

Chapter 5

Digestive efficiency of *Pheretima* sp. (Oligochaeta: Megascolecidae)

Introduction

A reason for the study on the feeding activity is the measurement of assimilation from consumption minus rejection (Petrusewicz and Macfadyen 1978). The purpose of this paper is the estimation of digestive efficiency of animals and the comparison of digestive efficiency between consumption minus rejection and production.

Method

1. Digestive efficiency (consumption minus rejection)

The digestive efficiency (consumption minus rejection) of *Pheretima* sp. (H-1) (Oligochaeta: Megascolecidae) was estimated. The materials obtained in the culture experiment were used for this determination (Chapter 4). It was difficult to detect the difference in weight between consumption and rejection. However, the difference in nutrient contents (Nitrogen and Carbon) between consumption and rejection was detectable.

The consumed nutrients are represented as follow

$$CN = 13.94 \times FC + 1.64 \times SC$$

$$CC = 222.93 \times FC + 22.51 \times SC$$

Where, CN is the consumed Nitrogen (mg per an individual per a day), CC the consumed Carbon. FC is the food consumption (g dry wt per an individual per a day) and SC the soil consumption. The soil consumption can be calculated as fecal pellet production minus food consumption. The values of 13.9 and 222.9 are the nitrogen and carbon content in the food (mg g^{-1} dry wt), respectively. The values of 1.64 and 22.5 are nitrogen and carbon content of the soil (mg g^{-1} dry wt), respectively. The carbon and nitrogen contents of 88 fecal pellet samples were determined with C.N corder (YANAGIMOTO). In each measurements, Pellet Samples of 400 mg dry wt were chosen from the fecal pellets produced by an individuals in a given period. The ejected nutrients are presented as follow

$$EN = PN \times FP$$

$$EC = PC \times FP$$

Where EN is the ejected Nitrogen and EC the ejected Carbon (mg per an individual per a day). PN is the Nitrogen content and PC the Carbon content, per gram dry weight of fecal pellet (mg g^{-1} dry wt). FP is the fecal pellet production of earthworms per day (g dry wt d^{-1}).

The digestive efficiency are represented as follow

$$DN = (CN-EN) / CN$$

$$DC = (CC-EC) / CC$$

Where DN is the digestive efficiency estimated on Nitrogen content and DC the digestive efficiency estimated on the Carbon content.

Another definition of digestive efficiency is consumption less rejecta $\{A=C-(F+U)\}$. It was impossible to separate from the true feces the components of nitrogenous and other excretion, as well as metabolized products such as digestive enzymes, mucus and gut lining, in the earthworms fecal pellets. Then, the ejection in the present determination (EN or EC) is equal to true feces plus nitrogenous and other excreta. Digestive efficiency was calculated on 88 pairs, in each nutrient element, of consumption and ejection.

2. Assimilation efficiency

Assimilation efficiency is total of production and respiration, per consumption. This calculation was employed for the cultivated individuals (Chapter 4). The production of individuals in term of energy was the energy in the weight gain per unit period ($21.133 \text{ KJ g}^{-1} \times \text{production in gram}$) (Chapter 3). The energy for the respiration of individuals per unit period was estimated by using the CO_2 expiration rate of *Pheretima* sp. (H-1) (Chapter 3), assuming that RQ was 0.79 and the caloric equivalent of O_2 was $4.775 \times 4.184 \text{ KJ}$. The energy consumption was total energy of food consumption and soil consumption ($11.661 \times \text{food consumption} + 0.887 \times \text{soil consumption}$, KJ per unit period). The metabolic rate of earthworms and the energy equivalent of materials were shown in earlier paper (Chapter 4).

Result

1. Digestive efficiency and the ratio of the food to total quantity consumed

The estimated value of digestive efficiency was in the range -179.2 to 51.6 % in Nitrogen and -255.7 to 50.0 % in Carbon (n=88). The mean values were 10.87 ± 20.43 in earlier and 10.41 ± 25.40 % in later (excluding two extreme values n=86). Figure 5-1a and 1b show the relations between the digestive efficiency and the ratio of the food consumed to total material consumed.

