Chapter 3

Population metabolism of Earthworm populations

Introduction

Knowledge of energy or matter flow through a population is important in determining the limiting factor of population and the role of population in an ecosystem. The importance of energy flow and the dominant role of earthworms as decomposer in many ecosystems have promoted several studies (Satchell 1963, 1967). Also, energetics permits the direct comparison of this study with those of an earthworm in other various environments. The objective of this paper is to construct an energy budget for several populations of Pheretima group (Oligochaeta: Megascolecidae).

Method

1 Measurement of various metabolic rate

1-1 Energy equivalent of animal tissue

The data on the energy equivalent of animal tissue is necessary for constructing the rate of the energy flow through animal population. *Pheretima* sp. (H-1) was used for this measurement. The specimens were collected in the experimental field of the department of Biology Kyushu University in June 1974. The earthworms were dissected and removed its gut contents and oven dried at 60 ºC for 24 hr. The anterior part of the matter was determined. The measurement was carried out with bon caloric meter (YANAGIMOTO).

1-2 Measurement of respiration

The data on the respiration of animal is also necessary for constructing the rate of energy flow through animal population. *Pheretima* sp. (H-1) was also used for this determination. The specimens were collected for the period from Feb. to July 1972 in the experimental field. CO_2 expiration rate of earthworms was determined with an infrared gas analyzer (URAS). The flow rate of air in the respiration chamber was maintained at a constant, 30 l per hour. A glass tube of 3 cm in diameter and 30 cm in length was used as the respiration chamber. Test specimens wrapped in moist filter paper were placed in the chamber. Because the movement of specimens was impeded in the rolled filter paper, the respiration in chamber was assumed to be standard metabolism.

The number of specimens tested per a measurement was changed within the range from 2 to 10 according to the weight of earthworms. When the weight of test specimen was between 60 and 200 mg fresh wt, ten individuals were used in a mass. When the weight of test specimens was between 200 and 2000 mg fresh wt, five individuals were in a mass. When the weight of test specimen was larger than 2000 mg fresh wt, two individuals were used in a mass. The standard deviation of the weight of test specimens within a mass did not exceed ten percent. Measurements were made at three temperature such as 15, 20 and 25 °C. The respiration chamber was immersed in a water bath, of which the water temperature was controlled by thermo-regulator in ± 0.25 °C. CO_2 expiration rate was recorded every 12 minute for 72 minute measurement of a run. The rate in later half of a run was averaged. The averaged value was regarded as CO_2 expiration rate in each measurement.

2. Energy conversion of biomass and respiration rate

Biomass and respiration were estimated on four populations of *Pheretima* sp. (H-1) (area H 1968, area D 1971 and 1972, and area G 1972), one population of *Pheretima vittata* (Goto et Hatai) (area H 1968) and one population of *Pheretima irregularis* (Goto et Hatai) Ohfuchi (area K 1968) for constructing the energy budget of population. The information on the density and the weight distribution were gained from the results of population studies (Chapter 1).

Biomass was calculated by summing of the dry weight of each individuals (mg dry wt m^{-2}). Production of a population in the time intervals t_1 to t_2 is given, under the linear assumption for the curves, by

$$P = -(L_{t1} - L_{t2})(W_{t1} + W_{t2})/2$$

where L_{t1} and L_{t2} are the number of survivals at the time t_1 and t_2, and W_{t1} and W_{t2} are the mean weight at the time t_1 and t_2 (Ono 1972). Figure 3-2 - 3-9 show the density and the mean body dry weight of every populations. Still, there were some irregular change in the mean weight of *Pheretima* sp. (H-1) in area H 1968 (Fig.3-2), and in the density of *Ph. vittata* in area H 1968 (Fig. 3-6), which would induced an over estimate on tissue production. Then, these irregular lines were corrected to the smooth lines with combining the average of neighboring values, to gain a proper estimate on tissue production.

Cocoon density and its weight (in wet weight) were studied on only two populations of *Pheretima* sp. (H-1) (area D 1971 and 1972) (Chapter 1). The water content of cocoon attained to 83.224 % of the weight (Sugi unpublished). From this, the cocoon production of these populations was estimated in dry weight.

