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DEVELOPMENTAL ENERGETICS IN NORTHERN LEAF-MINING INSECTS AT VARIOUS TEMPERATURES

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Developmental energetics were studied in the larvae of three sawfly species and the looper *Oporinia autumnata* feeding on birch leaves. The characteristics of energy balance were elucidated at low (9-12°) and high (17-19°) temperatures. It was shown that a high rate of food consumption, sharply increasing with increase in temperature, is a characteristic feature of the northern species of leaf-mining insects. The P/C coefficient of utilization of consumed food for growth is independent of temperature; its dependence upon food quality is discussed.

In studying the adaptations of insects to the conditions of life in the Subarctic, researchers have given considerable attention to adaptations to the leading extreme factor, which is low temperatures. At the same time they have shown interest primarily in the morphological, biological, and behavioral features (Fridolin, 1936; Strel'nikov, 1940; Shtakel' berg, 1944; Sdobnikov, 1957; Gorodkov, 1972; Downes, 1964, 1965) of northern insects while overlooking their energetics. Meanwhile the energetic features of northern insects are of considerable interest, since they assist in a more deep understanding of the adaptation of species to growth and development under conditions of the short and cool northern summer.

We began studying the energetics of development of certain leaf-mining insects common in the North in 1971. A number of features in the energetics were discovered and described: the high P/C coefficient of utilization of consumed food for growth, the high growth rate, and the high rate of food consumption, which were interpreted as adaptive features for northern species (Bogacheva and Dubeshkov, 1975; Bogacheva, 1977, 1980). However, the experiments were conducted conditions of rather high temperatures (15-22°C), while in nature the larvae must frequently develop at lower temperatures. In spite of this, they not only succeed in completing their development in the course of a season but also evidently flourish, maintaining comparatively high numbers from year to year. Which features of the energetics guarantee them successful passage of the larval stage during the period favorable to them? To answer this question it was necessary to study the development of leaf-mining insects at low temperatures.

The investigations were conducted in July-August 1980 in the city of Labytnangi (66°43' N Lat., forest-tundra zone). Three sawfly species from the family Tenthredinidae (all live in groups) and the looper *Oporinia autumnata* Bkh. were chosen for the experiments. They all feed on the foilage of birch *Betula tortuosa*, but the looper is a species with a spring-summer phenology of larval-phase development, while the sawflies are a species with a summer-autumn phenology.

Larvae weighing no less than 2-3 mg were placed singly in glass or polyethylene containers of 30-50 ml volume. A portion of the containers were kept in the laboratory at a temperature of 17-19° and a portion were kept at 9-12°. One or several birch leaves were placed in the container; a small piece of cotton, which was moistened daily, was placed on the bottom of the container to maintain the humidity. Each day at a single time the larvae were weighed, the food replaced, and the leaf areas consumed measured by superimposing the leaves on millimeter paper. Larval molting and changes in larval behavior were also measured. The experiments lasted until the larvae ceased eating.

The larval weight determined for live individuals had also to be expressed in milligrams dry matter. To do this larvae of the penultimate and ultimate instars were individually weighed, anesthetized, killed, dried, and weighed repeatedly. It is known that the percentage content of dry matter (as well as the caloric content) changes with the instars; however, the limited quantity of material compelled reliance on mean data for the last two instars.

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TABLE 1. Growth and Energetics of Larvae of the Sawfly *Croesus* sp. with Respect to Instars at Various Temperatures

T°, C	Instar	Instar duration, days	Weight on day of molting, mg dry matter	Food consumption, mg dry weight		Growth, % of body weight/day	$\frac{P+R}{C} \times 100\%$	$\frac{P}{C} \times 100\%$	$\frac{P}{P+R} \times 100\%$	$\frac{R}{C} \times 100\%$
				during instar	per 1 mg dry body weight/day					
9,1	III	4,3	0,8	7,7	0,96	23,7	—	32,8	—	—
	IV	5,0	2,5	19,3	0,95	25,3	35,0	32,0	91,4	3,0
	V	7,0	8,4	78,2	0,72	18,4	33,1	29,3	88,5	3,8
	VI	—	28,7	—	0,89	10,8	26,7	14,1	52,7	12,6
17,8	III	2,3	1,1	9,2	2,04	53,8	—	26,0	—	—
	IV	2,0	2,8	22,5	3,28	56,5	45,2	28,4	62,8	16,8
	V	3,5	9,1	97,6	2,17	50,3	45,3	26,8	59,1	18,5
	VI	8,5	29,7	286,9	1,62	19,4	43,4	12,9	29,8	30,5

Food consumption was intially determined in units of area and then expressed in wet and dry weight. To obtain data on the wet weight of a unit of leaf-blade area, slices of known area were weighed every four to five days. To determine the content of dry matter in the leaves, 10 samples from each of four leaves were weighed in parallel, then dried and weighed repeatedly. On the basis of the data obtained curves were constructed, from which the mean parameter values for each day were subsequently found. Leaves were taken for measurement and larval feeding from identical birch trees throughout the season.

