Cardinal Stefan Wyszyński University in Warsaw
Institute of Philosophy
Center for Ecology and Ecophilosophy

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Food Preferences in Two Detritivore Species: Laboratory Choice Tests Using Leaf Litters of Different Tree Species

Preferencje pokarmowe dwóch detrytofagicznych gatunków: laboratoryjne testy wyboru z wykorzystaniem ściółki różnych drzew liściastych

Gabriela Makulec[1], Krassimira Ilieva-Makulec[2]

[1] Medical University of Warsaw, Poland

[2] Cardinal Stefan Wyszynski University in Warsaw, Poland

ORCID KI-M https://orcid.org/0000-0002-7570-3822 • k.makulec@uksw.edu.pl

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Abstract: Soil fauna, including terrestrial isopods, millipedes and earthworms, play an important role in the decomposition of litter through the process of shredding it during consumption. In the present study, the food preferences in two detritivores, the common woodlouse (*Oniscus asellus*) and the earthworm (*Lumbricus rubellus*) over the leaf litter of four common tree species: common black alder (*Alnus glutinosa*), silver birch (*Betula pendula)*, small-leaved linden (*Tilia cordata*) and pedunculate oak (*Quercus robur*) were quantified in the laboratory. For each animal species, two sets of feeding mesocosms were prepared: one set with single litter species and another with mixed litter material (cafeteria-type test), where the animals were allowed to choose among the four litter species at once. The food preferences of the studied animals were determined on the basis of the consumption (mass loss) of litter for each litter species at the end of two-weeks lasting experiments. The results showed that the litter mass losses in both detritivores were significantly influenced by the tree species. The litter mass losses can be ranked in descending order as follows: alder, birch, linden, oak. In the case of *O. asellus*, litter mixing had no effect on litter mass loss when compared to single alder and birch litter, however mixing clearly accelerated litter mass loss compared to single lime or oak litter. For *L. rubellus*, litter mixing was found to slow litter mass loss compared to each single alder, birch and lime litter, while accelerating litter mass loss compared to single oak litter. For the interpretation of the results, the literature data on carbon to nitrogen ratio, as well as the proportion of difficult-to-degrade polyphenols and lignins in leaves of the studied tree species were used.

Keywords: litter consumption, *Oniscus asellus, Lumbricus rubellus*, earthworms, woodlice

Streszczenie: Fauna glebowa (stonogi lądowe, krocionogi i dżdżownice) odgrywa istotną rolę w rozkładzie ściółki poprzez jej rozdrabnianie podczas konsumpcji. Badania laboratoryjne przeprowadzono w celu określenia preferencji pokarmowych dwóch detrytofagicznych gatunków (stonogi *Oniscus asellus* oraz dżdżownicy *Lumbricus rubellus)* w stosunku do ściółki liściastej czterech pospolitych gatunków drzew: olszy czarnej (*Alnus glutinosa*), brzozy brodawkowatej (*Betula pendula*), lipy drobnolistnej (*Tilia cordata*) i dębu szypułkowego (*Quercus robur*). Dla każdego gatunku wykonano po dwa 14 dniowe eksperymenty. W pierwszym z nich oceniano atrakcyjność liści na podstawie masy zjedzonej ściółki tylko jednego gatunku, natomiast w drugim eksperymencie zwierzęta miały do wyboru liście ściółki 4-gatunkowej. Uzyskane wyniki wskazują na wyraźną selektywność obu gatunków wobec badanych ściółek. Najchętniej zjadane (a tym samym uznane zostały za najbardziej atrakcyjne) były liście olszy czarnej. Najrzadziej wybierana była ściółka dębu szypułkowego. Ściółki brzozy i lipy zajmowały miejsca pośrednie. W przypadku *O. asellus* stwierdzono, że ubytki ściółki mieszanej były podobne do ubytków jednogatunkowej ściółki olszy i brzozy, ale wyższe niż w przypadku jednogatunkowej ściółki lipy i dębu. W przypadku *L. rubellus* ubytki ściółki mieszanej były wyższe tylko w stosunku do jednogatunkowej ściółki dębowej, ale niższe w stosunku do ubytków pozostałych jednogatunkowych ściółek – olchy, brzozy i lipy. Do interpretacji wyników wykorzystano dane literaturowe dotyczące stosunku węgla do azotu, a także proporcji trudno rozkładalnych polifenoli i lignin w liściach badanych gatunków drzew.

Słowa kluczowe: konsumpcja ściółki, *Oniscus asellus, Lumbricus rubellus*, dżdżownice, stonogi

Introduction

All terrestrial ecosystems are maintained by the constant cycling of matter ("nutrients") and the flow of energy (Odum 1969; Trojan 1975). A key element in these transformations is the decomposition of the dead organic matter reaching the soil in the form of fallen needles, leaves, bark, small twigs, etc. The primary role in the litter decomposition is played by bacteria and fungi. However, the litter substrate becomes more accessible to these primary decomposers after it has been broken down into small particles. The role of "shredders" is fulfilled by soil macrofauna (terrestrial isopods, millipeds and earthworms). The fragmentation of litter by these animals during leaf consumption provides suitable substrates for fungi and bacteria, consequently leading to an increased rate of litter decomposition (Bohlen et al. 1997; Frouz et al. 2007; Frouz 2018).

