Trophic preferences of *Rossiulus kessleri* (Diplopoda, Julidae) for the litter of various tree species

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Abstract

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This article analyses the results of a 10-day laboratory experiment investigating the consumption preferences of *Rossiulus kessleri* (Lohm.) when the leaf litter of 16 tree species was offered. During this experiment the rate of microbiological decay of the leaves of each tree species in the litter varied from 0.6 to 4.1% per day. The maximum rate of litter consumption by *R. kessleri* was found for *Acer negundo* L. (0.75 mg/mg of body weight per day), *Quercus robur* L. (0.50), *Malus domestica* Borkh. (0.36) and *Cerasus vulgaris* L. (0.35). For other tree species under investigation it did not exceed 0.11 mg/mg of body weight per day. In the dynamics of acclimation of *R. kessleri* to a new diet there are three main tendencies: 1) sharp increase in body weight on the first day of the experiment and stabilization thereof at a high level on the next day (for *Fraxinus lanceolata* Borkh. there was a 39% gain in weight, for *Salix alba* L. 29%, respectively); 2) decrease during the first three days of the experiment and further stabilization of body weight at a level not significantly different from the initial one (for *Populus alba* L., *Acer platanoides* L., *Cerasus vulgaris* L., *Gleditsia triacanthos* L. and *Aesculus hippocastanum* L.); 3) long-term acclimation of about one-week's duration with return to initial (*Quercus robur* L., *Ulmus laevis* Pall.) or lower body weight (*Populus nigra* L. – 13% lower than initial weight, *Acer negundo* L. – 12% lower, *A. pseudoplatanus* L. – 9% lower, *Pyrus communis* L. – 8% lower, *Pinus sylvestris* L. – 7% lower). In the conditions of absence of food in the container, average body weight for 4 days decreased by 10%, while a 50% death rate of the starved millipedes was recorded on the 6th day. The maximum proportion of daily weight of faeces (dry weight) to live body weight was observed in *R. kessleri* fed on *Pinus sylvestris* L. (0.58%), *Robinia pseudoacacia* L. (0.57%), *Pyrus communis* L. (0.54%) and *Populus alba* L. (0.53%). The minimum average daily formation of faeces was recorded in millipedes fed on *Acer pseudoplatanus* L., *Cerasus vulgaris* L., *Malus domestica* Borkh. and *Aesculus hippocastanum* L. (0.20–0.23% of body weight). A discrepancy in rates of microbiological and zoogenic decomposition of litter was found for various tree species in the conditions of the laboratory experiment.

Key words

Diplopoda, forest litter, Julidae, litter consumption, trophic preferences

Introduction

Litter saprophages of the macrofauna play various roles in the decomposition of plant residues: earthworms intensify the processes of humification (Edwards et al., 1970; Coleman et al., 1983), while Diplopoda and Isopoda, on the contrary, accelerate mineralization of plant residues (Anderson et al., 1983; Dangerfield and Telford, 1989). Peculiarities of the role of individual taxonomic groups in decomposition of plant residues have not been sufficiently studied: the scientific literature deals with feeding behavior of, at most, 15 millipede species (e.g. Telford and Dangerfield, 1993; Hashimoto et al., 2004).

Trophic activity of saprophages is determined by a number of environmental factors: temperature (Striganova, 1972; Fujiyama, 1996), substrate wetting (Baker, 1980; Brygadyrenko, 2006), length of daylight (Boccardo and Penteado, 1995) and season of observations (Crawford, 1978; Dangerfield and Telford, 1991; Bailey and Kovaliski, 1993; David and Gillon, 2002), set of food substrates, degree of decomposition and depth of their occurrence in soil (Bocock and Heath, 1967), microbial population of intestines and food (Crawford et al., 1983; Márialigeti et al., 1985). Besides, saprophages as well as other animal species are often susceptible to diseases, in particular, in laboratory conditions (Federici, 1984). For this reason studies of the majority of saprophage species should be planned so as to eliminate the possibility of infections arising, which could otherwise influence the results of experiments.

The ratio of food components, i.e. leaf litter of various species of woody and herbaceous plants, has the greatest influence on the intensity of food consumption by saprophages (Bertrand et al., 1987; David et al., 2001; Alhamd et al., 2004; Ashwini and Sridhar, 2005). The issue of food selectivity of saprophages with regard to leaf litter has been insufficiently studied for most tree species (Hunter et al., 2003; Roy and Joy, 2009; Semenyuk and Tiunov, 2011). Species of Diplopoda, when consuming the litter contribute to its mechanical breaking down (Kheirallah, 1990), selectively consume it at the same time, or enrich it with definite groups of microorganisms (Kaneko, 1999; Maraun et al., 2003), digest it or, in contrast, increase the germination ability of plant species with fine seeds (Schowalter, 2011), eliminate helminth eggs and cysts of protozoan parasites (Szlavecz and Pobozsny, 1995). In areas of forest plantations disturbed by industrial forestry millipedes can actively participate in stabilization of the processes of litter decomposition (Topp et al., 2001; Salamon et al., 2008; Kulbachko and Didur, 2012).

