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## ENERGY BUDGET AND PRODUCTION EFFICIENCY OF *TRIBOLIUM CONFUSUM* DUVAL IN THE DEVELOPMENT CYCLE

**ABSTRACT:** All elements of energy budget of *Tribolium confusum* have been investigated. Consumption and excretion were determined using the method based on analysis of uric acid in faeces, production — by gravimetric and calorimetric methods, whereas respiration — using volumetric respirometer and cartesian divers microrespirometers. Full instantaneous and cumulative energy budget was given as well as indices of energy transformation efficiency:  $U^{-1}$ ,  $K_1$  and  $K_2$ . A great difference was observed in production and metabolism level between the male and the female. *T. confusum* was compared as regards bioenergy characters with an allied species *T. castaneum* Hbst. and other insect species.

**KEY WORDS:** *Tribolium confusum*, *T. castaneum*, energy budget, indices of energy transformation efficiency.

### 1. INTRODUCTION

The first energy budgets constructed at the beginning of the century (H i r a t s u k a 1920, I v l e v 1939) are at present a commonly used way of describing the energy flow through an individual or a group of individuals. Information on the budget is used in various kinds of ecological investigations, both on the level of an individual or a group of individuals. It can be useful for physiologists or biochemists including those that study phenomena controlling the population or the whole biocenosis. It is also used in applied sciences such as animal breeding, plant protection and others. Energy budgets of insects, store-pests, such as *Cryptolestes ferrugineus*, *Rhyssopertha dominica* Fabr. (C a m p e l l and S i n h a 1977), *Tribolium castaneum* (K l e k o w s k i et al. 1967, M. P r u s and T. B. P r u s 1977), *Trogoderma granarium* Everts. (K r a s z p u l s k i 1984), *Sitophilus oryzae* L. (S i n g h et al. 1976), *Sitophilus granarius* L. (S z w y k o w s k a-R e y 1974), are of special significance. They allow

to determine the amount of energy, which will be lost by the stored product. Together with demographical data they allow to predict the growth rate of pest population and the extent of damage it causes.

Beetles of the genus *Tribolium*, because of interesting biology and easy culture, attracted the attention of scientists not only as store pests, but as a perfect object of investigations in many fields. They became model species used in ecology and also in genetics, physiology etc. These animals had been of special significance in population studies. They helped to understand the role of factors affecting the population density, such as reproduction, mortality, migrations, the effect of structures: age, sexual, spatial — on population dynamics. They were used to study competition phenomena (P a r k 1954, P a r k et al. 1964).

P a r k et al. (1961), when investigating genetic strains of species *T. castaneum* and *T. confusum*, have presented a hypothesis concerning mechanisms controlling the population. Population of *T. castaneum* is relatively much more limited by the influence of physiological characters, whereas in the case of *T. confusum* it is more the result of intrapopulation interactions — mainly cannibalism. P r u s (1961, 1968) has investigated the effect of density and degree of environmental conditioning by animals on populations of *T. confusum* and *T. castaneum*. He has found that these two factors decrease the population growth, and the mechanisms of population control of these two species are very efficient. In case of *T. castaneum* it takes mostly the form of limiting the physiological fecundity, whereas the population control of *T. confusum* is mostly the result of increased cannibalism. Comparison of both *Tribolium* species from the point of bioenergetics will allow to state, whether the above mentioned differences in mechanisms controlling the population growth, are connected with differences in energy flow and bioenergetic efficiency of these two species.

The bioenergetics of *T. castaneum* species has been already investigated: energy budget has been made (K l e k o w s k i et al. 1967). Still, it is not a full budget as at the time there was no efficient method for estimating consumption. This analysis among animals living in flour is very difficult as the faeces get mixed with food. To divide these components is a tedious task. Some scientists try to dye the food but this does not help much as it may disturb the feeding of animals. Introduction to food of an unassimilated by animals indicator, e.g.,  $\text{Cr}_2\text{O}_3$  (M c G i n n s and C a s t i n g 1964) or radioisotopes — e.g.,  $^{32}\text{P}$  (D o m i n a s 1975) has the same defect. The method based on analysis of carbohydrates, which occur in the food but not in the faeces (K r i s h n a and S a x e n a 1962), is not sensitive enough.

The present paper gives a full energy budget of species *T. confusum*. Consumption, assimilation and excretion were determined using the method of uric acid content analysis, which allowed to determine the faeces content in the habitat (B h a t t a c h a r y a and W a l d b a u e r 1969a, 1970). All parameters of energy budget were determined after Ivlev's (1938) equation:  $C = P + R + F$ ,  $A = P + R$ , where  $C$  — consumption,  $P$  — production,  $R$  — respiration,  $F$  — faeces,  $A$  — assimilation. Also gross index of energy transformation efficiency was calculated  $K_1 = P/C$ , as well as net index of production efficiency  $K_2 = P/A$ , index of assimilation efficiency  $U^{-1} = A/C$ .

## 2. MATERIAL AND METHODS

The strain of *T. confusum* — bIV — from the group of four genetic strains of this species, cultured at the Chicago University (P a r k et al. 1961), was used in the investigations.

The cultures and particular experiments were conducted under the following conditions: at  $29 \pm 0.2^\circ\text{C}$ , relative air humidity 70–74%, dark incubator.

The culture medium was a mixture consisting of 95% wheat flour "Wrocławska" (up to 0.5% ash content in dry wt) and 5% of dried baker's yeast. Both the medium and all vessels and tools used in the culture were thermally sterilized to avoid infection with parasitic microorganisms (mainly *Adelina triboli*, Sporozoa).

Two series of individual cultures, 25 individuals in each, were conducted in vials containing 1 g of medium. Every 48 h particular individuals were separated from the medium by means of a plankton net of a mesh size 0.3 mm. Individuals were placed in aluminium foil chambers, weighed on an CAHN electrobalance model G, then placed again in vials on a fresh batch of culture. At the same time it was checked whether the exuvium is in the vial, in order to determine the development stage of the animal. Sex was determined in the pupa stage (S o k o l o f f 1972). After eclosion individuals were mated. Particular pairs were placed in vials in an 8 g medium. The measurement were then made every 72 h to determine the fecundity of *Tribolium* (P a r k et al. 1961). Every 72 h individuals were sieved, placed in aluminium foil pan with high walls preventing the animals from escaping, and weighed. The culture medium from vials was sieved through a net of a mesh size 0.3 mm in order to separate the eggs. The eggs were counted, weighed, and after 6-day incubation under standard conditions, their hatching ability was determined.

The mean weight was for egg together with the flour cover, sticking surface of each egg immediately after oviposition. In order to obtain the real egg weight, egg samples were rinsed of flour covering them in a water drop under the microscope and weighed. Thus the mean weight of flour cover was calculated.

Insect bodies from particular stages, age groups and sex, killed by short exposure at about  $80^\circ\text{C}$ , were collected. This material was then used to determine water and ash contents and energetic equivalent. It was weighed, dried at  $60^\circ\text{C}$ , homogenized in mortar.

Ash content was determined by combustion in muffle furnace at  $450^\circ\text{C}$  during 12 h (D o w g i a ł ł o 1975). The energetic equivalent was determined by combusting samples in bomb calorimeter (K l e k o w s k i and B ę c z k o w s k i 1973, P r u s 1975a). The microbomb calorimeter by formula of Phillipson (P h i l l i p s o n 1964) was used. The same methods were used to analyse water and ash contents and the energetic value of the culture medium. The weight of exuvia was determined by weighing samples containing 10–60 individuals on an electric balance CAHN, whereas their energetic equivalent was determined by combustion in bomb calorimeter.

The respiratory metabolism rate of animals was determined by two methods.

Respiration of eggs and young larvae — to the 8th day of development was determined by the method of cartesian divers microrespirometers (K l e k o w s k i 1975a). The eggs and 1–2 day old larvae were investigated in divers of a volume 3.8–11.8 mm<sup>3</sup> (particular individuals were used only for single series of measurements). The 2–8 day old larvae were investigated using divers of a volume 110–204 mm<sup>3</sup> (K l e k o w s k i 1984), placing them in divers with a little of culture medium. The production of carbon dioxide was also determined by the method of cartesian divers (K l e k o w s k i 1971).

For each age of an organism, 10–30 oxygen consumption measurements were made, this including 5–8 with measurements of CO<sub>2</sub> evolution and calculations of respiratory quotient. The respiration of other development stages was examined by the method of volumetric respirometers (K l e k o w s k i 1975b). Thus individual cultures were conducted in 1 mg culture medium, in respiration chambers every 2 days, connected to respirometers to make the measurements. Compensation chambers of respirometers also had 1 g of culture medium. Respiration chambers were darkened using aluminium foil. After measurements the animals were separated from the culture medium and weighed on CAHN balance. Next, they were placed in respiration chambers with fresh medium culture. The animals after attaining maturity were paired. They were separated into different chambers only during the measurements. This was done in order to keep the animals in the state of reproductive activity. Before pairing, both males and females were marked by dots of nitrocellulose laquer. Production of carbon dioxide was also determined by means of volumetric respirometers. The experiment was conducted in two repeats with 7 individuals. In the first repeat only oxygen consumption was measured, and in the second — also production of carbon dioxide. The respiratory quotient was calculated.

Determination of the food ration of animals feeding on flour is rather complicated. The gravimetric method — weight determination of food loss as a result of grazing, requires data on faeces content in the mixture remaining after animal grazing.

Faeces content was determined using the method described by B h a t t a c h a r y a and W a l d b a u e r (1969a) based on an analysis of uric acid content. It assumes constant amount of uric acid in faeces at simultaneous absence of this compound in the food. In order to determine consumption and faeces production, groups counting about 50 individuals were bred in 300–400 mg of culture medium, in 4 day periods. The weight loss of culture medium in particular cultures during the experiments was calculated, and afterwards medium samples were analysed for uric acid content. An enzymatic-spectrophotometric method of analysing uric acid content in faeces samples was used with uricase — a selective enzyme decomposing uric acid (B h a t t a c h a r y a and W a l d b a u e r 1969b). The uric acid content in faeces samples was also analysed. These results allowed to determine faeces content in medium when the culture terminated. Thus, it has been possible to determine consumption, faeces production and assimilation efficiency. Consumption and excretion equivalents are related to group cultures, they can not be used in the energy budget of individuals. Thus only the index of food assimilation efficiency  $U^{-1}$ , calculated acc. to parameters taken from the group experiment, was used.

Energy budget according to symbols used in the present paper is as follows:

$$C = \Delta B + B_{ex} + P_r + R + FU$$

where:  $C$  — consumption,  $\Delta B$  — body biomass increment,  $B_{ex}$  — biomass of exuvia (including egg shells),  $P_r$  — reproduction,  $R$  — respiration,  $FU$  — rejecta.

Budgets of instantenous and cumulative type are constructed using the method described by P r u s (1975b). The period of embryonic development was examined in 24 h intervals, further development in 2-day intervals, and reproduction period in 3-day intervals.

The consumption was calculated by dividing assimilation estimated as a sum of production and respiration by index of assimilation efficiency  $U^{-1}$  — determined in a group experiment separately for larvae and adult insects. The excretion was calculated from the difference:  $FU = C - A$ .

The  $t$ -Student's test was used to check the significance of differences in bioenergetic and physiological parameters between males and females and between particular moments of development of individuals. With the help of thest of  $t$ -Student or nonparametric ranged sign test (acc. to G r e ń 1978) the significance of differences of particular characters between species *T. confusum* and *T. castaneum*, were investigated.