Previous research has shown that litter quality, assessed by various plant characteristics, such as the C: N ratio and the type and amount of tannins, lignins, waxes and polyphenols they contain, constitutes the primary factor influencing the palatability of leaf litter to both phytophages and detritophages (Rief et al. 2012; Kajak 2016; Zhou et al. 2020; Steinwandter and Seeber 2020; Heděnec et al. 2022). The food preferences of different species of woodlice have been confirmed by a number of studies conducted over the past 10 years (Vos et al. 2011; 2013; Wood et al. 2012; Van de Weghe 2016). Similarly, there is quite a lot of work on the food selectivity of earthworms (Satchell 1971; Hendriksen 1990; Neilson and Boag 2003; Rief et al. 2012). Nevertheless, the existing scientific work does not provide unequivocal results, especially with regard to the choice and consumption of single- or multi-species litter. In the majority of previous studies, the mixing of litter from different plant species accelerates litter mass loss compared to single litter species, although mixing has also been found to slow, or to have no effects on mass loss in other studies (Patoine et al. 2017). Therefore, this topic requires further research.

The main objective of the present mesocosm experiments was to assess the food preferences of the two detritivore representatives, the common woodlouse (*Oniscus asellus* L.) and the earthworm (*Lumbricus rubellus* Hoffmeister) towards the leaf litter of four common tree species – common black alder (*Alnus glutinosa* L. Gaertn), silver birch (*Betula pendula* Roth), small-leaved linden (*Tilia cordata* Mill). and pedunculate oak (*Quercus robur* L.). The four tree species were chosen based on their frequent occurrence in Poland and their leaves having the range of carbon to nitrogen (C/N) ratios. Several studies (Brożek and Wanic 2002; Vesterdal et al. 2008; Parzych 2010; Królak et al. 2017) have indicated that the leaves of these species clearly vary in nitrogen content, from nitrogen-rich (alder leaves) to nitrogen-poor (oak leaves). The following questions were posed: i) whether woodlice and earthworms show an apparent food preference for leaves of certain tree species and ii) how this food preference influences the consumption of leaves in a 4-species litter.

1. Material and methods

1.1. Characteristics of the study species

The woodlouse *Oniscus asellus* L. represents terrestrial crustacean isopods within the family Oniscidae. Woodlice are commonly found in moist and dark habitats, usually hidden under stones, in cracks in walls, buried in the top layer of litter. They lead a nocturnal lifestyle. The woodlouse diet is dominated by dead organic matter of plant origin, although they can also feed on animal remains, fungal hyphae, as well as on the faeces of their own and other soil invertebrates. They have strong biting mouth apparatus that allow them to shred food (Maślak 2010).

Lumbricus rubellus Hoffmeister is an epi-endogeic, detritophagous litter-eating earthworm species of the family Lumbricidae. It inhabits and feeds in the litter and organically enriched surface layers of soil. It is typically found in fertile soils rich in organic matter such as litter at various stages of decomposition. *L. rubellus* is a highly mobile species, it does not dig channels but uses the macropores available in the soil (Plisko 1973; Kasprzak 1986; Brzeski and Makulec 1994). Earthworms lack jaws, instead they detect food and grasp it with their fleshy lips and then, via the oesophagus and crop, direct it to the gizzard (muscular stomach), where the food is grinded.

Specimens of *O. asellus* and *L. rubellus* were hand-collected at an allotment garden near Warsaw, and held (in plastic box with soil and litter from the area where they were picked) in a climatic chamber at 18°C for about two weeks until start of the experiment. For the experiments, adult specimens of the species were selected (*L. rubellus* specimens – length 6-8 cm and biomass – 0.374±0.02 g, *O. asellus* specimens – 1.3 × 0.4 cm in size and biomass – 0.065±0.01 g.

1.2. Feeding mesocosms

Aged leaf litters from four deciduous tree species: small-leaved linden (*Tilia cordata* Mill), silver birch (*Betula pendula* Roth), pedunculate oak (*Quercus robur* L)., black alder (*Alnus glutinosa* L. Gaertn). were used as food sources for the experiment. All litters were collected in the Młociński Park in Warsaw.

The dry tree leaves of all species were soaked for one hour in distilled water, dried on filter paper, and then circular leaf areas of 3.46 cm^2 each were cut out using a cork borer. An effort was made to ensure that all cut-outs contained leaf fragments outside the area of the main leaf nerves, as they could be less readily eaten by animals due to their hardness. The leaf circles were oven-dried at 60°C and weighted. Despite having the same surface area, leaf circles from different trees differed somewhat in mass, most likely due to differences in leaf blade thickness and the time of litter collection (Table 1). Feeding preferences of the two detritivores were conducted independently in two consecutive years.

