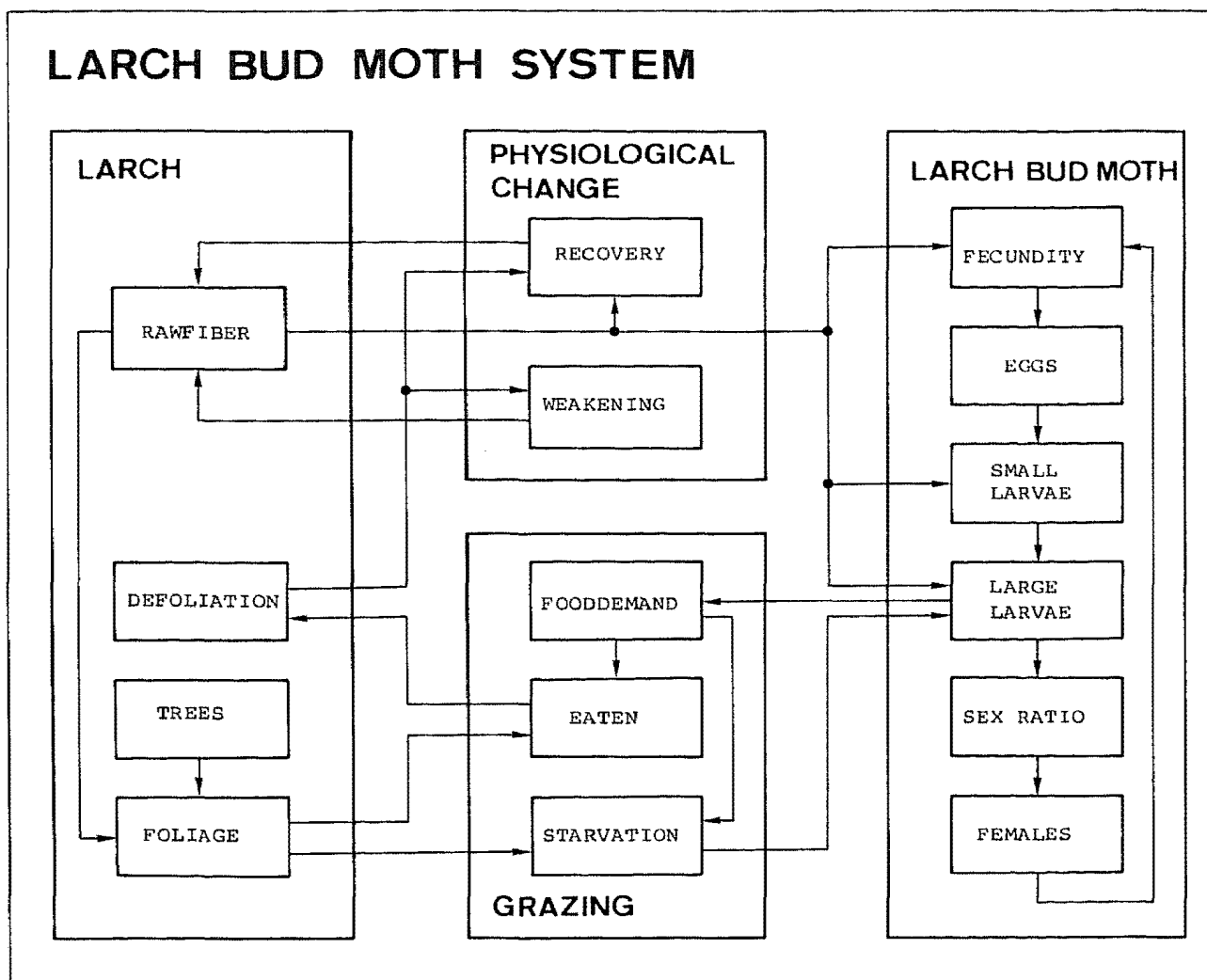


Fig. 4: Model structure of the larch-larch bud moth relationship.

If  $m_{eggs}$  includes also the hatching mortality, the number of newly hatched small larvae must be equal to the number of eggs determined by equation (1), which now can be rewritten:

