

**Measuring consumption in Eriocrania (Eriocraniidae,
Lep.) miners with reference to interaction between
the leaf and the miner**

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Abstract

HAUKIOJA, ERKKI. (Zoology Dept., Univ., 20500 Turku 50, Finland) Measuring consumption in *Eriocrania* (Eriocraniidae, Lep.) miners with reference to interaction between the leaf and the miner. REP KEVO SUBARCTIC RES STAT 11, 16—21. Illus. 1974. — Birch leaf consumption in the mining larvae of *Eriocrania* spp. (*sangii*, *semipurpurella* and *sparmanella*) was estimated in Finnish Lapland in 1973. In that year most of the larvae died at an early stage. As the faeces production could be estimated from mines, and assuming the relationship between faeces and consumption to be 0.65, it was estimated that on average a larva consumed about 3 mg dry weight of *Betula* leaf during its life-time in 1973.

Due to the reactions of the leaf against *E. sangii/semipurpurella* the leaves mined by these species were on average 10—60 mg smaller than predicted on the basis of their width. Thus the reactions of the leaf due to mining were probably more important in causing losses of plant biomass than direct consumption.

1. Introduction

When energy transfer relationships between a plant and its herbivores are evaluated, the amount of plant materials removed from the host is the measurement giving the direct impact of the consumer upon the host. Therefore, measuring the food intake and the amount of plant biomass wasted in the feeding process, is of basic importance in studying the functional importance of consumers in an ecosystem. During recent years research in this field has grown rapidly. The other side of the phenomenon, what is the effect of herbivores upon plants and especially upon their production, has received much less attention.

The birch (*Betula tortuosa*) is the dominant primary producer in northernmost Finnish Lapland (KÄRENLAMPI & KAUKHANEN 1972) and, accordingly, the action of herbivores on the birch was selected for intensive study in the Tundra IBP (Inter-

national Biological Programme) work at Kevo, Finnish Lapland.

The present paper deals with the herbivory by larvae of the miners of the genus *Eriocrania*, which according to their biomass figures belong to the most important herbivores of the birch (KOPONEN 1973) and were therefore selected for a closer study in 1973. The importance of this genus as birch herbivores has also been noticed in other parts of northernmost Fennoscandia (TENOW 1963; NUORTEVA 1966).

Consumption measurements in *Eriocrania*, as in other leaf-miners, are difficult using conventional gravimetric methods (WALDBAUER 1968), as feeding experiments are probably impossible without greatly disturbing the larva. However, leaf-miners also have an advantage in energetic studies due to their special life mode. In species which leave faeces inside the mine, it is easy to collect the larva and all its faeces at the same time. Estimates of the parameters in an energy

budget can therefore be made, although indirect deductions are needed (see FUNKE & WEIDEMANN 1971). An indirect approach is used also in the present paper when trying to determine consumption in *Eriocrania* species. At the same time reactions of the birch to the miner are discussed, and, finally some general aspects concerning herbivore research as part of ecosystem studies are discussed.

2. Materials

Miners of the genus *Eriocrania*, especially the species *sangii* and *semipurpurella*, were very abundant in northernmost Finland and Norway in 1973. At the places studied, 74–96 % of the larvae of the above two species died before emerging at the end of June — beginning of July. At that stage most of them were less than half-grown (KOPONEN 1974). The above two species have been treated as one group because it is difficult to determine the species from dead larvae (when differences in colour are not evident) and the measurements were made when most individuals had already died.

The place where *E. sangii/semipurpurella* were studied is situated at the top of the fell Jesnalvaara (approx. 310 m a.s.l.) near the Kevo Subarctic Research Station in northern Finland (69°45'N, 27°E). Some measurements of these species were made also from animals and leaves collected on the Petsikko fell (approx. 300 m a.s.l.) about 50 km south of Kevo.