The dried birch leaves and larvae were used to estimate the caloric content. The caloric content of the excreta of larvae maintained at various temperatures was determined separately.

The larval growth of northern leaf-mining insect species, the characteristics of their energy balance, and the influence on them of temperature conditions were followed in detail in the species — the sawfly *Croesus* sp. — for which the greatest quantity of data was obtained. The other two sawfly species were rare, and it was only possible to conduct experiments in three to five repetitions for each experimental variant. Few data suitable for analysis were also obtained for *O. autumnata*, since a considerable portion of the caterpillars taken for the experiment were infested with parasites. However, when the question is one of the patterns of development of northern insect species at low temperatures and of the general features of their energetics, material will be presented for all species studied.

Changes in Larval Weight during Individual Development (Table 1). The weight changes in *Croesus* larvae were followed after the third instar. *Croesus* sp. is a rather large species; the maximum larval weight averaged about 260 mg. The larval weight roughly tripled during each of the instars three through five, and in the sixth instar it doubled.

Earlier, in a study of Lepidoptera — the loopers *O. autumnata* and *Lygris prunata* L. and the cabbage butterfly *Pieris napi* L. (Bogacheva, 1980) — it was established that the caterpillar weight as a rule stabilizes or falls during molting periods. In sawflies the period of cessation of feeding associated with molting lasts only 5-6 h, in which connection no decline in weight was noted at this time in any of the three species studied, although the weight gains were minimum on molting days. The maximum weight gains (up to 70-80% of the body weight on the preceeding day) were observed on the day following the molt, while the average parameters for the instar were much lower.

The larval weight gains were held at approximately the same level in the third through the fifth instars and fell sharply during the last instar. This was caused both by a decline in the rate of larval feeding and by an increase in larval motor activity, as a result of which only a small portion of the food consumed was used for the creation of new body tissues. This will be examined in more detail below.

In speaking of larval development at different temperatures, it should be noted that during all instars the larval weight at 9° was less than that at 18° (see Table 1). However, these differences declined from the third to the sixth instar, comprising respectively 27.3, 10.7, 7.7, and 3.4%, whereas in the case of a temperature influence they would have been expected to increase. Probably, they were caused not by temperature but by other factors.

The influence of temperature on larval growth and accordingly on the duration of larval development was pronounced. The daily weight gains of larvae in the third through the fifth instars at 9° were approximately 20-25% of the body weight, while at 18° they were 50-55%. The duration of each larval instar also approximately doubled. (There are no data in Table 1 for the sixth instar at 9°, since most of the larvae at this temperature were unable to complete their development before the end of the experiment.)

Food Consumption. The larval food consumption was followed simultaneously with the change in larval weight. The total weight of the food consumed increased by 2.5- to 4.3-fold from instar (see Table 1), reaching a maximum during the sixth instar, when the larvae consumed more than 65% of the total quantity of food consumed during larval life.

It is interesting that, while attaining an identical weight, the larvae at 18° consumed 20-25% more food during each instar than the larvae at 9°. The rate of feeding was 2.0- to 3.5-fold greater during any larval instar at 18° than at 9°.

Energetic Coefficients. The subsequent fate in the organism of consumed food can be expressed by energetic coefficients. Larval energetics are described by the familiar equation $C = P + R + F$, where C is the consumption, P the weight increase, R the expenditures for respiration, and F the excreta. Three quantities were determined experimentally; the fourth (R) was calculated from the equation.

All quantities were initially substituted into the equation in calories. Therefore, the original data were first expressed in units of dry weight, and then in calories. It was established that in sawfly larvae the dry matter averages $21.4 \pm 0.3\%$ of the wet weight (36 larvae weighed); in birch leaves it averages 35.0%. The caloric content of birch leaves is 4.85 kcal/g dry matter; that of larvae is 5.60 kcal/g, while the caloric content of the excreta of larvae maintained at 9 and 18° is respectively 4.81 and 4.02 kcal/g. Subsequently, all quantities in the right-hand side of the equation were expressed in percentages of the consumption (C).