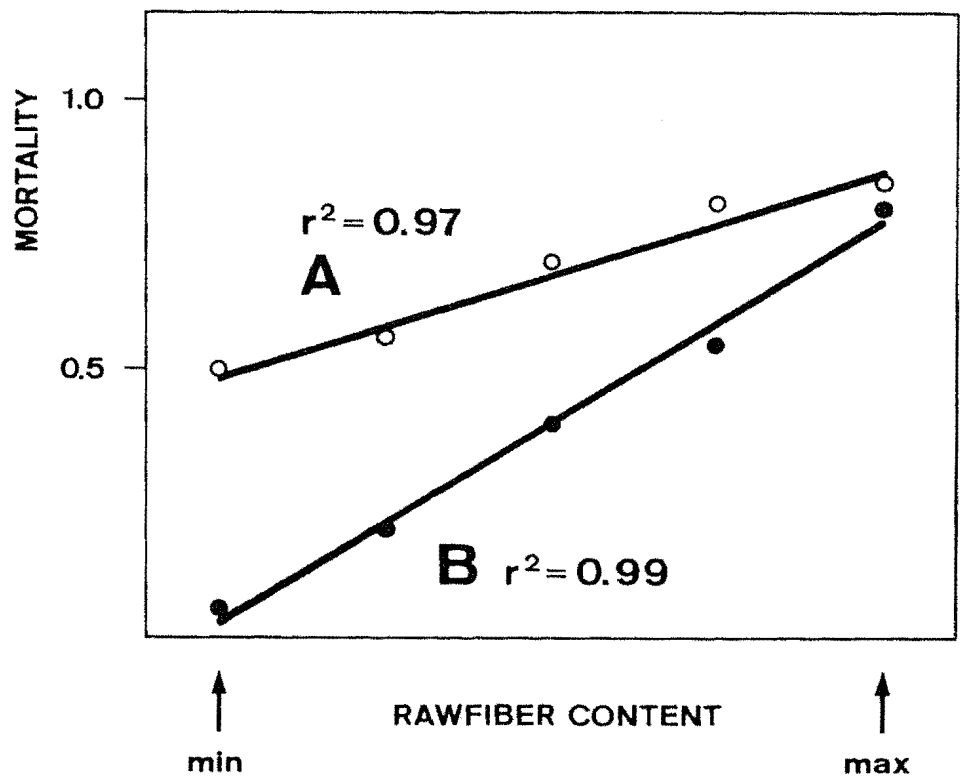
$$smallarvae := (1 - c_1) * eggs_k \quad (2)$$

The two first larval instars are biologically similar (MAKSYMOW, 1959) and therefore not differentiated. This allows to calculate at once the survival of the so defined small larvae (*smallarvae*). As above their number corresponds to the number of insects entering the next life stage, called large larvae (*largelarvae*). This model life stage includes the last three larval instars.

$$largelarvae := (1 - m_{smallarvae}^{(rawfiber)}) * smallarvae \quad (3)$$

According to the basic question only factors being affected by the plant-insect relationship may be included in the mortality of the small larvae. Hence the mortality  $m_{smallarvae}$  must not be considered as an overall mortality like the winter mortality  $m_{eggs}$ . It is merely caused by coincidence between larval development and needle growth, plus physiological deterioration. It appears from field

Fig. 5: Mortality of the larch bud moth larvae as a function of larch needle quality. A: mortality of small larvae ( $L_1, L_2$ ) due to incoincidence and physiological weakening; B: mortality of large larvae ( $L_3, L_4, L_5$ ) due to physiological weakening (data from BENZ, 1974; OMLIN, 1977; BALTENSWEILER *et al.*, 1977).



and laboratory data (BENZ, 1974; OMLIN, 1977; BALTENSWEILER *et al.*, 1977) that this mortality depends linearly on the raw fiber content of the larch needles, henceforth called *rawfiber*. The constants  $c_i$  in the following equation were obtained by linear regression using the data shown in fig. 5 (A).

$$m_{smallarvae} = c_2 * rawfiber + c_3 \quad (4)$$

Due to intraspecific competition for food and the limited carrying capacity of the larch, many larvae starve and even die at high population densities. The number of large larvae surviving starvation is calculated in the following way:

$$largelarvae := (1 - m_{starv}(fol, fooddem)) * largelarvae \quad (5)$$

By modelling the grazing process the auxiliary variable *fol* must be introduced for the food quantity foliage. It depends on the state variable *rawfiber*.

$$fol := g_{fol}(rawfiber) \quad (6)$$

Needle length and raw fiber content are negatively and linearly correlated (OMLIN, 1977). Assuming that the total amount of foliage biomass in kg fresh weight is determined by the needle length, a linear function  $g_{fol}$  is obtained.

$$g_{fol} = c_4 * rawfiber + c_5 \quad (7)$$

Only large larvae consume a considerable amount of foliage. When this grazing becomes significant, needle growth for the year is essentially depleted. Through laboratory studies (GERIG, 1966; BENZ, 1974) it was possible to establish the maximum consumption rate or food demand for the individual larva. To

calculate actual demand exerted by the total larval population, intraspecific competition must be taken into account. In this initial analysis the simple assumption of contest competition was adopted, not the more complex scramble competition (WATT, 1968; GRIFFITHS & HOLLING, 1969). Hereby the food demand *foddem* (an auxiliary variable) becomes directly proportional to the number of large larvae.

