G. On Methods of Analyzing Ecosystems: Lessons from the Analysis of Forest-Insect Systems*

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I. Introduction

There are various ways to analyze ecosystems. No approach is unanimously accepted (Ruesink 1976; Getz and Gutierrez 1982). One alternative to this seemingly unresolvable dispute is to analyze past experience in order to learn from it. A fair assessment of any scientific approach would be to compare its achievements with its initial objectives as defined by the scientists directly involved.

In this context forest-insect systems are of particular interest because they represent relatively natural ecosystems. Since forest pest insects cause often damages of high economical concern, several have been studied on a long-term basis.

Particularly challenging to ecology is the class of ecosystem with cyclic populations. They pose a challenge because the simplicity of their dynamics ought to allow for predictions about the temporal behavior of the cyclic population with relative ease. However, until the present, except for the most trivial extrapolations based on the periodicity of the phenomenon, we are not able to predict accurately population numbers for any well-defined set of environmental factors. If it should turn out that no predictions can be made, ecology as a scientific discipline would be at stake.

The main problem is that of population regulation. Today we have a set of competing hypotheses: natural enemies, host organisms, or self-regulation are proposed as main regulating mechanisms. Surprisingly enough, this set of hypotheses is arrived at in studies which deal with insects, such as the larch bud moth (Fischlin 1982) or the spruce budworm (Royama 1984) as well as with small mammals like snowshoe hares (Keith 1981) or voles (Krebs et al. 1973).

The larch bud moth, *Zeiraphera diniana* Gn., in the subalpine larch-cembran pine forests of the European Alps exhibits cyclic population fluctuations. Since it has been studied continuously for more than three decades, it provides a wealth of material to learn from in the context of this symposium.

This chapter discusses achievements and short-comings of the larch bud moth project. By contrasting these aspects with the goals the scientists involved have themselves defined, the historic development and the decision-making processes are reviewed. In

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particular, the influence of the prevailing spirit of the epoch on scientific activities, the importance of demecologically oriented research, the relevance of a balance between empirical and theoretical techniques, the difficulties in matching scales between real system, experiment, and model, the reasons which speak for an adaptive strategy, and finally the role personal relationships may play in scientific projects are discussed.

II. The Objective "Control"

The defoliation of subalpine larch trees in the Engadine (Swiss Alps) by the larvae of the larch bud moth at intervals of 9 to 10 years have been known since long (Coaz 1894). However, the coincidence of two circumstances triggered the idea of controling these periodic outbreaks. First, a very conspicuous outbreak in the dry summers of 1946 and 1947 led to much public concern about possible negative impacts on tourism to be revived after World War II. Secondly, the fame and availability of DDT combined with an optimistic attitude toward the potential of human technology, as it has been so accurately characterized by Perkins (1982) with the term "Paradigm of chemical control", called for human intervention.

The late Dr. Auer, who had profited from personal acquaintance with previous bud moth outbreaks, initiated a larval population census in 1948 with the goals (1) to estimate a mean population which may be considered as uninfluenced by immigration and emigration, i.e., an autochthonous population and (2) to detect local variations within this population (Auer 1961). The first goal reveals the intention to circumvent eventual difficulties due to the at the time much disputed Herdtheorie, whereas the second goal was motivated by the hope of detecting local concentrations of the so-called Eiserner Bestand, which could then be treated easily. Both goals comply to the overall objective, i.e., the control of the budmoth.

Thanks to Auer's farsighted approach, the larval census was not only pioneering but also scientifically and statistically sound from the very beginning (Kälin and Auer 1954). The first samples of larch branches were taken in the summer of 1949 in the Engadine Valley. From 1949 till 1956 samples were taken every year from an average of 1500 larch trees, randomly selected throughout the 6000 ha of larch-cembran pine forests. Thorough statistical analysis revealed for the first time the cyclic nature of the larch bud moth population dynamics (Fig. 1). It was possible to detect significant differences in the population levels from each year to the next. This is due to the dramatic changes in the growth rates of which the larch bud moth population is capable.

The need to distinguish the great variety of lepidopterous larval feeding on larch made it indispensable to involve professional entomologists at an early stage of the project. In addition, the forest service hoped that the entomologists might also suggest means, either biological or silvicultural, which could help to limit the economic impact of the outbreaks without their being forced to resort to insecticidal control (Bovey 1958; Bovey and Maksymov 1959). Thus, ideas stemming from the biotic school of population regulation (Tamarin 1978), i.e., the role of natural enemies, were incorporated into the project.

