Impact of ungulate browsing on leaf litter palatability for millipedes (Diplopoda)

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Immobile plants use various strategies to defend themselves against herbivores such as production of non-palatable or hardly decomposable chemical components in leaves. The objective of this study was to assess whether these biochemical changes persist through shedding of leaves and can affect litter palatability for decomposers. Millipedes were used as a model group of decomposers for an experimental study focusing on this aspect of ungulate – plant – soil invertebrate relationship. Leaf litter and millipedes (*Glomeris klugii, Glomeris hexasticha, Glomeris connexa, Julus scandinavius, Leptoiulus proximus, Megaphyllum projectum,* and *Unciger foetidus*) were collected at forest localities in the Křivoklátsko Protected Landscape Area and Biosphere Reserve, Czech Republic. Palatability of leaves from two different plots was compared. The first plot had been protected for 12 years from ungulate browsing and grazing (*fenced*), the second plot was an adjacent forest under permanent high pressure of ungulates (*grazed*). Leaf litter of beech (*Fagus silvatica*) and hornbeam (*Carpinus betulus*) was collected in autumn and spring in both plots and used in laboratory tests with millipedes. Consumption differed significantly between the individual experiments. Millipedes preferred hornbeam leaf litter over beech leaves, leaf litter from the *fenced* plot over that from the *grazed* plot, and *fresh* litter over *old*, overwintered leaves.

Keywords: Food preference, millipedes, leaf litter, ungulate browsing, soil fauna, decomposers.

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Introduction

In most natural temperate ecosystems, the actual density of large herbivores is relatively low. However, there are many areas of semi-natural or managed woodlands in Central Europe (at least in the Czech Republic), where densities of ungulates are unusually high and may have a marked impact on their environment, including the removal and consumption of herbage, trampling of soil and vegetation, and the input of excreta. However, there are also important indirect effects of herbivores on both above- and belowground properties and processes, which can govern the net effects of herbivores on ecosystem form and productivity (Bardgett et al., 1998). The effects of large herbivores on forest plant community structure and functioning (Reimoser and Reimoser, 1997; Hester et al., 2000; Kirby, 2001) and on above ground invertebrates, mainly insects (Suominem et al., 1999; Feber et al., 2001; Stewart, 2001; Suominen et al., 2003) have been widely studied and analyzed. The impact of ungulates on soil invertebrates in woodlands is expected to be mediated through the changes that ungulate grazing or browsing generates in the aboveground vegetation. The changes in structure, quantity and distribution of woodland undergrowth have effects on the amount and quality of litter and on the microclimate (Wardle et al., 2001). Browsed plants can defend themselves against herbivores by production of non-palatable or hardly decomposable chemical components in leaves. These plant secondary metabolites can limit the extent of microbial degradation in the rumen of large herbivores (Duncan and Poppi, 2008) and their persistence in leaf litter can influence the palatability by soil saprophagous invertebrates (Sakwa, 1974).

In this study, we experimentally tested whether potentially higher content of plant secondary metabolites in leaves persists through the shedding of leaves and whether it can affect leaf litter palatability for decomposers. In temperate woodlands millipedes represent one of the most important groups of soil and litter invertebrates. They accelerate significantly the decomposition rate of litter material and contribute to soil

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formation (Lavelle and Spain, 2001). Therefore millipedes were used in our tests as model decomposers.

Materials and methods

In 2005 and 2006, millipedes and leaf litter were collected in the Křivoklátsko Protected Landscape Area and Biosphere Reserve (Central Bohemia, Czech Republic). Millipedes were collected at three localities (the Červený kříž Nature Reserve, Benešův luh and Tři skalky) representing different types of woodland (subxerothermic oak, oak-hornbeam and beech forest, respectively). Leaf litter of two model trees species, beech (*Fagus silvatica*) and hornbeam (*Carpinus betulus*), were collected at the locality Benešův luh. A part of this locality has been protected from grazing by a fence since 1993 – leaf litter collected in this plot was called *fenced*; leaf litter from the surrounding forest with high density of ungulates (red deer and roe deer mainly) was called *grazed*. Leaves were collected in both plots of the locality directly from browsed and non-browsed young trees of comparable age just before they would have been shed in autumn 2005 (*fresh* leaves) or in early spring 2006 (*old*, overwintered leaves) and overdried under laboratory conditions.