$$foddem := c_6 * largelarvae \quad (8)$$

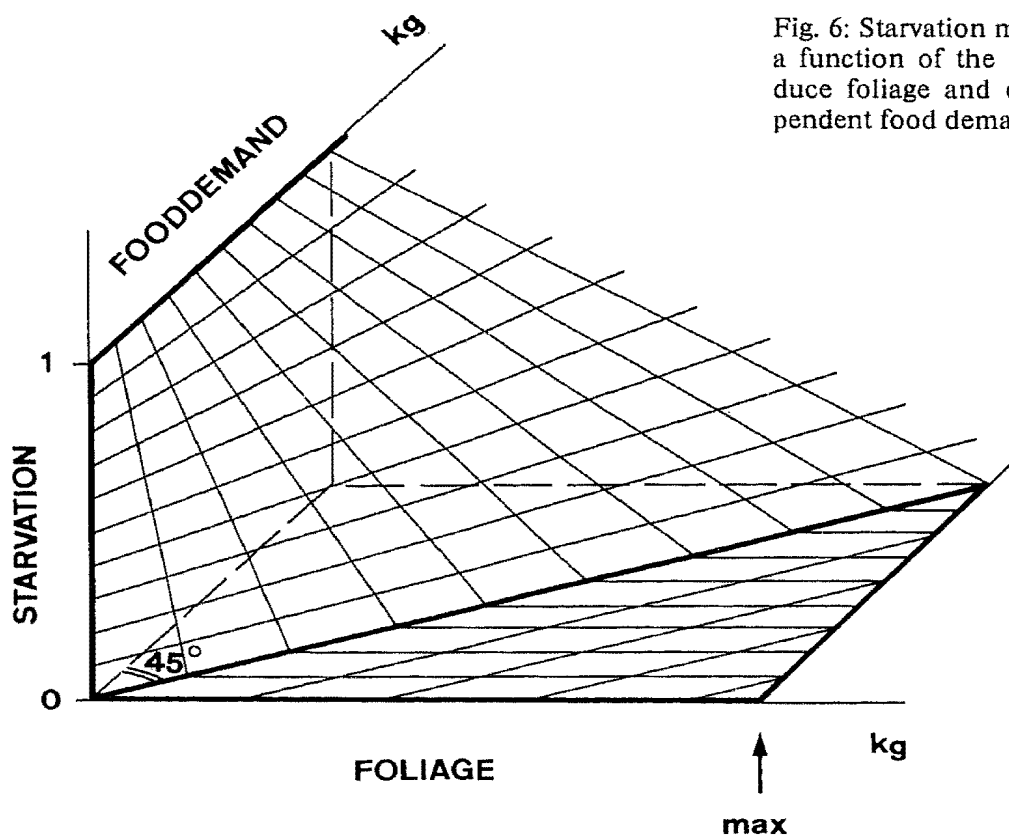


Fig. 6: Starvation mortality of large larvae as a function of the capacity of larch to produce foliage and of the larval density dependent food demand.

The starvation mortality  $m_{starv}$  then is a nonlinear function of the food demand and the amount of available food, i.e. foliage (fig. 6).

$$m_{starv} = \begin{cases} 0 & foddem < fol \\ (foddem - fol) / foddem & foddem \geq fol \end{cases} \quad (9)$$

Now the number of females may be calculated, using a sex ratio  $c_9$  averaged from observations (BALTENSWEILER, 1968).

$$females := c_9 * (1 - m_{l1pm}(rawfiber)) * largelarvae \quad (10)$$

Needle quality influences the vitality of large larvae ready to pupate, of pupae, and of newly emerged moths (BENZ, 1974). For all these life stages the mortality due to physiological weakening depends on *rawfiber*. Fig. 5 (B) shows



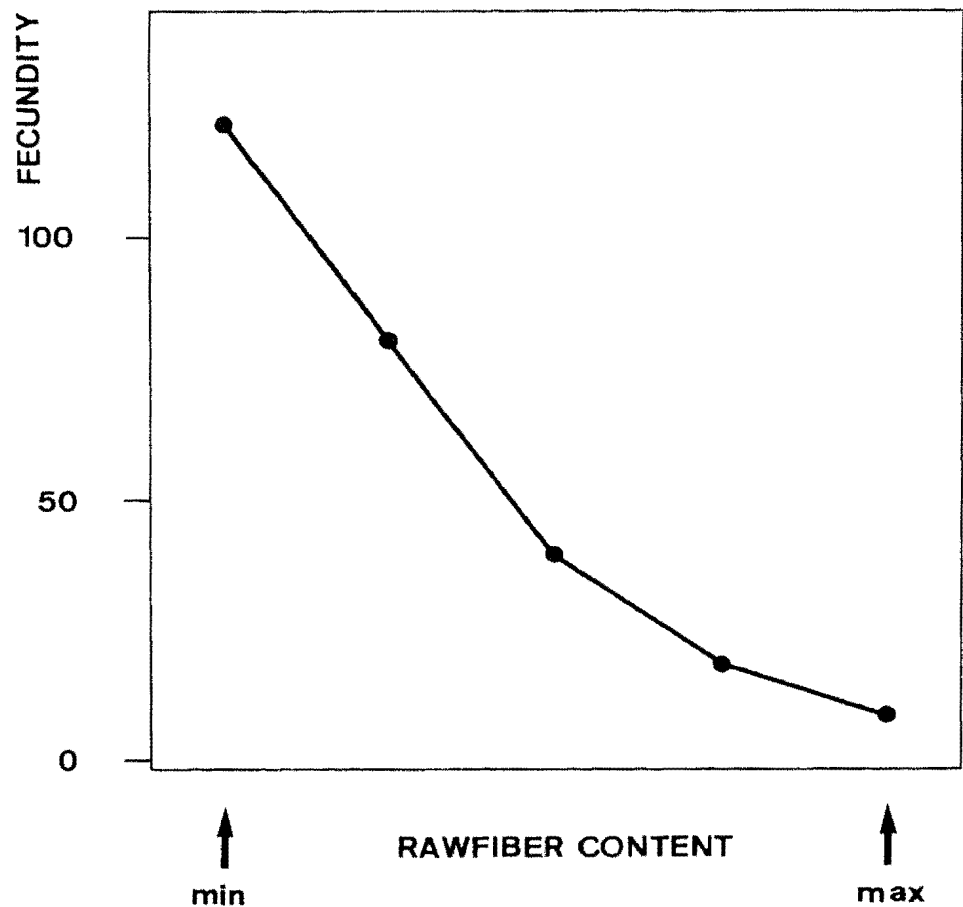
this linear mortality function  $m_{l1pm}$ , which was calculated from experimental data (BENZ, 1974).