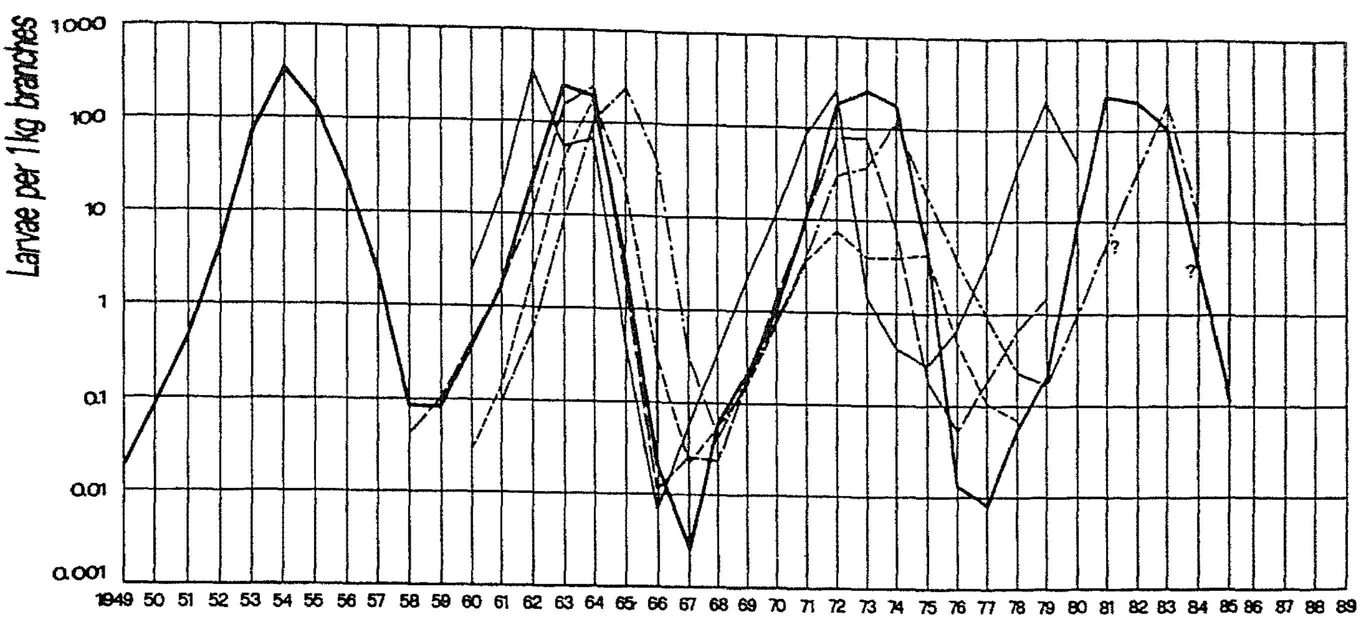

Fig. 1. Larch bud moth cycles as observed within five valleys of the European Alps. The data on larval densities are the result of the larval census as conducted within the so called optimum area of the larch bud moth. The samples have been taken from larch trees in the subalpine larch-cembran pine forests. The subalpine valleys represent the whole larch bud moth system, which ranges from the west to the east of the European Alps: Briançonnais (France) ——— , Goms (Switzerland) — — , Upper Engadine (Switzerland) ━━━ , Valle Aurina (Italy) - - - - - - , Lungau (Austria) — · — · . *Ordinate*: bud moth larvae per 1.0 kg larch branches; *abscissa*: years. [Data partially from Auer (1977); data after 1976 are published for the first time]

Studies on a larval virus disease (Martignoni 1957) and the complex of parasitoids (Baltensweiler 1958) were initiated. In 1954, at the peak of the first cycle (Fig. 1), the virus disease was killing large numbers of bud moth larvae, which coincided with a dramatic collapse of the population in the subsequent years. It is no surprise that the scientists involved were convinced that this disease was the main factor in the population regulation mechanism of the larch bud moth system (Martignoni 1957; Bovey 1958; Bovey and Maksymov 1959).

To summarize: the larch bud moth project was initiated on public demand by the provincial forest service in order to control the periodic outbreaks. The general public had no doubts about the potential of human technology to overcome any undesired properties of nature such as the defoliation of the larch forests by the bud moth. The main purpose for which the forest service established the annual larval census had to serve was the objective control. The main questions were: where and when should be treated? What is the effect of control measures?

The entomologists, for their part, believed that natural enemies, either disease or parasitoids, were the key to the understanding of the population regulation, and that it was essential to gain the relevant information in order to control the bud moth. Thus all protagonists in the larch bud moth team reflect clearly the prevailing spirit of the epoch.

A few years earlier, in 1945, the spruce budworm project had started in New Brunswick, Canada (Morris 1963). Despite the interesting fact that the two research groups did not know from each other until the mid 1950's, the two projects exhibit some strik-