Food consumed by saprophages can be assimilated with varying efficiency. The key factor in this case is the age of the animals: young millipedes feed more intensively and assimilate more efficiently the food consumed (Kondeva, 1980; Striganova and Prishutova, 1990; Brygadyrenko, 2004). Intensity of saprophage metabolism is directly evaluated by measuring oxygen consumption or emission of carbon dioxide (Dowdy, 1975; Penteado, 1987; Stamou and Iatrou, 1993; Webb and Telford, 1995; Maraun and Scheu, 1996). Indirectly, the metabolic rate is evaluated by increase in biomass of the animal or intensity of faecal formation (Van der Drift, 1975; Dangerfield, 1993). Addition of certain molecules (secondary compounds of plants) to the diet of saprophages or their exclusion leads to changes in the metabolic rate of saprophages (Sakwa, 1974; Cameron and Lapoint, 1978; Neuhauser and Hartenstein, 1978).

When carrying out laboratory experiments, it is important to evaluate changes in body weight of test animals, since in the course of experiments of several days duration there might be sharp deviations from the general tendency of changes in the animals' body weight (David, 1995). In most experiments, the body weight of each specimen is analyzed at the beginning and at the end of study, and intermediate data are neglected. Investigation of dynamics of substrate consumption processes shows a much more complex pattern in the system of changes in parameters (Couteaux et al., 2002).

Serious difficulties arise with assessment of trophic activity of animals in experiments lasting over one week since the feeding of saprophages at regular intervals and the concurrent uniform microbial decay of the litter necessitate subsequent simplification of experimental procedures and the introduction of corrective coefficients (Gere, 1956; Bertrand et al., 1987; David, 1998).

On the whole, the knowledge of the physiological peculiarities of Diplopoda (Hopkin and Read, 1992; Hertel, 2009) is still far less satisfactory than it is for the ecological and biological peculiarities of, for example, Isopoda (Lardies et al., 2004) and Lumbricidae (Lowe and Butt, 2005).

The ecology of *R. kessleri* has been studied in sufficient detail, compared with other Diplopoda species (Striganova, 1972, 1996; Prishutova, 2001a, 2001b; Brygadyrenko, 2004). However, the food preferences of this species with regard to various tree species have not been explored so far. Until now, no more or less complete analysis of the range of its trophic preferences has been carried out.

The objective of this paper is to evaluate the trophic preferences of *R. kessleri* for the leaf litter of 16 tree species, and assess the potential role of this Diplopoda species in the decomposition of the leaf litter of the most common tree species in its habitat.

Material and methods

Specimens of *R. kessleri* were taken manually on July 28–30, 2013 from the litter and soil surface in an artificial forest plantation of *Fraxinus lanceolata* Borkh. and *Robinia pseudoacacia* L. in the vicinity of Aleksandrovka village (48º45'01"N 34º58'10"E, Magdalynivka district, Dnipropetrovsk region of Ukraine). A total of 204 individuals of *R. kessleri* were used in the study: 17 experiments of 10 days duration were carried out, one for each of 16 plant species plus one control (without food). Before the beginning of the experiments all the millipedes were kept together in a single large container filled with a multi-species mix of leaf litter at optimum moisture. For each experiment there were 12 replicates involving a total of 12 Diplopoda specimens, each in its own separate container. Therefore each millipede was provided with 2 g of dry leaf litter of one species of tree for the duration of the experiment. The litter of the tree species used in the experiment (see Figs 1–6) was also collected from the forest plantation where the *R. kessleri* were obtained (this contained isolated trees of other species besides ash and acacia) or from nearby fruit orchards. The litter collected was formed from leaves that had fallen the previous autumn.

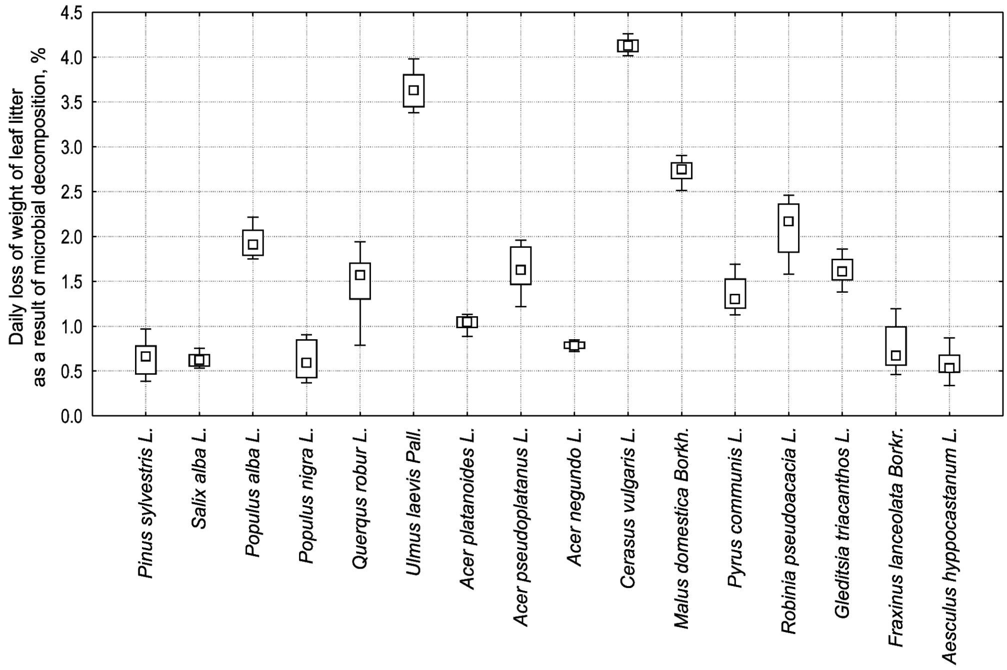

Fig. 1. Rate of microbial decomposition of the litter during experiment in the control (without food activity of *R. kessleri*): abscissa, tree species; ordinate, daily loss of weight of leaf litter as a result of microbial decomposition (%, $n = 12$).