$$m_{l1pm} = c_7 * rawfiber + c_8 \quad (11)$$

The number of eggs that a given female can lay during its lifetime depends on its vitality which can either be quantified by weight (VAČLENA, 1977) or derived from the needle quality. Thus fecundity is conceived as a nonlinear function  $g_{fec}$  of  $rawfiber$ , given by a table (BENZ, 1974) which may be linearly interpolated if necessary during a simulation run (fig. 7).

$$fecundity := g_{fec}(rawfiber) \quad (12)$$

Fig. 7: Fecundity of the larch bud moth females as a function of larch needle quality (data from BENZ, 1974).



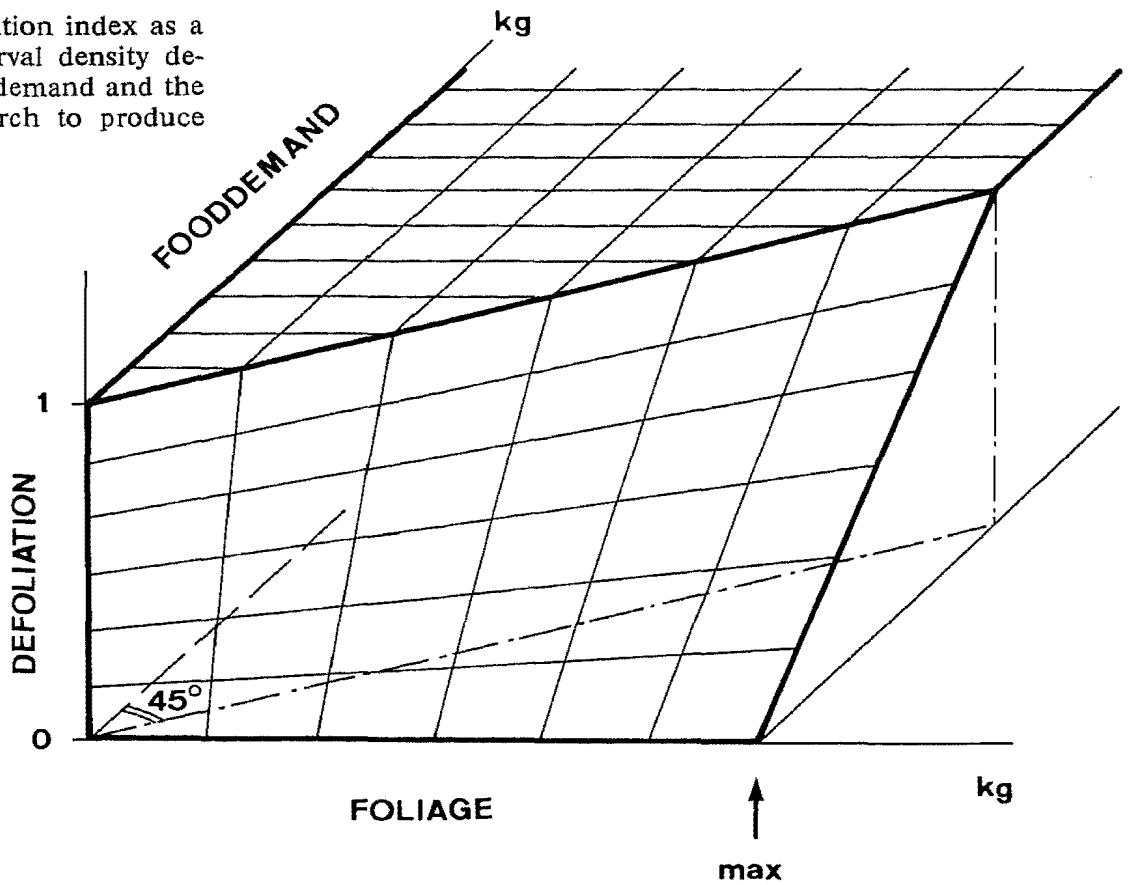
To finish the yearly iteration for the larch bud moth, the number of eggs  $eggs_{k+1}$  belonging to the new generation is calculated in the following way.

$$eggs_{k+1} := fecundity * females \quad (13)$$

From the previous assertions about the grazing process and competition it follows that the defoliation index is a nonlinear function of larval food demand and the actual available food quantity, the foliage (fig. 8).

$$defoliation = \begin{cases} fooddem / fol & fooddem < fol \\ 1 & fooddem \geq fol \end{cases} \quad (14)$$

Fig. 8: Defoliation index as a function of larval density dependent food demand and the capacity of larch to produce foliage.