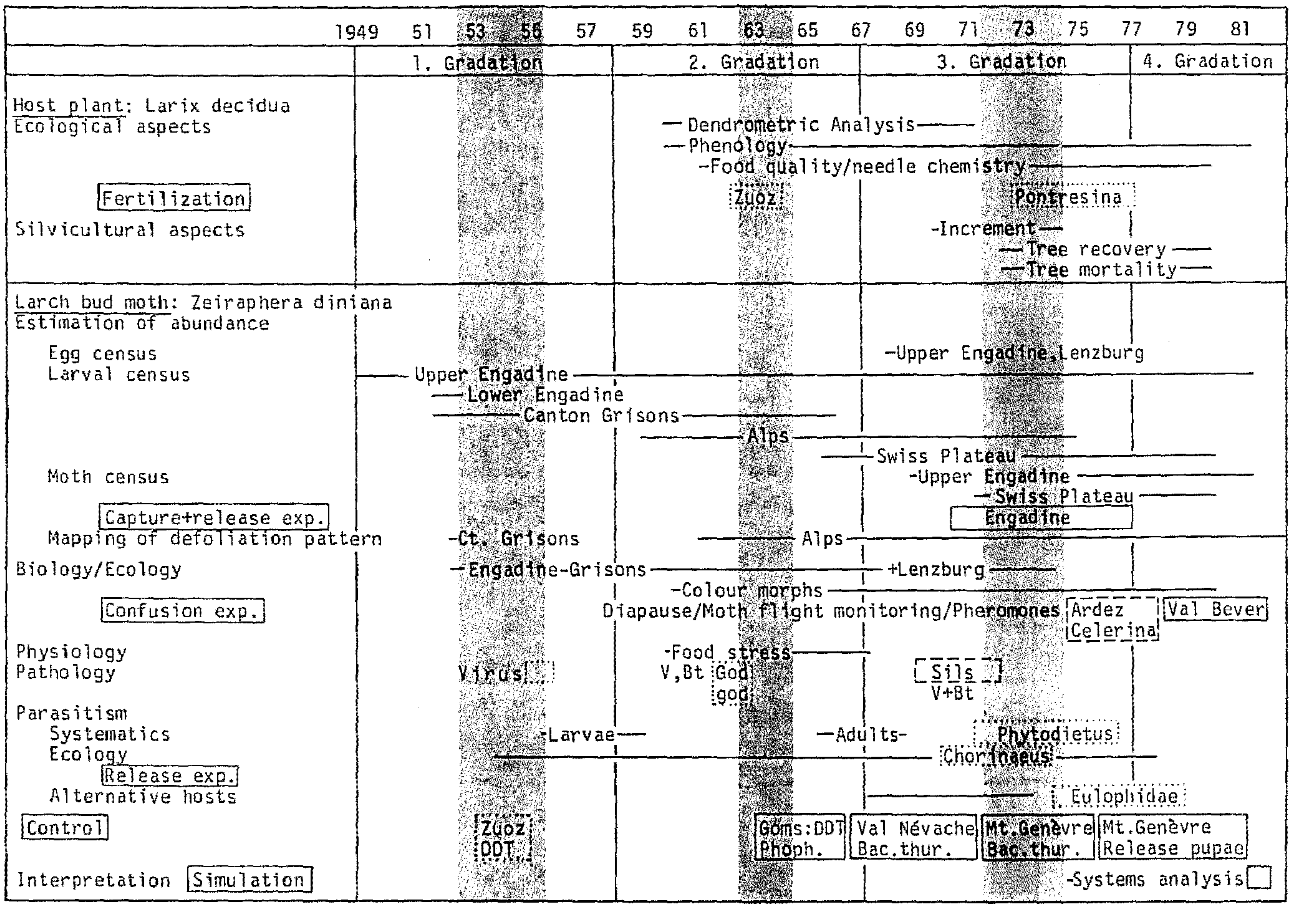

Fig. 2. Overview of the numerous scientific investigations conducted during the larch bud moth project 1949–1981. V = Granulosis virus; Bt = *Bacillus thuringiensis*.

Experiments ≤ 10 ha

Experiments ≤ 11–100 ha

Experiments ≤ 101–1000 ha

Experiments > 1000 ha

ing similarities. The projects differ fundamentally, however, in their approach to field studies: The life table studies of the spruce budworm project provide a rather detailed insight into the relevant biological processes. However, these results are of limited value, since they represent mainly local particularities for which spatial extrapolations have to remain mostly speculative. In contrast, the design of the larch bud moth project stressed the extensive registration of many biological phenomenons on a relatively larger, i.e., geographically more continuous, spatial scale, sacrificing intensive, detailed investigations and focusing on local factors.

In the larch bud moth project life table studies were begun in the mid 1960's only. This delay might be surprising, all the more as this approach, or precisely the "mortality tables", had been used in Germany already in 1936 (Schwerdtfeger 1968). Among other reasons, this late coming into use was due to the much greater difficulties in obtaining compatible population estimates in various life stage-specific universes, such as the lichen cover on larch branches, under which the egg stage overwinters, the needle clusters for the larval stage, and the forest litter for the pupae (Auer 1975). In contrast to these technical difficulties, the branch surface area of the balsam fir served as the basic unit to estimate life stage-specific densities of most *Choristoneura fumiferana* life stages.

According to the main objective, the control of the larch bud moth, great endeavors were dedicated to testing the feasibility of various control methods (Fig. 2). First control trials were undertaken on small areas by means of DDT spraying. As no biological product was available for large-scale treatments, 1700 ha of the Goms Valley (Swiss Alps) were treated with Phosphamidon and DDT in 1963, the peak of the second cycle observed during the project (Auer 1974).

Later on, in accordance with the world-wide trend away from the simplistic chemical control paradigm, new techniques were tested by investigating the rearing of the granulosis virus (Schmid 1973, 1974; Benz 1975), the application of *Bacillus thuringiensis* (Martouret and Auer 1977), biological control by enhancement of the parasitoid Eulophids (Herren 1976), and the application of sex pheromones according to the confusion technique (Baltensweiler and Delucchi 1979).

