INTEGRATING HOST, NATURAL ENEMY, AND OTHER PROCESSES IN POPULATION MODELS OF THE PINE SAWFLY

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INTRODUCTION

Explanation of population dynamics is one of the main problems in population ecology. There are two main approaches to the explanation: the factor approach and the dynamic approach. According to the first, an explanation is obtained when the effect of various environmental factors on population density is revealed. Such analysis is performed using well developed regression methods (Poole 1978). The resulting regression equations can be used for prediction of population density and their coefficients indicate the role of each factor in population change. This method of explanation considers the population as a black box with inputs and outputs. Population predictions obtained by regression are relevant only for stationary systems and only if mechanisms of population dynamics do not change.

The dynamic approach is oriented to the analysis of mechanisms of population change. It can predict the consequences of deliberate change of these mechanisms and, thus, it is more useful for population management than the factor approach. The dynamic approach deals with a system consisting of a population and its environment, a life system (Clark 1964). When applying the dynamic approach one must distinguish between factors and processes. A factor is a characteristic of the life system state. Clark et al. (1967) used the term "codeterminant" instead of "factor." But I prefer the term "factor" because its has became traditional in ecology. A process is a flow of similar ecological events that are taking place in a life system. Reproduction, mortality, growth, development, and migration are examples of ecological processes. There exist different mortality processes in each population. These processes correspond to different developmental stages of dying organisms and to different causes of mortality. For example, spontaneous larval and pupal mortality of a certain insect are different processes. Also, population decreases caused by predation and parasitism are the result of two different processes.

Life tables are widely used for the analysis of mortality in animal populations (Harcourt 1969, Varley et al. 1973). In these tables, mortality processes are termed as "mortality factors." This term is quite ambiguous because it includes both death processes and the factors affecting the rate of this process (Sharov 1985). But factors and processes cannot be identified for two reasons. First, there is no one-to-one correspondences between them. For example, insect mortality caused by predation depends not only on predator density but also on prey density, refuge capacity, temperature, and other factors as well. Temperature is a factor affecting the rates of many other processes: growth, reproduction, migration, and so on. Second, factors which influence the process rates may interact so that mortality levels cannot be attributed to individual factors. Thus, we reject the term "mortality factor."

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A life system can be described formally by a simulation model which uses the information about factor influence on process rates and factor change in the course of ecological processes. Simulation models are considered to be the basis for scientific explanation of population dynamics (Clark et al. 1967, Berryman 1981). But the behavior of a simulation model is often difficult to explain like the behavior of a real population.

Therefore, in practice the explanation of population dynamics is usually based not on simulation models but the statistical analysis of life tables. Using k-factor analysis one can reveal key mortality factors (Varley and Gradwell 1960, Podoler and Rogers 1975). Regression methods allow us to distinguish density-dependent factors which are believed to play a regulative role in population dynamics (Morris 1959, Varley et al. 1973). These methods have two main drawbacks. First, they use the term "mortality factor" which, as has been shown, leads to wrong interpretation. For example, temperature and humidity are usually not given in life tables and, therefore, they cannot be key factors despite their strong effect on population. Second, traditional methods of life table analysis do not provide us with sufficient information about life system structure. For example, the regulative role of ecological process in population dynamics is evaluated on the base of its density dependence, while ignoring its interaction with other processes. The possibility that density regulation is performed by process interaction is not taken into account. Thus it is not surprising that in many relatively stable populations, density dependent factor have not been revealed (Dempster 1983). The fact that some mortality factor is a key or density dependent one tells nothing about what will happen after its deliberate change.

Thus the dynamic approach, in spite of its advantages as compared with the factorial one, does not provide methods for evaluating factors and processes in population dynamics.

In this work I attempt to evaluate the role of factors and processes depending on their contribution to quantitative characteristics of population dynamics. This method allows us to reveal the role of process interactions.

Two approaches (empirical and simulational) can be applied in the analysis of the role of factors and processes in population dynamics. Using the empirical approach one should change factor values or process trends in the real life system and then consider the response of quantitative characteristics of population dynamics. In the simulational approach such experiments are simulated by a computer mathematical model. The latter approach is less expensive. Moreover, it is possible to simulate such changes of the life system that are not possible or not desirable in practice. However, the simulational approach is indirect, its precision depends on the validity of a simulation model. In this work we use the simulation approach.