Plastic boxes of 1,000 ml were used as feeding mesocosms in the experiment. The covers of the boxes contained a small hole (covered with mesh) for aeration and keeping animals within. Each mesocosm contained a 40 g of aquarium pre-dried sand (fraction size of 0.3-0.8 mm) in the case of epigeic woodlice and 80 g in the case of epi-endogeic earthworms. The sand was

Table 1. Dry weight (in g) of four-leaf circles cut from different tree species. Mean ± SD is given

Tree species	Litter used in woodlouse mecocosms	Litter used in earthworm mesocosms
A. glutinosa	0.070±0.002	0.070±0.002
B. pendula	0.068±0.005	0.067±0.002
T. cordata	0.064±0.002	0.065±0.004
Q. robur	0.074±0.004	0.087±0.003

used as an absorbent substrate to maintain humidity and to prevent the litter from sticking to the bottom of the mesocosms.

Two sets of feeding mesocosms were prepared: one set with single litter species and another set with mixed litter material (cafeteria-type test). The food preferences were determined on the basis of the consumption (mass loss) of litter of each tree species (lime, birch, oak or alder) during the entire experiment.

In the case of earthworms, on the sand surface of the mesocosms were placed four leaf circles (of known mass) of a single tree species or one leaf circle of each tree species tested (4 circles in total) in the first and second experiment, respectively. In both experiments, earthworms were inserted individually in the middle of the mesocosms.

In the case of woodlice, 12 pre-weighed leaf circles of the single tree species were used for the first experiment and 4 leaf circles of each tree species in the cafeteria-type experiment. In both experiments, 6 woodlice were introduced into each mesocosm, which combined mass was comparable to that of one earthworm.

For both species, all the experiments were conducted in 3 replicates. Before the earthworms and woodlice were introduced into the mesocosms, the leaf circles and sand were sprayed with 10 ml (for woodlice) or 20 ml (for earthworms) of the water used to soak the leaves (before the leaf circles were cut). This allowed the leaves to be softened, micro-organisms to be re-established and ensured a similar microflora composition in the mesocosms.

Feeding mesocosms were kept in the dark in a climate chamber (at 18°C and 75% humidity) for the entire experiment. Each day, observations were made on the behaviour and condition of the animals. The duration of the experiments was 14 days. Two weeks appears to be a sufficiently short period of time for there to be no significant loss of litter under the influence of microorganisms. At the end of the experiment, the remaining litter of each tree species were dried (at 60°C) and weighted.

1.3. Statistical analysis

To test whether the tree species significantly affects the litter mass loss, a one-way ANOVA (F-test value) was used. The significance of differences between means was compared using the Tukey post-hoc test and a probability value of $p<0.05$. In addition, Pearson's correlations were calculated between the initial litter C/N ratio and the and the litter mass losses at the end of the experiment. For this purpose, the following C/N data available in the literature were used: for alder leaves – 14.3, birch – 17.6, linden – 28, oak – 31.4 to 42 (Brożek and Wanic 2002; Vesterdal et al. 2008; Parzych 2010; Królak et al. 2017).

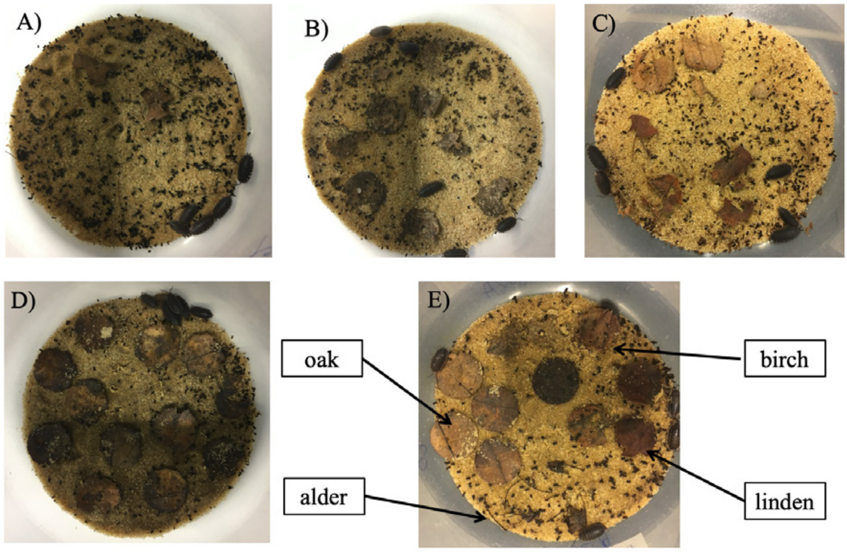
2. Results

Daily observations during the experiment revealed, on the one hand, that the animals were maintained in good condition and, on the other, that no shortage of food was occurring. Additionally, the constant observations made it possible to capture visually the differences in the rate of the litter cover reduction in the different mesocosms over time (Photographs 1 and 2).