For the laboratory experiments, 180 millipedes of seven species were used : *Glomeris klugii* Brandt, 1833; *Glomeris hexasticha* Brandt, 1833; *Glomeris connexa* C.L.Koch, 1847; *Julus scandinavius* Latzel, 1884; *Leptoiulus proximus* (Němec, 1896); *Megaphyllum projectum* (Verhoeff, 1894) and *Unciger foetidus* (C.L.Koch, 1838). The millipedes were kept and the individual experiments were carried out in a thermostat chamber, under standardized conditions at 15°C and a high relative air humidity. Millipedes were placed into small plastic boxes with plaster substrate and fed in preferential tests. Palatability of leaf litter from two different variants was compared in each set up. Four experiments were done with different combinations of leaves. Millipedes chose between leaves from the same tree species, which differed in origin (*grazed* vs. *fenced*) or in age (*fresh* vs. *old*). Before each experiment millipedes were starved for 2 days. After collecting of faecal pellets, the millipedes were fed with 2 leaves (weighed after drying at 60°C and remoistened by distilled water). After 4 days the rests of leaves were removed from the boxes, overdried at 60°C and reweighed to determine consumption rate. Differences of food intakes were evaluated by ANOVA with Tukey tests to pair difference.

Results and discussion

Consumption of leaf litter from individual experiments differed significantly (Fig. 1) (ANOVA, F = 9.36, P = 0.0001). Consumption of beech leaves was significantly lower than that of hornbeam leaves. In addition to this significant difference, we found in the case of hornbeam leaves significant preference for *fresh* litter compared to the *old*, overwintered leaves in the experiment with leaves from the *grazed* site. The most interesting result was the significant preference for *fresh* hornbeam leaf litter from the *fenced* site over the leaves from the *grazed* site (Fig. 1).

Studies aimed at the response of soil fauna to changes in herbivore pressure are rare. Changes in plant species composition resulting from herbivory caused changes in decomposition, although mainly due to different microhabitat conditions in litter (Hector et al., 2000). Although Wardle et al. (2001) found an impact of browsing of non-native ungulates on the density of millipedes, simple manipulation with litter quality (adding organic matter or man-made fertilization) had no effect on millepede density (Salamon et al., 2006).

Plants can decrease the palatability of their own tissues in response to herbivore pressure (Duncan and Poppi, 2008). Tree species differ in intensity of defence against herbivores and it is known, that leaves of species unpalatable for herbivores (like snails) have a longer decomposition time (Cornelissen et al., 1999).

The results from our laboratory experiments revealed significant differences in litter consumption. Millipedes exhibited a stronger preference for hornbeam leaf litter than for beech leaves. This result is not surprising, because differences in palatability of leaves among tree species are already well known (Lyford, 1943; Kondeva, 1980; Bano and Krishnamoorty, 1981). Similarly to our observation, in Lyford's trials the millipede *Cylindroiulus caeruleocinctus* (Wood, 1864) consumed leaf litter from hop hornbeam (*Ostria virginiana*) 30-times more than leaves of beech (*Fagus grandifolia*) (Lyford, 1943). Kondeva (1980) showed that hornbeam leaves are consumed more quickly than leaves of oak by the millipede *Pachyiulus varius* (Fabricius, 1781). Finally, if millipedes have not a choice and must consume less palatable leaves, they mature in a shorter time and reach maturity at lower weights (Banerjee, 1970).