### 3. RESULTS

Mean development time from the hatching of larvae to the emergence of an adult individual is  $27.6 \pm 1.7$  days. Adding the 5.6 days for embryonic development (P a r k et al. 1961), one obtains a development cycle lasting 33.2 d. This is only a mean result, as within a population there are two groups, distinctly differing in the number of larval stages and development time (B i j o k 1986). This difference is about 3.2 d. The differences occur also in the growth rate and body weight.

The growth of *T. confusum* larvae approximates the logarithmic curve. Maximum body weight, being on the average 3.15 mg, occurs shortly before the prepupa stage. Then, the body weight decreases in the stage of pupa and adult individual.

During the embryonic development, both the percentage of dry weight and ash in egg, increase. These values decrease once the larva is hatched. Their further changes are connected with the growth and eclosion (Fig. 1). Adult females have higher ash content and body hydration than males.

Energetic equivalent of one milligramme of dry eggs' weight (Fig. 2) ranges between 5.8 and 6.0 cal (24.3 — 25.1 J). One milligramme of dry weight of just hatched larvae has a much higher energetic equivalent — 6.29 cal (26.3 J). This equivalent decreases fast and then begins to increase during a long time, attaining the maximum just before the larvae pass into the inactive stage — 7.20 cal (30.1 J). Characteristic for the inactive stages is the gradual drop of energetic equivalent. Females, when entering the reproduction period, show a decrease of energetic equivalent, which becomes significantly lower than in males ( $P < 0.01$  on the 38th day,  $P < 0.001$  on the 46th day).

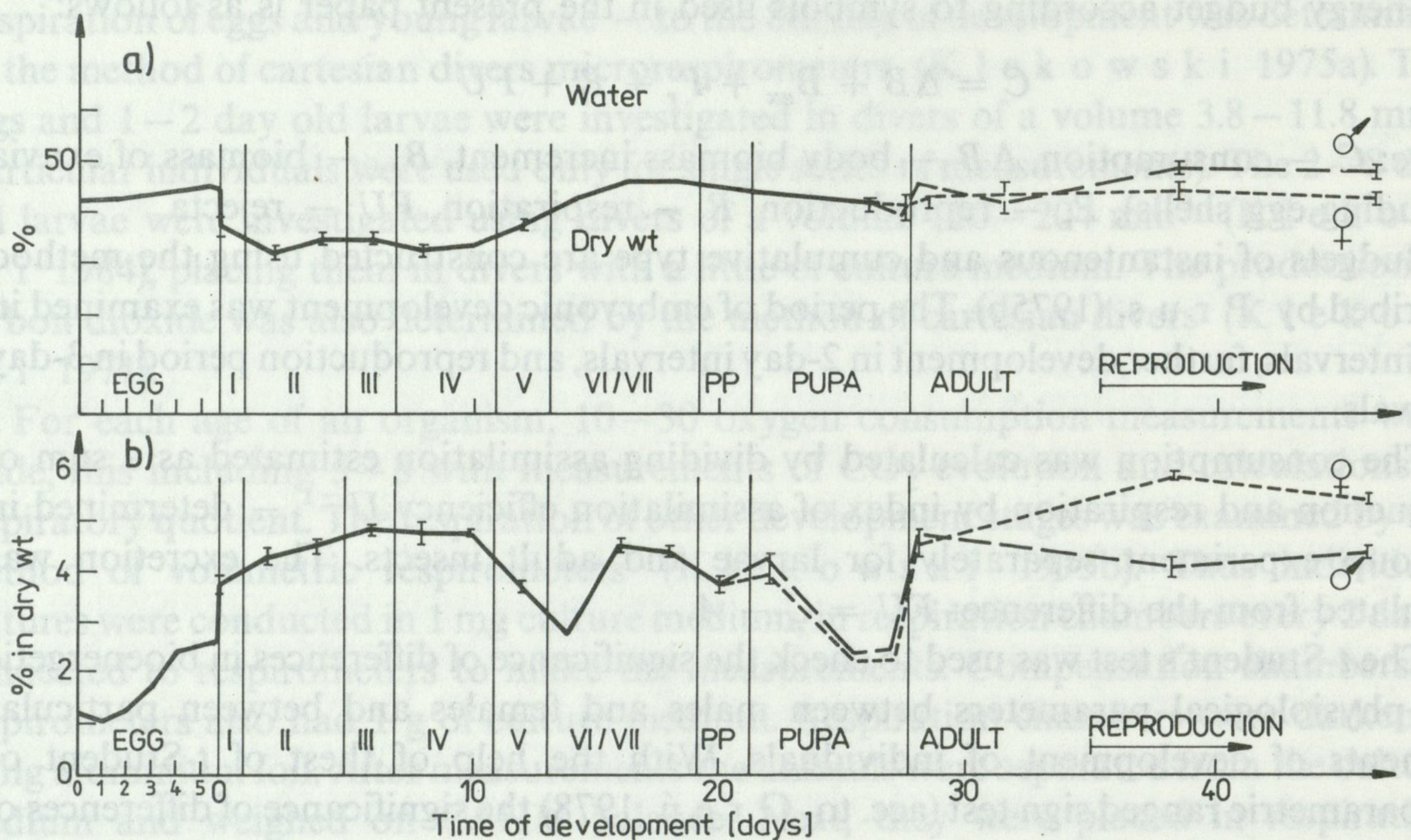


Fig. 1. Changes in water, dry weight (a) and ash (b) content of *T. confusum* body in its development (means  $\pm$  SD)

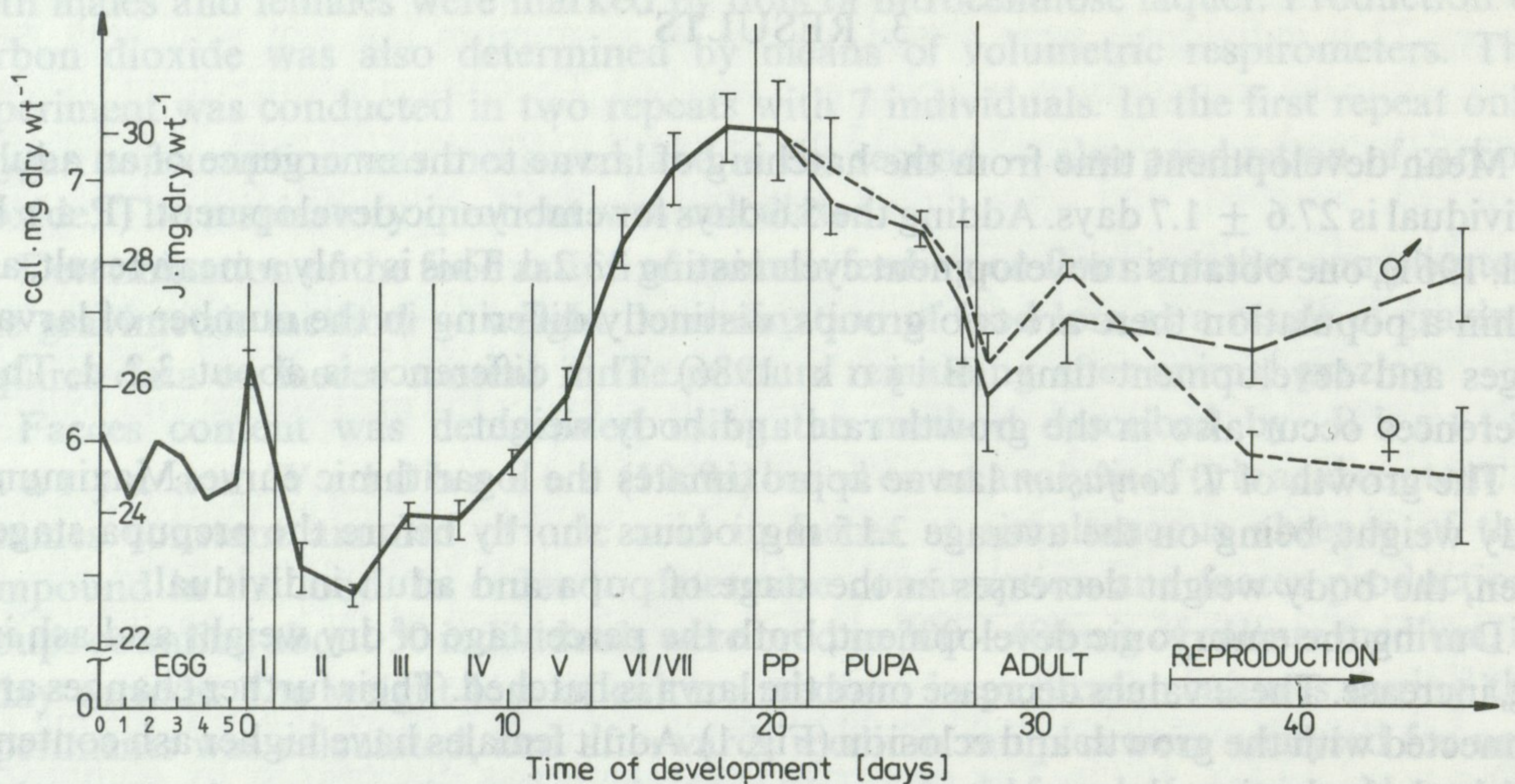


Fig. 2. Changes of energetic equivalent of 1 mg dry wt of *T. confusum* body in its development (means  $\pm$  SD)

On the 46th day these equivalents are 5.88 and 6.64 cal/mg (24.6 and 27.8 J/mg) for males and females, respectively.

An increase of total energetic value of body of an average *T. confusum* individual (Fig. 3) during the period of greatest body increment, i.e., between the 10th and 18th day of development, is rather even. After storing the maximal amount of energy — 10.45 cal