The process of food assimilation is characterized by the coefficient of assimilation $(P + R)/C$ or A/C. It declined somewhat from the younger instars to the older (see Table 1). It is interesting that at 18° the larvae assimilated a greater fraction (43-45%) of the consumed food than at 9°, although at the higher temperature the food passed through the gut much more rapidly.

The energy assimilated from the food is expended primarily for the needs of the organism itself, i.e., for respiration (R). These expenditures are partially determined by the larval motor activity. It is known that motor activity increases from instar to instar and particularly increases towards the end of the last instar (Crossley, 1966). Both in the wild and to a still greater extent in the containers, where an increase in activity could also have been caused by the experimental conditions (small container volume, comparatively small quantity of food, etc.), activity and the expenditure of energy for respiration increased markedly during the sixth instar relative to the preceeding instars. These parameters further increased sharply with increase in temperature, which can also be explained by an increase in larval mobility with temperature increase, the intensification of the processes of nutrition, etc.

The principal energetic coefficient is the P/C coefficient of utilization of consumed food for growth, since specifically this coefficient determines the larval growth rates. At the same time, growth (production) represents the final stage in the utilization of matter (and energy) in the organism: that which is assimilated but not expended for the respiration of the body tissues is used for the creation of new tissues. Metabolic expenditures increased with the increase in larval motor activity during the sixth instar, while the $P/(P + R)$ coefficient — the utilization of assimilated food for growth — correspondingly fell. It is this, as well as a certain decline in assimilation with larval growth, that caused the P/C coefficient to decline during the sixth instar to half that in the fifth. As a whole throughout the developmental period the coefficient was approximately 18% in the *Croesus* sawfly (in Table 2 for comparison with the other species, whose caloric content we did not determine, the P/C is expressed in g/g dry weight × 100%).

Influence of Temperature on Larval Growth and Energetics. As already indicated above, larval weight was apparently independent of the temperature at which the larvae developed; other investigators also have failed to note such a dependence. Only Haukioja and Iso-Iivari (1976), studying the development of the sawfly *Dineura viridídorsata* in northern Finland, explained the difference in the mean larval weights in 1972 and 1973 by the temperature condi-

TABLE 2. Most Important Characteristics of Larval Nutrition in Certain Northern Species of Leaf-Mining Insects at Various Temperatures (1980)

Taxonomic classification of object	Experimental dates	Mean daily temperature of period, °C	Quantity of daily data	Rate of food consumption, g/g body weight (dry weight)/day	P/C, g/g · 100%
Tenthredinidae, Croesus sp.	4.VIII—16.VIII 4.VIII—17.VIII	9,1 17,8	100 83	0,86±0,03 2,09±0,07	16,0 16,3
Tenthredinidae, sp. 2	29.VII—4.VIII 29.VII—1.VIII	11,5 18,1	28 12	1,44±0,10 2,42±0,22	11,7 13,6
Tenthredinidae, sp. 3	30.VII—17.VIII 30.VII—11.VIII	9,4 17,9	19 32	1,50±0,08 2,22±0,15	15,2 14,1
Geometridae, O. autumnata	11.VII—21.VII 9.VII—1.VIII 8.VII—17.VII (1978 r.)	12,0 18,5 22,0	9 56 52	0,85±0,14 1,32±0,10 1,60±0,13	27,7 19,7 23,2

tions of the summer seasons. However, these these conditions must have affected the food plant (birch), as well as the chemistry of its leaves; and the fact that larval weight depends upon the composition of the food is generally known.

The expenditure of energy in the larval organism proceeded differently at different temperatures: assimilation and expenditure for respiration increased with increase in temperature. Since both these processes occurred simultaneously, the P/C coefficient remained nearly constant (Table 2). The observed increase in the rate of larval growth at high temperature is explained not by an increase in the fraction of food energy used to build the larval body but by an intensification of larval feeding. This is the only or, in any case, the most important means of increasing growth and reducing larval development times during the brief periods of relatively high temperatures.

Features of the Energetics of Northern Spceies of Leaf-Mining Insects. We have considered a high P/C coefficient as one such feature (Bogacheva and Lubeshkov, 1975; Bogacheva, 1977. 1980). In connection with the studies of 1980, our understanding of this was modified somewhat.