Despite the many attempts, up to the present no technique has brought satisfying results in suppressing the larch bud moth populations. Already after the first decade of the project it was realized that the attempts to control seemed to be more difficult than had been anticipated initially. Thus it had been found that the bud moth populations increased not, as had been hoped, from a few local pockets providing optimal growth conditions, but that growth conditions were sufficient to allow for the reaching of defoliation densities throughout the whole Engadine valley. Also by 1974 it became definitely evident that the formerly so promising granulosis disease was unfeasible as a control method (Schmid 1974). The problem had grown to a surprising complexity.

III. The Objective "Basic Research"

Although it is true that the larch bud moth project was initiated with the objective of control in mind and that it was dominated by this goal for its first half, it would be wrong to overlook the efforts which went into basic research from the very beginning (Fig. 2).

During the first cycle (1949–1958), a major effort was made to analyze the biology and autecology of larch bud moth (Maksymov 1959). The parasite complex was studied without really having an explicit goal of biological control in mind.

Aspects like the phenological coincidence between larval and host tree development (Baltensweiler 1984), weather influences, the behavior of the larch bud moth (Meyer 1969) and its diapause (Bassand 1965) were studied during the second cycle (1959–1967).

During the third cycle (1967–1975) more aspects, like that of a color polymorphism (Baltensweiler 1977) and the role of migration (Baltensweiler and Fischlin 1979; Fischlin 1982, 1983) were studied. These studies on moth migration profited very much from the analysis of the sex pheromone of the larch form, as the Trans-11-tetradecenyl-acetate in 1971. In order to trace immigration from the subalpine outbreak areas, the monitoring network was widened subsequently to cover the entire Swiss plateau. Furthermore, great efforts were made from 1975 to 1980 to evaluate the feasibility of the confusion method at low population densities (Baltensweiler and Delucchi 1979). The study of the complex of parasitoids was completed (Delucchi 1982), and some first simulation studies were undertaken (Van den Bos and Rabbinge 1976). Detailed investigations were also conducted to shed light on the food quality aspect by Benz (1974). Surprisingly enough, it is worth noting that forestry aspects were not seriously studied before this third cycle (Baltensweiler and Rubli 1984). We will return to this later. A chronological overview of many of these scientific activities is depicted in Fig. 2.

It is quite obvious that a wealth of data was collected in the course of all these research activities. However, despite the large data base, no conclusive theories, for instance on population regulation, resulted from all these efforts. An analogous situation had developed in the spruce budworm research, too; however, we believe for different reasons (Holling 1978; Royama 1981). In order to understand this argument we propose a simple, generally useful scheme to classify some of the research management decisions typically made in the course of the evolution of such projects (Fig. 3).

It is based on the following reasoning: in order to resolve a particular scientific problem, both empirical as well as theoretical knowledge is required. These two sources of information sum up to a particular "amount of information", which is usually determined by some uncontrolled properties of the real system to be studied. At a given point in time this amount of information can be considered to be constant (Fig. 3A).

In the situation where the needed amount of information is less than that provided by established knowledge, e.g., many civil engineering tasks belong to this class, the problem can be readily resolved (Fig. 3B). This situation may be rarely applicable to a biological problem.

Figure 3C exhibits a considerable discrepancy between total currently available information, empirical as well as theoretical, vis-a-vis the amount needed in order to resolve the problem (Case C). It might be argued that we miss only a yet unknown theorem or some new theoretical method to bridge the remaining information gap. If this were correct, it would follow that the only ingredient needed to resolve our problem would be to find the talented scientist, capable of having the brilliant flash of thought, the idea which fills the gap. Beside limits to his imagination there could exist no constraints which were capable of threatening the success of the theoretical investigation. As a result would follow: by simple theoretical reasoning there is always a possibility to extrapolate our knowledge beyond the current limits to the situation we strive for, the one depicted in Fig. 3E.

An analogous situation arises if there is plenty of empirical data, but only little theoretical knowledge at hand (Case D). Similar to case C it might be argued that there are just some relevant experimental data missing, which may be easily gathered by conducting some morefield observations or some clever experiments, in order to bridge the remaining information gap. If this were correct, it would follow that the only thing needed is to enlarge the empirical data base. Beside limits of time, opportunities to visit the field, and human as well as financial resources, there could exist no constraints which were capable of threatening the success of such a data collection. Similarly to the previous case would follow: by simply collecting more empirical data, there is al-