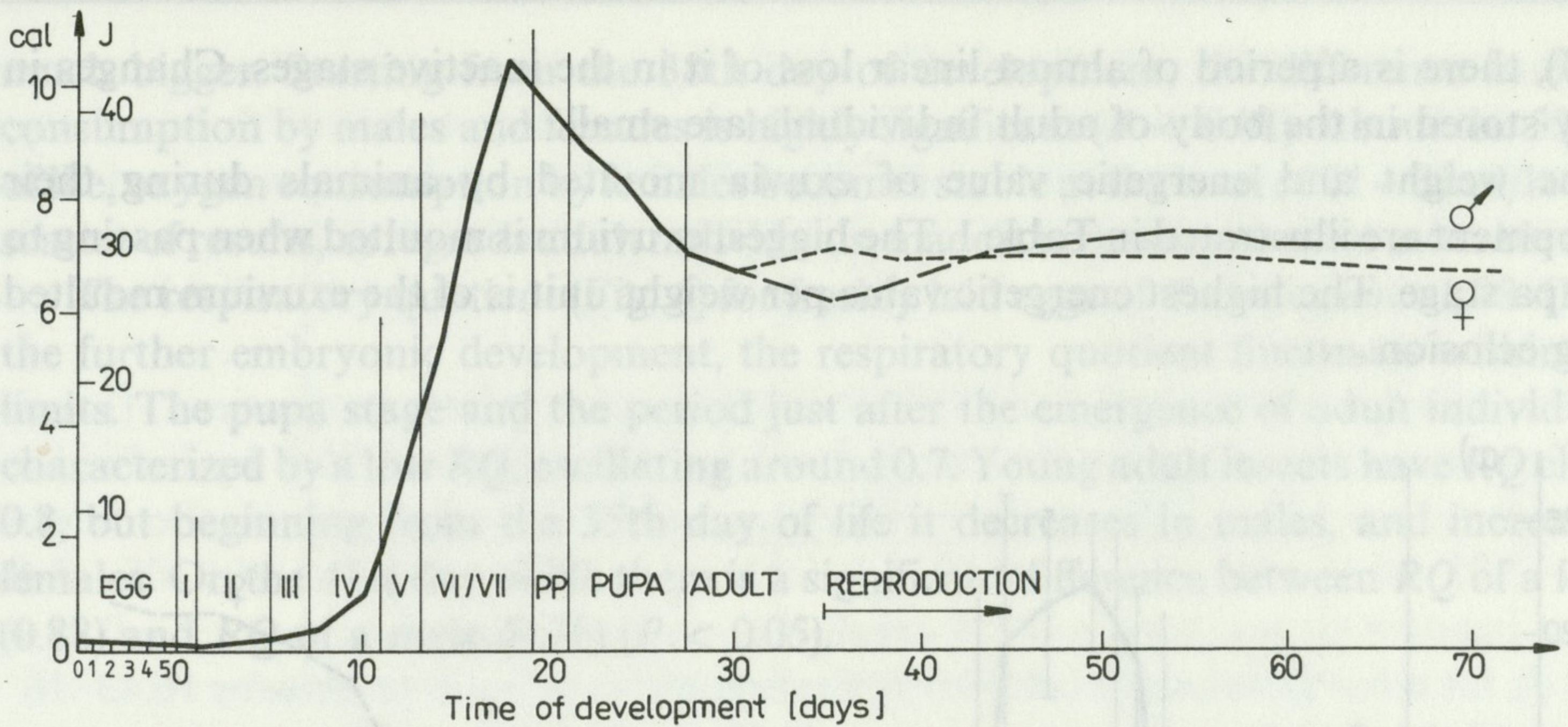


Fig. 3. Changes of energetic value of one individual *T. confusum* in its development

Table 1. Characteristics of exuvia occurring between particular development stages of *Tribolium confusum* (Roman numerals – larval stages)

Stages	Moment of exuvium appearance (days of growth)	Mean dry wt $\pm$ SD $\mu$ g	Energetic equivalent of 1 mg dry wt $\text{cal} \cdot \text{mg}^{-1}$ ( $\text{J} \cdot \text{mg}^{-1}$ )	Total energetic value mcal (mJ)
Egg – I*	0	$5.0 \pm 1.14$	—	7.266 (30.44)
I – II	1	$1.74 \pm 0.11$		7.865 (32.93)
II – III	5.04	$5.67 \pm 0.30$		25.62 (107.2)
III – IV	7.08	$9.59 \pm 0.39$		43.55 (181.5)
IV – V	10.57	$20.48 \pm 0.70$	$4.52 \pm 0.22$ ( $18.92 \pm 0.92$ )	92.57 (387.6)
V – VI	13.08	$44.53 \pm 2.16$		201.3 (842.6)
VI – VII	16.85	$55.69 \pm 4.41$		251.7 (1054)
Prepupa – pupa	21.25	$64.14 \pm 1.61$	$4.62 \pm 0.21$ ( $19.34 \pm 0.88$ )	296.3 (1241)
Pupa – adult	27.61	$31.98 \pm 1.38$	$5.12 \pm 0.22$ ( $21.44 \pm 0.92$ )	163.7 (685.5)

\*Egg shell.

(43.7 J), there is a period of almost linear loss of it in the inactive stages. Changes in energy stored in the body of adult individuals are small.

The weight and energetic value of exuvia moulted by animals during their development are illustrated in Table 1. The biggest exuvium is moulted when passing to the pupa stage. The highest energetic value per weight unit is of the exuvium moulted during eclosion.

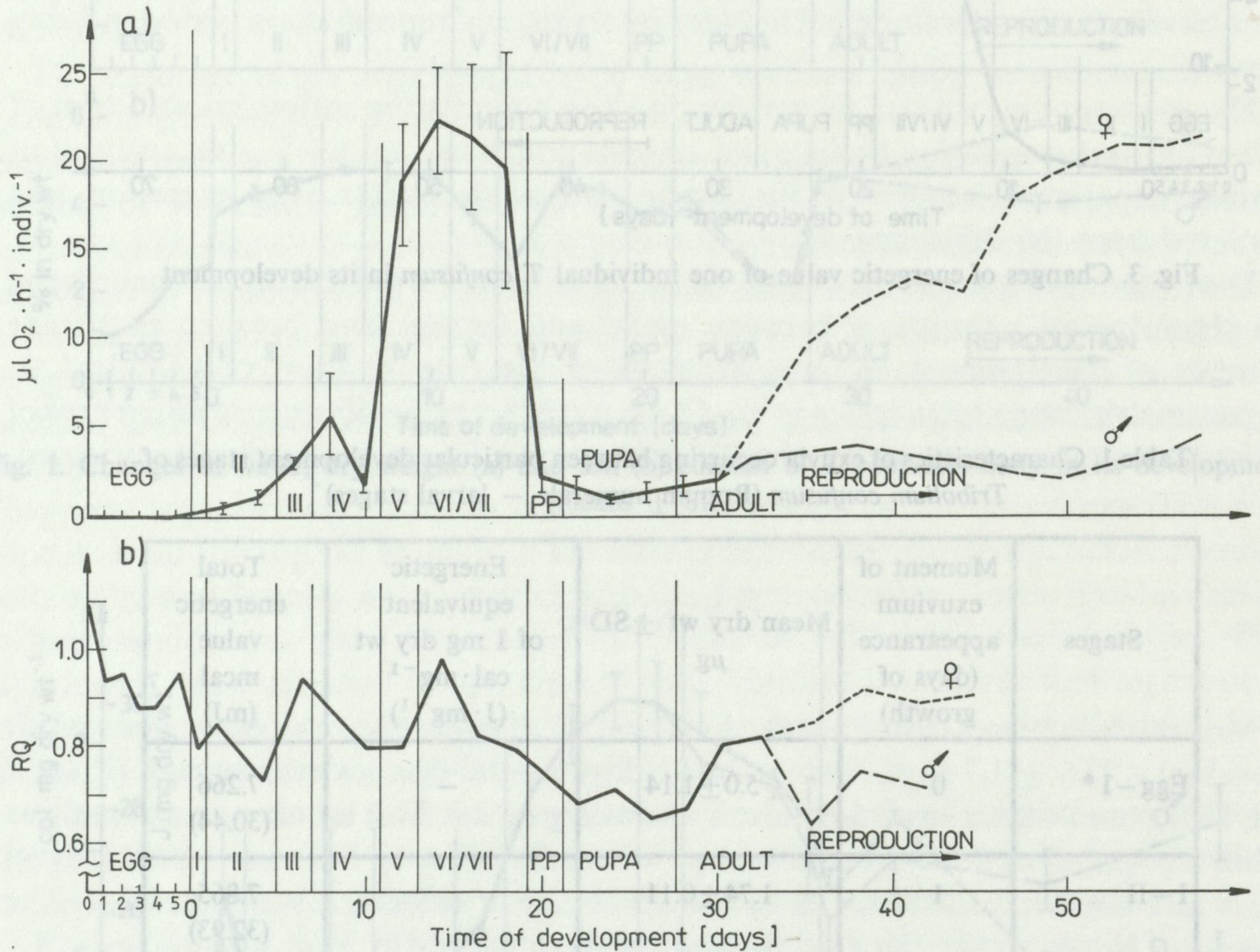


Fig. 4. Oxygen consumption (a) and respiratory quotient (b) of *T. confusum* in its development (means  $\pm$  SD)

Oxygen consumption in a freshly laid egg of *T. confusum* is  $9.5 \cdot 10^{-3} \mu\text{l/h}$ . Logarithmic growth of oxygen consumption rate during the larval period (Fig. 4) is disturbed by metabolism decrease on the 10th day of development. Oxygen consumption by a 10-day larva is only slightly higher than of a 4-day larva. This decrease in metabolism is statistically highly significant ( $P < 0.001$ ) and was also distinct in two series of the experiment. Between the 12th and 18th day of development oxygen consumption remains on a high level — on the average  $18.9 - 22.4 \mu\text{l/h}$ . The period of inactive stages — prepupa and pupa, and two first days of life of adult individuals are characterized by very low oxygen consumption, not exceeding  $2.3 \mu\text{l/h}$ . The minimum falls more or less in the middle of this period, i.e., on the 24th day of development —  $1.02 \mu\text{l/h}$ . From about the 32-nd day of development (i.e., some 4 days since the transformation), begins the period of increasing metabolism. In case of males it is small — oxygen consumption does not exceed  $5 \mu\text{l/h}$ . In females, the metabolism increase is



much bigger. Starting from the 38th day of development, the difference in oxygen consumption by males and females is highly significant ( $P < 0.01$ ). About the 53d day of life, oxygen consumption by females becomes stable at the level of 21 – 22  $\mu\text{l}/\text{h}$ . Great scatter of results, as regards adult individuals, made it necessary to use a movable mean.

The respiratory quotient (Fig. 4) for freshly laid eggs of *T. confusum* is 1.08. During the further embryonic development, the respiratory quotient fluctuates within some limits. The pupa stage and the period just after the emergence of adult individual, is characterized by a low  $RQ$ , oscillating around 0.7. Young adult insects have  $RQ$  close to 0.8, but beginning from the 35th day of life it decreases in males, and increases in females. On the 41st day of life there is a significant difference between  $RQ$  of a female (0.88) and  $RQ$  of a male (0.76) ( $P < 0.05$ ).