High P/C coefficients (from 20 to 30%) were found in species of the spring—summer group (sawfly *Amauronematus harpicola* Zhel., leaf beetle *Phytodecta pallidus*, Lepidoptera *O. autumnata*, *Lygris prunata* L.). Similar data have been obtained by other authors. Thus, in the leaf beetle *Melasoma collaris* in alpine habits of southern Norway on willow this coefficient fluctuated from 20 to 26% (Hagvar, 1975); in the leaf bettle *P. pallidus* in Sweden it reached 29% (Axelsson et al., 1974). However, in 1980 we obtained lower values of the P/C coefficient for the group of summer—autumn sawfly species (12-16%, see Table 2). Even smaller values of this parameter are possible. A sawfly *Dineura virididorsata* has been described (Haukioja and Niemelä, 1974) with a P/C coefficient of only 9%. This species completes development by mid September under the conditions of the field station Kevo.

Cates (1980) believes that nutrition on young and mature leaves represents two opposing strategies. Young leaves are superior in food value since they are rich in protein; however, they contain substances that inhibit metabolic processes in herbivorous insects. Specialized species that have been able to adapt to such leaves are compensated by a more valuable food substrate, and their P/C coefficient is accordingly higher. The species that must feed on mature foilage, which no longer contain inhibitory substances and whose food value is low, have a low P/C coefficient.

Thus, the P/C coefficient in large measure depends upon food quality. Insofar as there are species of both the summer—spring and the summer—autumn groups in the north, a high P/C coefficient cannot be considered invariable for northern species. Furthermore, only species with a spring—summer larval-phase phenology and, consequently, a high P/C coefficient reach high numbers in the North.

We shall now examine the feeding rate. This parameter is mainly dependent upon temperature and is primarily responsible for the rate of larval growth. The feeding rate of the larvae of north species was already rather high at low temperatures (9-12°; see Table 2); it corresponds to the level observed at 20-30° in species of temperate and tropical zones (Carne, 1966; Reichle and Crossley, 1967, cited in Naukioja and Niemelä, 1974; Van Hook and Dodson, 1974; Mathavan and Pandian, 1975; Scriber, 1977).

At a temperature of 18-22°, which in northern species is apparently close to the optimum, the food consumption increased to 1.6-2.4 g/g dry body weight per day. These are very high values. Thus, V. Kaczmarek (1967) believes that active, feeding arthropods (larvae of beetles hymenopterons, and butterflies) consume per day a quantity of food that averages 0.75 of their own body weight. According to other data (Reichle and Crossley, 1967, cited in Haukioja and Niemelä, 1974) all leaf-mining insects fall within 0.5 to 1.5 g/g. A mean food consumption rate of 1.3 g/g dry body weight/day has been reported for lepidopterous dendrophages (Scriber and Feeny, 1979). Only sawflies, which feed on conifers (a food with a low nitrogen content), are characterized by a higher food consumption: up to 3.6 g/g dry body weight per day during the penultimate instar (Fogal and Kwain, 1972; Fogal, 1974; Larsson and Tenov, 1979; Wagner, 1980, cited in Slansky, 1980). It is probably more correct to consider the high rate of food consumption characteristic of the northern species of leaf-mining insects as an adaptation to larval development at low growing-season temperatures, when it is very important to them that they utilize the brief periods of favorable temperatures with the maximum advantage for growth.

On the basis of the foregoing the following conclusions can be made:

1. Temperature conditions influence the energetics of larval development. Assimilation and, simultaneously, the metabolic expenditures of larvae increase with increase in temperature. The fraction of the food energy used to increase the larval body mass remains approximately constant.

2. The P/C coefficient is much more highly dependent upon food quality than upon temperature in leaf-mining insects of the Subarctic, as well as in insects of other latitudes.

3. Temperature conditions do not exert a marked influence on larval weight.

4. North species of leaf-mining insects are even at low temperatures (9-12°) characterized by a rather high rate of feeding (0.8-1.4 g/g dry body weight per day), which corresponds to the feeding rate of insect dendrophages of intermediate and southern latitudes at 20-30°.

5. The rate of food consumption increases by 2.0- to 2.5-fold in northern insect species with an increase in temperature to 18-20°. The larval growth rate correspondingly increases, and the times of larval development are reduced.

6. The high feeding rate at low temperatures makes it possible for larvae to complete development even during an unfavorable summer and, when the temperature increases, permits utilization of the brief periods of the most favorable temperatures with maximum advantage.

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