The proposed method of a population analysis is applied to the common pine sawfly, *Diprion pini* L., a dangerous pest of pine plantations. It overwinters as an eonymph (prepupa) in cocoons in the litter or the upper soil layers. Eonymphs having visible rudimentary pupal eyes are called pronymphs. There are 2 to 34 percent pronymphs among hibernating sawflies (Avramenko 1970). Overwintered sawflies have two flight periods: late April to early May and late July to early August (Sharov and Safonkin 1982). Sawflies hibernated as pronymphs emerge in both periods (about 60 percent in the first period and about 40 percent in the second period), while sawflies hibernated as eonymphs emerge only in the second period (about 35 percent). The remaining eonymphs maintain their diapause during the next whole year or longer.

Female sawflies oviposit into a split made along the edge of the pine needle. Eggs laid by one female usually occupy a needle cluster (Dusaussoy and Geri 1966). Larvae hatched from an egg cluster form a colony. In July eonymphs make cocoons in pine crowns and from September to October in the litter and soil. Emergence of sawflies from summer cocoons nearly coincides in time with the second flight period of the overwintered generation. Thus in August there are larvae of the first and second generations. To avoid confusion, we use the term "wave of development" instead of "generation."

Sawflies developing in May to June belong to the first wave of development, and the sawflies developing from August to October belong to the second wave. In the Rostov region the common pine sawfly has outbreaks of mass reproduction within 3 to 6 years (Kharlashina 1984). Outbreaks usually follow those years with hot, dry summers.

METHODS

Simulation Modelling

The model proposed in this paper is based on our previously published data on the life cycles and survival of the common pine sawfly and its parasitoids (Sharov 1982, 1983, 1986b, 1987, 1988, Sharov and Safonkin 1982). Principles of modelling were adopted from the model of winter moth (Varley et al. 1973). The mean temperature in May to September is an input variable. Parameters of the model were partially taken from experimental data and partially found by the maximum likelihood procedure. The model validity was evaluated on a qualitative level by its ability to predict pest outbreaks. Information about sawfly outbreaks in the Rostov region (Kharlashina 1984) and temperature from 1956 to 1983 were used as a test.

Quantitative Characteristics of Sawfly Population Dynamics

Sawfly population dynamics as a whole was characterized by the mean level and standard deviation of a log-transformed (natural logs) late-instar larvae density in the second wave of development. Pest density in the first wave of development has not been considered because it was smaller than the density in the second wave. Log-transformation is necessary because of a log-normal distribution of population density. Mentioned characteristics were estimated using the simulation of a population dynamics. The real mean temperature from May to September during the 28-year-period from 1956 to 1983 was taken as an input variable.

The population dynamics pattern of the common pine sawfly is complex because of repeated outbreaks of the pest. We analyzed each period of an outbreak separately. Isaev and Khlebopros (1974) distinguished five periods in the phase portrait of an outbreak cycle of forest insect pests: period of stability, increase, maximum, collapse, and depression. The common pine sawfly has a very short period of maximum, and thus we considered only the other four periods.

The period of stability is characterized by coefficients of m- and v-stability (in previous publications (Sharov 1986a) they were called coefficients of buffering and homeostasis, respectively), describing different aspects of population density regulation. They were estimated using the simulation model with the mean temperature from May to September being constant and equal to 18.6°C, which is the average temperature in non-drought years. Let $\bar{x}$ be the mean log-transformed late-instar larvae density in the second wave of development and $\bar{z}$--the mean log-transformed larvae survival in the same wave of development before the measurement of population density. In both cases, averaging was performed across a number of years. If the value $\bar{z}$ becomes lower due to additional mortality, the value $\bar{x}$ decreases. The coefficient of m-stability is defined as

$$MS = (d\bar{x}/d\bar{z})^{-1} \qquad (1)$$

It indicates how difficult it is to suppress the population density. The greater its value, the more additional mortality is needed for population suppression.