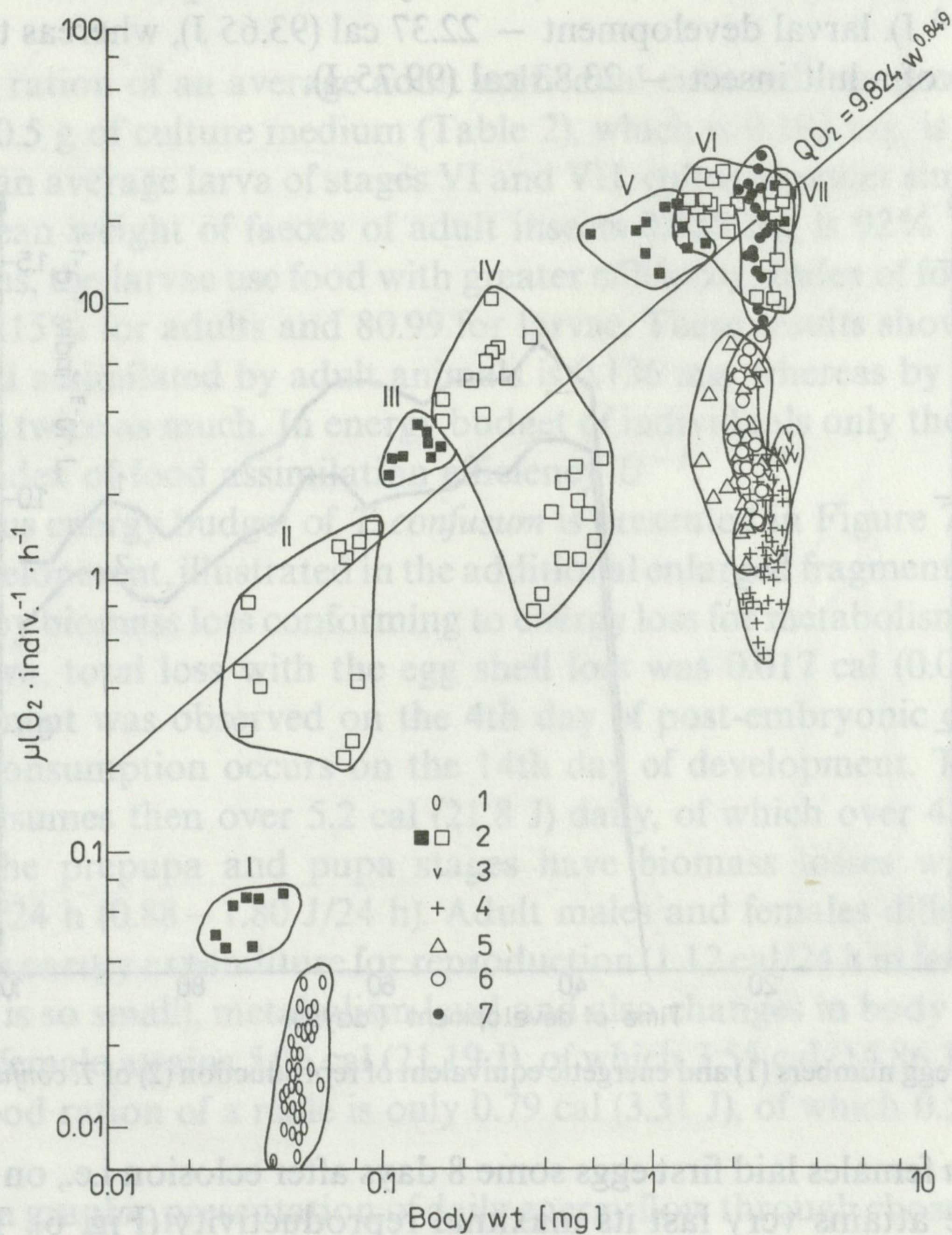


Fig. 5. Weight dependance of oxygen consumption in *T. confusum*

Generalised equation for growing larval stages (II–VII), 1 – eggs, 2 – larval stages, 3 – prepupae, 4 – pupae, 5 – adult males, 6 – adult females not reproducing yet, 7 – reproducing females, Roman numerals mean larval stages

Correlation coefficient between body weight of larvae from the II<sup>nd</sup> to VII<sup>th</sup> stage and the oxygen consumption by them is  $R = 0.826$ . This relation can be presented in

the form of line  $QO_2 = 9.824 w^{0.849}$ , which in the double logarithmic system is presented by regression line (Fig. 5). Points corresponding to the IVth larval stage concentrate in two groups, corresponding to the 8th day of development and to the characteristic decrease of metabolism on the 10th day. In drawing the regression line eggs, larvae of the I stage (not growing), pupae, prepupae and adult individuals were not taken into consideration.

Oxycalorific equivalents for particular values of respiratory quotient (Lusk 1928) were used to calculate the energy used for metabolism in 24 h by individuals of a given age. Thus, the daily metabolism values for eggs are in the interval  $1.14 - 3.95 \cdot 10^{-3}$  cal ( $4.77 - 16.54 \cdot 10^{-3}$  J), for larvae:  $0.0049 - 2.259$  cal ( $0.0205 - 9.458$  J), for inactive stages:  $0.115 - 0.258$  cal ( $0.481 - 1.080$  J), for adult males: ca 0.48 cal (2.01 J), for adult females: 2.5 cal (10.5 J). Embryonic development absorbs  $16.43 \cdot 10^{-3}$  cal ( $68.77 \cdot 10^{-3}$  J). larval development — 22.37 cal (93.65 J), whereas total growth till the emergence of adult insect — 23.83 cal (99.75 J).

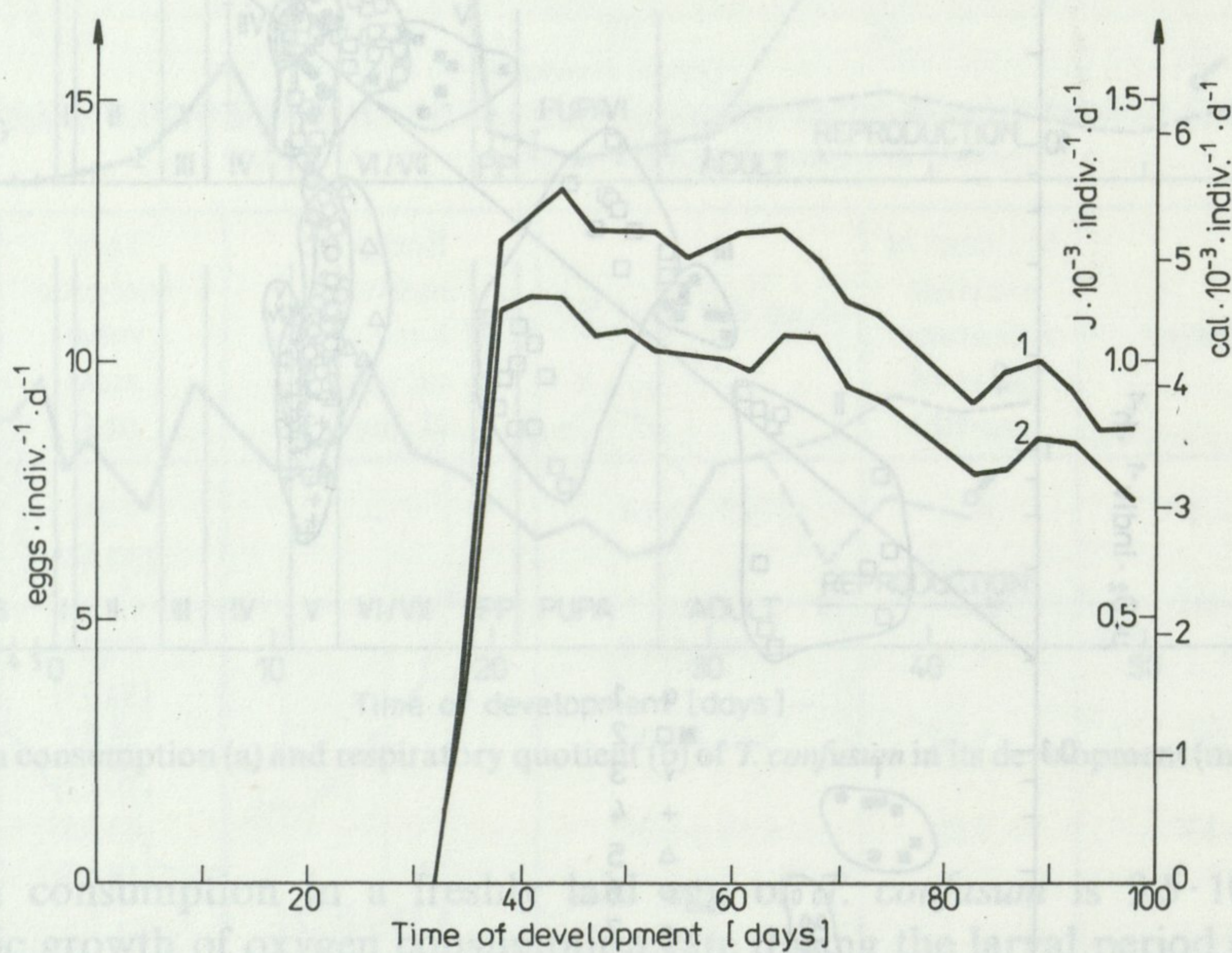


Fig. 6. Changes in egg numbers (1) and energetic equivalent of reproduction (2) of *T. confusum* female per day

*T. confusum* females laid first eggs some 8 days after eclosion i.e., on the 35th day of life. The female attains very fast its maximal reproductivity (Fig. 6). Then, the value  $12 \text{ eggs} \cdot \text{female}^{-1} \cdot 24 \text{ h}^{-1}$  in the initial stage of high fecundity (about the 40th day of life), decreases gradually to less than  $9 \text{ eggs} \cdot \text{female}^{-1} \cdot 24 \text{ h}^{-1}$  (about the 100th day of life). Also the hatching capability of eggs tends to decrease with the age of females. Thus, the number of live progeny hatched from eggs laid by females in 24 hrs decreased from 7.3 individuals in the initial stage of reproduction, to some 4 individuals at the end of observations (100th day of life). The energy located by females in eggs decreases from 1.1 cal (4.6 J) on the ca 40th day of life to over 0.7 cal (3 J) on the 100th day of life.

Table 2. Daily consumption and excretion as well as assimilation efficiency of *Tribolium confusum* individuals in group culture (mean values  $\pm$  standard deviations)

Stage	Consumption mg · ind. <sup>-1</sup>	Faeces mg · ind. <sup>-1</sup>	Assimilation efficiency $U^{-1}$ %
Adult	0.193 $\pm 0.027$	0.057 $\pm 0.006$	70.15 $\pm 0.75$
Larva	0.326 $\pm 0.012$	0.062 $\pm 0.004$	80.99 $\pm 0.23$

Daily food ration of an average adult individual cultured in a group of a density 50 animals in 0.5 g of culture medium (Table 2), which is 0.193 mg, is hardly 60% of food ration of an average larva of stages VI and VII, cultured under similar conditions (0.326 mg). Mean weight of faeces of adult insects 0.057 mg is 92% of larval faeces (0.062 mg). Thus, the larvae use food with greater efficiency. Index of food assimilation efficiency is 70.15% for adults and 80.99 for larvae. These results show that the daily amount of food assimilated by adult animals is 0.136 mg, whereas by larvae — 0.264 mg, i.e., almost twice as much. In energy budget of individuals only the abstract value was used — index of food assimilation efficiency  $U^{-1}$ .

Instantaneous energy budget of *T. confusum* is presented in Figure 7. The period of embryonic development, illustrated in the additional enlarged fragment of this figure, is characterized by biomass loss conforming to energy loss for metabolism. On the day of hatching a larva, total loss with the egg shell loss was 0.017 cal (0.071 J). The first biomass increment was observed on the 4th day of post-embryonic development.

Maximal consumption occurs on the 14th day of development. The larva of the VIth stage consumes then over 5.2 cal (21.8 J) daily, of which over 4.2 cal (17.6 J) is assimilated. The prepupa and pupa stages have biomass losses within the range 0.21–0.43 cal/24 h (0.88–1.80 J/24 h). Adult males and females differ considerably, both as regards energy expenditure for reproduction (1.12 cal/24 h in females, not given for males as it is so small), metabolism level and also changes in body biomass. Daily food ration of female attains 5.06 cal (21.19 J), of which 3.55 cal (14.86 J) is assimilated, whereas the food ration of a male is only 0.79 cal (3.31 J), of which 0.56 cal (2.34 J) is assimilated.