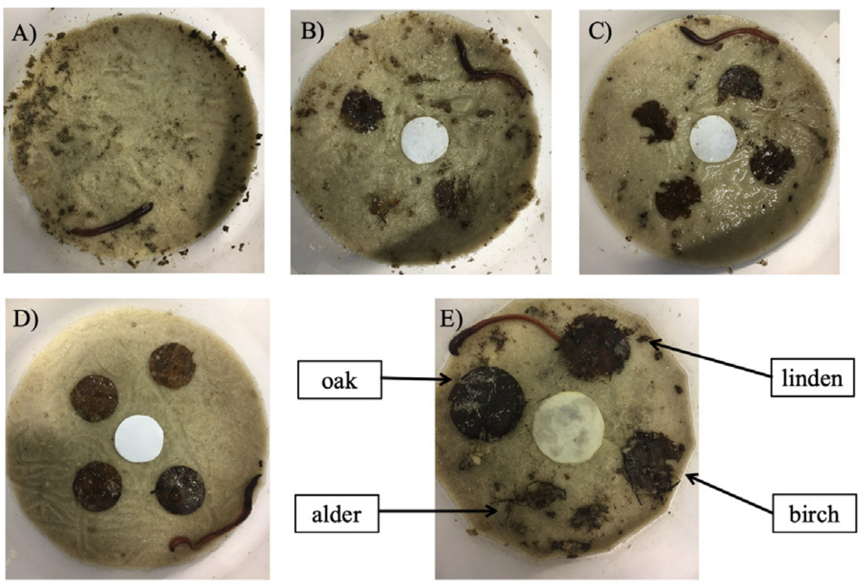
2.1. Litter consumption by *O. asellus* and *L. rubellus* when fed on single-species litter

Litter consumption by woodlice and earthworms when they were fed on a single leaf species is shown on Figs. 1A and 2A. The litter mass losses of the different tree species can be ranked in descending order as follows: alder, birch, linden, oak. Alder litter was the most readily eaten. Over a two-week period, six adult woodlice consumed approximately 0.140 g d.w. of alder litter. Conversely, oak litter was the least attractive food. The woodlice consumed almost four times less oak leaf litter compared to alder, which was only about 0.040 g d.w. (Fig. 1A).

Over a period of 14 days, alder litter (0.07 g d.w.) was completely consumed by one



Photograph 1. Remaining mass of litter in *O. asellus* foraging mesocosms at the end of the experiment: alder (A), birch (B), linden (C), oak (D) and litter mixture (E)



Photograph 2. Remaining mass of litter in *L. rubellus* foraging mesocosms at the end of the experiment: alder (A), birch (B), linden (C), oak (D) and litter mixture (E). The white paper circle was only placed when the photo was taken to illustrate the initial size of the litter circles

earthworm. During the same period, oak litter was consumed to the least extent – as little as 0.004 g of dry matter, which was 14 times less than that of alder (Fig. 2A).

The results of the analysis of variance (ANOVA, $F=13.65$; $p<0.05$ for woodlice, $F=53.46$; $p<0.001$ for earthworms) showed that litter mass loss was significantly influenced by the tree species.

Woodlice consumed significantly more alder, birch and linden litter than oak litter and additionally more alder than linden litter ($p<0.05$, Tukey's post-hoc test). No significant differences in litter mass loss were found between alder and birch, as well as between birch and linden (Fig. 1A).

In the mesocosms with earthworms significant differences in litter mass losses were found among all tree species ($p<0.05$, Tukey's post-hoc test) (Fig. 2A).

The litter mass losses in relation to the litter initial weights are shown on Fig. 1B and 2B. As it can be seen the percentage leaf mass losses differed significantly between the tree species. For both detritivores the percent of leaf mass loss was significantly the lowest for the oak and the highest for the alder.

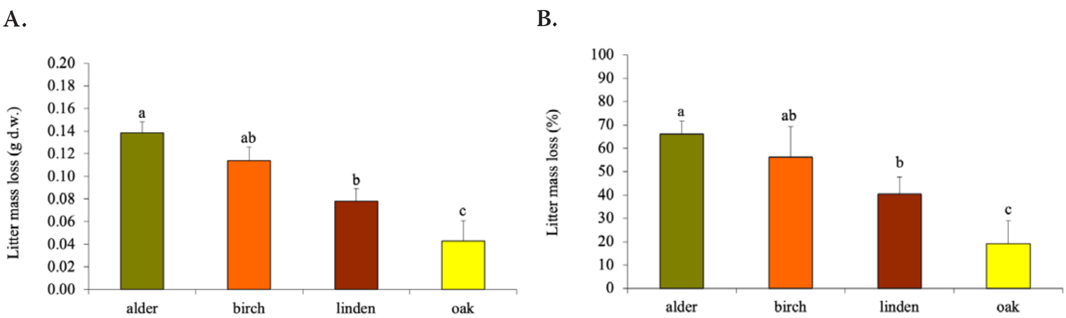


Figure 1. Litter consumption (A) and percentage of litter consumed (B) by six woodlice *O. asellus* when fed on single-species litter. Bars represent mean values+SD. Different letters indicate statistically significant differences ($p < 0.05$)