Another important aspect of population regulation is the v-stability, which prevents the increase of the amplitude of density fluctuations. It is described by the coefficient of v-stability:

$$VS = (ds^2_x/ds^2_z)^{-1} \quad (2)$$

where s^2_x and s^2_z are variances of the log-transformed sawfly larvae density, x, and the log-transformed survival, z . When s^2_z is infinitesimal and the system is in a stable state, then:

$$VS = s^2_z/s^2_x \quad (3)$$

The rate of an increase of sawfly density at the beginning of the outbreak is characterized by the index $\ln(N_o/N_s)$, where N_s and N_o are late-instar larval densities in the second wave of development per 1 m^2 in the period of stability and during the outbreak, correspondingly. The rate of density decrease at the period of population collapse is characterized by the index $\ln(N_o/N_c)$, where N_c is the larval density after an outbreak.

Rates of population density fluctuation were estimated using the simulation model. We assumed that the mean temperature from May to September was 18.6°C and it did not change from year to year (the period of stability); then it increased up to 21.1°C for only one year (the simulation of a drought) and after that it was stable at the initial level. The density N_s was measured in the year before the drought, N_o in the next year after drought and N_c in the second year after drought.

In a period of depression of a sawfly population, drought generally does not cause repeated outbreak; if it does, outbreak is less intensive. This property is characterized by the coefficient of "refractoriness"

$$R = \sum_{i=2}^{4} \ln(N_o/N_i) \quad (4)$$

where N_o is the larval density in the next year after the first drought and N_i is the same density in the next year after the second drought which happens i years after the first drought. For i more than 4 the refractory effect is lost. The coefficient R was estimated using the simulation model. The drought was simulated by rising the mean May to September temperature from 18.6°C to 21.1°C.

Confidence limits for all quantitative characteristics estimated using the simulation model were found by the following method: a set of versions of the initial model was obtained by independent stochastic variation of the 32 most important parameters of the model. Standard deviations of these parameters were equaled to their standard errors. For selection of adequate model versions the population dynamics was simulated assuming the droughts occurred periodically every 4 years. Then the estimated parasitization rate of sawfly eggs and eonymphs was compared with our empirical data obtained from 1977 to 1979. As a result 10 model versions, including the initial one, were selected for simulation of the dynamics of the sawfly's parasitization rate.

Each quantitative characteristic was estimated using all 10 model versions and then the mean value, standard deviation "s" (in this case it is taken as standard error) and half of the confidence interval "ts" ("t" is the student's criterion for P = 0.05) were found for each characteristic. In the following text half of the confidence interval is given after the signs "$\pm$".

Analysis of Process and Factor Contributions to the Quantitative Characteristics of Population Dynamics

The contribution of individual processes and their interactions to the quantitative characteristic y_i of population dynamics was evaluated using the equation:

$$y_i = ß_o + ß_1 v_1 + ß_2 v_2 + ß_{12} v_1 v_2 + ß_3 v_3 + \ldots , \quad (5)$$

where v_j is an integer variable indicating the dependence of the j-th ecological process on factors, and β_j is the coefficient representing the contribution of the j-th ecological process or process interaction (if the coefficient has more than one index) to the value y_i. The variable v_j has only two meanings: $v_j = 1$ if the rate of j-th process naturally depends on factors and $v_j = 0$ if this rate is fixed at the equilibrium level peculiar to the period of stability. Process rates were fixed only in that period of an outbreak cycle, in which we wanted to examine the role of these processes. The value y_i was estimated using the model with different combinations of processes having the fixed rate. Then coefficients β_j were obtained by the multi-factor regression technique (Maximov 1980).

The "refractoriness" of the sawfly population is associated with a special postoutbreak state of the life system. We analyzed what factors peculiar for this state gave the greatest contribution to the coefficient of refractoriness R. In the course of simulation the value of different factors was changed in winter following the outbreak of the sawfly population. Values peculiar to the period of stability were given to these factors. The refractory role of factors was evaluated by the response of the coefficient of refractoriness to factor change.

The role of parasitoids in sawfly population dynamics was examined by simulation of their exclusion from the life system. The change of the mean value and standard deviation of the log-transformed sawfly larvae density was analyzed.