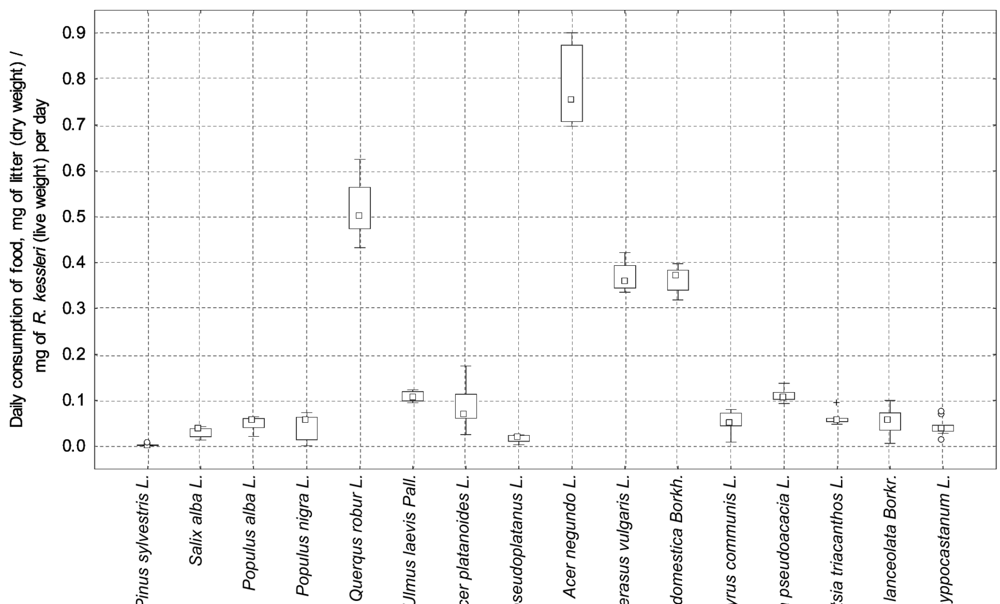

Fig. 2. Rate of consumption of leaf litter of various tree species by *R. kessleri*: abscissa, tree species; ordinate, daily consumption of food (mg of litter (dry weight) / mg of *R. kessleri* (live weight) per day, $n = 12$).