By completing the yearly iteration also for the larch, the transformation of the needle quality, indicated by the raw fiber content, must be defined.

$$rawfiber_{k+1} := g_{regr}(fol, rawfiber_k) * rawfiber_k \quad (15)$$

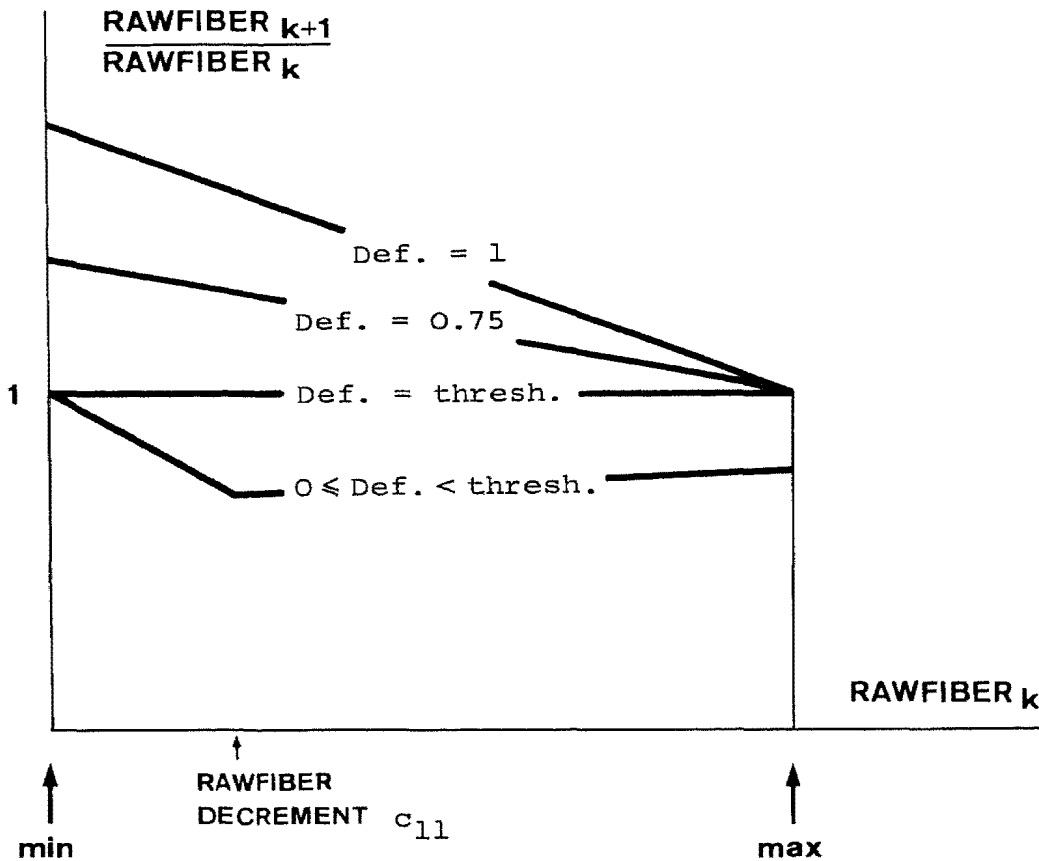


Fig. 9: Annual recruitment functions for raw fiber content. The ratio between raw fiber content of two succeeding years depends on the previous raw fiber content and the defoliation index (Def.). Four curves, each with their particular defoliation indexes, are given.

If severe defoliation occurs, the tree is physiologically weakened due to lost primary production and subsequent new sprouting in August, i.e. the middle of the vegetational season. As observed in the field this leads in the following year to an increase of the raw fiber content, usually to its maximum value  $c_{12}$  (BENZ, 1974; OMLIN, 1977). If there is no significant defoliation, a weakened tree will begin to «recover», and raw fiber content falls. Below this threshold of defoliation  $c_{13}$  the rate of recovery was assumed to be constant at high initial raw fiber values, but tending towards zero as raw fiber approaches its minimum value  $c_{10}$ . Because only scanty field data were available, a large set of postulated recovery rates were identified by simulation runs.

Fig. 9 shows this mathematical relationship, plotted as annual recruitment functions (RICKER, 1954; CLARK *et al.*, in press) for raw fiber content at different levels of defoliation. The region above the value 1 indicates physiological weakening of the larch, i.e. an increase in the raw fiber content. In the region below 1 the larch recovers, this means the raw fiber content decreases.

$$g_{reer} = \left\{ \begin{array}{ll} \frac{c_{10}}{rawfiber_k} & (defoliation < c_{13}) \wedge ((rawfiber_k - c_{10}) < c_{11}) \\ \frac{rawfiber_k - c_{11}}{rawfiber_k} & (defoliation < c_{13}) \wedge ((rawfiber_k - c_{10}) \geq c_{11}) \\ \frac{1}{rawfiber_k} & defoliation = c_{13} \\ \frac{(defoliation - c_{13})(c_{12} - rawfiber_k)}{(1 - c_{13})c_{10}} + 1 & defoliation \geq c_{13} \end{array} \right. \quad (16)$$

In order to provide a better overview all the equations (2) to (16), which represent the simulation model, were condensed into one system of equations (17). Hereby the so called mathematical model was obtained<sup>3</sup>. It consists of discrete time, nonlinear equations<sup>4</sup>. It is of second order with no input (driving)

<sup>3</sup> Although much more variables were introduced in the simulation model than in the mathematical model, both are mathematically equivalent to each other. All the variables additionally defined for the simulation model, the so called auxiliary variables, are implicitly given by the expressions of the mathematical model. Though in some sense arbitrary, the choice of the state variables seems to reflect the structure of the real system most naturally. Moreover, by this choice the linkage with a migration model becomes yet possible.