RESULTS

Simulation Model

The proposed model simulates the multiple year dynamics of the common pine sawfly population. It has been described in detail (Sharov 1986b). A year is the basic time unit. There are four blocks describing the sawfly population, its host tree *Pinus sylvestris* L., and two groups of parasitoids developing in sawfly eggs and eonymphs. The model describes the change of population density of the sawfly and its parasitoids in their life-cycle and the dynamics of the amount of needles on the pine trees. Sawfly mortality caused by parasitoids was described by the modified model of Rogers (1972). In this model I assumed that the area of discovery (a) depends on the parasitoid density (P) in accordance with the model of Hassell and Varley (1969): $a = Q\,P^{-m}$, where Q and m were parameters. Sawfly-host plant interaction was described by the model of Semevski (1971). According to this model the pest space distribution is log-normal. The number of surviving larvae on each tree was assumed to be equal to the number of food units on the tree. If food is in plenty there is no mortality due to food shortage. The initial distribution of needles on trees was assumed to be uniform.

Sawfly fecundity is constant. Young larval survival increases with the size of a colony, the group effect (Sharov 1988). The size of a colony, in turn, depends on egg mortality due to parasitism. Last-instar larval and eonymph mortality was assumed to depend on mortality caused by food shortage and on mean May to September temperature in the previous and current years. The effect of temperature on larval mortality in the model is an explication of the effect of host-plant quality, dependent on weather. It is known that pine tree weakening caused by water deficiency is usually associated with high temperature and favors sawfly development (Schwenke 1964, Kharlashina 1984).

Reactivation of diapausing sawfly eonymphs depends on temperature in a dose-effect manner. The temperature increases the reactivation rate in the second flight period of the current year and the first flight period in the next year (Sharov and Safonkin 1982). The reactivation rate in the first flight period is considerably reduced after an outbreak. In the model it depends on sawfly larvae density in the previous year.

The model appeared to be adequate at the qualitative level. It "predicted" five out of six sawfly outbreaks in the Rostov region from 1956 to 1983 (Sharov 1986b). It is important that this model not only predicts pest outbreaks (they can be predicted by a simple regression model as well), but that it also describes mechanisms of a population alteration. It shows that its basic assumptions are sufficient for simulation of the high rate of sawfly density increase at the beginning of an outbreak.

Role of Processes and Factors in Population Dynamics

The role of six ecological processes in the dynamics of the common pine sawfly population was examined: 1) egg mortality caused by parasitoids, 2) eonymphs mortality caused by parasitoids, 3) larval mortality caused by food shortage, 4) sawfly reactivation in the first flight period, 5) sawfly reactivation in the second flight period, and 6) larval mortality caused by diseases.

In the period of stability the coefficients of m- and v-stability of the sawfly population appeared to be MS = 0.70 $\pm$ 0.12, VS = 0.30 $\pm$ 0.19. Population m- and v-stability are linked mainly with the interaction of the sawfly with the parasitoids (Table 1). Parasitoids of eggs and eonymphs give an approximately equal contribution to the coefficient of m-stability in the sawfly life system ($ß_1$ = 0.51, $ß_2$ = 0.41). Eonymph parasitoids give the greater contribution to the coefficient of v-stability of the host $ß_2$ = 0.68) than egg parasitoids ($ß_1$ = 0.20). Interaction of mortality processes associated with two groups of parasitoids destabilizes the sawfly population dynamics ($ß_{12}$ = -0.59).

The model predicts the high rate of sawfly density increase after drought. In a dry year the late-instar larval density in the second wave of development becomes 101 $\pm$ 36 m^{-2} as compared with 34 $\pm$ 11 m^{-2} in the period of stability. In the next year it increases to 995 $\pm$ 368 m^{-2}. The reduction in larval mortality caused by diseases after drought when host plants are weakened is most important in population density increase ($ß_6$ = 0.55) (Table 1). Mass reactivation of sawflies in the first flight period is also important ($ß_4$ = 0.35).

The sum of regression coefficients (5) for process interactions (2.32) is much greater than that for individual processes (1.05). Thus, process interactions but not individual ones play an important role in the increase of sawfly density at the beginning of an outbreak. The most important are interactions of temperature-dependent processes (No. 4-6) with that of egg mortality caused by parasitoids ($ß_{16}$ = 0.46, $ß_{15}$ = 0.37, $ß_{14}$ = 0.32).