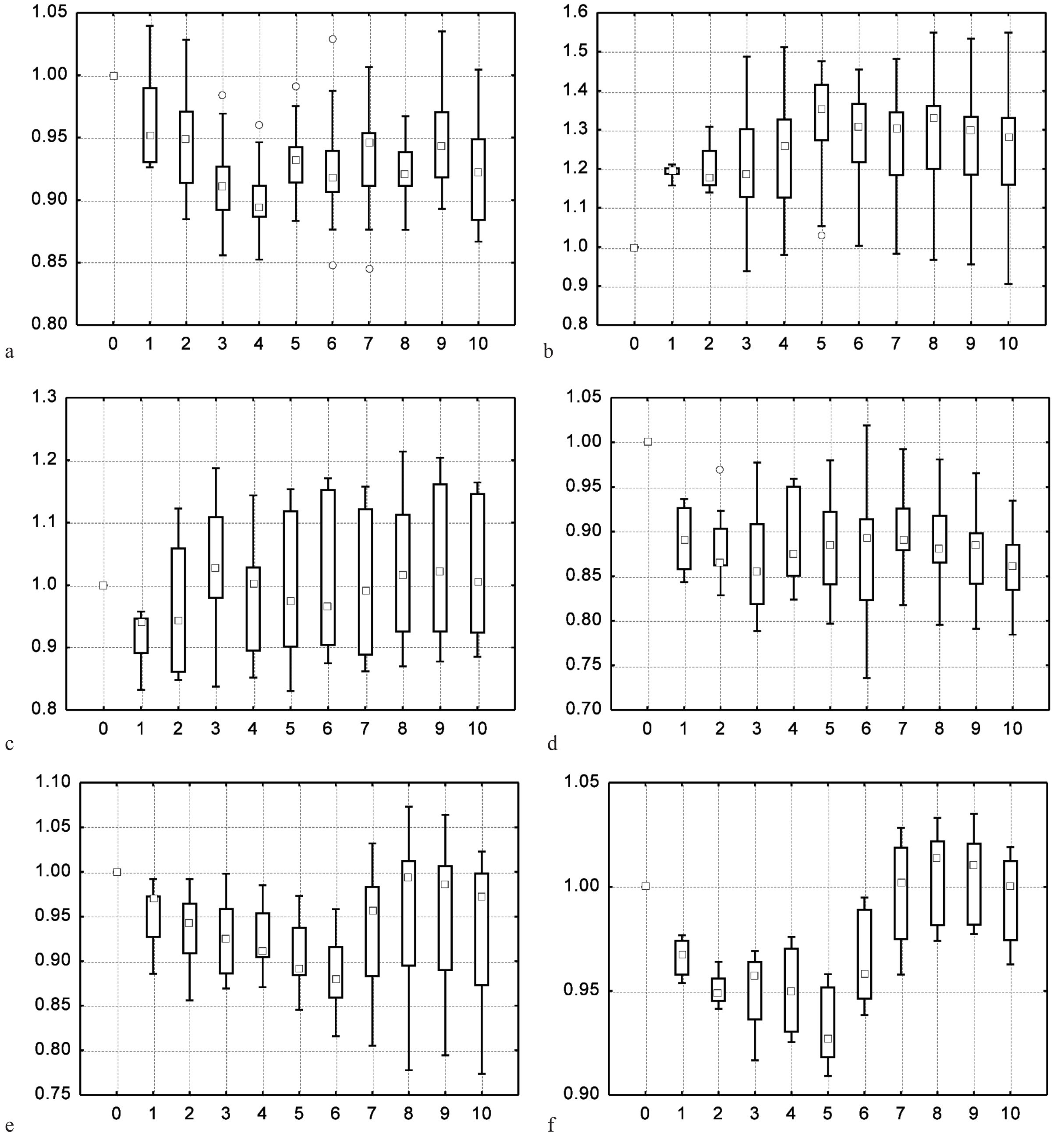

Fig. 3. Dynamics of *R. kessleri* body weight, when it is fed on litter of various tree species: a, *Pinus sylvestris*; b, *Salix alba*; c, *Populus alba*; d, *P. nigra*; *e*, *Quercus robur*; fV, *Ulmus laevis*; abscissa, time (days from the beginning of experiment); ordinate, ratio of *R. kessleri* body weight to its weight before the experiment (in all variants of the experiment $n = 12$).

For the experiments, millipedes (347 ± 86 mg by live weight) were placed in plastic cups of 0.5 l in volume. The weight of the millipdedes, their faeces and the litter was determined with the use of a torsion balance (with accuracy of 0.5 mg). The millipedes were weighed separately before and on each day of the experiment. The faeces of each millipede were weighed only at the end of the experiment after the excrement had been separated from the leaf litter. The leaf litter in each container was weighed in its dry state (prior to sprinkling) before the experiment and, having been dessicated, after the experiment. Throughout the study, a consistent temperature of +26 to +28 ºC and air humidity of 75–90% were maintained in the laboratory. To maintain constant humidity in the containers, the litter was periodically and evenly sprayed with distilled water using spray cans. With a view to reducing moisture evaporation, the cups were covered with paper.