These relation are approximated by following linear equations

$$Y = 0.6378 \times X - 15.2448 \quad r=0.5445 \quad \text{in Nitrogen} \quad (5-1)$$

$$Y = 0.5805 \times X - 12.4840 \quad r=0.4503 \quad \text{in Carbon} \quad (5-2)$$

Where, Y is the digestive efficiency and X the ratio of the food consumed to total material consumed. The figures show that the digestive efficiency was positively correlated with the quality of the consumed material. However, these linear equations show the low reliability ($r=0.54$ in Nitrogen and $r=0.45$ in Carbon). Some part of this low reliability may due to biased samples from the fecal pellet materials. However, the following is certain. When earthworms consumed a nutrient poor material, the digestive efficiency falls to a very low level or to minus.

2. The relation between digestive efficiency and weight

Figure 5-2 shows the ratio of food to the gross weight of the taken material. The ratio plots the age of earthworm. The younger individuals take the richer resource than those of the elder individuals. This result predicts the relation between digestive efficiency and earthworm's weight. The values of digestive efficiency were plotted to weight of earthworms in Fig. 5-3. Mean values of

digestive efficiency in each cultivation series was also plotted in same figure. The efficiency of small immature less than 1000 mg scattered in wide range -50 % to 50 %. The range decreased with the increase of weight. The value of large immature more than 2000 mg wet weight wt was in range -20 to 30 %. Mean values of efficiency decrease from 30 to 5-10 % with the increase of weight. The minus value of digestive efficiency was seen in wide range of weight. The minus value due to the efficiency of the earthworms consuming the food at the lower rate, regardless of weight (Fig. 5-1).

3. The effect of digestive efficiency on growth rate

Several earthworms showed the minus digestive efficiency. A digestive efficiency is defined as $A=C-(F+U)$, where F is true faeces and U excreta. Namely, if the earthworm take the food at lower rate less than 21 % of total material consumed, the quantity of assimilated material is less than that of the excreted material which contain a digestive fluid, mucus and gut lining. These raise the question that the earthworms eating a nutrient poorer material showed the weight decrease or losses. Now, it is able to calculate the growth rate in a given period from the results of the cultivation (Chapter 4). The growth rate was the ratio of the increased weight to the initial weight in given period. Figure 5-3 show the relation between growth rate and digestive efficiency according to the cultivation temperature and the weight class. In this figure, the decrease in weight by the minus digestive efficiency is not seen. Younger earthworms usually ingest the nutrient richer resource, and get the high efficiency of digestive and the higher rate of weight growth than those of elder earthworms (Fig. 5-1, Fig. 5-2 and Fig. 5-3, and Formula 4-1,4-2 and 4-3 in Chapter 4). Still, the cultivated earthworms ingested the various quality of resource (Fig. 5-2), and showed the wide range of digestive efficiency (Fig. 5-1, Fig 5-2 and 5-3). For example, the large earthworms of 1 g weight cultivated at 25 °C ingested the food at the rate between 10 % and 60 %, and showed the wide range of digestive efficiency (Fig. 5-2). It is reasonable to assume that certain earthworms ingest the fixed quantity of the food and soil in long period, in spite of daily change. True digestive efficiency of earthworm is not a mean of measurements. But true digestive efficiency is the efficiency of earthworms ingesting the food at the averaged rate.

4. Assimilation efficiency of Production plus Respiration

Figure 5-4 showed the assimilation efficiency estimated by $A = (P+R) / C$. The values of $A = (P+R) / C$ ranged from 1.17 % to 3.72 %. Its average value was 2.17 %. The result means that, the cultivated earthworms required 2.17 % of assimilation efficiency for them to sustain the basal metabolism (P+R). This value was far lower than the digestive efficiency of the cultivated earthworms estimated from $A=(C-F)/C$.

Discussion

1. The digestive efficiency of the cultivated earthworms

The simple averages of the digestive efficiency of the cultivated earthworms were 11.27 % in Nitrogen and 10.41 % in Carbon. These values did not reflect the true average digestive efficiency

of the cultivated earthworms. The true value can be estimated by adopting the average ratio of the food consumed to total material consumed. It had been estimated that the cultivated earthworms having a same distribution of weight to that of the field population in area D 1972 consumed the food at 35.5 %. This value is answer to 7.397 % for Nitrogen and 8.124 % for Carbon, of the digestive efficiency of the cultivated earthworms.