<sup>4</sup> Reasons for having chosen a deterministic local model were already discussed in the previous section. Still some mathematical questions are worth discussing. From systems theory it can be deduced that linear, stable (in the sense of LIAPUNOV), and autonomous systems can not produce periodic cycles as observed in the abundance of the larch bud moth. Large scale applications of insecticides, reducing the number of larch bud moth larvae, indicated that the real system exhibits stability in the sense of LIAPUNOV (GRISON *et al.*, 1971; AUER, 1974). Moreover it is true that the real system is potentially able to cycle endlessly. Hence already these reasons are calling for a nonlinear system.

variables. Larval density expressed as number of larvae per kg larch branches is considered as output variable. Not the least because the larch bud moth is an univoltine insect, the time step was chosen equal to one year.

$$\begin{aligned}
 e_{k+1} &:= g_{fec}(r_k) \cdot (1 - m_{starv}(p_3 r_k + p_4, p_1 r_k \cdot e_k + p_2 e_k)) \cdot (p_5 r_k^2 + p_6 r_k + p_7) \cdot e_k \\
 r_{k+1} &:= g_{recr}(p_3 r_k + p_4, r_k) \cdot r_k
 \end{aligned}
 \tag{17}$$

(abbreviations used:  $e$ :: = eggs,  $r$ :: = rawfiber,  $p_i$ :: = parameters; for not explicitly stated nonlinear functions see (9), (12) and (16)).

## RESULTS AND DISCUSSION

The present-day opportunities to utilize inexpensive computing facilities can be very misleading. Experience has shown that one should avoid building models which are very large and too complex. These hardly bring new, deeper insights. Of course the task to develop models which are simultaneously realistic, holistic, simple and general is difficult, not to say impossible (HOLLING, 1968). The solution is not to maximize realism, holism, simplicity and generality all together. Rather it is the one that optimizes all these aspects according to the basic purpose of the investigation. Hence the basic purpose limits how much one gains, say, of generality instead of realism, or holism instead of clearly understandable simplicity. By studying the causes of the cycles, our basic purpose is to understand the mechanisms of population regulation, since a control of the larch bud moth for large areas has been found to be neither feasible nor economic (BALTENSWEILER, 1978). Therefore in the model presented generality is preferred to detailed realism, and simplicity to a holism not based on rigorously definable assumptions.

Taking all these statements into account, the modelling approach used in this paper seems to match the basic question – of how the observed gradation cycles arise – better than the type of approach utilized by VAN DEN BOS & RABBINGE (1976). From that simulation study resulted a very complex (27th order) model system, besides simulation more or less resistant to any further (e.g. mathematical) treatment. So far no analysis of that model could bring satisfactory elucidation of which factors were most responsible for discrepancies between that model and the real system, perhaps because it was not dedicated to such purposes as giving clear insights into the mechanisms of population regulation.

Because it is not yet possible to compare the basic model formulated in this first step with the other models envisioned in table 1, its behaviour and sensitivity have been elucidated by simulations.

The model system is of second order, thus its behaviour is fully characterized by two variables each selected from a set representing the larch and the larch bud moth respectively (fig. 4).

For the larch bud moth was defined as output variable the so called «simulated» larval density. Using proportions found in the field (AUER, 1952–1975) among small larvae, large larvae, and foliage, this density was calculated from the variables of the model. Fig. 10 shows the final simulation results compared to the range of observed mean densities among sections within the Upper Engadine valley. The comparison between a model cycle and the observed «average cycle» is given in fig. 11.