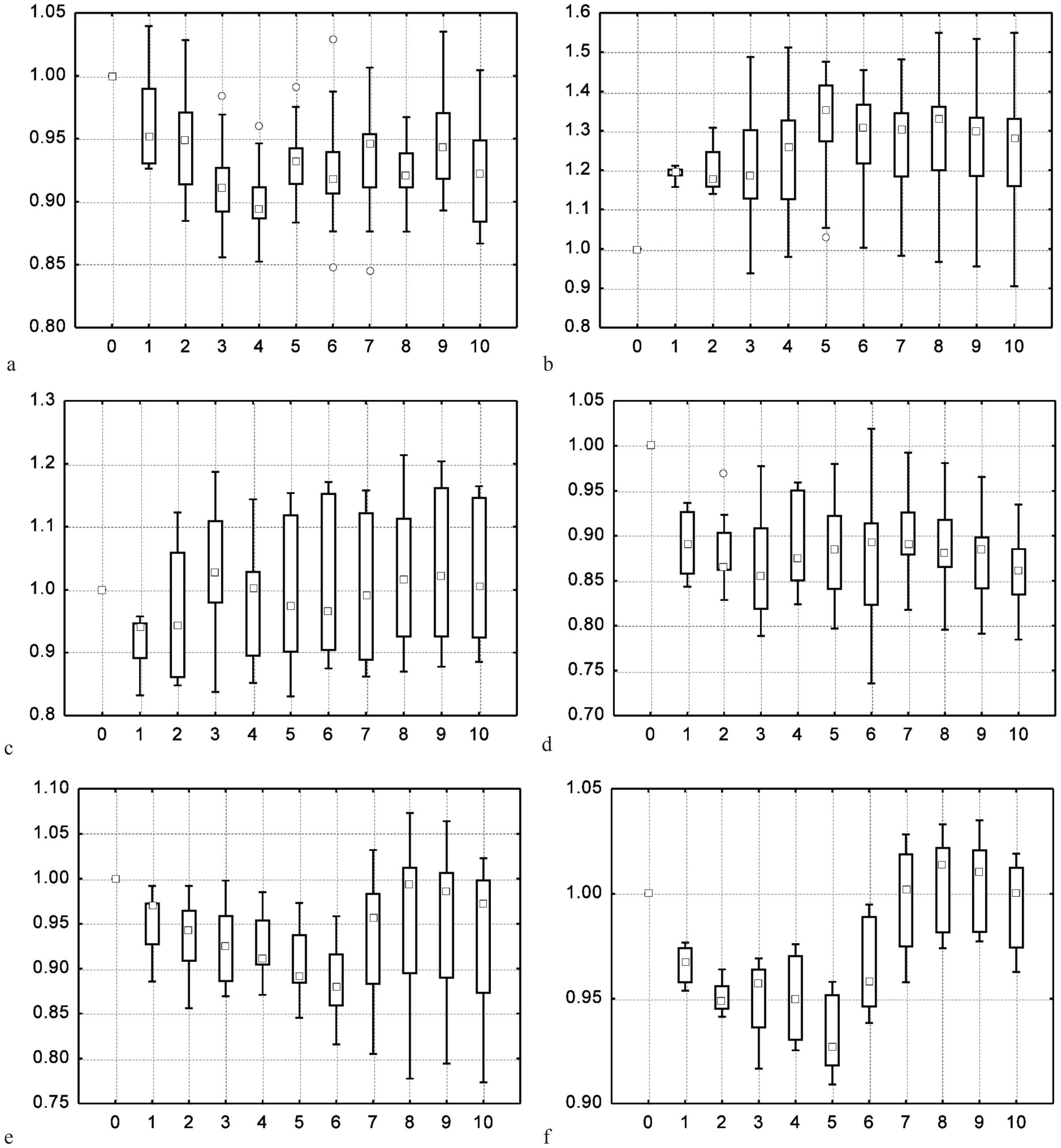

Fig. 4. Dynamics of *R. kessleri* body weight, when it is fed on litter of various tree species: a, *Acer platanoides*; b, *A. pseudoplatanus*; c, *A. negundo*; d, *Cerasus vulgaris*; e, *Malus domestica*; f, *Pyrus communis*; abscissa, time (days from the beginning of experiment); ordinate, ratio of *R. kessleri* body weight to its weight before the experiment (in all variants of the experiment n = 12).

Food consumption (C_1^*) was calculated by a modified formula of David (1998):

$$C_1^* = (M_0 - M_0D - M_n) / (1 - D)^{1/2},$$

where M_0 – initial food weight (dry weight) offered to millipede for consumption, M_n – food weight (dry weight) at the end of the experiment not consumed by the millipede, D – coefficient of reduction of food weight as a result of its microbiological decomposition calculated with the use of control set of experiments (n = 12) in identical containers without millipedes ($D = (M'_0 - M'_n) / M'_0$, where M'_0 and M'_n – dry weight of food at the beginning and at the end of control experiment without the presence of millipedes).

Primary processing of measurement results was performed in MS Excell software package. All data (rate of microbial decay, rate of consumption of leaf litter, changes in *R. kessleri* body weight, daily formation