Figure 8 is a graphic presentation of daily energy flow through chosen development stages of *T. confusum*. Thus, in the case of pupa and egg, the whole metabolism is covered at the expense of biomass loss of organism. In the case of young larva (I stage) and young adult individual, the assimilated energy does not cover entirely the expenditure for respiration, and in the case of a larva — also that for exuvium production. The deficit is replenished at the expense of body biomass. In all these cases it is a “negative production”, i.e., own body biomass loss. In the case of an adult male, the production is practically none and the whole assimilated energy covers the

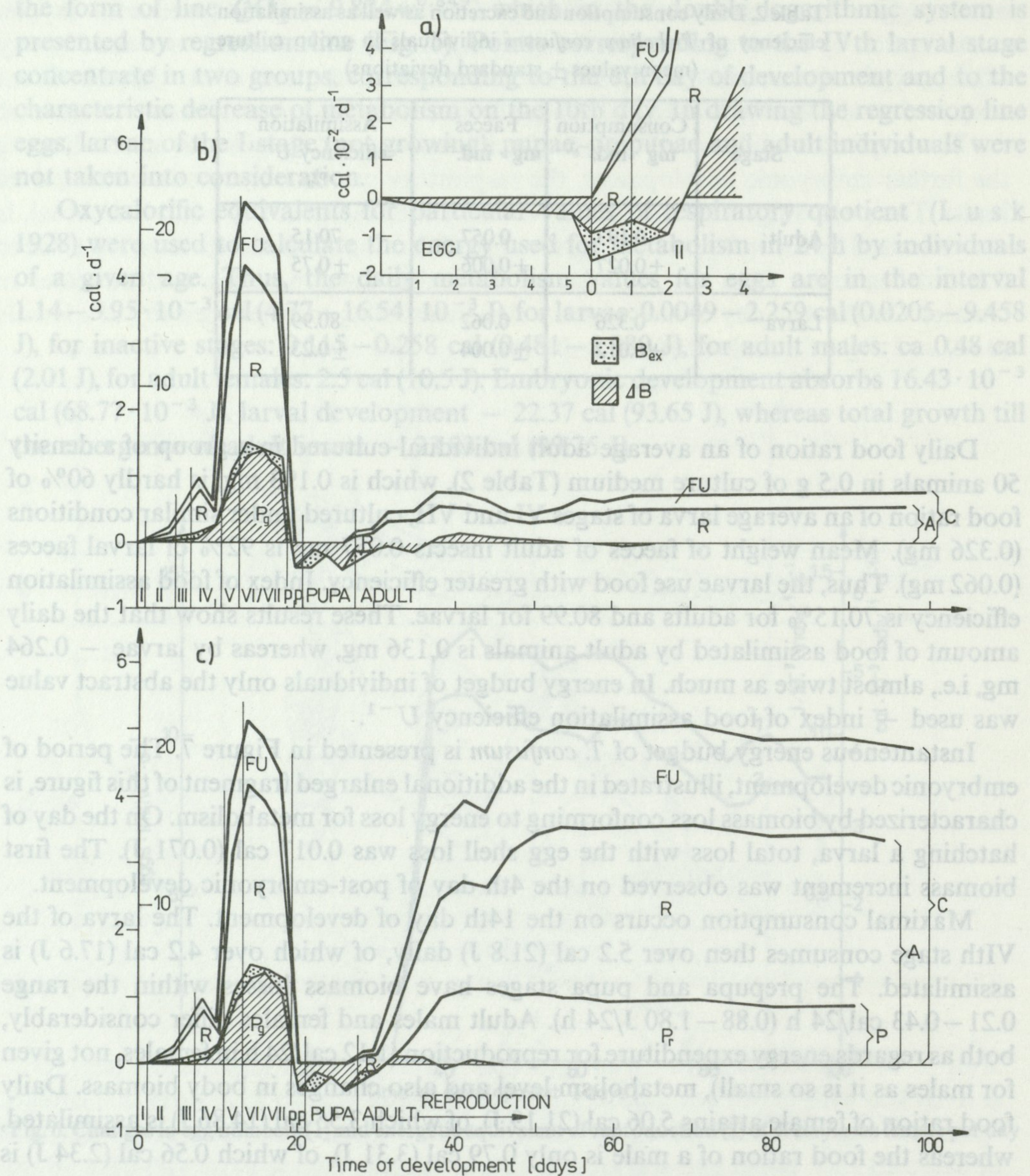


Fig. 7. Instantaneous energy budget of *T. confusum*

a – early developmental stages, b – males, c – females,  $\Delta B$  – change in biomass,  $B_{\text{ex}}$  – biomass of exuvia,  $P_g$  – growth production (body + exuvia),  $P_r$  – reproduction,  $P$  – total production,  $R$  – respiration,  $FU$  – faeces,  $A$  – assimilation,  $C$  – consumption

metabolism expenditure. When the larva grows, the production consists of body increment and moulting of exuvia, whereas in the case of adult female – of egg production. The course of variation of indices of production efficiency (Fig. 9) is discontinuous as there are periods of “negative production”. For young larvae (II and

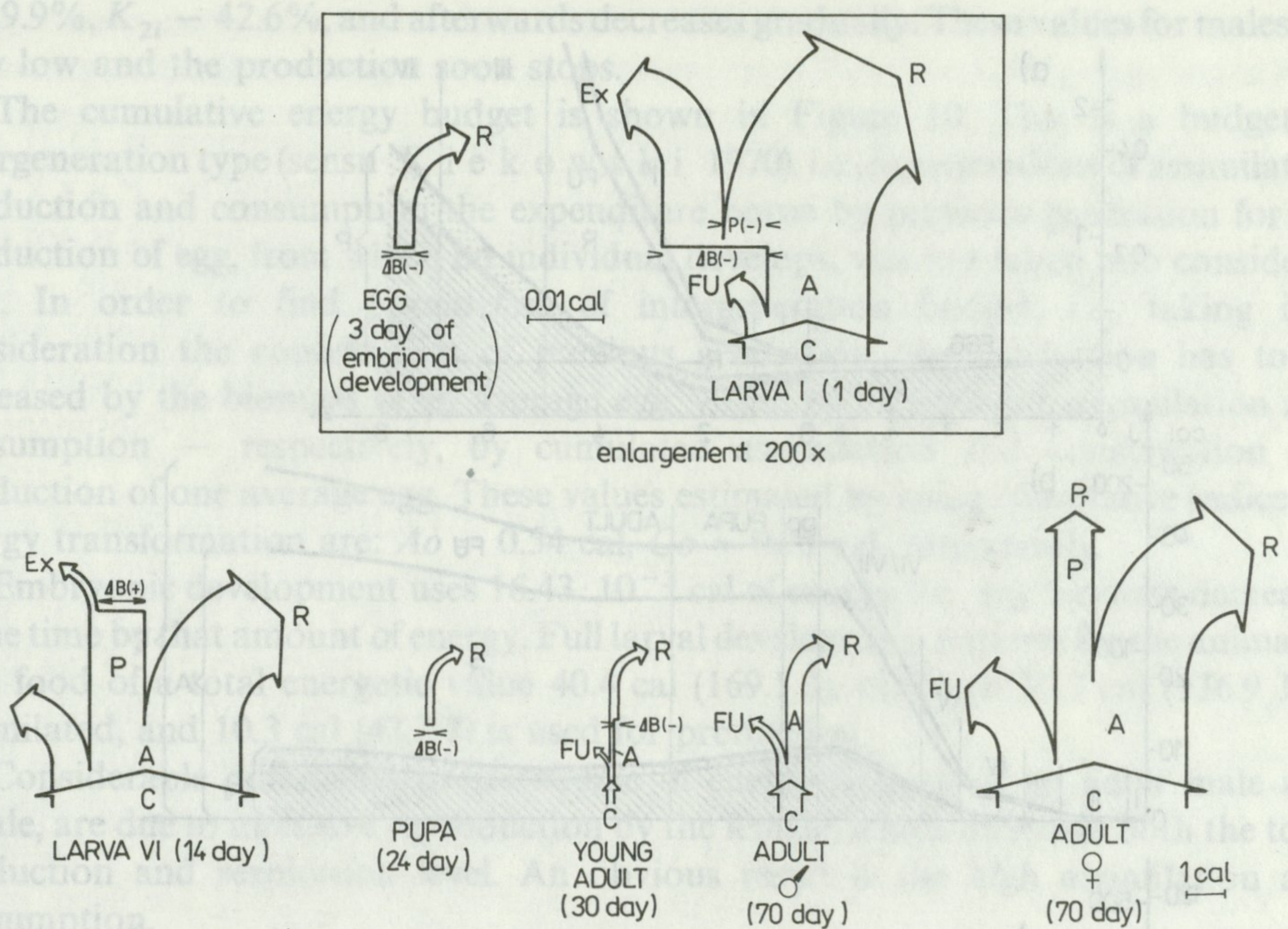


Fig. 8. Energy flow through *T. confusum* individual in some moments of its development

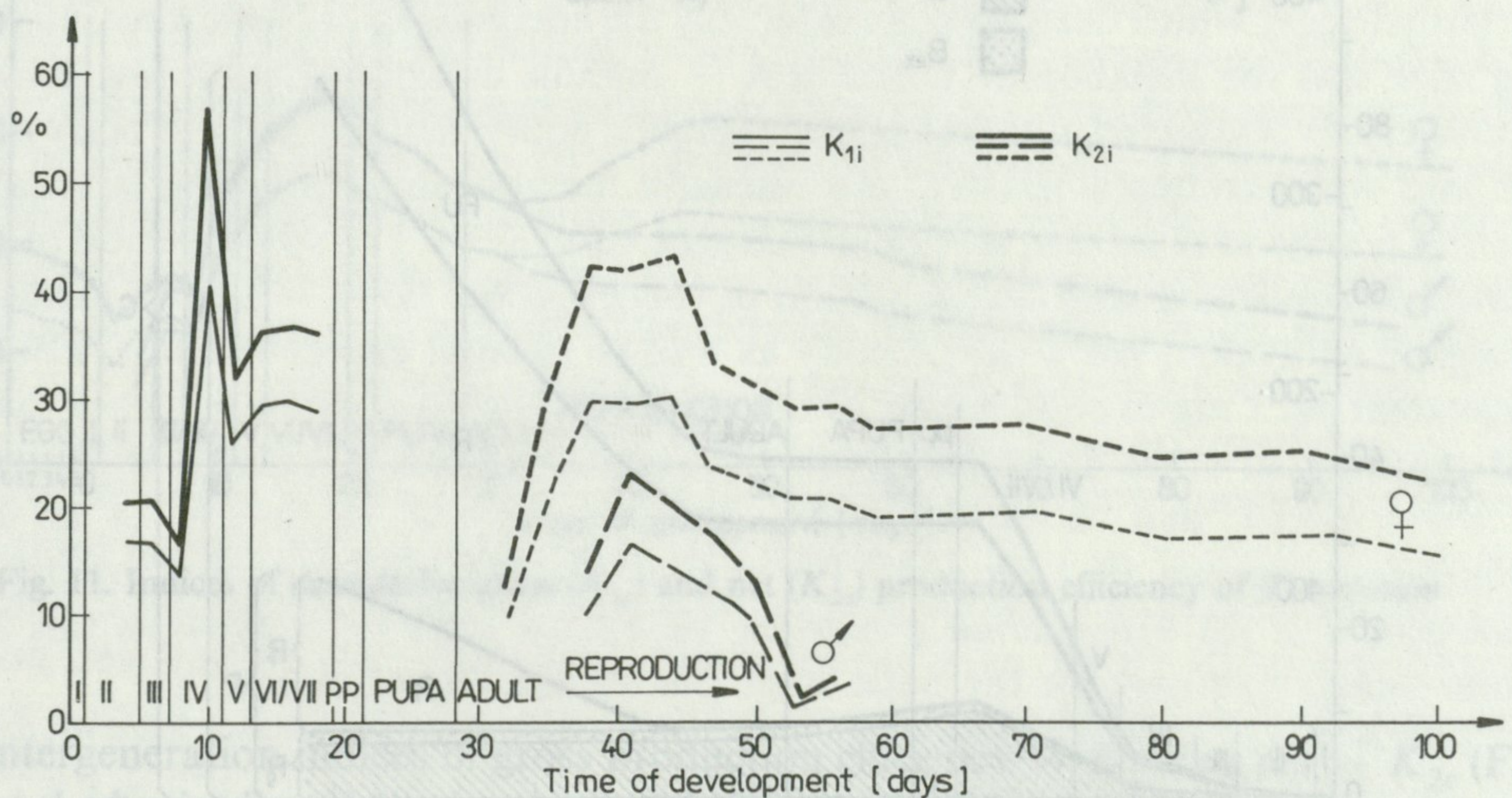


Fig. 9. Indices of instantenous gross ( $K_{1i}$ ) and net ( $K_{2i}$ ) production efficiency of *T. confusum*