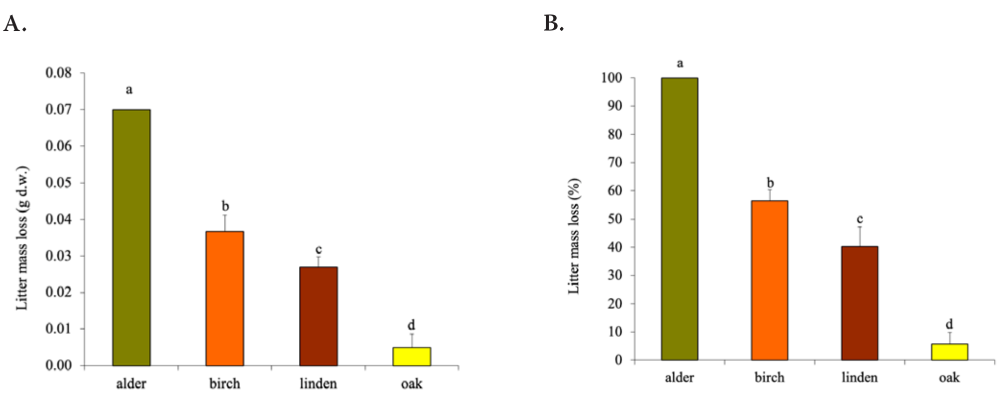


Figure 2. Litter consumption (A) and percentage of litter consumed (B) by one earthworm *L. rubellus* when fed on single-species litter. Bars represent mean values+SD. Different letters indicate statistically significant differences ($p < 0.05$)

2.2. Litter consumption by *O. asellus* and *L. rubellus* when fed on four-species litter mixture

In the experiment with the four-species litter, the woodlice and earthworms confirmed their food preferences. It was found, they also consumed the most alder litter and the least oak litter (Fig. 3A and 4A). The results of ANOVA (F=61.1; $p<0.05$ for woodlice, F=54.72; $p<0.001$ for earthworms) again indicate that the litter mass losses were influenced significantly by the tree species.

In the mesocosms with woodlice, significant differences in litter mass loss were found between alder and each of the three other leaf species and between birch and oak ($p<0.05$, Tukey's post-hoc test). Litter losses of birch and linden as well as linden and oak did not differ significantly (Fig. 3A).

In the mesocosms with earthworms, significant differences in litter mass losses were found among all tree species ($p<0.05$, Tukey's post-hoc test) (Fig. 4A).

The total mass of litter mixture consumed (total of the four tree species) by woodlice was similar to the consumption of each single alder and birch litter but higher than the consumption of each single lime or oak litter (Figs. 1A and 3A). Meanwhile, the total mass of litter mixture consumed by earthworms was lower compared to the consumption of single alder, birch and linden litter but higher than the consumption of single oak litter (Figs. 2A and 4A).

Over the 14 days, in the litter mixture experiment, woodlice consumed the most, almost 90% of the available alder litter, and the least, less than 20% of the oak litter. There were no significant differences between the percentage losses of birch and linden litter (Fig. 3B).

Within 14 days, earthworms consumed 80% of the available alder litter and only 3% of the oak litter. There were no significant differences between the percentage losses of birch and linden litter (Fig. 4B).

Considering the initial total mass of the four-species litter, we found that woodlice and earthworms within 2 weeks consumed the available leaf material to the extent of 44% and 35%, respectively (Fig. 3B and 4B).

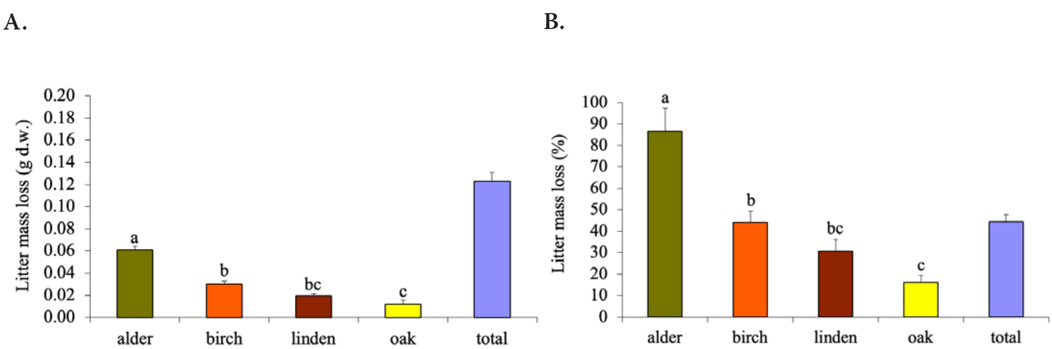


Figure 3. Litter consumption (A) and percentage of litter consumed (B) by six woodlice ***O. asellus*** **when fed on 4-species litter mixture. Bars represent mean values+ SD. Different letters indicate statistically significant differences ($p < 0.05$)**