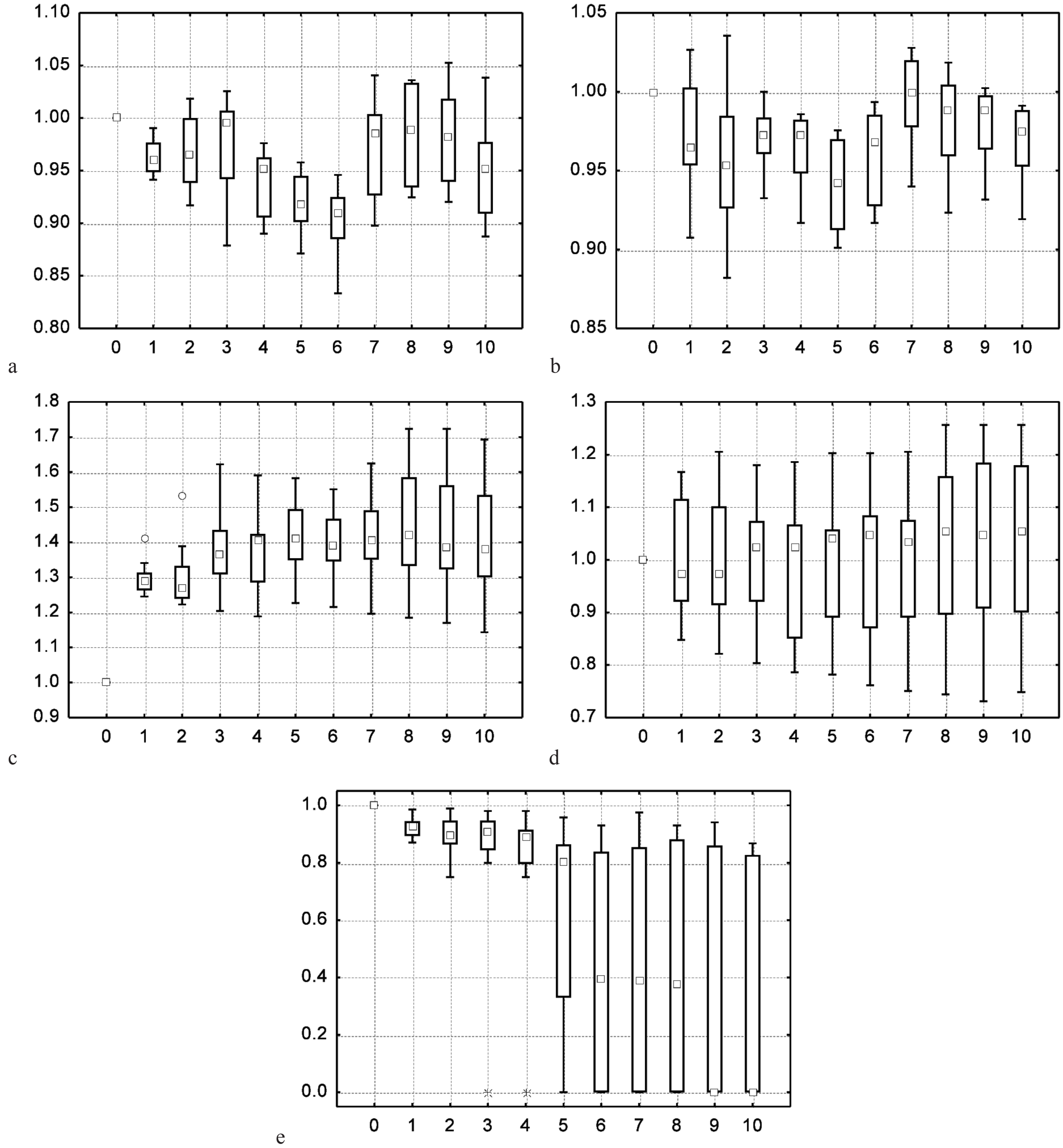

Fig. 5. Dynamics of *R. kessleri* body weight, when it is fed on litter of various tree species: a, *Robinia pseudoacacia*; b, *Gleditsia triacanthos*; c, *Fraxinus lanceolata*; d, *Aesculus hippocastanum*; e, absence of food; abscissa, time (days from the beginning of experiment); ordinate, ratio of *R. kessleri* body weight to its weight before the experiment (in all variants of the experiment $n = 12$).

of faeces) were calculated for individual specimens of millipedes for each specific day of the experiment (Figs 3–5) or for the 10-day study as a whole (Figs 1, 2, 6). Further statistical data analysis was performed in Statistica 8.0 software package. For characteristic of samples, the figures show the median, 25% and 75% quartiles. Differences between samples were considered significant at $P < 0.01$ in one-way analysis of variance.

Results

The rates of litter mass loss in the substrates under study varied by a wide range: from 0.6 to 4.1% per day (Fig. 1). The highest rate of leaf litter mass loss caused by microorganisms was featured by *Cerasus vulgaris* L., *Ulmus laevis* Pall. and *Malus domestica* Borkh. (2.8–4.1% per day). A two-three times lower rate of

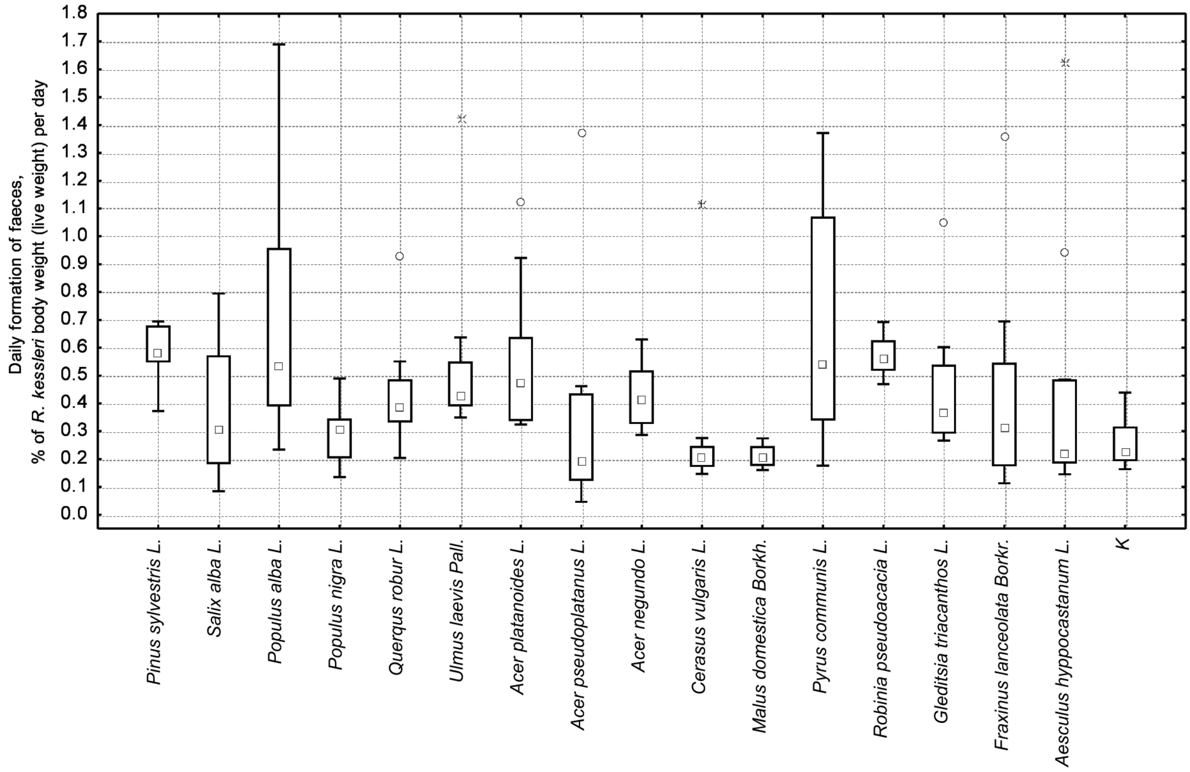

Fig. 6. Daily formation of faeces by *R. kessleri*: abscissa, tree species; *K*, control; ordinate, daily formation of faeces (% of *R. kessleri* body weight (live weight) per day, $n = 12$ for each variant of food).

litter mass loss was observed for *Robinia pseudoacacia* L., *Populus alba* L., *Gleditsia triacanthos* L., *Acer pseudoplatanus* L., *A. platanoides* L., *Quercus robur* L., *Pyrus communis* L. (1.0–2.2% per day). A minimum rate of mass loss through microbial decay was characteristic for *Fraxinus lanceolata* Borkr., *Pinus sylvestris* L., *Salix alba* L., *Populus nigra* L., *Acer negundo* L. and *Aesculus hippocastanum* L. (0.5–0.8% per day). Differences are connected with various periods of formation of the leaf litter, varying conditions of its fermentation in the forest ground litter before commencing the experiment, and peculiarities of the gut microflora of each specimen.