Energy equivalent of biomass and production was estimated with the energy equivalent of tissue of *Pheretima* sp. (H-1). The cocoon productions of two populations were converted to calorie, assuming that the energy equivalent of cocoon was equal to that of body tissue. Bolton and Phillipson (1976) determined the energy equivalent of the cocoon of eight Lumbricid species as 21.481 - 22.083 KJ per total dry weight and 22.966 - 22.501 KJ per gram ash free weight, which were almost same to those of body tissue.

CO_2 expiration of population was estimated by using the data on the body wet weight frequency of populations, the CO_2 expiration rate of *Pheretima* sp. (H-1) under experimental condition, field temperature, and Q_{10} formula by assuming that the use of Q_{10} formula involve the hypothesis of an exponential increase of metabolic rate with temperature. Assuming the respiratory quotient of earthworm is 0.79 and using oxycaloric coefficient of 4.775 Kcal l^{-1} O_2 of oxygen (19.979 KJ) l^{-1} O_2, CO_2 expiration of population was converted to the energy consumption for respiration. The diet for the earthworm consists of a mixture of organic debris, fungi and probably protozoa. Then, it is safe to use the energy equivalent of 19.979 KJ $l^{-1}O_2$ quoted by O'conner (1967) (Heilbrunn 1947). The value of RQ is assumed 0.79 following Macfadyen (1963) for animal feeding on a mixed plant matter.

The populations of soil dweller Pheretima were composed by several generations. The age compositions of these species were analyzed with Cassie's method. From this result, the growth curves for individual and the survivor ship curve of every generation were constructed (Chapter 1). By using these curve, the annual production and annual respiration of soil dweller Pheretima can be approximated with same method used for litter dweller Pheretima. This calculation was made on the generations of *Pheretima heterochaeta* (Baird) starting in early summer of 1971 in area D, and area G (Chapter 1). The curves on the survivor rate and the weight growth, of these generations showed some irregular change. Particularly, the large irregular changes were seen in the survivor ship curve. This was due to the vertical movement of earthworms to deeper zone than 20 cm depth for hibernation in winter and spring. Then, the densities in these months were estimated from the difference of density between before and after hibernation. Other irregular change in density and growth were corrected to the smooth lines, combining with an average of neighboring values. The respiration rate of litter dweller: *Pheretima* sp. (H-1) was used for the estimation of the respiration of soil dwellers, extrapolating the body fresh weight of soil dweller to formula 3-1, 3-2, and 3-3. Byzova (1965) reported that the respiration rate of soil dweller Lumbricid were lower than that of litter dweller Lumbricid. Then, the estimated respiration of soil dweller Pheretima might be slightly larger than the true rate in field. However, there were no available data on the respiration rate of soil dweller Pheretima. Because of the absence of the information on the vertical movement of earthworms for hibernation and on the respiration rate of soil dweller Pheretima, the population metabolism of soil dweller Pheretima is the provisional estimation.

Result

1. Measurement of various metabolic rate

1-1. Energy equivalent of animal tissue

The energy equivalent of animal tissue of *Pheretima* sp. (H-1) was 21.133 ± 0.916 J mg^{-1} dry wt (n=7). This value is slightly higher than that of *Lumbricus terrestris* L. (4.1256×4.184 KJ g^{-1} dry wt, Cummins and Wuycheck 1971). Bolton and Phillipson (1976) determined the energy equivalent of body tissue of Lumbricid species as the range 18.885 - 22.075 KJ per dry weight minus gut content in three endogees Lumbricid, and the range 22.204 - 23.968 KJ per g^{-1} ash free weight in eight Lumbricid species. The value of *Pheretima* sp, (H-1) was within the range of those of Lumbricid per dry weight minus gut content.

1-2 Respiration rate

Figure 3-1 shows the respiration rate of *Pheretima* sp. (H-1). The CO_2 expiration rate can be represented as follow

$CO_2\ h^{-1} = 111.23\ W^{0.69271}$ at 25 °C (3-1)

$CO_2\ h^{-1} = 76.50\ W^{0.69296}$ at 20 °C (3-2)

$CO_2\ h^{-1} = 58.50\ W^{0.73654}$ at 15 °C (3-3)

W is the weight of the earthworms in g fresh wt.