More surprising was the result, that millipedes preferred *fresh* leaf over *old*, overwintered one. Several studies have confirmed that palatability of leaf litter increase with time. David and Gillon (2002) found that fresh leaf litter of *Quercus ilex* was avoided and that 6 month old litter was most palatable. This is caused by decreasing content of polyphenols and tannins in dead leaf tissues during the process of their aging (Coulson et al., 1960; Bocock, 1964). This pattern of changes in palatability seems to be general, although Kheirallah (1979) found a more complicated one: freshly fallen ash leaves (2-3 months old) were highly palatable for the millipede *Julus scandinavius*; then their palatability decreased over the next 5 months and later increased again (during 8 to 14 months) until the litter was completely decomposed. Perhaps leaves of hornbeam have a similar pattern of palatability as ash leaves, which are tastier for millipedes at the age of one month (our *fresh* litter) than at the age of 7 months (our *old* litter). In comparison, according to Kheirallah (1979) the beech leaves were the most palatable 12 months after their fall.

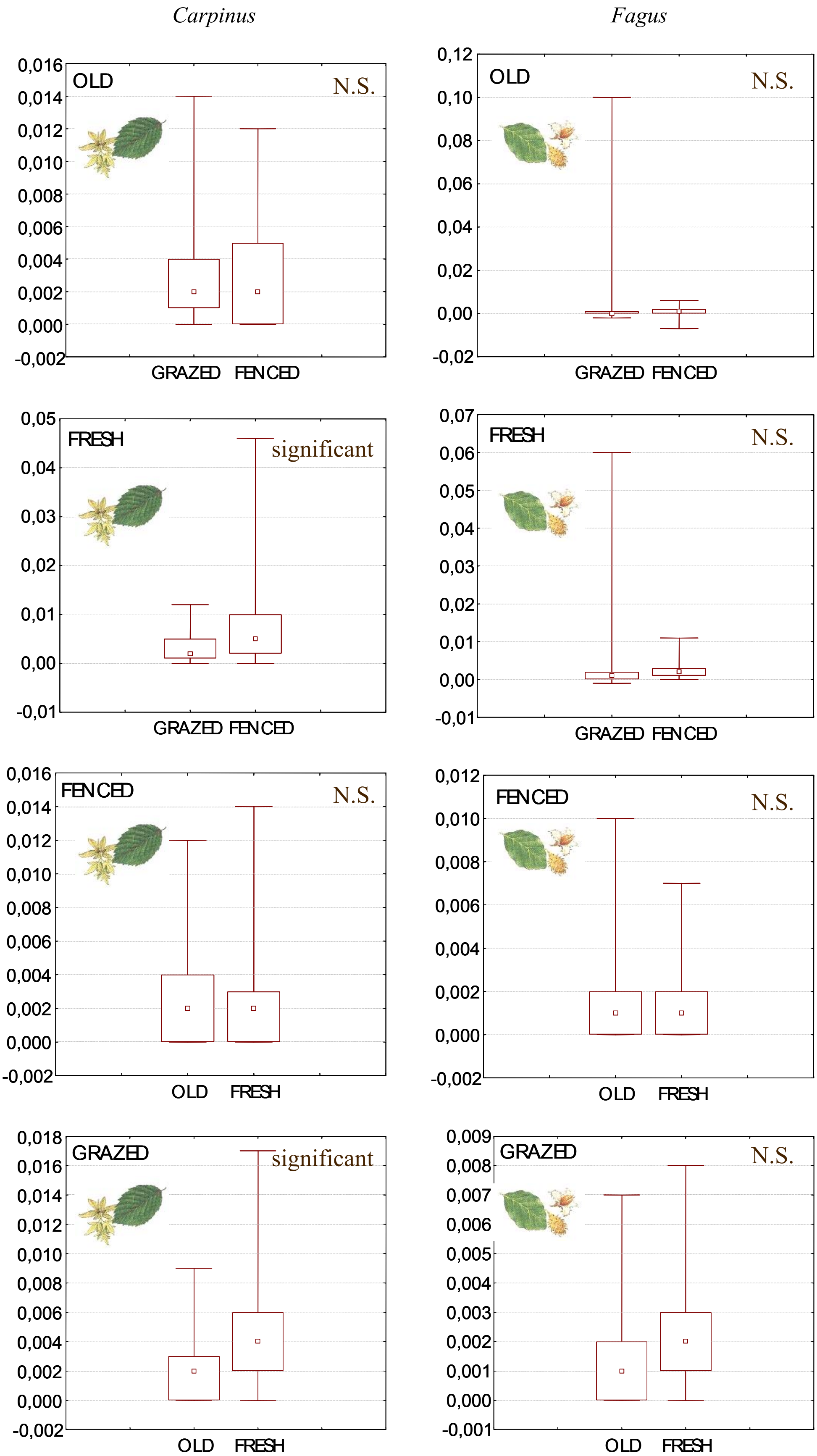

Fig. 1. Food intake (g/ind. per 2 days) by millipedes in cross-preference tests with hornbeam (*Carpinus*) and beech (*Fagus*) leaf litter (median, 25-75% interval and min-max interval).

Gere (1956) came to a similar conclusion under field conditions, when millipedes preferred older leaves from the F_X layer over those from the F_1 layer. Also Hassall et al. (1987) and Rushton and Hassall (1983) reported that terrestrial isopods preferentially consumed decaying leaf litter characterized by reduced toughness and low contents of phenolics and other deterrent compounds (Kuiters and Sarink, 1986).

In our tests the millipedes significantly preferred leaf litter from non-browsed trees (*fenced*) over the leaves from overgrazed shrubs and trees (*grazed*). Herbivory evokes defence of plants at different time scales, from immediate production of volatiles (Snoeren et al., 2007) to evolutionary differences in the content of polyphenols and tannins (Gilbert and Bocock, 1960; Coulson et al., 1960; Bocock, 1964). A medium time scale was found in birch (Tuomi et al., 1988), which produced leaves with higher content of phenols one year after browsing occurred. Our results imply, that some chemical defensive components produced by plants against herbivores cause decreased palatability for detritivores as well, and that millipedes can distinguish these differences in presence or quantity of non-palatable chemical compounds in leaves.

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References

Banerjee, B., 1970. Effects of unmixed and mixed leaf litter of three species of plants on the development and growth of *Polydesmus angustus* Latzel. Experientia, 26: 1403-1404

Bano, K., Krishnamoorty, R.V., 1981. Consumatory responses of the millipede *Jonespeltis splendidus* (Verhoeff) in relation to soil organic matter. Proc. Indian Acad. Sci. (Anim. Sci.), 90: 631-640

Bardgett, R.D., Wardle, D.A., Yeates, G.W., 1998. Linking above-ground and below-ground interactions: How plant responses to foliar herbivory influence soil organisms. Soil Biol. Biochem., 30: 1867-1878

Bocock, K.L., 1964. Changes in the amounts of dry matter, nitrogen, carbon and energy in decomposing woodland leaf litter in relation to the activities of the soil fauna. J. Ecol., 52: 273-284

Cornelissen, J.H.C., Perez-Harguindeguy, N., Diaz, S., Grime, J.P., Marzano, B., Cabido, M., Vendramini, F., Cerabolini, B., 1999. Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. New Phytologist, 143, Special Issue: Variation in Leaf Structure: 191-200

Coulson, C.B., Davies, R.I., Lewis, D.A., 1960. Polyphenols in plant, humus, and soil. I. Polyphenols of leaves, litter, and superficial humus from mull and moor sites. J. Soil Sci., 11: 20-29

David, J.-F., Gillon, D., 2002. Annual feeding rate of the millipede *Glomeris marginata* on holm oak (*Quercus ilex*) leaf litter under Mediterranean conditions. Pedobiologia, 46: 42-52

Duncan, A.J., Poppi, D.P., 2008. Nutritional Ecology of Grazing and Browsing Ruminants. In: Gordon, I.J., Prins, H.H.T. (eds.), The Ecology of Browsing and Grazing. Ecological Studies, Volume 195, Springer-Verlag Berlin Heidelberg, p. 89-116

Feber, R.E., Brereton, T.M., Warren, M.S., Oates, M., 2001. The impact of deer on woodland butterflies: the good, the bad and the complex. Forestry, 74: 271-276