E. sangii and *semipurpurella* reach their larval stage early in the summer. As leaves of *Betula tortuosa* attain their maximum weight in the middle of July in the Kevo region (Haukioja & Koponen, unpublished), a large proportion of the consumption by these miner species occurs at a time when leaves are still growing. This leads to asymmetric growth of the leaf so that the tip of the leaf usually turns to the side of the mine.

Some measurements that could not be made for *E. sangii/semipurpurella* due to the sudden decline of the population were made on *E. sparmanella*. It was not as common as *E. sangii/semipurpurella* at any of the 24 places in northern Norway and Finland where *Betula* leaves were studied for signs of herbivory in 1973 (unpublished). Materials in this paper for *E. sparmanella* were taken mainly from Leirpollskogen (70°25'N, 28°35'E), northern Norway.

E. sparmanella occurs later in the summer than *E. sangii/semipurpurella* and its larvae survived better. Because of the later occurrence, most or all of the consumption by *E. sparmanella* larvae takes place during the phase when the *Betula* leaves are full-grown. Therefore the leaves retain their normal form in spite of the presence of a mine.

3. Methods and results

3.1. Basic terminology

Using the symbols recommended by PETRUSEWICZ (1967), the parameters of energy intake and output in an individual or in a population can be related to each other e.g. in the following way:

$$MR - NU = C = P = R = FU$$

where

MR = materials removed in the feeding process from *Betula* leaves

NU = wasted parts of food

C = consumption

R = respiration

P = production of new biomass and

FU = excreta.

In *Eriocrania* mines the net production can be measured from the weight of the larva. Also the FU term can be evaluated directly as all faeces are present in the mine. The value of the term NU is in practice 0. Thus $MR = C$.

It is worth stressing that the above relationship is applicable only when the feeding process is considered from the point of view of the herbivore population. From the viewpoint of the whole ecosystem, the situation can be quite different. VARLEY (1967) mentioned that defoliating caterpillars on oak caused increment losses more than ten times their own secondary production. As the ratio P/C of the larvae is generally of the order of 0.25 (e.g. in SMITH 1972), we should use, when studying herbivore action and not just the energy flow through a herbivore population, a relationship

$$\text{total losses of plant biomass} = L + MR$$

where L = material losses of the plant due to the reactions to damage by herbivores.

In the example of VARLEY (1967), $L > 2.5 \times C$.

In the following attempts to measure MR and L are described.

3.2. MR — measurements

C or MR in *Eriocrania* during its life-time can easily be measured by adding together the values for P, R and FU. P and FU are also easy to measure in practice, but measuring R in the manner used by FUNKE

& WEIDEMANN (1971), is dependent on the assumption that the leaf quality is the same in controls as in the mined area and its immediate vicinity. As shown later, the validity of this assumption is questionable. Therefore, in the following an indirect method for estimating the FU/C ratio in invertebrate herbivores by using literature references is applied.

The following assumptions must be made:

- change in the dry weight or energy content of FU is negligible,
- when using dry weights only, then energy content of FU and MR is about the same,
- it is possible to collect faeces accurately enough from the mine, and
- pertinent literature references can be found.

For point a) no data are available, but it may be mentioned that the faeces in *Eriocrania* mines are dry and therefore probably do not favour bacterial growth. FUNKE & WEIDEMANN (1971) were of the same opinion. For b) HAUKIOJA (1973) gives values of 5.1 and 5.3 kcal/g for the food (*Betula* leaf) and faeces of *Dineura virididorsata* (Hym., Tenthredinidae) at Kevo. As far as point c) is concerned, experience in the field seems to support this assumption, and Fig. 1 shows