The period of density increase is naturally followed by the period of collapse. According to the simulation, in the first year after the outbreak, sawfly larval density becomes approximately only one-third as large as in the period of stability. The larval mortality caused by food shortage plays the dominant role in the fall of population density ($ß_3$ = 1.61). The sum of regression coefficients for process interactions (2.02) is greater than that for individual ones (1.92). This indicates the importance of process interactions in the sawfly density increase. The interaction of larval mortality caused by food shortage with that of eggs caused by parasitism is particularly important ($ß_{13}$ = 1.75). If food is in plenty, parasitoids cannot suppress the sawfly population ($ß_1$ = -0.83, $ß_2$ = 0.69). Eonymph parasitoids cannot decrease the host density even in conditions of food shortage (coefficient $ß_{23}$ is non-significant).

In the period of depression, the life system of the common pine sawfly is characterized by a decrease in density of "new" eonymphs diapausing less than 1 year, increased density of "old" eonymphs with diapause period more than 1 year, elevated density of parasitoids, and decreased amount of needle as compared with the period of stability. After the change of 1) "new" eonymph density, 2) "old" eonymph density, 3) amount of needle in trees, 4) density of egg parasitoids, and 5) density of eonymph parasitoids to the value peculiar for the stability period, the coefficient of refractoriness

Table 1. Effect of ecological processes on quantitative characteristics of the common pine sawfly *Diprion pini* L. population dynamics.

ß coefficients of equation (5)*	Quantitative characteristics of population dynamics **			
	y_1 = MS	y_2 = VS	$y_3 = \ln(N_o/N_s)$	$y_4 = \ln(N_o/N_c)$
0	0	0	0	0.62 ± 0.15
1	0.51 ± 0.17	0.20 ± 020	0	-0.83 ± 0.38
2	0.41 ± 0.11	0.68 ± 0.09	0	0.68 ± 0.26
12	-0.22 ± 0.10	-0.59 ± 0.10	0	0.54 ± 0.35
3	-0.01 ± 0.01	-0.02 ± 0.01	0	1.61 ± 0.50
13	0.01 ± 0.01	0.02 ± 0.01	0	1.75 ± 0.52
23	0.01 ± 0.01	0.02 ± 0.01	0	-0.15 ± 0.20
123	-0.01 ± 0.01	-0.02 ± 0.01	0	0.51 ± 0.52
4	0	0	0.35 ± 0.12	0.45 ± 0.15
14	0	0.01 ± 0.01	0.32 ± 0.11	0.12 ± 0.16
24	0	0	0.05 ± 0.03	-0.34 ± 0.15
124	0	0	0.05 ± 0.03	-0.28 ± 0.16
34	0.01 ± 0.01	0.02 ± 0.01	0	-0.36 ± 0.11
134	-0.01 ± 0.01	-0.02 ± 0.01	0	-0.35 ± 0.19
234	-0.01 ± 0.01	-0.02 ± 0.01	0	0.26 ± 0.12
1234	0.01 ± 0.01	0.02 ± 0.01	0	0.33 ± 0.26
5	0	0	0.15 ± 0.09	0
15	0	0	0.37 ± 0.27	0
45	0	0	0.13 ± 0.04	0
145	0	0	0.17 ± 0.12	0
6	0	0	0.55 ± 0.15	0
16	0	0	0.46 ± 0.15	0
46	0	0	0.24 ± 0.07	0
146	0	0	0.13 ± 0.12	0
56	0	0	0.20 ± 0.05	0
156	0	0	0.29 ± 0.16	0
456	0	0	-0.05 ± 0.02	0
1456	0	0	-0.22 ± 0.07	0
Sum of the coefficients	0	0	0.18 ± 0.14	0
Total	0.70 ± 0.12	0.30 ± 0.19	3.37 ± 0.45	4.56 ± 1.08

* Numbers of ecological processes: 1) egg mortality due to parasitoids, 2) eonymph mortality due to parasitoids, 3) larval mortality due to food shortage, 4) sawfly reactivation in the first flight period, 5) sawfly reactivation in the second flight period, and 6) larval mortality due to diseases.

** MS and VS are coefficients of m- and v-stability of the sawfly population in the period of stability; N_s, N_o and N_c are population densities of sawfly larvae per 1 m^2 in the second wave of development in the period of stability, outbreak and collapse, correspondingly.

appeared to be 1) 8.0 $\pm$ 3.4, 2) 8.5 $\pm$ 2.6, 3) 6.8 $\pm$ 4.2, 4) 6.8 $\pm$ 2.0, 5) 1.2 $\pm$ 1.6, correspondingly. In the control where no factor was deliberately changed, the coefficient of refractoriness was equal to 7.5 $\pm$ 3.5. Thus the refractoriness of the sawfly life system in the period of depression is associated with the elevated density of eonymph parasitoids. The other factors including density of egg parasitoids and amount of needles in the trees has no refractory effect.