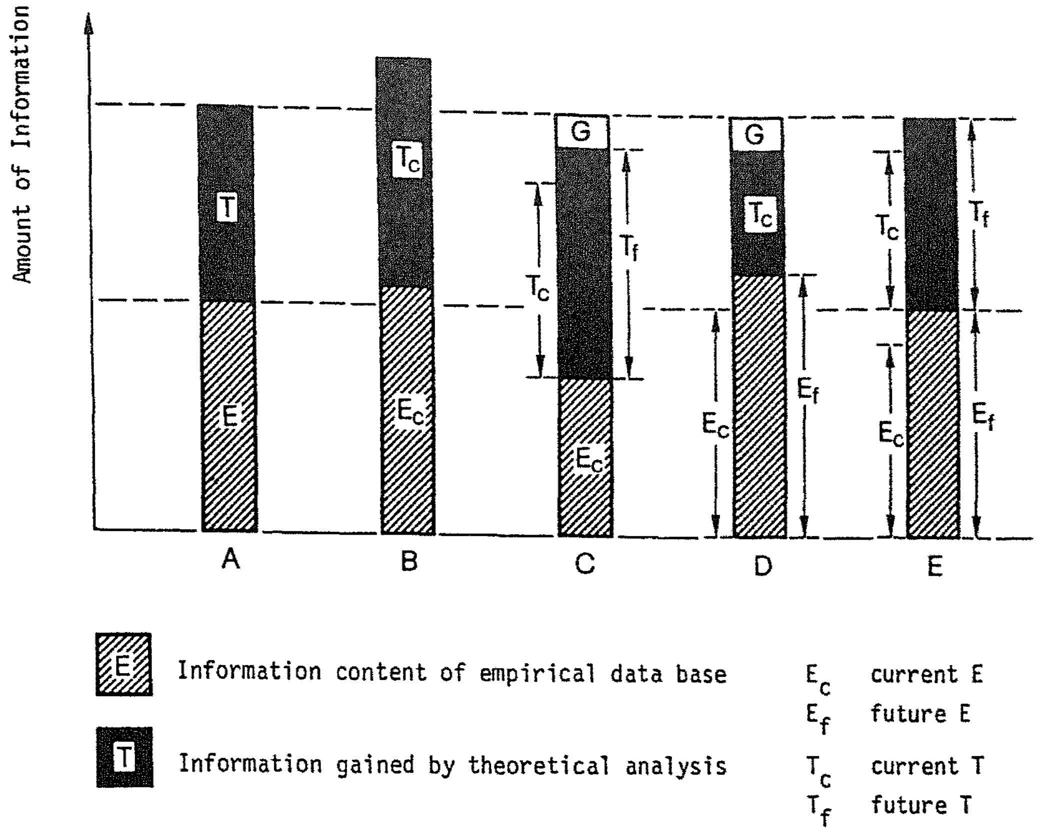

Fig. 3. Mental scheme to illustrate considerations during the decision-making process when research resources have to be allocated. *A* information needed to resolve the pest problem; *B* data base as often encountered in civil engineering problems, surpassing both the empirical as well as the theoretical data requirements; *C* attempt to overcome an information gap by stressing theoretical investigations; however, a gap remains due to the restricted, empirical data base. *D* analogous to case C, but this time the limited theoretical knowledge constrains the success. *E* well-balanced efforts enlarging both the empirical and the theoretical foundations of the project in order to resolve the research problem in an optimal way; the resulting information matches optimally the needs as defined by the real system which is studied (see also *A*)

ways a possibility of extrapolating our knowledge beyond the current limits to the situation we strive for, the one depicted in Fig. 3E.

However, we believe that there are limits which may not be overcome in either of the latter cases. For case C we think that intrinsic constraints, mainly determined by the information content extractable from the set of empirical data acquired from the real system, will so limit all theoretical reasoning beyond a certain boundary that no brilliance could ever bridge the remaining, irreducible information gap (Fig. 3C see G). Any theoretical study working beyond these limits would be purely speculative and of no practical value in terms of the solution of the problem at hand. Similarly, we believe that irrespective of the quantity and quality of the empirical information gathered, its interpretation is limited by the relevant theoretical framework.

Therefore the cases C and D are analogous. Both lack information in order to match the information requirements posed by the problem. However, they differ in as much as case C is short of sound empirical data, case D is short of theory. Consequently the remedy to bridge the information gap is substantially different and may only be confounded at high costs. For instance much effort and many financial resources went into theoretical studies of the spruce budworm system; they have not lived up to their original expectations (Clark 1979). Early in the 1970's the situation was assessed to be similar to case D, although it was rather that of case C (Royama 1984). Could these resources have been spent differently? Only lately has the Canadian Forestry Service begun to emphasize again thorough and serious field studies, recognizing the situation as being that of case C, hopefully leading to a more optimally balanced study.

What seems to be crucial at any stage of a research project is to find means to identify properly the situation in which the study currently is. Theoretical as well as empirical investigations have to be well balanced in order to make progress, i.e., to reach the goal by resolving the problem (case E). Unfortunately, much too often, the correct identification of the situation can be made only later with hind-sight.

At the early 1970's it was felt that the larch bud moth project was in a situation similar to case D. By making big efforts to introduce systems analysis to the project, attempts were made to balance the available empirical information against theoretical knowledge. However, it should also be mentioned that earlier modeling studies have also been made. They were either a Fourier analysis (Auer 1968) or a key-factor analysis (Auer 1971), both approaches we now know are of limited value. But fortunately, as early as 1970, first contributions by simulation studies were made (van den Bos and Rabbinge 1976). The situation was perceived to be that of case D, and consequently efforts went into successful, theoretical studies which finally helped to rank the competing hypotheses on the population regulation (Fischlin 1982).