The respiration of some Lumbricidae species *L. terrestris* was measured by Byzova (1965), and Cosgrobe and Schwarz (1965) with Warburg method. They reported that the O_2 consumption rate of *Lumbricus terrestris* was expressed as $O_2\ h^{-1} = 83.5\ W^{0.71}$ at 19 °C and $156\ W^{0.69}$ at 25 °C, respectively. Where, W is the wet weight of earthworm in g fresh wt. Assuming that RQ is 0.79 because animal feed on a mixed plant matter, the O_2 consumption of *Pheretima* sp. (H-1) can be described as $O_2\ h^{-1} = 96.8\ W^{0.6929}$ at 20 ℃, and $141.8\ W^{0.69271}$ at 25 °C, respectively. Phillipson and Bolton (1976) reported that the O_2 consumption rate of *Allolobophora rosea* (Savigny) by individuals of 60-225 mg was 91.34-156.8 $O_2\ g^{-1}$ fresh wt h^{-1} at 15 ℃. The O_2 consumption of *Pheretima* sp. (H-1) by same size individuals is estimated as 109.69-155.39 $O_2\ g^{-1}$ fresh wt h^{-1} at 15 °C. These results may mean there are no large difference in O_2 consumption rate between Lumbricidae and *Pheretima* sp. (H-1). Still, the respiration rate of *Pheretima* sp. (H-1) in respiration chamber may refer to basal metabolism. It have been known that the respiratory rate of *L. terrestris* is affected by activity of earthworm and by expose to light in addition to ambient temperature (Satchell 1967). Then, the respiratory rate of *Pheretima* sp. (H-1) in field is likely to be larger than that measured in respirometer.

2. Biomass, production and respiration of abundantly populations

Figure 3-2 - 3-9 show the seasonal change in density, average weight, biomass and respiration of populations (four populations of *Pheretima* sp. (H-1), one population of *Pheretima vittata*, one population of *Ph. irregularis,* and two populations of *Ph. heterochaeta).*

***Pheretima* sp. (H-1) in area H 1968:**

The biomass of *Pheretima* sp. (H-1) in area H 1968 increased rapidly after 20 March, and has reached maximum biomass 2.982 g dry wt m^{-2} (63.011 KJ m^{-2}) on July 6, 1968. The average biomass from March 20 to Sept. 2, 1968 was 0.779 g fresh wt m^{-2} (16.485 KJ m^{-2}) (Fig. 3-2). The production was estimated at 4.065 g dry wt m^{-2} (85.772 KJ m^{-2}). Respiration increased after March 20, 1968 and reached the maximum of 2.013 KJ $m^{-2}\ d^{-1}$ on July 6, 1968. Total respiration was calculated with 138.239 KJ m^{-2}.

***Pheretima* sp. (H-1) in area D 1971:**

The biomass of *Pheretima* sp. (H-1) in area D 1971 increased after March, reached the maximum of 3.324 g dry wt m^{-2} (70.249 KJ m^{-2}) on June 10, 1971. The average biomass was 1.729 g dry wt m^{-2} (36.526 KJ m^{-2}) (Fig. 3-3). The production was estimated at 7.688 g dry wt m^{-2} (162.339 KJ m^{-2}). The density of cocoon was 108.8 m^{-2} on late August 1971 and its average weight was 19.6 mg fresh wt. This is equivalent to 7.544 KJ m^{-2} of cocoon production: 21.133 × 108.8 × 0.0196 × (1

- 0.83224). The respiration rate increased after March 8 and reached the maximum rate of 2.423 KJ m^{-2} d^{-1} on June 10, 1971. Total respiration of this population was 193.669 KJ m^{-2}.