According to the simulation, the exclusion of each group of parasitoids from the life system of the host leads to an increase of the mean log-transformed sawfly density (Table 2). Egg parasitoids suppress the mean host density to a greater extent than parasitoids of eonymphs. The standard deviation of log-transformed sawfly density decreased significantly after the exclusion of egg parasitoids. This fact indicates the destabilizing role of the parasitoids in population dynamics of their host.

DISCUSSION

Mechanisms of common pine sawfly population dynamics in the Rostov region are similar to those in western Europe (Dusaussoy and Geri 1966, Eichhorn 1977, 1982, Geri and Goussard 1984). Nevertheless there are some differences. The primary one is connected with the mechanisms of reactivation of overwintered sawflies. There are three flight periods of the common pine sawfly in western Europe instead of just two as in the Rostov region. The additional flight period takes place in July and is often the most intensive one.

In France outbreaks of mass reproduction of the sawfly have been recorded at time intervals of 17 to 28 years (Geri and Goussard 1984), less often as compared with the Rostov region where the average time interval between outbreaks is 4 years (Kharlashina 1984). This outbreak pattern is common in all geographical regions. The provoking event is apparently drought that weakens a host plant and thus increases sawfly survival. The reactivation rate of the pest also increases, particularly in the first flight period in the year following drought. As a result, the seasonal cycle of the pest becomes mainly bivoltine instead of monovoltine in the stability period. Consequently, the population growth rate increases. The parasitization rate of the sawfly decreases, which might be interpreted as the escape from parasitoids. In the period of a population decline the parasitization rate increases greatly up to 100 percent (Urban 1962, Eichhorn 1982, Kristek and Petruska 1982). Mortality caused by diseases and proportion of diapausing sawflies increase as well. In some cases lowered fertility has been observed (Urban 1962, Eichhorn 1982, Geri et al. 1990). After the outbreak the rate of parasitism decreases gradually. In the Rostov region we have observed all these effects except the lowered sawfly fertility at the end of an outbreak (Sharov 1982, 1986b, 1987).

But enumeration of peculiarities of different outbreak periods does not explain a population alteration. It is necessary to prove that a given set of phenomena considered is enough for adequate outbreak simulation, and to evaluate quantitatively the role of each ecological process in a population dynamics. It has not been done before.

Known mechanisms of common pine sawfly population dynamics do not allow us to explain its fast population growth at the beginning of an outbreak. According to Kharlashina (1984), larval mortality caused by disease, host tree resistance, and other factors comprises not more than 30 percent of the total mortality. If the mortality level from drought-induced host plant weakening were three times lower, the sawfly density would be 1.29 times higher in 1 year. Taking into account transformation of the seasonal cycle from monovoltine to bivoltine, the pest density might be 1.29^2 = 1.65 times as high. Such a density alteration is too small to escape parasitoids. When considering the effect of parasitism, one can explain a two- to threefold increase in sawfly density, but natural population density rises two orders of magnitude during an outbreak.

Table 2. Consequences of parasitoid exclusion from the life system of the common pine sawfly (based on data simulation)

Presence of egg parasitoids	Presence of eonymph parasitoids	Mean log-transformed sawfly larvae density in the second wave of development	Standard deviation of log-transformed sawfly larvae density in the second wave of development
Yes	Yes	3.85 ± 0.20	1.53 ± 0.24
Yes	No	4.62 ± 0.27	1.36 ± 0.34
No	Yes	5.66 ± 0.39	0.46 ± 0.12
No	No	5.94 ± 0.36	0.40 ± 0.05

There are no explanations for the increased rate of parasitism during population collapse. Elevated parasitoid performance can be associated with their increased density. But in this explanation the greater population growth rate of the sawflies compared to that of parasitoids has not been taken into account. Thus the parasitism rate can only grow if some other factors inhibit the growth of the host population.