IV. Balance or Shift in Objectives?

Initially, control was the main objective of the larch bud moth project, toward the end basic research dominated the study. Why this shift? Was it necessary in order to develop a control program, or were just the selfish interests of university scientists responsible for it? One could also argue that this shift simply reflects the need for a good balance between applied and basic research, which mutually depend on each other. The change would then be nothing else than the pendulum striking back, oscillating around the golden mean. Another argument is that the shift reflects a general trend in the scientific community.

The latter is partially true, since the need for a thorough understanding of pest systems in order to be able to develop management programs is the result of many scientific efforts within the last two decades. Too many conventional pest management programs have failed, and it was necessary to search for alternatives, whereby an ecologically sound understanding of the systems to be managed has been shown to be required and quantitative methods have been regarded as being indispensable.

It must be admitted that the diverse short-term interests between control and basic research have led during the course of the bud moth project to sometimes even dramatic tensions. On several occasions it was heavily disputed whether the larval census should be reduced or even dropped completely in order to allow for other investigations such as, e.g., life table-oriented research. Obviously priorities had to be attached to the various subprojects which interested the individual scientists most. The arguments narrowed to a confrontation of locally intensified field research versus extensive sampling throughout the European Alps. Interestingly enough, this issue was never decided decisively. In retrospect, we are tempted to say, fortunately not! The results of the two approaches have stimulated each other in continuous interactions. Many seemingly unrelated details stemming from one or the other approach can be understood at a higher level of organization. A fascinating example of this is the reduction of the amplitude of the bud moth cycle the lower the altitude of the study site. The underlying causes for the populations becoming extinct temporarily on the Swiss Plateau, however, still await evaluation.

Similarly, it is also true that, thanks to the continuity in the larval census over more than 12 population cycles a rich compatible data base has been collected. It has allowed results to be related to each other which have been obtained in completely separate locations or times. Conversely, it appears in hind-sight that the many resources allocated to the larval census work could have been optimized in such a way that no other research work would have had to be delayed or substantially hampered.

All in all, it appears that the tension between the counterparts control and basic research has been fruitful. The combination of these two objectives in the case of the larch bud moth project has provided the necessary finances, a good motivation up to an actual need for a rigorous understanding of the real system, which resulted in one of the most exciting long-term studied ecological systems. Looking back we are convinced that such long-term studies are necessary. Observing a system as complex as an ecological system for only a short time is quite likely to be very misleading. The reader may be reminded of the rather euphoristic situation at the end of the first cycle, when it was generally believed that the virus disease could be applied for the control of the bud moth outbreaks. Only the course of the following second cycle, when the granulosis disease appeared in an enzootic manner only, disproved this misconception immediately.

Finally it should not be forgotten that ecological research is expensive. Not all species to be studied can please us in this respect to the extent that the winter moth does, whose flightlessness allowed Varley and Gradwell (1960) to constrain their studies to a small location, like that of the famous five oak trees in the University forest Wytham Wood near Oxford. Since the success of a pest program depends so strongly on the correct understanding of the natural population regulation, ecology can hope for some of the most valuable contributions made from the side of control oriented research on pest dynamics. These studies most probably will be financed by those most interested in the ecological results, not by academic institutions having difficulties to guarantee the necessary long-term interest in the subject.

V. Lessons We Can Learn

We made attempts to summarize some of the lessons we learned which appeared to us to be of the greatest interest to other ecologists:

1. It is wise to verify critically the implicit assumptions on which the objectives of the project are based; too often the prevailing spirit of the epoch influences the ap-

proach to the pest problem to a degree which leads to suboptimal results. Too often, simple but basic questions are hardly ever asked, only because of prevailing paradigms.

For instance, an important, implicit assumption made at the beginning of the larch bud moth project proved to be wrong: although the larch bud moth causes conspicuous defoliation, this does not necessarily imply that it is also a pest. As the more recent studies have shown (Baltensweiler and Rubli 1984), the damage caused is generally negligible, since tree mortality occurs only occasionally and overall increment loss amounts to just 10%. In contrast, the consumption of 50–100% of the larch needle biomass considerably accelerates nutrient cycling. This aspect is proposed for further investigations as to possibly positive impacts on the productivity of the ecosystem.

The other belief that larch bud moth is controllable has also proved to be wrong. Results from simulation studies (Fischlin 1982) in accordance with results from field experiments (Auer 1974) indicate that the larch bud moth population is extremely resilient. It appears to be quite unlikely that any of the envisaged control strategies would have led to either permanent or substantial control of the larch bud moth population.

Thus despite the obvious nature of many of the required steps in pest problem resolving as depicted in Fig. 4, the sequence is too often not obeyed.

2. Demecological problems should be resolved before we attempt to tackle synecological ones. Many pest problems are demecological problems, and resolving them will provide some of the most valuable contributions to ecology.