***Pheretima* sp. (H-1) in area D 1972:**

The biomass of *Pheretima* sp. (H-1) in area D 1972 increased after Feb., reached a maximum level on May 23. This highest level has been maintained for the period of the rainy season (Fig. 3-4). The maximum biomass was 8.378 g dry wt m^{-2} (177.067 KJ m^{-2}) on June 8, 1972. The average biomass was 4.368 g dry wt m^{-2} (92.299 KJ m^{-2}). The production was estimated at 11.489 g dry wt m^{-2} (242.672 KJ m^{-2}). The density of cocoon was 128.6 m^{-2} and the average weight of cocoon was 18.97 mg fresh wt. These mean 8.648 KJ m^{-2} of cocoon production. The respiration rate increased after Feb., reached a maximum level on June 19 and maintained the level for June. The maximum rate of respiration was 6.510 KJ m^{-2} d^{-1} on June 30, 1972. Total respiration was calculated as 589.275 KJ m^{-2}.

***Pheretima* sp. (H-1) in area G 1972:**

The population of *Pheretima* sp. (H-1) in area G 1972 was a part of the population of same species in area D 1972. The maximum biomass and the maximum respiration rate in area G appeared on June 1. They were 0.76 g dry wt m^{-2} (16.067 KJ m^{-2}) and 0.531 KJ m^{-2} d^{-1}, respectively (Fig. 3-5). The average biomass was 0.268 g dry wt m^{-2} (5.661 KJ m^{-2}). Total respiration was 44.124 KJ m^{-2}. The production was estimated as 1.174 g dry wt m^{-2} (24.686 KJ m^{-2}).

***Pheretima vittata* in area H 1968:**

The biomass and the respiration of *Ph. vittata* in area H 1968 showed a similar change with those of *Pheretima* sp. (H-1) in area H. Still, the biomass and the respiration of *Ph. vittata* continued till late autumn. The maximum biomass and the maximum respiration appeared on August 3. They were 1.964 g dry wt m^{-2} (41.505 KJ m^{-2}) and 1.473 KJ m^{-2} d^{-1}, respectively (Fig. 3-6). The average biomass was 0.883 g dry wt m^{-2} (18.661 KJ m^{-2}). Total respiration was calculated as 126.566 KJ m^{-2}. The production was estimated at 3.217 g dry wt m^{-2} (68.199 KJ m^{-2}).

***Pheretima irregularis* in area K 1968:**

The maximum biomass and the maximum respiration rate of *Ph. irregularis* in area K 1968 appeared on 3 July. These were 0.725 g dry wt m^{-2} (15.322 KJ m^{-2}) and 0.523 KJ m^{-2} d^{-1}, respectively (Fig. 3-7). The average biomass was 0.226 g dry wt m^{-2} (0.523 KJ m^{-2}) and total respiration was calculated at 43.639 KJ m^{-2}. The production was estimated at 0.827 g dry wt m^{-2} (17.573 KJ m^{-2}).

***Pheretima heterochaeta* in area D 1971-1973:**

The biomass increased in summer, and reached the autumn peak of 709.68 mg dry wt m^{-2} on Oct. 5, 1971 (Fig. 3-8). After the autumn peak, it increased again but decreased in winter and spring months. After, it increased to the maximum of 1368.3 mg dry wt m^{-2} on June 8, 1972. In July 1972, the biomass showed an abruptly decreased by the disappearance of matured individuals.

Afterwards, biomass's low level continued until January 1973. The average biomass for the active months was 694.73 mg dry wt m^{-2}. The production was estimated as 1597.62 mg dry wt m^{-2} (33.765 KJ m^{-2}). The respiration showed a similar change to that of the biomass, except the winter decrease of respiration due to low temperature condition. The respiration showed the autumn peak of 0.607 KJ m^{-2} d^{-1} on Oct. 5, 1971 and the maximum of 1.699 KJ m^{-2} d^{-1} on July 15, 1972. Total respiration was 234.467 KJ m^{-2}.