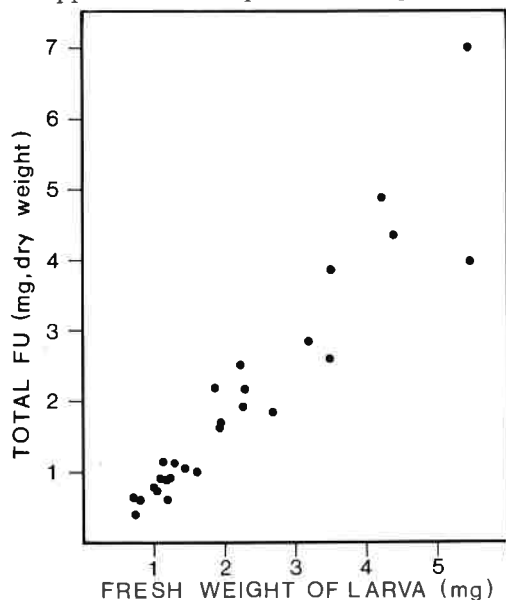


Fig. 1. Relationship between the amount of faeces in the mines of *Eriocrania sparmanella* and the weight of the larva.

that there is at least a clear correlation between the weight of the larva (*E. sparmanella*) and the weight of the collected faeces. This indicates that the random variation in faeces collecting is not large. Point d) is the most difficult. There do not seem to be any published results of the FU/C ratio measured directly in leaf miners. Table 1 gives some

Table 1. FU/C percentages in some leaf-eating caterpillars.

Species	FU/C-%
<i>Operophtera brumata</i> (Smith 1972)	64.5
<i>Oporinia autumnata</i> (Haukioja & Niemelä, in prep)	62.6
<i>Cidaria caesiata</i> (Haukioja & Niemelä, in prep)	60.5
<i>Hydriomena furcata</i> (Smith 1972)	63.9
<i>Erannis</i> spp. (Smith 1972)	63.7
<i>Cosmia trapezina</i> (Smith 1972)	61.4

Table 2. Proportions of dead and living *Eriocrania sangii/semipurpurella* with mean weights on Petsikko fjell in June — July 1973.

Date	living	dead		mean weight (mg)	
		N	%	living	dead (fresh)
27. 6.	129	81	39	1.04	—
5. 7.	43	292	87	3.12	—
10. 7.	0	201	100	—	1.57
18. 7.	0	155	100	—	—

figures for this ratio in leaf-eating caterpillars. On the basis of these figures an estimate of 0.65 was chosen for use in *Eriocrania*. Table 2, made from materials collected on Petsikko fell, shows that the majority of *E. sangii/semipurpurella* died in the first days of July in 1973. At that time the mean weight of larvae was about 2 mg (fresh). In the Kevo region the weight development was about the same (mean weight for 12 living *sangii/semipurpurella* was 1.6 mg on June 26, 1973). As the dry weight of faeces produced by a larva of 2 mg fresh weight was about 2 mg (Fig. 1), the mean life-time consumption was ca 3 mg dry weight of *Betula* leaf. This figure is valid only for 1973 when the majority of the larvae died at an early stage.

3.3. Loss of leaf tissue (L)

Mining of a *Betula* leaf by *E. sangii/semipurpurella* usually leads to curving of the

leaf tip towards the mined half. In addition to this it was observed that mined leaves are on average broader and/or shorter than unmined leaves. This was tested using a sample of leaves collected from Petsikko fell from which the breadth/length ratio was calculated. The length of a leaf was measured along the middle vein, taking curvature into account, and the width was taken from the (unmined) half of the same leaf. The results were as follows:

unmined leaves	0.404
mined leaves	0.432

The difference was statistically significant (analysis of variance, $p < 0.01$).

Later in this paper it will be shown that it is essential to know if the difference in the morphology of unmined and mined leaves is due to abnormal increase in width in the unmined half or in retarded growth in length. The impression, that mined leaves are shorter and not wider, was supported by the fact that as materials for this paper were collected on Jesnalvaara fell in July, it was easy to find leaves broader than 30 mm (half diameter) for the control group but not easy to find mined leaves with a half diameter larger than 25 mm. About one third of *Be-*

tula leaves there were mined by *E. sangii semipurpurella*. This indicates that abnormal growth in width is not the correct explanation.