We consider the understanding of the demecology of key organisms in an ecosystem a prerequisite for a successful, long-term management of a pest system. Depending on the mechanisms of natural regulation, controllers may behave in completely the opposite way than has been planned during their design. Hence, success or failure of a pest management program is bound to the correct understanding of the dominating natural regulation processes. As systems engineering taught us, even in cases of the simplest technical systems it is quite unlikely that by a mere accident a system synthesis (Design of a controller) based on an incorrect systems analysis (Development of model of the unregulated system) yields a correct controller, let alone in the cases of the more complex ecosystems. Only if the preceding step of systems analysis (Understanding of natural regulation of pest population) has resulted in an at least qualitatively correct model system, will the subsequent controller design step (Design of pest management program) have a chance to succeed, i.e., to result in the design of a working controller (pest management scheme) (see also Fig. 4).

The experience with larch bud moth, indicating that it plays a key role in the whole ecosystem and how difficult it was to tackle just the demecological problems, leads us to the following statement: demecology comes first, synecology second. Several case studies (larch bud moth, spruce budworm, pine looper, and pine processionary) clearly show how much expensive data collection as well as theoretical analysis is needed in order to develop a thorough understanding of the functioning of the studied systems.

In general, it appears to be a useful principle to stratify research efforts with regard to a hierarchical, functional order within the ecosystem wherever and whenever possible. Only thanks to its relative simplicity has it been possible to gain as much understanding of the larch bud moth system as we have today. It is relatively simple because of its small number of species (6 host species, larch bud moth itself, 3 egg, 55 lar-

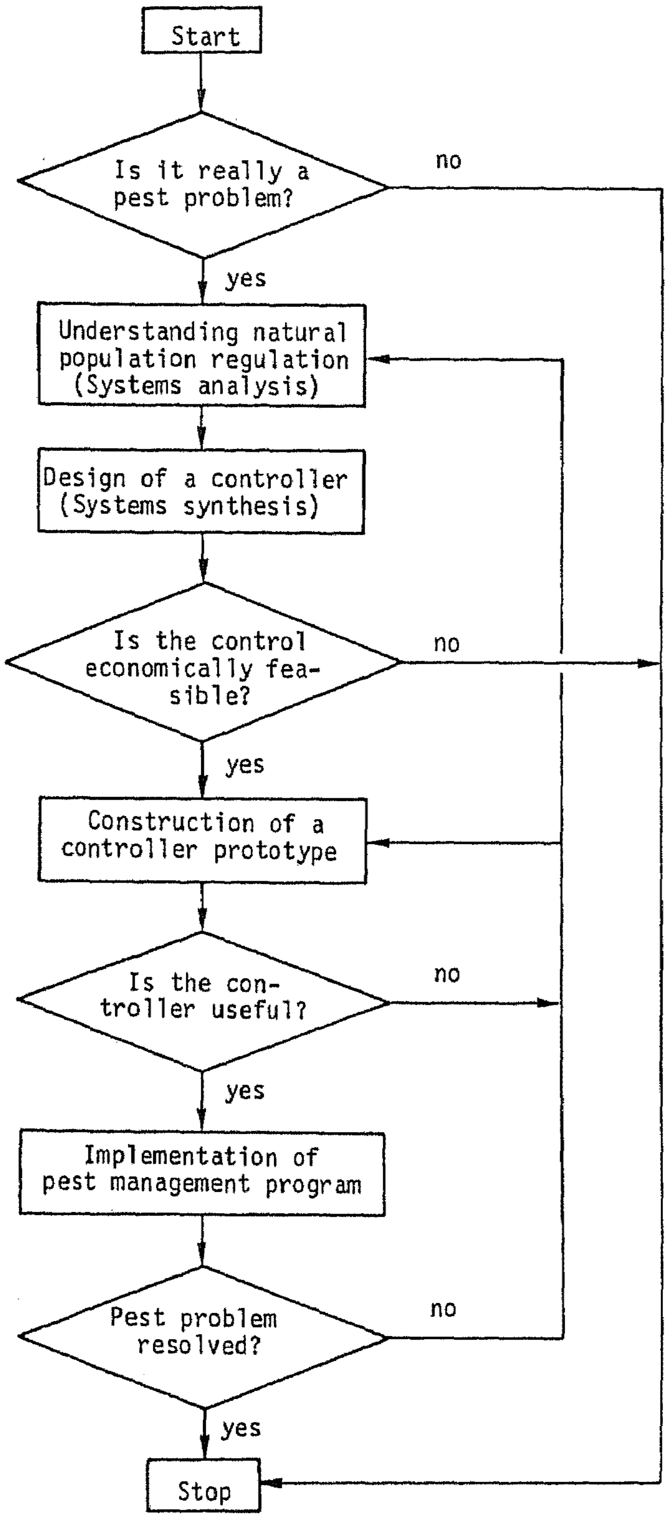

Fig. 4. Flow chart for the resolving of pest problems. Although almost trivial, experience has shown to what surprisingly large extent it is ignored. Some of the simple but fundamental questions are never asked, let alone answered

val, 2 pupal life stage attacking predators or parasitoids, 15 herbivorous competitors), its cyclic dynamics, i.e., the periodic solution, its great amplitude, which resulted in relatively low requirements in terms of data precision, its relatively short periodic length, compared for instance to that of 35 years of the spruce budworm, and the fact that larch bud moth is a key species dominating the rest of the system. This dominance over all other arthropods relies on the depletion of the larch needle biomass by the fast-developing bud moth larvae. Despite all these advantages, it has been necessary to simplify procedures whenever and wherever possible in order to minimize the efforts of research.