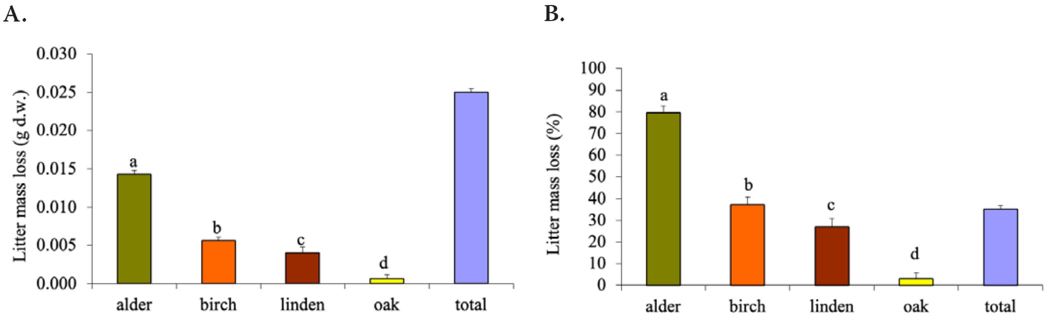


Figure 4. Litter consumption (A) and percentage of litter consumed (B) by one earthworm *L. rubellus* when fed on 4-species litter mixture. Bars represent mean values+ SD. Different letters indicate statistically significant differences ($p < 0.05$)

2.3. Relationships between litter mass loss and C/N ratio of tree leaves

For both detritivores we found a negative correlation between the litter mass loss (data from our study) and the known from the literature C/N ratios of leaves for the used tree species. The relationship was highly significant, indicating a decrease in litter consumption as the carbon/nitrogen ratio of the leaves increases (Fig. 5A and 5B).

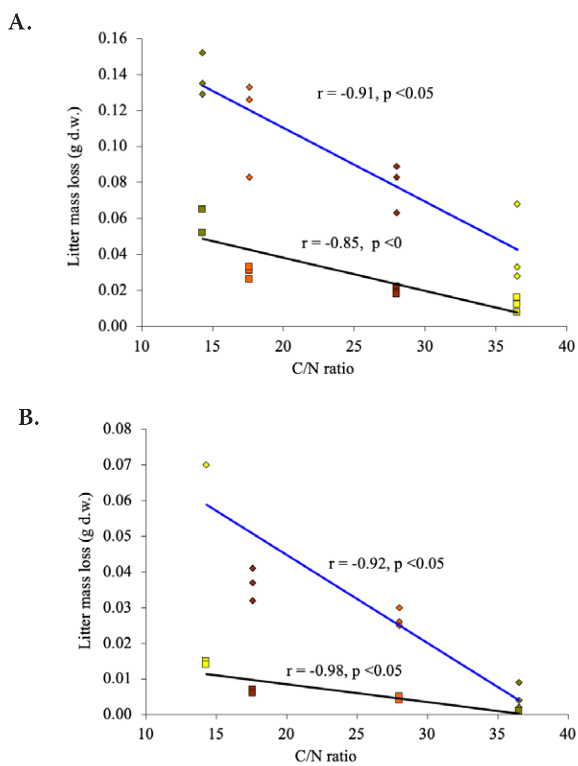


Figure 5. Relationships between litter mass loss (our research) and C/N ratio of different species leaves (based on literature data, sources given in the text). A – *O. asellus* mesocosms, B – *L. rubellus* mesocosms. The strength of the relationship is given as Pearson correlation coefficient (r) and significance of each relationship (p). Colour legend indicating the different litter species: see figure 1. Blue line – trend line for single-species litter, Black line – trend line for 4-species litter

3. Discussion

The results of our study indicate that *L. rubellus* and *O. asellus*, two detritivores belonging to two different types of organisms – annelids and arthropods, respectively have similar feeding preferences for litter from *Alnus glutinosa*, *Betula pendula*, *Tilia cordata* and *Quercus robur*. Alder litter was the most preferred and consumed by both species, while oak leaves were the least preferred. Intermediate positions were occupied by birch and lime litter.

It is widely recognised that the attractiveness of litter to saprophages depends on the proportion of readily available organic matter, including nitrogen compounds (Rief et al. 2012; Kajak 2016; Zhou et al. 2020; Hedĕnec et al. 2022). A good indicator of the palatability of leaf litter for microflora and saprophages is its carbon to nitrogen ratio (C:N ratio). The leaves of the four tree species used in the study show a considerable variation in this parameter, from value of 14 for alder leaves, through 17-28 (for birch and lime, respectively) and exceeding 40 for oak leaves (Brożek and Wanic 2002; Vesterdal et al. 2008; Parzych 2010; Królak et al. 2017).

The correlations of these C/N values with litter mass losses, as determined in our study, were found to be very high. Thus, our results, indicating a very clear decrease in the consumption of litter by both detritivores as the carbon/nitrogen ratio of the leaves increases, seem to confirm the statement presented above. The content of nitrogen compounds in plant tissues is mainly determined by the availability of mineral forms of this element in the substrate or by the ability of plants to use symbiotic organisms capable of fixing atmospheric nitrogen. Among the four tree species used in the study, only alder grows in relatively fertile habitats and is able to use symbiotic organisms (actinomycete *Frankia* sp.) to assimilate atmospheric nitrogen (Górny 1975; Kajak 2016).

Consequently, alder leaves are relatively rich in various compounds, including proteins, and are found to be readily eaten by both herbivores and saprophages. The palatability of litter with high nitrogen content to woodlice has been already observed in a number of studies (Vos et al. 2011; 2013; Wood et al. 2012; Van de Weghe 2016). Similarly, the attractiveness of high-nitrogen-containing litter to earthworms has been also observed previously (Satchell 1971; Hendriksen 1990). These authors, earlier than we did, found that earthworm species belonging to the genus *Lumbricus* tend to select leaves with high (elm, ash, alder) or medium nitrogen content (lime and hazel) and avoid leaves of trees (oak and beech) with a high content of tannins and resin-derived substances. Contrary to our results, finding from other work indicated a lack of food selection by *L. rubellus* earthworms (Neilson and Boag 2003; Rief et al. 2012).