For measuring the effects of mining on the leaf the following method was used.

A sample of *Betula tortuosa* leaves (395 exx) not eaten in any way and regular in form, was collected for controls from the top of the fell, Jesnalvaara. The width from the middle vein to the edge of the leaf was measured. Their stalk was removed and they were dried at 105°C to a constant weight. Fig. 2 gives the mean weight of leaves in

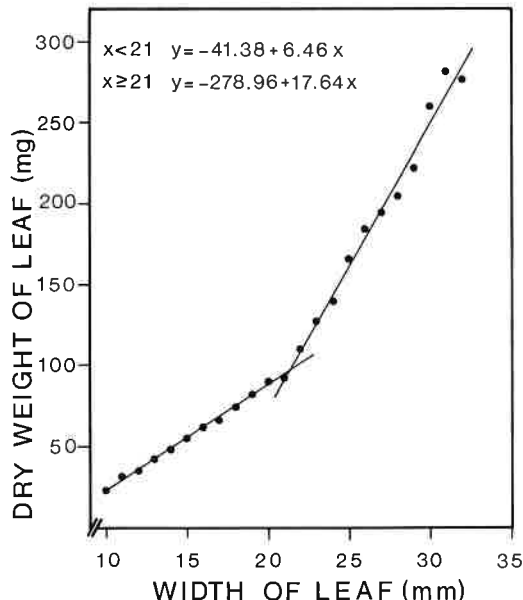


Fig. 2. Relationship between the half-diameter of *Betula tortuosa* leaf (from middle vein to edge) and the dry weight of the leaf.

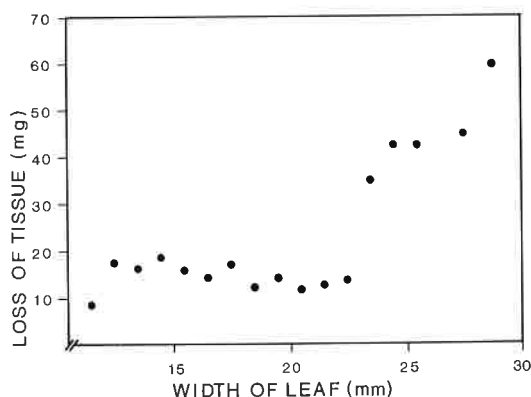


Fig. 3. Mean biomass losses in leaves mined by *Eriocrania sangii/semipurpurella* compared with expected values calculated from the half-diameter of the leaf by using a regression equation from Fig. 2.

relation to their half-diameter. The weight increases steeply after the 21–22 mm half-diameter class. Two regression lines, with the point of inflection at 21.25 mm, gave reasonably good representation of the relationship between the size and the weight of intact leaves.

From the same location 191 leaves with (dead) miners inside were analysed by removing the stalk, remains of the larva, faeces, parasite larvae, etc., by measuring the width of the non-eaten half and drying the leaf. After that the expected weight for each leaf was calculated using the measured width of the leaf and a regression equation based on Fig. 2. Deviations from the expected weights are given in Fig. 3.

3.4. Conclusions

The main results obtained are as follows:

— the consumption of a miner was of the magnitude of 3 mg dry weight of *Betula* leaf during the life-time of a larva

— the biomass reduced from mined leaves compared with the expected value for unmined leaves was 10–60 mg more than that taken by the miner and was dependent on the size of the leaf.

The bulk of material losses from a leaf is therefore caused by the reactions of the plant against the miner and this effect is 3–20 times more than the consumption. This does not necessarily mean that e.g. the photosynthetic surface of a plant or its energy reserves were reduced very much, because the results presented only give the situation in a single leaf. It may be that the losses are to some extent compensated e.g. in other leaves. There is some evidence which indicates that some kind of compensation can occur even in the intact half of a mined leaf.