3. It is crucial to balance empirical and theoretical efforts. The larch bud moth study has recently gained thanks to a more balanced project in this respect. The objective of control made it necessary to invest in long-term field studies on which it has been possible to base extensive theoretical investigation. For the first time it has been possible to identify conclusively a major factor, the larch-larch bud moth relationship, regulating the larch bud moth population (Fischlin 1982). From this positive experience we conclude that quantitative data as well as analytical methods are crucial in dealing with the complexity of ecological research.

4. Research efforts have to be matched with the temporal and spatial scales of the real system. Unmatched scales lead only to unsatisfying results (Klomp 1973). Hereby the design of the larval census may serve as an illustration. Initially samples were collected within the Engadine valley only. However, after the first cycle (1949–1958) it became evident that not only the sampling area had to be expanded but that the sampling effort per unit area could be reduced by a factor 3 without loss of precision. Thus resources could be reallocated to an enlarged sampling schema encompassing the entire Alps by sampling in representative valleys along the alpine arch (Fig. 1). This approach has proven very successful. Some of the most valuable data revealing important aspects of the larch bud moth system, such as the population peak below defoliation threshold in the Vallee Aurina (Fig. 1, 1972–1975) or the asynchrony in population trend between 1972–1979, have been detected only thanks to this strategy.

5. Despite the need to maintain compatibility of data as long as possible, it is necessary to adopt an adaptive strategy. Several successful changes have been made during the larch bud moth project. One of them has just been mentioned, the expansion of the larval census over the area of the whole European Alps. Another important adaptation in research endeavors which led to a change in interpretation was the introduction of the large-scale monitoring program of the bud moth flight by means of pheromones. The similarity in population increase in the various valleys along the alpine arch from 1958 till 1964 was considered at the end of the second cycle to represent pure autochthonous population growth. However, the results of the monitoring program, together with the mapping of the defoliation pattern throughout the Alps, revealed the importance of long-range dispersal of moths. However, actual observation could not be done before the invention of the pheromone traps. Only this new method allowed for an actual testing of the Herdtheorie hypothesis by monitoring immigration distinct from emigration.

6. Take care of human aspects in a research group in order to ensure the collaboration of coworkers over a long-enough period by actively supporting cooperation and maintaining motivation. This aspect is too often overlooked and neglected. Without going into painful details it may be allowed to state the following: in particular in long-term projects relationships between participants tend to lead to serious problems. Being more aware of these dangers could have helped in many situations. Caring for human relationships wherever and whenever possible can substantially improve the situation and helps to ensure the success of the whole project. This is mainly the responsibility of project leaders and they should be more often selected according to these needs. A caring leader can contribute substantially to the improvement of personal re-

lationships by observing a few rules of mutual respect and considering personal interests and needs of the team members.

It is also wrong to assume that good human relationships among project participants develop themselves naturally without any particular efforts. The contrary is the case: the more the project institutions provide active support of good interpersonal relationships, the more likely is the working ambiance to become fruitful. In particular, uncertainties in the pursuit of research due to the funding system may trouble an already hardly institutionally supported teamwork to such a degree that it almost breaks down. The ups and downs during the larch bud moth project have demonstrated this on numerous occasions.

VI. Conclusions

The following list summarizes the main points we would like to stress:

- Ecological research could profit from being more aware of the fact that implicit assumptions tend to influence our decisions to an undesirable degree. Hampering of progress could be reduced by critical reflection of the prevailing spirit of the epoch.
- Demecology of key organisms in an ecosystem, in particular in the case of pest populations, can contribute worthwhile results to ecology. Demecological understanding of a pest is also a necessity for a successful, long-term management of a pest system. Demecology by itself is already difficult enough, and it is required for the study of real synecological systems. Let's do the simple first, the too complex later.
- It is crucial to balance empirical and theoretical efforts. We need not only modern field research, ecology also needs sound theoretical techniques. Quantitative methods are crucial to the success of ecological research in both areas, in field research as well as in systems analysis.
- Research efforts have to be matched with the temporal and spatial scales of the real system. If the scales do not match, resources are going to be wasted; illusionary savings turn out to have devastating effects in the end. This also implies that it is no good strategy to concentrate all efforts on one single location or problem. Marginal areas or problems deserve some attention too. They help to corroborate the main issues.
- Despite the need to maintain comparability of data as long as possible it is necessary to adopt an adaptive strategy. Modern techniques can become so beneficial that one cannot afford not to use them, even if some other efforts have to be sacrificed during the adaptation phase.
- Take care of the human aspects in a research group in order to ensure the collaboration of coworkers over a long-enough period by actively supporting cooperation and maintaining motivation.

Obvious and trivial as many of these points may appear, experience has shown us how often we fail to remember them. We hope that future research projects will be even more exciting than the one we were lucky to have been part of.

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