The digestive efficiency of field population: The quality of the material consumed effects on digestive efficiency of earthworm (Fig. 5-2a, b). Then, we can attain to the good estimate of the average digestive efficiency of the field earthworms, if there are the information on the average quality of the materials consumed by the field earthworms. The nutrient content in the materials consumed by the field earthworms were 6.42 mg of Nitrogen g^{-1} dry wt and 72.15 mg of Carbon g^{-1} dry wt. These values were equivalent to 38.89 % for Nitrogen and 24.77 % for Carbon, of the ratio of the food consumed to total material consumed. The digestive efficiency of the field earthworms was estimated at 9.559 % in case of Nitrogen, and was estimated at 1.895 % in case of Carbon, respectively, by adopting formulas 5-1 and 5-2. These results are summarized in Table 5-1. The difference in the estimated digestive efficiency between Nitrogen and Carbon was due to the difference in the C/N ratio of the food resource between field and cultivation. Carbon content is the more fundamental indicator on estimating the metabolic rate of the earthworms in field, by the reason that sucrose was detectable for earthworms sensory organ (Laverack 1960) (Chapter 4). Thus, the value of 1.895 % should be the true digestive efficiency of the earthworms in field.

2. Several figure of digestive efficiency

Table 5-1 summarized several figures of digestive efficiency of *Pheretima* sp. (H-1). The digestive efficiency scattered in the range between 1.9 % and 10 %. The efficiency of the cultivated earthworms were far larger in digestion (C-F)/C than basal metabolism (P+R)/C. The excess energy (digestion minus assimilation) were far larger in younger than elder (Fig. 5-1). Also, the growth rate of the cultivated earthworms was far larger in younger than in elder (Chapter 4). The excess energy and material assimilated by younger earthworms must be expended to gain the higher growth rate.

The digestive efficiency (C-F)/C were far larger in cultivation than in field. The lower efficiency of the field earthworms may explain the smaller maximum weight and the lower rate of weight growth than the cultivated earthworms. Also, the weight decrease after maturation in field may be due to the lower digestive efficiency besides limited quantity of resource in field.

Crossley et al (1971) estimated the digestive efficiency of three Lumbricid fed on leaf litter by using the radio isotope technique 11.6 % for *Octolasion lacteum* (Orley), 28.5 % for *Allolobophora hortensis* (Michaelsen) and 25.4 % for *Lumbricus terrestris* L.. The efficiencies reported by Crossley et al are akin to that of immature *Pheretima* sp. (H-1) ingesting the food at high rate (Fig. 5-2). Still, they said that *Octolasion* fed on soil only did not show the detectable assimilation of ^{137}Cs . Bolton and Phillipson (1976) reported that the assimilation efficiency

(P+R)/C of *Allolobophora rosea* (Savigny) fed on bramble soil were less than 2.4 %. This figure are similar to the assimilation efficiency (P+R)/C of *Pheretima* sp. (H-1).

3. The speculation on the excreta

The relation between digestive efficiency and the quality of resource was approximated with a linear equation (The formula 5-1 and 5-2). Using this empirical equation, some speculation on digestion and excreta was made. The definition of digestive efficiency is consumption less rejecta $C-(F+U)/C$. Rejecta contain the components of nitrogenous and other excretion as well as metabolized products such as digestive enzymes, mucus and gut lining besides the true feces. The equations 5-1 showed the minus digestion in the range less than 21.5 % in Carbon and than 23.9 % in Nitrogen, of the food to total material consumed. The minus digestion may be partly due to the earthworm's selectively ingestion of nutrient rich material from the soil which was filtrated through the 1 mm mesh. It is very difficult to assume the selectively ingestion of earthworms from the soil, because the soil used for cultivation consisted of nutrient poor sandy soils. Crossley et al (1971) reported that the radioactive decay of *Lumbricid* fed on the soil tagged with ^{137}Cs was made by a single component (K1) showing only the elimination of the ingested soil. This result demonstrates that no detectable ^{137}Cs was assimilated from the tagged soil ingested by *Octolasion*. Bolton and Phillipson (1976a) said that *Allolobophora rosea* (Savigny) preferentially selects the more organic fractions of the soil for ingestion. Bolton and Phillipson (1976b) reported that the energy equivalent of feces produced by *Allolobophora rosea* (Savigny) after being kept in the homogenized mull type soil were consistently higher than those for the soil medium (2.586 KJ g^{-1} dry wt of the homogenized mull type soil, and 3.402 - 3.540 KJ g^{-1} dry wt of feces). The author believes that *Pheretima* sp. (H-1) could not assimilate the material from the soil. *Pheretima* sp. (H-1) was the litter feeder and the energy equivalent of the soil used was very low (chapter 4). Then, the minus assimilation of the earthworms consuming only the soil might due to the excreta of the nitrogenous substance such as digestive fluid, muco protein and gut lining.