***Pheretima heterochaeta* in area G 1971-1972:**

Biomass and respiration of the population starting in summer 1971 in area G showed a similar change to that of same species in area D. However, the level of the value is different. Namely, the biomass showed the autumn peak of 2807.35 mg dry wt m^{-2} on Nov. 7, 1971 and the summer maximum of 2889.11 mg dry wt m^{-2} on June 1, 1972 (Fig.3-9). The average biomass for the active months was 1631.93 mg dry wt m^{-2}. The respiration showed the autumn peak of 1.427 KJ m^{-2} on Nov. 7, 1971 and the summer maximum of 3.799 KJ m^{-2} d^{-1} on July 19, 1972. Total respiration was 659.465 KJ m^{-2}. The production was estimated at 4724.3 mg dry wt m^{-2} (99.839 KJ m^{-2}).

Discussion

In general, the energy assimilated by population may be approximated by Assimilation = Production + Respiration (+ Cocoon production), so A are given as 224.001 KJ m^{-2} (P+R) for *Pheretima* sp. (H-1) in area H 1968, 356.008 + 7.544 KJ m^{-2} (P+R+CP) for *Pheretima* sp. (H-1) in area D 1971, 831.917 + 8.648 KJ m^{-2} (P+R+CP) for *Pheretima* sp. (H-1) in area D 1972, 68.810 KJ m^{-2} (P+R) for *Pheretima* sp. (H-1) in area G 1972, 194.765 KJ m^{-2} (P+R) for *Ph. vittata* in area H 1968 and 61.212 KJ m^{-2} (P+R) for *Ph. irregularis* in area K 1968, 268.232 KJ m^{-2} (P+R) for *Ph. heterochaeta* in area D 1971 - 1972 and 759.304 KJ m^{-2} (P+R) for *Ph. heterochaeta* in area G 1971 - 1972.

Using A, P and R, some ecological important ratio: P/B (Production /Average biomass), P/Bmax (Production / Maximum biomass) and R/A (Respiration / Assimilation) are calculated. Production turn over rate mean the fraction of the total population which enters it in a given period or the fraction of population which is release in a given period. Turn over rate is defined as

P/B or E/B

Namely, this is an index of efficiency of biomass production (Petrusewicz and Macfadyen 1970). Ono (1972) and Morisita (1975) aroused a question about the average biomass (B). If the biomass of population is not changed with the passage of time, the ratio of the net production to the mean biomass will show a true over rate. However, if the biomass is greatly changed with the passage of time, the ratio of the pure production to the average biomass will become a meaningless index. Morisita (1975) proposed the new conception, an average appearance time of the unit biomass. He maintained, it is necessary to define the turn over rate of the population into which the biomass is greatly changed as a ratio of the net production to the maximum biomass. A new definition of the turn over rate means the following. How many times does the unit biomass change places in the average appearance time of the unit biomass? New turn over rate (P/B_{max}) is used in this thesis just like past turn over rate (P/B). Table 3-1 summarizes these ratios with those of *Pheretima sieboldi* (Horst) (Sugi and Tanaka 1978 a) and of *Pheretima* sp. (H-1) under the artificial environment condition (chapter 10). Each animal's energy buget reflects each animal's thermodynamics characteristic (Ono 1972). The productivity efficiency of Pheretima species will be compared with those of various animals.

There are small difference in the ratios among eight populations of litter dweller (Table 3-1), these being litter feeder or raw humus feeder. This may be due to the similar food resource requirement, despite some difference of density change (Sugi and Tanaka 1978 a). On the other hand, the ratios of soil dweller Pheretima were very different from those of litter dweller Pheretima. Productivity was slightly lower in soil dweller than in litter dweller, and respiration cost were higher (Table 3-1). The difference in Productivity depends on the difference between the length of the life period and the pattern of growth of each group. The soil dweller hardly grows up after passing the winter. On the other hand, the litter dweller keeps growing up excluding the growth stop of *Pheretima sieboldi* for the period of passing the winter. Byzova (1965) reported that soil dwelling Lumbricid showed lower respiration rate than that of Soil-litter or litter dwelling Lumbricid. The soil dweller maintains the biomass for a longer period compared with the litter dweller. High respiration cost of soil dweller Pheretima depends on long longevity. Satchell (1980) said that endogeic K-selected Lumbricid showed a lower productivity and larger cost for respiration than those of epigeic r-selected Lumbricid. Therefore, it is thought that a thermodynamics difference of each Pheretima group reflects each life type for each Pheretima group.