The least preferable oak leaves, meanwhile contain a medium number of nitrogenous compounds, along with a substantial quantity of difficult-to-degrade complex substances in the nature of tannins, lignins, waxes or polyphenols. It is likely that, for this reason, they were unattractive to earthworms and woodlice in our study. Our results are consistent with those of van de Weghe (2016), who also found low rate of litter loss and lack of shredding of oak leaves by woodlice.

In agreement to Patoine et al. (2017), our results showed that the effect of litter mixing (from four tree species in our study) on litter mass loss compared to single litter species is not unambiguous. For *O. asellus*, mixing had no effect on litter mass loss when compared to single alder and birch litter. However, mixing clearly accelerated litter mass loss compared to single lime or oak litter. A similar effect of avoiding poorer quality litter when woodlice were given a choice was also observed by Wos et al. (2011). They speculated that, in this case, other factors such as the activity of the microflora colonising the litter or the substitution of direct leaf consumption by coprophagy, may determine the outcome.

For *L. rubellus*, contrary to expectations, mixing was found to slow litter mass loss compared to each single species of alder, birch and linden, while accelerating litter mass loss compared to single oak litter. This indicates that earthworms of the species *L. rubellus* are less able than woodlice to avoid litter of lower quality when given a choice.

Our results indicate that the strength of the preference for high-quality litter seems to be higher in the *O. asellus* compared to *L. rubellus.* Moreover, while both detritivores preferred consuming alder leaves, woodlice seem to be more selective than the earthworms. The food selection by detritophagous organisms can have major consequences for ecosystem functioning. In fertile alder and riparian forests, the pool of attractive litter is rapidly depleted, and the released nutrients are already utilized in the following season. The situation will be different in oak and mixed forests, where the reluctant and difficult to decompose oak or pine litter often remain for 2-3 years (Górny 1975; Kajak 2016).

In conclusion, our results confirm that the two detritovore species, the earthworm *L. rubellus* and the isopod *O. asellus* play a significant role in shredding litter fallen on the soil surface. Additionally, both species are quite selective in choosing leaves of specific species from the litter, thus exerting a significant influence on the composition of the litter and, consequently, on the rate of decomposition.

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References

Brożek, Stanisław, and Tomasz Wanic. 2002. "Impact of forest litter of *Alnus glutinosa* (L.) Gaertn., *Alnus incana* (L.) Moench, *Alnus viridis* (Chaix) Lam. et DC, *Abies alba* Mill., and *Fagus sylvatica* L. on chosen soil properties." *Electronic Journal of Polish Agricultual Universities* 5(1): #01. http://www.ejpau.media.pl/volume5/issue1/forestry/art-01.html

Brzeski Michał, and Grzegorz Makulec. 1994. *Dżdżownice, ich produkty w ogrodach, działkach i tunelach [Earthworms, their products in gardens, allotments and greenhouses].* Gdańsk: HOST.

Bohlen, Patrick J., Robert W. Parmelee, David A. McCartney, and Clive A. Edwards. 1997. "Earthworm effects on carbon and nitrogen dynamics of surface litter in corn agroecosystems." *Ecological Applications* 7: 1341-1349. https://doi.org/10.1890/1051-0761.

Frouz, Jan, Dana Elhottová, Václav Pižl, Karel Tajovský, Monika Šourková, Tomáš Picek, and Stanislav Malý. 2007. "The effect of litter quality and soil faunal composition on organic matter dynamics in post-mining soil: A laboratory study." *Applied Soil Ecology* 37: 72-80. https://doi. org/10.1016/j.apsoil.2007.04.001.

Frouz Jan. 2018. "Effects of soil macro- and mesofauna on litter decomposition and soil organic matter stabilization." *Geoderma* 332: 161-172.

Górny, Mieczysław. 1975. *Zooekologia gleb leśnych [Zooecology of forest soils].* Warszawa: Wydawnictwo Naukowe PWRiL.

Heděnec, Petr, Haifeng Zheng, David Siqueira, Yan Peng, Inger Schmidt, Tobias Frøslev, Rasmus Kjøller, Huan Li, Jan Frouz, and Lars Vesterdal. 2022."Litter chemistry of common European tree species drives the feeding preference and consumption rate of soil invertebrates and shapes the diversity and structure of gut and faecal microbiomes." *Soil Biology and Biochemistry* 177: 108918. 10.1016/j.soilbio.2022.108918.

Hendriksen, Niels Bohse. 1990. "Leaf litter selection by detritivore and geophagous earthworms." *Biology and Fertiity of Soils* 10: 17-21.

Kajak, Anna. 2016. *Biologia gleby [Biology of soil].* Warszawa: Wydawnictwo SGGW.