It is able to estimate the quantity of the excreted nutrient element by using the minus assimilation of the earthworms consuming only the soil. These quantities can be calculated

$$\text{EN2} = 1.64 \times 15.2488/100 = 0.250 \text{ mg N g}^{-1} \text{ dry wt}$$

$$\text{EC2} = 22.5 \times 12.484 /100 = 2.809 \text{ mg C g}^{-1} \text{ dry wt}$$

Where EN2 is the quantity of the excreted Nitrogen, EC2 the quantity of the excreted Carbon, 1.64 the nitrogen content of the soil (N mg g^{-1} dry wt of the soil), 22.5 the carbon content of the soil (C mg g^{-1} dry wt of the soil), 15.2448 the constant value b in the formula 5-1 and 12.484 the constant value b in the formula 5-2.

Assuming that one gram of animal protein contain 530 mg C and 160 mg N and that most part of the excreted material was composed by protein, it is able to estimate the approximated quantity of the excreted protein. Namely, the excreted protein was estimated as 1.563 mg Protein g^{-1}

dry wt of the soil ejected in basing on Nitrogen or as 5.3 mg protein g⁻¹ dry wt of the soil ejected in basing on Carbon. There are large difference in the estimate between Nitrogen and Carbon. It is unknown whether this difference was due to the excretion of the Carbon rich material such as Lipid or the error in the estimation on the constant values "b" between the formula 5-1 and the formula 5-2.

It is able to estimate the total quantity of the secretion matter accumulated in the fecal pellets produced by the field population. In earlier paper (Chapter 4), the total quantity of the fecal pellet production of *Pheretima* sp. (H-1) in area D 1972 was estimated at 13247.09 g dry wt m⁻². These values mean the excretion of 20.71 g protein m⁻² in Nitrogen, or 70.21 g protein m⁻² in Carbon. Assuming 4.0 × 4.184 KJ g⁻¹ dry wt of protein, the above values corresponds to 346.603 KJ m⁻² or 1174.867 KJ m⁻², respectively. The majority is not considered in total production (P), though a part of this amount of energy might be reflected in the weight decrease of the field population after late June 1972 in area D. The unseen production corresponds to 41.6 - 141.1 % of total assimilation (P+R = 832.198 KJ m⁻²) of this population.

I do not have comparable data concerning this hidden production now. Even if the digestive efficiency is defined as $A=(C-F)/C$ without the separation between true feces and excretion, the study on energy - material balance of animals will not induce large inconsistency. We must obtain enough data on the rejecta for exact understanding on hidden production.

Summary

1) The digestive efficiency of the cultivated earthworms was estimated with the difference in the quantity of nitrogen and carbon between consumed minus ejected. The estimated efficiency was in wide range from -200 % to 80 %.

2) The relation between the digestive efficiency and the quality of the material consumed was approximated by following equation $A = 0.58028 X - 12.624$, where X is the ratio of the food consumed to total material consumed. The average ratio of the food consumed to total material consumed was estimated as 35.5 % in cultivation condition. The digestive efficiency of the cultivated earthworms was calculated at 7.397 %.

3) Assimilation efficiency of the cultivated earthworm can be estimated another process $\{A = (P+R)/C\}$. Average efficiency from (P+R)/C was calculated at 2.17 %. The values from (C-F)/C were far larger than that from (P+R)/C. Particularly, the excess absorption (total absorption minus basal metabolism) was larger in younger earthworm than in elder earthworm. It was discussed that the excess energy assimilated by younger earthworms must be expended for their mobility and their specific dynamic action to gain the larger weight increase.

4) The digestive efficiency of the field earthworm ($A=(C-F)/C$) could be estimated at 1.895 %, the value of which was deduced from Carbon content in the gut material of the field earthworms. This value was far lower than the average value of the cultivated earthworm. It was discussed that

the lower digestive efficiency of the field earthworms than that of the cultivated earthworms might be another reason why the weight and the growth rate were far lower in field than in cultivation.

5) The equation between digestive efficiency and the quality of the material consumed indicate that the earthworm consuming the nutrient poor resource showed the minus digestive efficiency. From this, it was discussed on the hidden production arising from the excretion of the nitrogenous substance such as digestive fluid, muco protein and gut lining.

Reference

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