Respiration cost of the litter dweller Pheretima was in the range from 0.554 to 0.708. Those of the soil dweller Pheretima is from 0.874 to 0.869 (Table 3-1). Tanaka (1970) summarized the bio-energetic data of terrestrial arthropoda in a table. His table showed that R/A ratios such as Spittle bag, grasshoppers, and Collembola composed of two or more generations are distributed within the range of 0.55-0.65. These numerical values are approximated to the value of two Pheretima species well.

The values of P/B ratio of Pheretima species was in the range from 2.630 to 5.218 for litter dweller and 2.300 - 2.895 for soil dweller, also the value of P/B_{max} was in the range from 1.371 to 2.313 for litter dweller, and 1.168 - 1.635 for soil dweller (Table 3-1). P/B and P/B_{max} of Collembola are 12.06 and 5.37 respectively for *Isotoma trispinata* MacGillivray, and 8.14 and 3.66 respectively for *Onychiurus* sp.. (P/B_{max} of Collembola was calculated from Tanaka's data (1970)). Mishima (1973) reported that P/B of fresh water snail; *Semisulcospira bensoni* (PHILLIPI) was 6.1. Morisita (1975) summarized the values of P/B and P/Bmax of aquatic insects. His table show that P/B value is distributed between 2.4 and 9.7, and also P/B_{max} value is distributed between 0.8 and 3.7. P/B value and P/B_{max} value of *L. terrestris* are 0.33-0.47 and 0.22-0.32 respectively for Merlewood population, and 0.42-0.56 and 0.37-0.49 respectively for Heaning population (Lakhani and Satchell 1970). P/B_{max} ratio of *L. terrestris* were calculated, using the data of Lakhani and Satchell's paper. Nowak (1975) reported that P/B ratio of *Allolobophora caliginosa* (Savigny) was 0.39-1.3 in pasture land of Poland.

Among the above values, the values of Collembola are highest and the value of *L. terrestris* is smallest. As Tanaka (1970) said, the smaller body animal have a higher turn over rate compared with those of larger weight animals. However, *A. caliginosa* have a smaller weight and showed the lower turn over rate than those of many Pheretima species. *Lumbricus terrestris* and *Allolobophora caliginosa*: both take several years for maturation and live for more. Earlier Lumbricid was anesic (Litter - Soil dweller) and later Lumbricid was endogeic (soil dweller) (Satchell 1980). Then, the difference in productivity between Lumbricid and Pheretima might be due to the difference in longevity of life time but not in body size.

Summary

1) The energy equivalent of animal tissue of *Pheretima* sp. (H-1) was 21.133 ± 1.213 KJ g^{-1} dry wt. Respiration rate of *Pheretima* sp. (H-1) were 58.5 - 111.23 CO_2 for an individuals having one wet weight.

2) The energy budgets of several populations of Pheretima species were estimated. The assimilation (P+R) of *Pheretima* sp. (H-1) were 224.011 KJ m^{-2} in area H 1968, 356.008 KJ m^{-2} in area D 1971, 831.917 KJ m^{-2} in area D 1972 and 68.810 KJ m^{-2} in area G 1972. The assimilation of *Ph. vittata* was 194.765 KJ m^{-2} in area H 1968. The assimilation of *Ph. irregularis* was 61.212 KJ m^{-2} in area K 1968. The assimilation of *Ph. heterochaeta* were 268.322 KJ m^{-2} in area D 1971-1973 and 759.304 KJ m^{-2} in area G 1971-1972.

3) The R/A ratio of Pheretima were ranged between 0.544 and 0.713 for litter dweller Pheretima and 0.869-0.874 of soil dweller Pheretima. The values of litter dweller Pheretima were slightly smaller than those of Lumbricidae species.

4) P/B ratio, and P/B_{max} of litter dweller Pheretima were ranged between 2.631 and 5.218, and between 1.141 and 2.313, respectively. Also, the values of soil dweller Pheretima were 2.300-2.895 and 1.168-1.635, respectively. The values of litter dweller Pheretima were larger than those of Lumbricidae species.

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