Gere, G., 1956. The exemination of feeding biology and humificative function of Diplopoda and Isopoda. Acta Biologica Hungarica, 6: 257-271

Gilbert, O., Bocock, K.L., 1960. Changes in leaf litter when placed on the surface of soils with contrasting humus types. II. Changes in the Nitrogen content of oak and ash leaf litter. J. Soil Sci., 11: 10-19

Hassall, M., Turner, J.M., Rands, M.R.W., 1987. Effects of terrestrial isopods on the decomposition of woodland leaf litter. Oecologia, 72: 597-604

Hector, A., Beale, A.J., Minns, A., Otway, S.J., Lawton, J.H., 2000. Consequences of the reduction of plant diversity for litter decomposition: effects through litter quality and microenvironment. Oikos, 90: 357-371

Hester, A.J., Edenius, L., Buttenschon, R.M., Kuiters, A.T., 2000. Interactions between forests and herbivores: the role of controlled grazing experiments. Forestry, 73: 381-391

Kheirallah, A.M., 1979. Behavioural preference of *Julus scandinavius* (Myriapoda) to different species of leaf litter. Oikos, 33: 466-471

Kirby, K.J., 2001. The impact of deer on the ground flora of British broadleaved woodland. Forestry, 74: 219-229

Kondeva, E.A., 1980. Feeding activity of the millipede *Pachyjulus flavipes* (C.L. Koch, 1847) (Diplopoda, Pachyjulidae) and its role in the decomposition of leaf litter. Doklady Akademii Nauk SSSR, 254: 1511-1514

Kuiters, A.T., Sarink, H.M., 1986. Leaching of phenolic compounds from leaf and needle litter of several deciduous and caniferous trees. Soil Biol. Biochem., 18: 475-480

Lavelle, P., Spain, A.V., 2001. Soil Ecology. Kluwer Academic Publishers, Dordrecht, 654 pp.

Lyford, W.H., Jr., 1943. The palatability of freshly fallen forest tree leaves to millipedes. Ecology, 24: 252-261

Reimoser, F., Reimoser, S., 1997. Game damage and game benefit - objective assessment of the ungulate impact on the forest vegetation. Zeitschrift für Jagdwissenschaft, 43: 186-196

Rushton, S.P., Hassall, M., 1983. Food and feeding rate of terrestrial isopod *Armadillium vulgare*. Oecologia, 57: 415-419

Sakwa, W.N., 1974. Consideration of the chemical basis of food preference in millipedes. Symp. Zool. Soc. London, 32: 329-346

Salamon, J.-A., Alphei, J., Ruf, A., Schaefer, M., Scheu, S., Schneider, K., Sühring, A., Maraun, M., 2006. Transitory dynamic effects in the soil invertebrate community in a temperature deciduos forest: Effects of resource quality. Soil Biol. Biochem., 38: 209-221

Snoeren, T.A.D., de Jong, P.W., Dicke, M., 2007. Ecogenomic approach to the role of herbivore-induced plant volatiles in community ecology. J. Ecol., 95: 17-26

Stewart, A.J.A., 2001. The impact of deer on lowland woodland invertebrates: a review of the evidence and priorities for future research. Forestry, 74: 259-270

Suominen, O., Danell, K., Bryant, J.P., 1999. Indirect effects of mammalian browsers on vegetation and ground-dwelling insects in an Alaskan floodplain. Ecoscience, 6: 505-510

Suominen, O., Niemela, J., Martikainen, P., Niemela, P., Kojola, I., 2003. Impact of reindeer grazing on ground-dwelling Carabidae and Curculionidae assemblages in Lapland. Ecography, 26: 503-513

Tuomi, J., Niemela, P., Rousi, M., Siren, S., Vuorisalo, T., 1988. Induced accumulation of foliage phenols in mountain birch: branch response to defoliation? Am. Nat., 132: 602-608

Wardle, D.A., Barker, G.M., Yeates, G.W., Bonner, K.I., Ghani, A., 2001. Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. Ecological Monographs, 71: 587-614