Analysis of the role of an ecological process in the alteration of a sawfly population helps explain the phenomenon. Previous attempts to explain the pattern of sawfly population dynamics failed because the interaction of ecological processes were taken into account. We have revealed the dominant role of the process interactions in the course of a sawfly outbreak. Simulation modelling is the only correct method for the description of process interactions. Thus an explanation of population dynamics can be obtained only by this method.

Some mechanisms previously not taken into account were included in our model. For example, we found that the rate of eonymph reactivation in the second flight period increased with temperature (Sharov and Safonkin 1982). The model showed this as an important mechanism of the sawfly density increase after drought.

Table 1 indicates escape of the sawfly population from parasitoids at the beginning of an outbreak as an interaction of temperature dependent processes (No. 4-6) with an egg mortality caused by parasitoids. In the collapse period parasitoids do not play any important role, but their interaction with larval mortality caused by food shortage is important. This interaction is interpreted as follows: sawflies increase their density until food exhaustion, and then parasitoids have the time to outnumber their host and to suppress the host population. Unlike eonymph parasitoids, egg parasitoids are more important in host suppression because their interaction with the sawfly occurs in an earlier phase of the life cycle. When the number of host eggs is sufficiently reduced by egg parasitoids, some hosts are available for eonymph parasitoids.

In the depression period, repeated drought does not provoke an extra outbreak because the increased density of eonymph parasitoids controls the population number of their host. Approximately 3 years after an outbreak the parasitism rate of the sawfly eonymph decreases. The next drought, in turn, will cause a new outbreak of the pest. After an outbreak, the density of egg parasitoids decreases faster compared to parasitoids of the eonymphs. This is due to the absence of a prolonged diapause in egg parasitoids. Thus they are not able to support refractoriness of the sawfly life system.

In the period of stability, the sawfly population is regulated by parasitoids. Both groups of parasitoids prevent the mean density alteration of the host, however only the eonymph parasitoids stabilize host density fluctuations. These regulation mechanisms are rather weak and cannot maintain population density at the equilibrium level during drought. Consequently another outbreak will begin.

In general, an outbreak pattern of sawfly population dynamics is determined primarily by egg parasitoids. On the one hand, they are not able to maintain a low host density under unstable weather conditions; on the other hand, they prevent continuation of a high pest density during an outbreak. Eonymph parasitoids maintain the refractoriness of a sawfly life system after an outbreak and play a certain role in the "escape effect" during host density increase.

These conclusions are supported by the simulation experiment with parasitoid exclusion. Sawfly outbreaks do not occur without egg parasitoids, however, the mean sawfly density increases. Thus egg parasitoids suppress and destabilize the host population. Similar parasitoid effects on host insect population dynamics was reported earlier for *Prieria sinica* Moore (Shiotsu and Tsubaki 1986) and for *Epinotia tedella* Gl. (Munster-Swendesen 1985).

Thus the proposed method for explanation of population dynamics pattern allows us to describe quantitatively the role of factors and processes in the common pine sawfly life system. The process interaction was shown to play the dominant role in the course of an outbreak of the pest. This fact is evident through the "entirety" of the life system and shows the necessity of the system's approach to life system analysis.

SUMMARY

The role of ecological factors and processes in the population dynamics of the common pine sawfly, *Diprion pini* L., was examined using a simulation model. Consequences of fixation of density- and temperature-dependent process rates were determined. Results were processed by methods of multi-factor analysis. In the absence of drought the sawfly density is low and fluctuates within the steady state. Density regulation described by coefficients of m- and v-stability is associated with host-parasitoid interactions. Parasitoids developing in eggs and those in eonymphs prevent the change of the mean host density level (m-stability), but only parasitoids of eonymphs stabilize host density fluctuations (v-stability). Sawfly outbreaks are initiated by droughts which weaken the host plant and interrupt eonymph diapause. Both increase and decrease of sawfly density during the outbreak are caused by process interactions rather than individual processes. In the postoutbreak period, repeated drought cannot initiate a new outbreak because of high eonymph-parasitoid density. In general, the outbreak character of sawfly population dynamics is associated with the presence of egg parasitoids that suppress but destabilize the host density. The role of each ecological process is determined not only by its own properties but by the whole life system including the population and its effective environment. The role of processes in population dynamics should be analyzed using simulation models that can describe adequately the interaction of these processes in the life system.

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