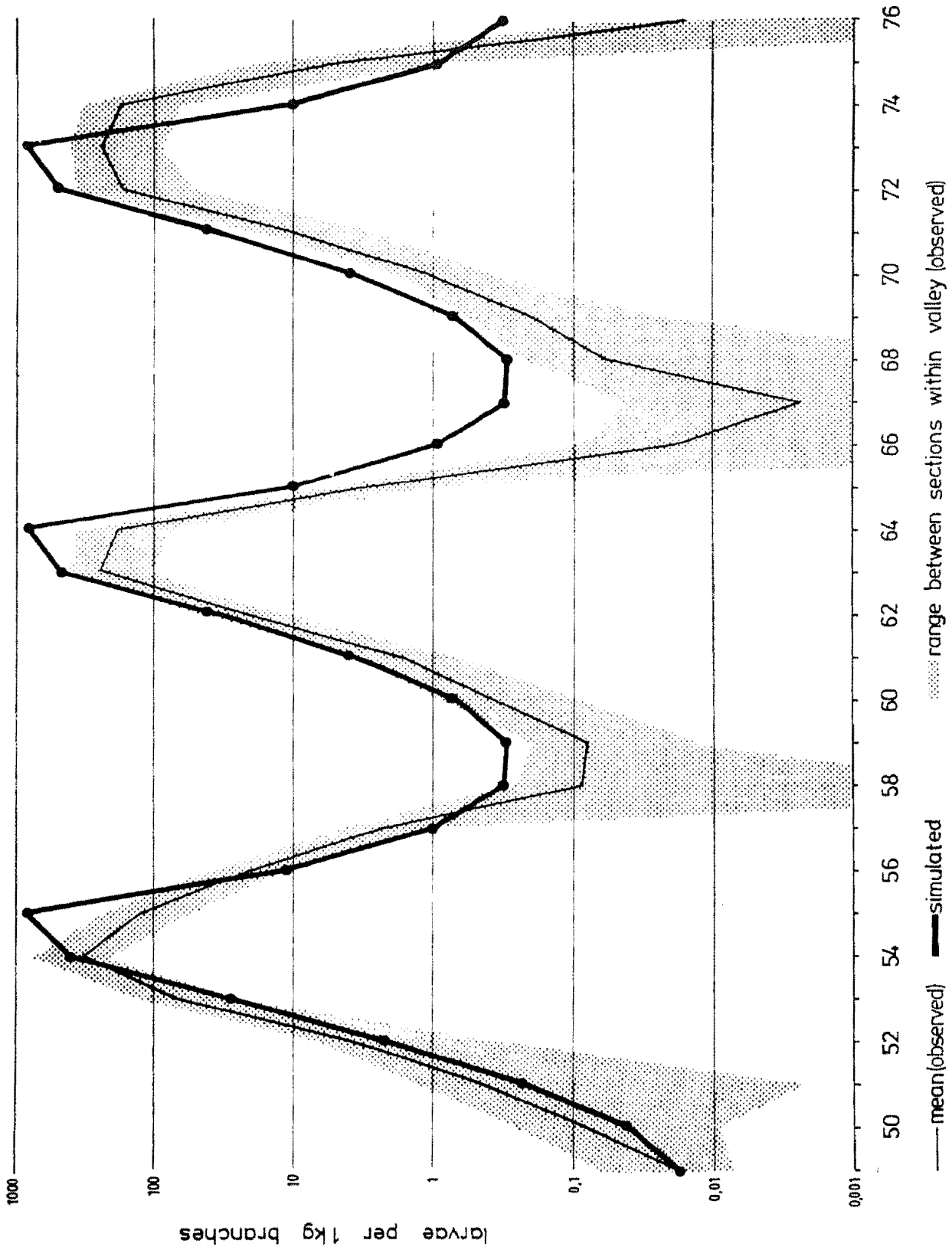


Fig. 10: Simulated model behaviour compared to real system behaviour (abundances of larch bud moth larvae) (Observed values from AUER, 1977).

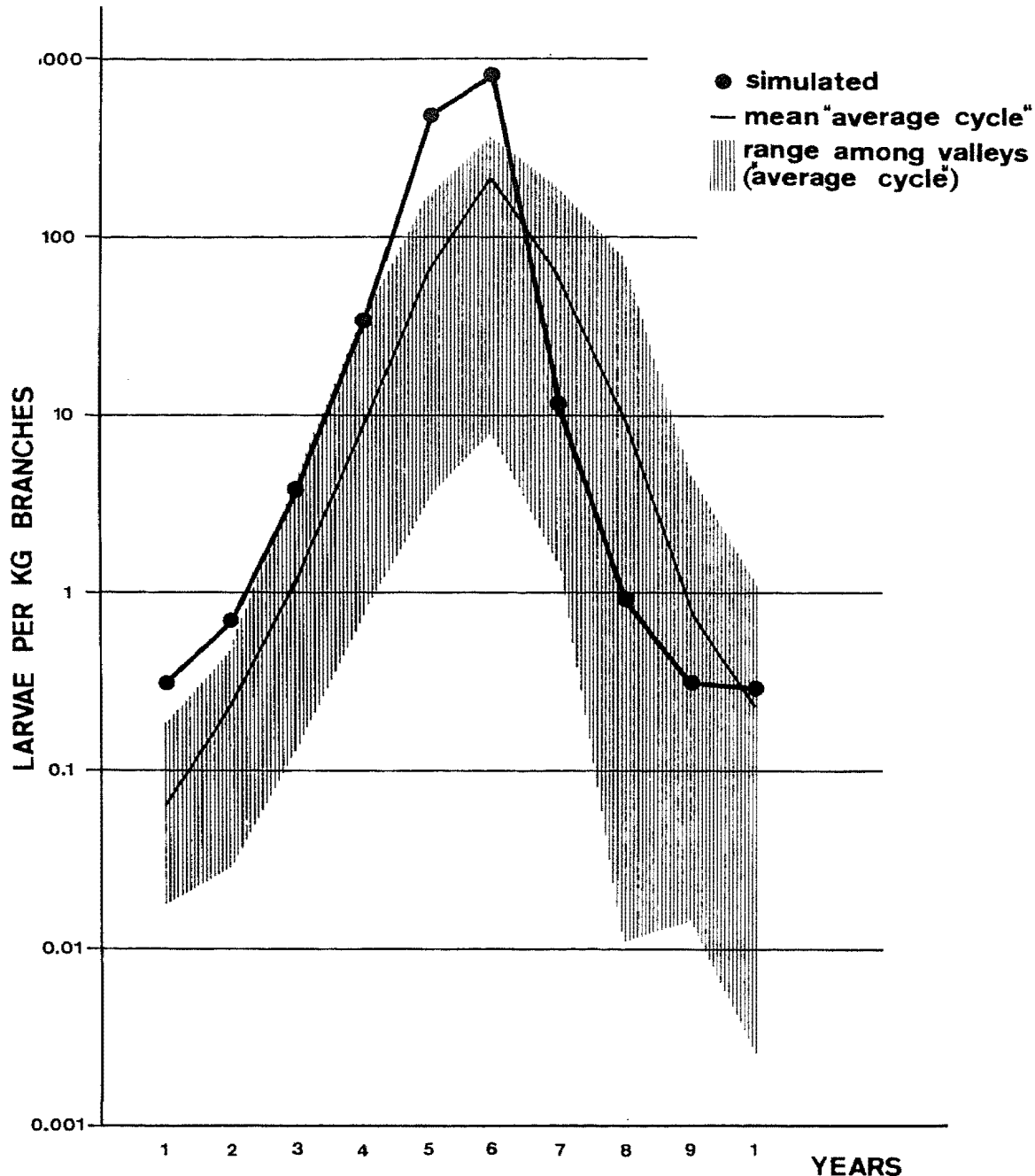


Fig. 11: Simulated cycle of the larch bud moth density compared to the observed «average cycle» (mean of the «average cycle» calculated from data observed by AUER, 1977).