The maximum rate of leaf litter consumption by *R. kessleri* was found for *A. negundo* – 0.75 mg/mg of body weight per day (Fig. 2). The second by the rate of consumption was *Q. robur* (0.50), the third place was shared by *M. domestica* (0.36) and *C. vulgaris* (0.35 mg/mg of body weight per day). For *U. laevis* and *R. pseudoacacia* the rates of consumption ranged around the level of 0.11, and for all the other tree species under study they did not exceed 0.10 mg/mg of body weight per day. The leaves decomposed by microorganisms at the highest rate (Fig. 1) were also those consumed by *R. kessleri* at maximum rates (Fig. 2). The given tendency was not revealed for the leaf litter of *P. alba*, *G. triacanthos*, *A. pseudoplatanus*, *A. platanoides* and *P. communis*, having medium to high rates of microbiological decomposition and very low level of consumption by millipedes.

When millipedes were fed on pine needles (Fig. 3a), their weight decreased during four days and then stabilized at the level of 92–95% of their initial weight. Fluctuations in body weight are, probably, connected with acclimation to consumption of food not typical for the population under study (millipedes for the experiment were collected in an ash-tree-acacia plantation). As all the containers were equally sprinkled with water and then covered by paper to ensure consistent moisture conditions it is unlikely that fluctuations in the millipedes' body weight was due to changes in body water content. When animals were fed on leaves of *S. alba*, on the contrary, their weight for the first day of experiment increased by 20% (Fig. 3b). This continued to increase until the fifth day when it reached a peak of about 36% above the weight on the first day of the experiment, which was followed by a slight decline by the tenth day.

Millipedes feeding on *P. alba* showed no significant changes in body weight during 10 days of the laboratory experiment (Fig. 3c). A diet of leaf litter of *P. nigra*, instead, reduced the millipedes' body weight by 15% by the third day of experiment; however, a certain acclimation occurred subsequently (with the body weight returning to 90% of the initial level).

Oak litter (Fig. 3e) throughout the first week of the experiment caused a practically linear reduction of the animals' body weight (by 12%). Thereafter acclimation took place, and body weight returned to the initial (pre-experiment) level. A similar period of acclimation of *R. kessleri* to leaves of *U. laevis* (Fig. 3f) was one day shorter but the dynamics of body weight change were similar.

The consumption of maple leaves had various effects on the experimental animals (Fig. 4a, b, c). 5–12% gain in body weight after a three-day period of acclimation was observed for *A. platanoides*. Feeding on leaves of *A. pseudoplatanus* and *A. negundo* led to a lengthening of the acclimation period to 6–8 days and a total reduction of body weight by 10–13% by the end of the experiment.

Feeding on leaves of *C. vulgaris* (Fig. 4d) did not significantly change the body weight of *R. kessleri* by the end of the 10-day laboratory experiment. The acclimation period lasted 3 days. A diet of *M. domestica* and *P. communis* (Fig. 4e, f) led to a significant reduction of body weight, down to 92–93% of the initial level by the end of the experiment. The period of acclimation to the diet was 5–6 days.

A diet comprising leaves of *R. pseudoacacia* and *G. triacanthos* (Fig. 5a, b) insignificantly (by 2–5%) reduced the millipedes' body weight by the end of the experiment. The acclimation period was 6–7 days.

The fastest and most stable gain in the body weight of *R. kessleri* (29% of body weight on the first day of experiment reaching, with mild fluctuations, 39% by the end of the experiment) was caused by feeding on the litter of *F. lanceolata* (Fig. 5c).

A diet of leaf litter of *Ae. hippocastanum* led to a gradual increase in body weight of 7% by the end of the experiment (Fig. 5d). The acclimation period was three days.

In the conditions of absence of food in the container the first and the second millipedes died on the third and fourth days of the experiment and the average body weight of the remaining specimens during the first four days decreased by 10% (Fig. 5e). A 50% death rate of the starving animals in the cups was recorded on the sixth day of the experiment.

In the experiment we observed infrequent but rather significant deviations of body weight in individual millipedes from their body weight on the previous day. Compared with the body weight of each individual on the previous day (12 millipedes * 10 days of experiments – 120 measurements of body weight for each diet) sizeable and sharp fluctuations were recorded (70–90 mg increase/decrease in body weight) for *F. lanceolata*, *S. alba*, *A. platanoides*, *A. pseudoplatanus*, *C. vulgaris*, *Ae. hippocastanum* and some other tree species, not attributable to errors in the instruments or records of experimental results.

Average daily formation of faeces by millipedes (Fig. 6) is an indicator of their contribution to mechanical grinding of organic debris on the soil surface, and their role in soil-forming processes as a whole. In terms of the daily mass proportion of faeces to live body weight in *R. kessleri*, the first place among the tree species studied is taken by *P. sylvestris* (0.58%), followed by *R. pseudoacacia* (0.57%), *P. communis* (0.54%) and *P. alba* (0.53%). The minimum average daily formation of faeces is recorded in millipedes fed on *A. pseudoplatanus*, *C. vulgaris*, *M. domestica* and *Ae. hippocastanum* (0.20–0.23% of body weight). It is possible that a diet of leaf litter from these species produces a constipative effect on the millipedes. It is interesting to note that the control group of millipedes which were not fed during the 10-day experiment produced the same faecal mass (0.23% of body weight) as the millipedes fed on the four plant species listed above.