III stage) the gross index  $K_{1i}$  is 16.5%, whereas net index  $K_{2i}$  — 20.5%. The maximum 40.6 and 57.0%, respectively, is observed for the characteristic 10th day of development, when metabolism decreases considerably maintaining the growth rate. At the end of larval development, the indices are 29 and 36%, respectively. Production efficiency of adult female increases when starting the reproduction, attaining  $K_{1i}$

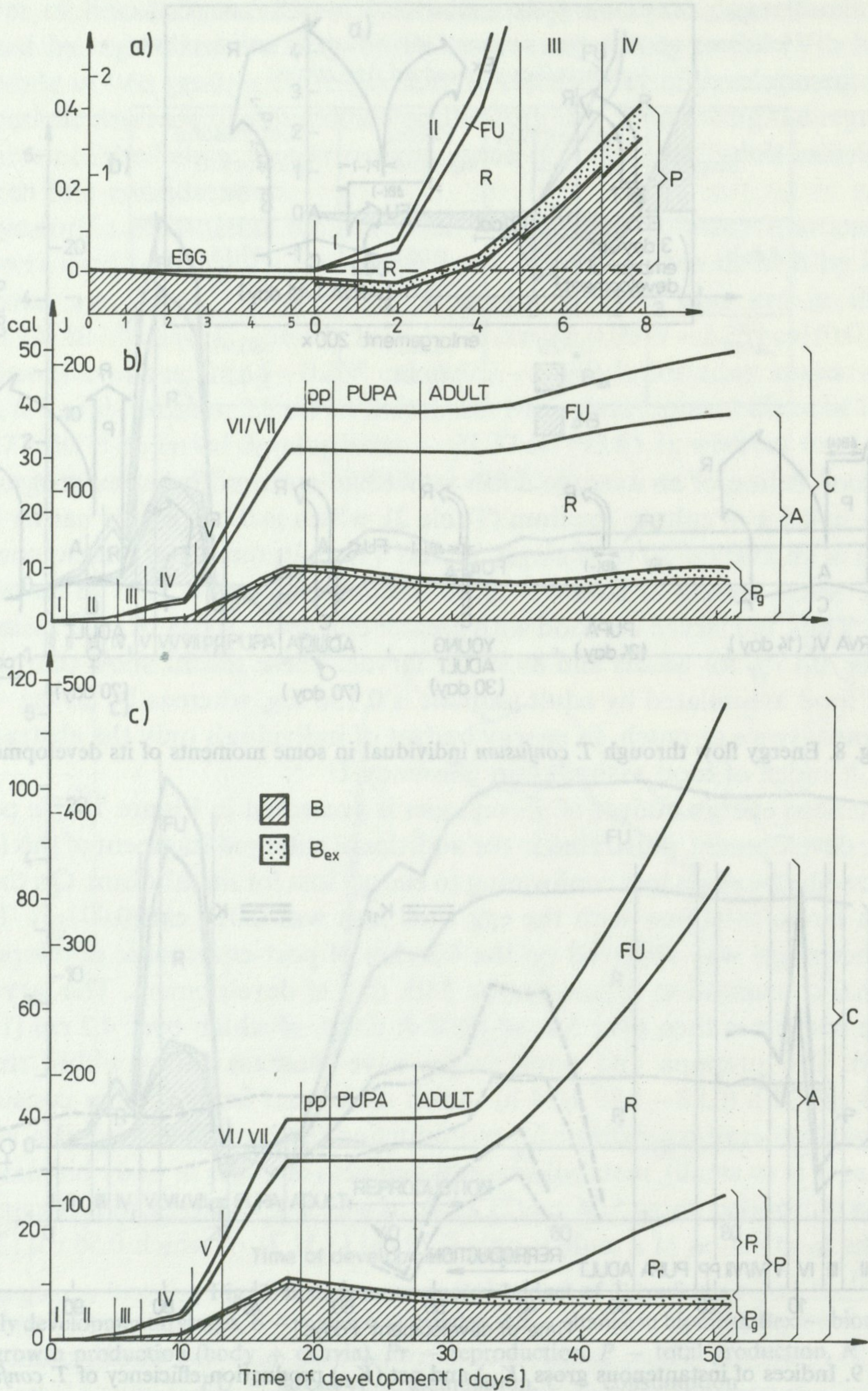


Fig. 10. Cumulative energy budget of *T. confusum*

a - early developmental stages, b - males, c - females,  $B$  - body biomass,  $B_{ex}$  - biomass of produced exuvia,  $P_g$  - growth production (body + exuvia),  $P_r$  - reproduction,  $P$  - total production,  $R$  - respiration,  $FU$  - faeces,  $A$  - assimilation,  $C$  - consumption

— 29.9%,  $K_{2i}$  — 42.6%, and afterwards decreases gradually. These values for males are very low and the production soon stops.

The cumulative energy budget is shown in Figure 10. This is a budget of intergeneration type (sensu K l e k o w s k i 1970), i.e., in estimations of assimilation production and consumption the expenditure borne by previous generation for the production of egg, from which an individual develops, was not taken into consideration. In order to find parameters of intergeneration budget, i.e., taking into consideration the contribution of previous generation, the production has to be increased by the biomass of an average egg — i.e., by 0.10488 cal, assimilation and consumption — respectively, by cumulated assimilation and consumption per production of one average egg. These values estimated by using cumulative indices of energy transformation are:  $A_0 = 0.54$  cal,  $C_0 = 0.75$  cal, respectively.

Embryonic development uses  $16.43 \cdot 10^{-3}$  cal of energy, i.e., egg biomass decreases at the time by that amount of energy. Full larval development requires for the animal to take food of a total energetic value 40.4 cal (169.1 J), of which 32.7 cal (136.9 J) is assimilated, and 10.3 cal (43.3 J) is used for production.

Considerable differences in the course of energy budget, of an adult male and female, are due to intensive reproduction by the female, which increases both the total production and respiration level. An obvious result is the high assimilation and consumption.

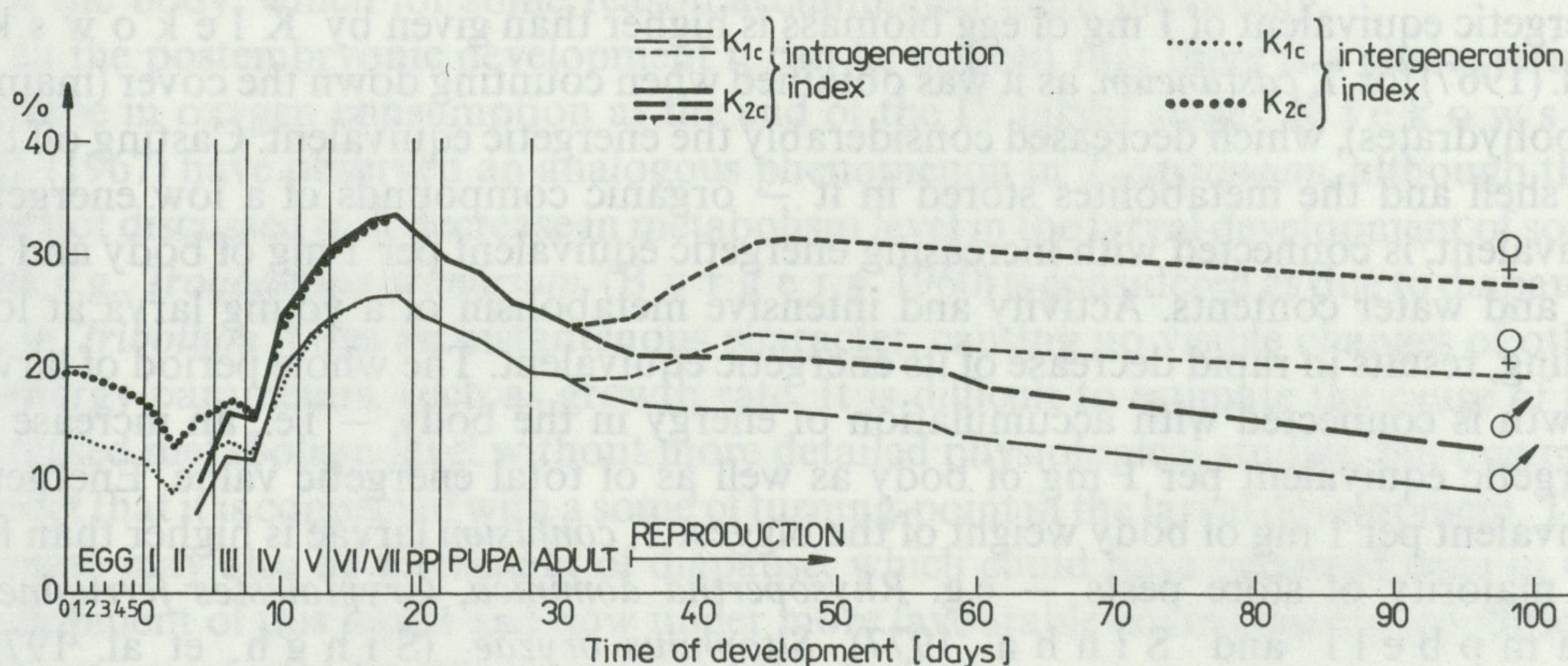


Fig. 11. Indices of cumulative gross ( $K_{1c}$ ) and net ( $K_{2c}$ ) production efficiency of *T. confusum*

Intergeneration indices of gross production efficiency —  $K_{1c}$  and net —  $K_{2c}$  (Fig. 11), at the beginning of development, are 13.95 and 19.88%, respectively. Intergeneration indices can be estimated only when the production begins to assume positive values. Maximum production efficiency is attained at the last larval stage. The indices are then:  $K_{1c}$  — 26.72%,  $K_{2c}$  — 33.01%, respectively. Production efficiency of adult females attains the maximum on about the 44th day of their life. The indices being then:  $K_{1c}$  — 23.29%,  $K_{2c}$  — 31.01%, respectively. For males the indices decrease asymptotically to zero.

#### 4. DISCUSSION

The mean time of an *Tribolium confusum* individual development is 33.21 days. Comparing this with the time of *T. confusum* development obtained by Park et al. (1961) — 32.24 days, so it can be said that the difference less than one day is not great, and considering the great variability within a strain as regards growth rate — is not significant. Thus conditions under which all manipulations with developing animals were made (i.e., mainly temperature and humidity) approximated sufficiently those planned for the experiment to prevent any significant changes of the development rate.