Kasprzak, Krzysztof. 1986. *Skąposzczety glebowe, III. Rodzina dżdżownice (Lumbricidae) [Soil oligochaets, III. Family Earthworms (Lumbricidae)].* Warszawa: Wydawnictwo Naukowe PWN.

Królak, Elżbieta, Beata Piskorz, and Ewelina Kotowska. 2017. "Wpływ dodatku liści brzozy brodawkowatej, robinii akacjowej i jarzęba pospolitego na zmiany właściwości rekultywowanych po pożarze gleb leśnych w dwóch typach siedlisk [Influence of the addition of silver birch, Black locust and rowan leaves on changes in the properties of post-fire rehabilitated forest soils in two habitat types]." *Inżynieria Ekologiczna* 18: 159-165.

Maślak, Magdalena. 2010. "Życie w glebie [Soil life]." *Zeszyty Edukacyjne Śląskiego Ogrodu Botanicznego* vol. 3. Accessed November 5, 2023. http://www.obradzionkow.robia.pl/uploaded3/zmniejszone/pdfy/1609.pdf.

Neilson, Roy, and Brian Boag. 2003. "Feeding preferences of some earthworm species common to upland pastures in Scotland." *Pedobiologia* 47: 895-899.

Odum, Eugene Pleasants. 1969. *Ekologia [Ecology].* Warszawa: Wydawnictwo Naukowe PWRiL.

Patoine, Guillaume, Madhav P. Thakur, Julia Friese, Charles Nock, Lydia Hönig, Josephine Haase, Michael Scherer-Lorenzen, and Nico Eisenhauer. 2017. "Plant litter functional diversity effects on litter mass loss depend on the macro-detritivore community." *Pedobiologia*: 29-42. https://doi.org/10.1016/j.pedobi.2017.07.003

Parzych, Agnieszka. 2010. „Azot, fosfor i węgiel w roślinności leśnej Słowińskiego Parku Narodowego w latach 2002–2005 [Nitrogen, phosphorus and carbon content of the forest vegetation of the Slovinski National Park in the years 2002-2005]." *Ochrona Środowiska i Zasobów Naturalnych* 43: 45-64.

Plisko, Jadwiga Danuta. 1973. *Lumbricidae, dżdżownice (Annelida: Oligochaeta). Fauna Polski 1 [Lumbricidae, earthworms (Annelida: Oligochaeta].* Warszawa: Wydawnictwo Naukowe PWN.

Rief, Alexander, Brigitte A. Knapp, and Julia Seeber. 2012. "Palatability of selected alpine plant litters for the decomposer *Lumbricus rubellus* (Lumbricidae)." *PLoS ONE* 7(9): e45345.

Satchell, John E. 1971. "Dżdżownice [Earthworms]." In *Biologia gleby [Soil biology]*, edited by Alan Burges, and Frank Raw, 258-319. Warszawa: Wydawnictwo Naukowe PWRiL.

Steinwandter, Michael, Julia Seeber. 2020. "The buffet is open: Alpine soil macro-decomposers feed on a wide range of litter types in a microcosm cafeteria experiment." *Soil Biology and Biochemistry* 144: 107786. https://doi.org/10.1016/j.soilbio.2020.107786.

Trojan, Przemysław. 1975. *Ekologia ogólna [General Ecology].* Warszawa: Wydawnictwo Naukowe PWN.

Van de Weghe, Tom. 2016. *Interactions between woodlice and millipedes for leaf litter breakdown under changing environmental conditions.* MSc thesis. University of Gent. available online: https://lib.ugent.be/fulltxt/RUG01/002/304/328/RUG01-002304328_2016_0001_AC.pdf.

Vesterdal Lars, Inger Kappel Schmidt, Ingeborg Callesen, Lars Ola Nilsson, and Per Gundersen. 2008. "Carbon and nitrogen in forest floor and mineral soil under six common European tree species." *Forest Ecology and Management* 255: 35-48.

Vos, Veronique C.A., Jasper van Ruijven, Matty P. Berg, Edwin T.H.M. Peeters, and Frank Berendse. 2013. "Leaf litter quality drives litter mixing effects through complementary resource use among detritivores." *Oecologia*. 173: 269-280.

Vos, Veronique C.A., Jasper van Ruijven, Matty P. Berg, Peeters Edwin T.H.M., and Frank Berendse. 2011. "Macro-detritivore identity drives leaf litter diversity effects." *Oikos* 120: 1092-1098. https://doi.org/10.1016/j.apsoil.2018.07.010

Wood, Camila Tim, Carolina Casco Duarte Schlindwein, Goncalves Soares Geraldo Luis, Paula Beatriz Araujo. 2012. "Feeding rates of *Balloniscus sellowii* (Crustacea, Isopoda, Oniscidea): the effect of leaf litter decomposition." *ZooKeys* 176 (176): 231-45. https://doi.org/10.3897/zookeys.176.1940

Zhou, Shixing, Olaf Butenschoen, Sandra Barantal, et al. 2020. "Decomposition of leaf litter mixtures across biomes: The role of litter identity, diversity and soil fauna." *Journal of Ecology* 108: 2283–2297. https://doi.org/10.1111/1365-2745.13452.