Discussion

Rates of microbial decay of leaves are different for various stages of their decomposition. The results of our unpublished experiments prove that the rate of consumption of ash-tree leaves by *R. kessleri* fluctuates widely by a factor of up to 18.4 over a period of 1–12 months after their falling, due to the varying stages of activity of bacteria and fungi in the process of decomposition of the leaf litter. It is rather difficult to reveal here which factor has the greatest influence on the rate of leaf litter consumption: the degree of leaching and microbiological decomposition of secondary compounds in the leaf, organic nitrogen content, successional changes of microorganisms at various stages of substrate decomposition or other factors (Sakwa, 1974). It is not possible to differentiate these factors at the present stage of development in soil zoology. Therefore, fragments of last-year's leaves served as a substrate for this study. Visually the leaves of each tree species were distinct and so leaves of different species varied considerably in the degree of their decomposition. The data obtained allow us to compare food consumption, gain in body weight and rate of faeces formation of *R. kessleri* when fed on 16 tree species in the second half of the vegetation season (at the beginning of August). In natural conditions in the steppe zone of Ukraine, where millipedes are able to select specific leaves at optimal stages of decomposition from the litter mixture, the trophic load is redistributed in response to seasonal changes in the forest environment, the principal factors being humidity and temperature (Kondeva, 1980; Hopkin and Read, 1992).

It is important to note a sharp divergence of the rates of microbiological and zoogenic decomposition of the litter for various tree species in the conditions of laboratory experiments (Figs 1, 2). For example, *A. negundo* features the highest rate of food consumption by the millipedes, compared with most other tree species, and at the same time one of the lowest rates of microbial decay of litter. Cherry tree and apple tree leaves were consumed by the millipedes at practically equal rates, while the rate of microbiological decomposition of apple tree leaves was 47% lower than that for those of cherry trees. We have not found similar results in the literature we have searched.

There are three tendencies in the dynamics of acclimation of *R. kessleri* to new diets.

1. Sharp increase in body weight during the first day of the experiment and further stablization thereof at a definite level, for example, for *S. alba* (Fig. 3 b) and *F. lanceolata* (Fig. 5 c).
2. Short-term decrease in body weight during three days of the experiment and further stablization thereof at the level not significantly differing from the initial weight, for example, for *P. alba* (Fig. 3c), *A. platanoides* (Fig. 4a), *C. vulgaris* (Fig. 4d), *G. triacanthos* (Fig. 5b) or *Ae. hippocastanum* (Fig. 5d).
3. Long-term acclimation (for about one week) with return to initial (*Q. robur* (Fig. 3e), *U. laevis* (Fig. 3f)) or lower body weight (*P. sylvestris* (Fig. 3a), *A. pseudoplatanus* (Fig. 4b), *M. domestica* (Fig. 4e), *P. communis* (Fig. 4f)).

As a result of the laboratory experiment, it was found that consumption of leaf litter of *F. lanceolata* significantly increased the body weight of *R. kessleri* by 39% in 10 days, *S. alba* – by 29%. A diet comprising semi-decomposed leaves of *P. nigra* in 10 days significantly decreased the miillipedes' body weight by 13%, *A. negundo* – by 12%, *A. pseudoplatanus* – by 9%, *P. communis* – by 8%, *P. sylvestris* – resulted in a 7% body weight reduction. No statistically significant tendencies in millipede body weight change were found for other tree species.

With equal consumption of food of different types a larger mass of faeces resulting from consumption of a particular food item is evidence of the lower food assimilation (Nicholson et al., 1966). Our experiment has shown that for the four tree species (*A. pseudoplatanus*, *C. vulgaris*, *M. domestica* and *Ae. hippocastanum*) the mass of formed faeces did not significantly differ from the variant with full absence of food. Interesting results were obtained for cherry trees, consumption of which is ranked third among 16 tree species studied (Fig. 2), yet the amount of faeces formed on this diet is the same as in the variant without food (Fig. 6).

R. kessleri is the dominant Diplopoda species in the studied region and the European part of the former USSR (Striganova, 1996; Brygadyrenko, 2006). Food preferences of this species in various tree plantations can be both of theoretical and practical interest. Formation of tree plantations resistant to penetration of steppe species under their canopy is possible only with a stable and strong litter layer (of 30–40 mm thick) required for deceleration of germination of seeds of steppe plants, reduction of moisture evaporation from the soil surface, increase in quantity of litter zoophages which destroy forest pests. The Diplopoda species studied in this paper has great importance in the regulation of the rate of mineralization of plant litter and forest litter.

Conclusions

Our results allow us to detect significant differences in the rates of consumption of leaf litter of various tree species by the Diplopoda species studied. The three types of dynamics of adaptation by *R. kessleri* to diet change documented in the study require further investigations at the physiological (estimation of rate of metabolic processes in the millipede), biochemical (study of the content of secondary compounds and other critical components of the diet in a food substrate) and ecosystem levels (determination of the role of individual groups of microflora in the processes of adaptaion to diet changes). It may be concluded that the results presented here will provide the basis for constructing a simulation model of decomposition of plant litter in forest ecosystems by *R. kessleri* and other species of litter saprophages.

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