Generally the growth of *T. confusum* individuals approximates that of *T. castaneum* (Prus 1976) (characteristic rapid growth of last larval stages). This type of growth occurs, amongst others, in such insects as: store product pests as *Sitophilus oryzae* (Singh et al. 1976) and *Trogoderma granarium* (Kraszpulski 1984). Maximum body weight of *T. confusum* is higher than of *T. castaneum* by 0.5 mg, on the average. Thus, *T. confusum* is a species attaining greater weight at a slightly longer development cycle. When comparing the total daily weight increment (visible in Fig. 7) with analogous values for *T. castaneum* (Klekowski et al. 1967), a considerable prevalence of *T. confusum* is observed. Generally the changes in weight are similar.

During the embryonic development, the reserves stored in egg are used, mainly organic compounds, which cause proportional increase of ash content (Fig. 1). Energetic equivalent of 1 mg of egg biomass is higher than given by Klekowski et al. (1967) for *T. castaneum*, as it was obtained when counting down the cover (mainly carbohydrates), which decreased considerably the energetic equivalent. Casting off the egg shell and the metabolites stored in it — organic compounds of a low energetic equivalent, is connected with increasing energetic equivalent per 1 mg of body and its ash and water contents. Activity and intensive metabolism of a young larva at low feeding, results in rapid decrease of its energetic equivalent. The whole period of larval growth is connected with accumulation of energy in the body — i.e., an increase of energetic equivalent per 1 mg of body as well as of total energetic value. Energetic equivalent per 1 mg of body weight of the biggest *T. confusum* larvae is higher than for the majority of store pests — e.g. *Rhyssopertha dominica*, *Cryptolestes ferrugineus* (Campbell and Sinha 1977), *Sitophilus oryzae* (Singh et al. 1976), *Tribolium castaneum* (Klekowski et al. 1967). This value can be compared with analogous one for *Trogoderma granarium* (Kraszpulski 1984) as this beetle stores energy not only for the pupa stage but for the rest of its life.

The decrease in ash content during the most intensive development, may prove that it is the period of storing mainly highly energetic compounds. Klekowski et al. (1967) have observed rapid growth of lipid content in *T. castaneum* body in this period.

The female in pupa stage and before beginning the reproduction probably has some energy stored to begin egg production — and therefore higher energetic value. This reserve is probably used very quickly and the energetic value drops below the characteristic value for males. Similar relationship can be observed looking at the data on *Sitophilus oryzae* species (Singh et al. 1976), where energetic equivalent of



young females body was higher than of young males, but already after 2–3 days this difference practically no longer existed. A female intensively producing eggs has in her body more water than the male. S h l i e p e r (1936) has already shown that the rate of metabolism changes in the body is connected with the degree of body hydration.

Mean oxygen consumption during the embryonic development does not differ much from the equivalent characteristic for *T. castaneum*. However, the total energy used in the embryonic period for metabolism by *T. confusum*, is higher because of longer development than in *T. castaneum*.

Low respiratory quotient at the beginning of the embryonic development was also observed among grasshoppers (E d w a r d s 1953).  $RQ$  over one unit shown by *T. confusum* egg immediately after being laid by a female, has been also recorded by K l e k o w s k i et al. (1967) in *T. castaneum*. Such high  $RQ$  values are characteristic for different biochemical processes. One of them can be the synthesis of lipids from carbohydrates (K l e i b e r 1961). Such a process can be expected in an egg, taking into consideration the data of K l e k o w s k i et al. (1967) showing low lipid content in a laid egg (less than 20%), increasing with the body growth. According to E d w a r d s (1953), metabolization of organic acids also gives a  $RQ$  above 1. As the recorded  $RQ$  values are a sum of biochemical processes in the organism, the actual  $RQ$  value over 1 should be treated, e.g., as a total effect of carbohydrate metabolism ( $RQ$  near 1 – L u s k 1928), synthesis of lipids ( $RQ > 1$ ) and expelling carbon dioxide from the body, which for some reason accumulated there previously.

In the postembryonic development it can be noticed that there is a characteristic decrease in oxygen consumption at the end of the IV larval stage. K l e k o w s k i et al. (1967) have observed an analogous phenomenon in *T. castaneum*, although they have not discussed it. A decrease in metabolism level in the larval development of some pests, e.g., *Trogoderma granarium* (B u r g e r s 1960) is considered as due to diapause, but in *Tribolium* it has an instantenous character, causing no visible changes of other bioenergy parameters, such as growth rate. It is difficult to estimate the cause of the decreased metabolism level without more detailed physiological studies, but one may suspect that it is connected with a some of turning-point in the larval development. This decrease may also be a remnant of diapause, which could have occurred once in the development of this insect and now under more favourable environmental conditions of the store infested by this insect, is on the decline.

Analysis of oxygen consumption in the larval stage shows a relatively long period of intensive respiration (12–18th day), much longer than in *T. castaneum* species (K l e k o w s k i et al. 1967) or several other insects, where a single peak is observed. In case of *T. confusum* the period of increased respiratory activity is much longer than in *T. castaneum*, but simultaneously the metabolism level is much lower and so the development is longer but less rapid. However, the comparison of total energy engaged in metabolism during the larval period shows that it is higher in *T. confusum*, despite a milder course of respiration rate.

Analysis of the relationship between the weight and oxygen consumption by growing stages (regression line in the form of  $R = aW^b$ ) shows that the exponent  $b = 0.849$  seems to be identical as in case of *T. castaneum* (K l e k o w s k i et al.

1967). Coefficient  $a$  of equation, much lower than in case of *T. castaneum* proves the lower metabolism level per body weight unit, i.e., generally lower metabolic activity of the species.

Passing through the pupa stage is illustrated by typical  $U$ -shaped curve of respiration rate (E d w a r d s 1953) with minimal values more or less in the middle of that period.  $RQ$  values are here very low, proving mainly the lipid metabolism. This phenomenon is being commonly observed in holometabolic insects and is so distinct that can even change the respiratory quotient of the whole population, when great numbers of pupae appear (M. P r u s and T. B. P r u s 1977).

Metabolism changes in adult females are quite different from those observed in *T. castaneum* by K l e k o w s k i et al. (1967). The main reason is the difference in the course of experiment. In the case of *T. castaneum* we are dealing with a typical individual culture, in which animals do not have a chance of developing their reproduction activity. Thus it is a metabolism connected with the life of organism and not reproduction. Thus the difference between the metabolism in females and males is so small. In case of *T. confusum*, particular pairs of individuals were almost in constant contact (separated only for few hours, every three days when measuring respiration), providing conditions for reproduction. Thus, their metabolism attained the level indispensable for reproduction. Inputs of matter and energy on reproduction are incomparably greater in the case of female than the male, and it is not surprising that their metabolism level is distinctly higher. In the case of males the shape of curves for *T. confusum* and *T. castaneum* do not differ significantly. Intensive egg production by females can be the cause of higher respiratory quotient — e.g., as a result of synthesis of lipids from food containing mainly carbohydrates.

Consumption and faeces production values in the experiment provide information on the extent of losses and pollution of flour by greatly concentrated insect populations. But these data can not be used directly in the energy budget of individuals. When constructing the energy budget only the abstract value was used — index of assimilation efficiency  $U^{-1}$ , assuming that it depends to a smaller extent on population density than on consumption and faeces production.

Food assimilation efficiency by *T. confusum* larvae of the last stages is distinctly higher than in adult individuals. C a m p b e l l and S i n h a (1977) have observed a similar relation in species *Cryptolestes ferrugineus*. They have also noticed that index  $U^{-1}$  is even higher in the earliest development stages of larvae. Similar are the observations of H i r a t s u k a (1920) in this studies on silkworm (*Bombyx mori*). As it can be seen, a young organism having the main task of the fastest and most effective body production, uses maximally the available food for building its own tissues. It can be expected that the food utilization by an adult female, engaged in equally intensive production, would be more effective than that of the male. Such is the case, for example, of silkworm (H i r a t s u k a 1920).

High  $U^{-1}$  index is typical for store pests grazing on food having high nutritive value, composed of food relatively easy to digest and assimilate (Table 3). Index  $U^{-1}$  for *T. confusum* larvae calculated by B h a t t a c h a r y a and W a l d b a u e r

Table 3. Comparison of indices of energy transformation in chosen insect species

Species	Food	Stage	$U^{-1}$	$K_1$	$K_2$	Author
<i>Tribolium confusum</i>	wheat flour + yeast	larva	80.99	25.6	31.6	Bijok present paper
		adult ♂		19.1–9.6	23.7–12.8	
		adult ♀		23.0	31.2	
<i>T. castaneum</i>	wheat flour + yeast	larva	—	—	30.0	Klekowski et al. 1967
		adult	—	—	22–47	
<i>Sitophilus granarius</i>	enriched cereal food	larva	87.7	12.4	14.2	Baker 1974
<i>S. oryzae</i>	enriched cereal food	larva	95.8	24.1	24.9	Baker 1974
<i>S. oryzae</i>	wheat grain	larva	78.30	16.4	20.9	Singh et al. 1976
		adult ♂	79.81	10.6	13.7	
		adult ♀	81.20	9.9	12.2	
<i>Cryptolestes ferrugineus</i>	wheat grain	larva	66–79	1–16	3–23	Campbell and Sinha 1977
		adult	66–69	—	22	
<i>Trogoderma granarium</i>	wheat germs	larva	40.6	17.9	44.0	Kraszpulski 1984
		adult ♂	30.2	13.9	46.0	
		adult ♀	40.1	12.0–13.9	34.6	
<i>Bombyx mori</i>	mulberry leaves	larva	45.85	29.2	64.0	Hiratsuka 1920
<i>Lestes sponsa</i>	animal food	larva	35–46	25–35	65–90	Fischer 1970

(1970) as 62.9% is slightly lower than given in the present paper as it is for the whole larval development together.

General diagram of energy flow through an individual in particular development stages (Fig. 8) does not differ much for the typical one for holometabolic insects grazing on stored food products. There are periods when the energy budget is negative — i.e., energy expenditure of an organism is higher than the energy sampled by animal (Fig. 8). These are inactive stages: egg, prepupa and pupa as well as development stages immediately following them — i.e., young larva and young adult individual — which take little food.

Differences in the energy flow through adult males and females observed by K l e k o w s k i et al. (1967) are much smaller than those described here. This is so, because at respiration measurements *T. castaneum* individuals not contacting one another, i.e., not reproducing, were used. Here, it has been shown that intensive reproduction by a female requires high metabolism level resulting in an almost seven times higher energy flow through the female than through the male (Figs. 7, 8).

The intrageneration budget applied gives an idea about the energy flow within one individual, assuming as the initial point the moment of egg laying, from which this individual developed. However, this does not give any idea as to the energy flow between one generation and the second one in a given population. Thus the population is not treated as a continuous phenomenon from the point of view of bioenergetics, but only as a description of changes within one individual at a physiological level. Therefore, for a more ecological conclusion, the budget of intergeneration type (K l e k o w s k i 1970) should be used. In the case of *T. confusum* the difference between these two budgets is significant only in the initial development stage, when “inherited” energy after the previous generation contributes considerably to the budget. Intergeneration budget can be constructed assuming the energy stored in an egg as production at zero point, whereas the assimilation and consumption for egg production should be calculated using indices taken from the intrageneration budget.