A sample of leaves mined by *E. sangii/semipurpurella* but which had, however, retained their original symmetric form was collected from Jesnalvaara. Interpretation of the symmetry of a leaf is of course subjective, but the 16 leaves chosen fulfilled this condition well. They were cut into two parts along the middle vein and the width of the unmined half of the leaf was measured and its dry weight was taken. After that the expected value for the dry weight of the unmined half was calculated from its width by using the regression equations in Fig. 2, and dividing the result by two. If the growth of the unmined half were normal, the calculated weights in the sample should be distributed around the measured values of respective leaves. However, in 15 out of 16 possible cases the expected value was lower than that actually measured; the deviation from an even (8–8) distribution is statistically significant ($p = 0.015$, Fisher's exact probability test).

If similar results were obtained with larger materials it would show that some compensation mechanism operates at least in the intact half of the leaf. This does not affect

the validity of the earlier results given in the present paper.

It is also an indication that there are qualitative differences between the unmined half of a mined leaf and an unmined leaf. That is why no attempts to carry out respiration measurements and to use them for consumption determination (p. 00) were made. It does not, however, necessarily invalidate the practice proposed by FUNKE & WEIDEMAN (1971) but calls attention to the need for detailed study of the reactions of a leaf against a miner before using the method for respiration measurements.

4. Energy studies of populations in ecosystem studies

When energy flow through an ecosystem is studied, the work is done by a lot of people who usually work on different systematic or functional groups. In herbivore studies the normal practice would seem to be to study a population with much the same kind of methods as are used in population energy studies. In most respects these studies give usable results also for ecosystem studies but in others more emphasis is needed than is usually given them. In the following some points are discussed which are relevant to this kind of work on leaf-miners and, more generally, on herbivorous invertebrates.

Of the population parameters the most frequently used are perhaps assimilation (A) and production (P) and the aim seems to be to determine the secondary production of the population. This depends at least to some degree on the influence of the IBP programme the task of which was to determine the production potentials of the main biomes of the world (PETRUSEWICZ & MACFADYEN 1970).

It is possible to determine production without measuring consumption, perhaps unfortunately, because it can be maintained that C or MR are at least as important parameters as A and P from the point of view of the ecosystem. When the situation is studied only from the viewpoint of a (herbivore) population, the importance of production is central but from the point of view of the ecosystem the importance of P is more evident as potential food for the next trophic

level. Quantitatively it is much less than the materials which the herbivore population has removed from the preceding trophic level, from primary producers. The importance of a population in channelling the energy flow through an ecosystem along certain paths can be better evaluated by knowing the magnitude of MR and C. However they also give only an imperfect picture of the population in the energy flow of the ecosystem as the regulatory mechanisms of populations in ecosystem energy flow are known only very incompletely.

As shown earlier in this paper, the symbols MR and C, used in population energy studies, only tell what is the *direct* impact of a herbivore population upon the plants they use for food. The indirect effects are in the present case larger than the direct ones, and, in spite of difficulties in studying them, require considerable emphasis in research.

A third phenomenon that can be traced in differences between an ecosystem-orientated view and a population-orientated view, is found in energy flow studies in invertebrate herbivores. More than 60 % of the energy content of the ingested material is lost in the form of faeces. However, the main interest and research is frequently spent on determining the fate of the minor path, i.e. that part of energy, less than 40 %, which is assimilated. This trend is not pertinent e.g. in mammalian herbivores (e.g. DROZDZ et al. 1971) where the proportion of assimilated energy is larger than that of FU.

The above examples indicate that, perhaps due to the short time span that energy relationships have been studied in terrestrial ecosystems, some strategies adopted in consumer studies are not especially applicable to ecosystem studies. One of the main reasons for this might be found in the sharp division into botanical, zoological and microbiological research, but a more thorough discussion of this topic is beyond the scope of the present paper.

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