No equivalent field data are available concerning larch. Chemical analyses of needles were made during the past years of the regression phase of the last cycle for only a few, individual larch trees (BENZ, 1974; OMLIN, 1977). Therefore any graphical representation of the raw fiber content of larch needles is omitted. Instead, the simulated raw fiber content of a complete cycle is given in table 2.

The model sensitivity was evaluated in several ways. The effects of changes in structure and in various parameters were tested in simulation runs. The model system revealed a remarkable robustness. Of the functions which could not be specified with a fair amount of certainty from experimental data, only changes to the recovery rate of the needle quality (i.e. the decline rate of *raw fiber*) led to dramatic changes in the system behaviour. A plausible increase in the rate of recovery produced cycles of shorter period and lower amplitude than those shown in fig. 10 and 11, while a decrease produced the reverse.

year	percentage of raw fiber content
1959	15.1
1960	14.1
1961	13.1
1962	12.1
1963	11.1
1964	18.0
1965	18.0
1966	17.0
1967	16.0

Table 2: The simulated raw fiber content of larch needles for the second observed cycle in the Upper Engadine valley (1959-1967).

Two conclusions result from this study. The first accepts the basic structural hypothesis underlying the model as correct. If this is true and assumed that the growth potential of the larch bud moth population has not been overestimated nor the mortality underestimated, the recovery rate of the needle quality must be really as slow as is indicated by the model. Measurements of the needle length only partially support the latter view. Unfortunately the lack of directly measured raw fiber content prohibits rigorous, empirical validation of this point. As mentioned above, chemical analyses were made only through the years 1970 to 1975. However it would have been much more important to sample during the years 1967 to 1969, at the beginning of the progression phase.

The second conclusion accepts that some other processes than grazing and physiological reactions would have to be included into the model to obtain more realistic behaviour. This aspect is best evaluated by comparing the model presented here with other models as proposed in table 1. The present study encourages such a comparative modelling procedure and it is hoped that better understanding of the contribution of the various system components to the overall system behaviour, as mainly characterized by the larch bud moth dynamics, may be achieved through such an approach.

One broader conclusion may also be drawn. The model was constructed by incorporating only properties about the larch-larch bud moth relationship, without aiming at a cyclic system behaviour. Because the model system does cycle with a large amplitude and a realistic period it may be concluded that this behaviour follows from the larch-larch bud moth relationship. The suggestion thereby arises that this relationship represents a basic component of the larch bud moth system, and that without it there would be no such cycles in the abundance of the larch bud moth at all.

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CORRIGENDA

p.281 replace (14) with

$$\text{defoliation} := g_{\text{defol}}(\text{fol}, \text{fooddem}) \quad (14a)$$

$$g_{\text{defol}} = \begin{cases} \text{fooddem}/\text{fol} & \text{fooddem} < \text{fol} \\ 1 & \text{fooddem} \geq \text{fol} \end{cases} \quad (14b)$$

p.282 replace (15) with

$$\text{rawfiber}_{k+1} := g_{\text{regr}}(g_{\text{defol}}(\text{fol}, \text{fooddem}), \text{rawfiber}_k) * \text{rawfiber}_k \quad (15)$$

p.283 replace (16) with

$$g_{\text{regr}} = \begin{cases} \frac{c_{10}}{\text{rawfiber}_k} & (\text{defoliation} < c_{13}) \wedge ((\text{rawfiber}_k - c_{10}) < c_{11}) \\ \frac{\text{rawfiber}_k - c_{11}}{\text{rawfiber}_k} & (\text{defoliation} < c_{13}) \wedge ((\text{rawfiber}_k - c_{10}) \geq c_{11}) \\ 1 & \text{defoliation} = c_{13} \\ \frac{(\text{defoliation} - c_{13})(c_{12} - \text{rawfiber}_k)}{(1 - c_{13})c_{10}} + 1 & \text{defoliation} \geq c_{13} \end{cases} \quad (16)$$

p.284 replace (17) with

$$\begin{aligned} e_{k+1} &:= g_{\text{fec}}(r_k)^{(1-m)} \text{starv}_{;3}^{(p_3 r_k + p_4, p_1 r_k e_k + p_2 e_k)} (p_5 r_k^2 + p_6 r_k + p_7) e_k \\ r_{k+1} &:= g_{\text{regr}}(g_{\text{defol}}(p_3 r_k + p_4, p_1 r_k e_k + p_2 e_k), r_k) r_k \end{aligned} \quad (17)$$

(abbreviations used:  $e$  ::= eggs,  $r$  ::= rawfiber,  $p_i$  ::= parameters; for not explicitly stated nonlinear functions see (9), (12), (14b) and (16)).