S t ę p i e ń (1970) has calculated these values according to equations:

$$C_c = P_c/K_{1c} \quad \text{and} \quad A_c = P_c/K_{2c}$$

where  $C_c$  and  $A_c$  are appropriately cumulated consumption and assimilation for production of an average egg,  $P_c$  — production, i.e., energetic equivalent of an average egg, and  $K_{1c}$  and  $K_{2c}$  — cumulative indices of gross and net production efficiency taken from the intrageneration budget for half of the life of an average individual. Indices  $K_{1c}$  and  $K_{2c}$ , however, provide information only about the utilization of energy (consumed or assimilated, respectively) for total production, and not only for reproduction. Thus it seems right to use here other indices informing about utilization of energy for reproduction. They could be called indices of reproduction efficiency

$$\text{gross} - P_{rc}/C_c \quad \text{and} \quad \text{net} - P_{rc}/A_c$$

where  $P_{rc}$  is the cumulated reproduction (in this case eggs). Only thus defined indices allow to estimate proper consumption and assimilation for production of an average egg.

When comparing the species *Tribolium confusum* with a number of insects — store pests (Table 3) as regards production efficiency, it can be said that its position is quite high. Among the pests in the table, only *Trogoderma granarium* shows higher net production efficiency, whereas its gross production efficiency is lower because of less efficient food assimilation. The net production efficiency of adult *T. castaneum* individuals in the table is higher than the analogous one of *T. confusum*. However, one should look for the causes of it in the incompatibility of experimental methods. K l e k o w s k i et al. (1967), when working on the energy budget of *T. castaneum*, have assumed the weight of eggs produced by this insect as the total weight of eggs together with flour covers, which similarly as in *T. confusum* stick to the surface of egg shell immediately after being laid. This increases considerably the production calculated for the period of maturity. Furthermore, these authors, as it has been already mentioned, estimated the metabolism of individuals, i.e., individuals not engaged in production, much underrated, especially in the case of females. This results in further overrating of production efficiency indices. Thus it can be expected that adult *T. castaneum* individuals do not have to be always more efficient as regards bioenergy than *T. confusum* individuals. For the purpose of comparison the energy budget of *T. confusum* was again calculated adapting it to research methods from the paper by K l e k o w s k i et al. (1967). Therefore, egg production values were reestimated adding the flour covers. Respiration of an average male was assumed as respiration of an average adult individual, assuming that the metabolism level of not reproducing female and male is similar as shown by K l e k o w s k i et al. (1967). Thus calculated budget shows that the energy input for egg production is higher in *T. confusum*. Also

Table 4. Comparison of chosen parameters and bioenergy indices of *T. confusum* and *T. castaneum*

Parameters compared	<i>T. confusum</i>			<i>T. castaneum</i>	
Total energetic value of one individual (cal)					
larva	9.92	(b)*	>	7.02	(k)*
adult	7.0	(b)	>	5.1	(k)
egg with egg shell	0.221	(m)*	>	0.101	(k)
Energetic equivalent of 1 mg dry wt (cal · mg <sup>-1</sup> )	5.4–7.2	(b)	>(z)**	4.9–6.7	(k)
Metabolism level: coefficient $a$ of regression equation $QO_2 = aW^b$	9.8	(b)	<	19.9	(k)
Daily energy expenditure for production of eggs (cal)	1.2	(b)	>	1.0	(k)
$K_{2i}$ (%) larva (max)	56	(b)	(z)	50	(k)
$K_{2i}$ (%) adult (mean)	67	(m)	>(z)	48	(k)
Larval growth $K_{2c}$ (%)	31.6	(b)	>(z)	30.0	(k)
Adult (100th day) $K_{2c}$	56.78	(m)	>(z)	44.0	(k)

\* Authors: (b) — B i j o k — present paper, (k) — K l e k o w s k i et al. 1967, (m) — B i j o k — data from the present paper adapted to methods of (k), \*\* (z) — significance of difference was investigated using test of ranked signs.

indices of production efficiency of adult *T. confusum* individuals are higher than analogous ones characteristic for *T. castaneum* (Table 4). Before transforming the budget the conclusion was just the opposite (Table 3).

*Tribolium confusum* does not have much different production efficiency from other species of phytophagous plants. But it is lower as regards efficiency indices from, for example, the predatory species — larva of dragon-fly *Lestes sponsa* (Table 3).

The comparison of bioenergy parameters of two allied species *T. confusum* and *T. castaneum* (Table 4) shows that: (1) *T. confusum* attains a greater body weight — also the energetic equivalent of both the whole body and the body weight unit is higher. Similar is the case of eggs oviposited by females of these species. (2) *T. castaneum* is a more fertile species, although daily energy expenditure for egg production is slightly higher in *T. confusum*. (3) *T. castaneum* is characterized by higher level of respiratory metabolism. (4) *T. confusum* is more effective as regards transformation efficiency of available energy.

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## 5. SUMMARY

Full energy budget of *Tribolium confusum* was made. Strain bIV (P a r k et al. 1961) was used in the investigations. All elements of energy flow through an individual were investigated, such as consumption, excretion, food assimilation, production, respiration.

Consumption and excretion were determined using the method of analysis of uric acid in faeces (B h a t t a c h a r y a and W a l d b a u e r 1969a). Gravimetric and calorimetric methods were used to determine production. Respiration was estimated by volumetric respirometers and cartesian divers.

Two species were compared as regards bioenergy: *T. confusum* and *T. castaneum*, which despite being closely related, differ distinctly by the mechanism of population density control (P a r k et al. 1961, P r u s 1961, 1968).

Amongst others, it was found that the growth of *T. confusum* larvae approximates the logarithmic form. The maximum being on the average 3.15 mg is attained at the end of larval development. Energetic equivalent of 1 mg dry weight of body ranges between 5.8 and 6.0 cal/mg, whereas it is higher in adult males than in females (Fig. 2). The females are characterised by higher hydration and ash content in the body (Fig. 1). Logarithmic growth of rate of respiratory metabolism of a larva is disturbed by a decrease on the 10th day of development (Fig. 4). Food assimilation efficiency by a larva (80.99%) is higher than by an adult individual (70.15%) (Table 2).

There are periods, when the energy budget of *T. confusum* is negative, i.e., energetic expenditure is higher than energy taken by the organism (Fig. 8). A great difference was observed in the energy flow through a male and female. It consists of a difference in the metabolism level and in reproduction (Fig. 7). Cumulative energy budget was constructed (Fig. 10). The embryonic development uses  $16.43 \cdot 10^{-3}$  cal ( $68.8 \text{ J} \cdot 10^{-3}$ ) of energy and the full larval development requires together with food 40.4 cal (169.1 J) of energy, of which 32.7 cal (136.9 J) is assimilated, whereas 10.3 cal (43.3 J) is assigned for production.

Instantaneous maximum of production efficiency is attained on the 10th day of development  $K_{1i} = 40.6\%$ ,  $K_{2i} = 57.0\%$  (Fig. 9). Cumulative indices of production efficiency (Fig. 11) for the period of larval development are  $K_{1c} = 26.72$  and  $K_{2c} = 32.01\%$ , respectively (Fig. 11). For adult females these values are  $K_{1c} = 22.29$  and  $K_{2c} = 31.01\%$ , respectively. *T. confusum* has a rather high position among insects — stored product pests, as regards efficiency of energy transformation (Table 3).

The comparison of bioenergetic parameters of *T. confusum* and *T. castaneum* (Table 4) shows that *T. confusum* attains a greater weight body of and of eggs laid, as well as energetic equivalent. *T. castaneum* is more fertile, although its daily energy expenditure for reproduction is lower than in *T. confusum*. *T. castaneum* shows higher level of metabolism, *T. confusum* is however more efficient as regards energy transformation efficiency.

## 6. POLISH SUMMARY

Sporządzono pełen budżet energetyczny *Tribolium confusum*. Do badań użyto szczepu bIV (P a r k et al. 1961). Zbadano wszystkie elementy przepływu energii przez osobnika, jak konsumpcja, wydalanie, asymilacja pokarmu, produkcja, respiracja.

Do oznaczenia konsumpcji i wydalania zastosowano metodę z zastosowaniem analizy kwasu moczowego w fekaliach (B h a t t a c h a r y a i W a l d b a u e r 1969a). Do określenia produkcji użyto metod grawimetrycznych i kalorymetrycznych. Respirację określono przy użyciu respirometrów wolumetrycznych i nurków kartezyjskich.

Porównano pod względem bioenergetycznym dwa gatunki: *T. confusum* i *T. castaneum*, które mimo bliskiego pokrewieństwa różnią się wyraźnie mechanizmem regulacji liczebności populacji (P a r k et al. 1961, P r u s 1961, 1968).

Stwierdzono m.in., że wzrost larw *T. confusum* jest zbliżony do postaci logarytmicznej. Maksimum wynoszące średnio 3,15 mg jest osiągnięte pod koniec rozwoju larwalnego. Wartość energetyczna 1 mg suchej masy ciała utrzymuje się w granicach 5,8 – 6,0 cal/mg, przy czym jest wyższa u dorosłych samców niż u samic (rys. 2). Samice natomiast charakteryzują się wyższym uwodnieniem i udziałem popiołu w ciele (rys. 1). Logarytmiczny wzrost tempa metabolizmu oddechowego larwy jest zakłócony spadkiem w 10. dniu rozwoju (rys. 4). Wydajność asymilacji pokarmu przez larwę (80,99%) jest wyższa niż przez osobnika dorosłego (70,15%) (tab. 2).

Istnieją okresy, gdy bilans energii *T. confusum* jest ujemny, tzn. wydatki energetyczne są wyższe niż energia pobrana przez organizm (rys. 8). Zaobserwowano ogromną różnicę w przepływie energii przez samca i samicę. Składa się na nią różnica w poziomie metabolizmu oraz produkcji generatywnej (rys. 7). Skonstruowano kumulatywny budżet energetyczny (rys. 10). Rozwój embrionalny pochłania  $16,43 \cdot 10^{-3}$  cal ( $68,8 \text{ J} \cdot 10^{-3}$ ) energii, a pełny rozwój larwalny wymaga pobrania z pokarmem 40,4 cal (169,1 J) energii, z czego zasymilowane zostaje 32,7 cal (136,9 J), a na produkcję przeznaczone 10,3 cal (43,3 J).

Chwilowe maksimum wydajności produkcji jest osiągnięte 10. dnia rozwoju  $K_{1i} = 40,6\%$ ,  $K_{2i} = 57,0\%$  (rys. 9). Kumulatywne wskaźniki wydajności produkcji (rys. 11) za okres rozwoju larwalnego wynoszą odpowiednio  $K_{1c} = 26,72\%$  oraz  $K_{2c} = 32,01\%$  (rys. 11). Dla dorosłych samic wartości te wynoszą odpowiednio  $K_{1c} = 22,29\%$  oraz  $K_{2c} = 31,01\%$ . *T. confusum* zajmuje dość wysoką pozycję wśród owadów – szkodników magazynowych pod względem wydajności konwersji energii (tab. 3).

Z porównania parametrów bioenergetycznych *T. confusum* i *T. castaneum* (tab. 4) wynika, że *T. confusum* osiąga większy ciężar ciała i składanych jaj oraz wyższą wartość energetyczną. *T. castaneum* jest płodniejsze, aczkolwiek jego dobowy wydatek energetyczny na reprodukcję jest niższy niż u *T. confusum*. *T. castaneum* charakteryzuje się wyższym poziomem metabolizmu. *T. confusum* jest natomiast efektywniejsze pod względem wydajności konwersji energii.

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