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SHORT COMMUNICATION

Leakage of Nutrients Into The Soil Due to Carrion Decomposition Can Enhance Plant Growth

Elke Wenting[1,2] · Patrick A. Jansen[1,3] · Mathijs J. B. Laugeman[2] · Frank van Langevelde[1]

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Abstract
Carrion decomposition has potentially far-reaching effects on nutrient cycles. Recent studies have demonstrated changes in soil-nutrient dynamics and enhanced plant growth because of nutrient leakage from decomposing carrion. However, only macronutrients have been evaluated so far, overlooking effects on a wide range of other essential or ecotoxic elements. This study aimed to examine how leakage affects the chemical composition of soil below decomposing carrion for a wide range of chemical elements, and how this in turn affects plant growth. We performed an experiment in which we let carrion fluid leak from dead mice for different periods of time and measured 22 elemental concentrations in the soils underneath. Then, we grew F1 maize plants on these soils and measured plant biomass. We found that leakage elevated concentrations of 13 essential elements (C, Ca, Co, Fe, K, Mg, Mn, Mo, Na, Ni, P, Se, and Zn) beneath the carrion. None of the potential ecotoxic elements turned out significant. Plant growth was up to nine times higher in soils enriched by carrion fluid. Our results demonstrate that a wide range of chemical elements leak into the soil as result of carrion decomposition, in concentrations that enhanced net plant growth. Our study must be considered as a first step towards a more comprehensive approach for investigating elemental leakage in the soil due to carrion decomposition. Further research may consider larger carcasses, more comprehensively examine the effects of multiple elements on plant growth, and examine how factors like scavenger activity, which may intercept carrion before elemental leakage can happen, affects leakage into the soil.

Keywords Carrion · Decomposition · Soil Chemistry · Nutrient Cycle

1 Introduction

Carrion is an ephemeral but highly nutritious resource for many organisms, so-called scavengers (e.g. Barton et al. 2013; DeVault et al. 2003; Wilson and Wolkovich 2011). Carrion decomposition has potentially far-reaching effects on nutrient cycling, a key driver of ecosystem functioning (Ngai and Srivastava 2006). Animals play a crucial role in this cycle by accumulating large amounts of nutrients in their bodies, collected over long timespans and large areas (Doughty et al. 2016). These include essential elements such as cobalt (Co) and selenium (Se), which are scarce and hard to gather for all lifeforms (Crowe and Bradshaw 2014). When animals die, their bodies—including all the accumulated elements—enter the detritus pool in the form of carrion at a single point in time and space (e.g. Barton et al. 2013), marking the start of the decomposition process.

While large parts of carrion decompose through consumption by scavengers and decomposers, some parts may leak into the soil in the form of 'carrion fluid'; a mixture of bodily

✉ Elke Wenting
elke.wenting@wur.nl

Patrick A. Jansen
patrick.jansen@wur.nl

Mathijs J. B. Laugeman
mlaugeman@gmail.com

Frank van Langevelde
frank.vanlangevelde@wur.nl

1 Department of Environmental Sciences, Wageningen University and Research, Box 47, 6700 AA Wageningen, The Netherlands

2 Department of Animal Ecology and Physiology, Radboud Institute for Biological and Environmental Sciences, Radboud University, Box 9010, 6500 GL Nijmegen, The Netherlands

3 Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Balboa, Ancon, Panama

fluids, decomposition products and microbial byproducts that drain from the carrion. This has been shown to alter local soil concentrations of macronutrients (e.g. Bump et al. 2009; Barton et al. 2016; Keenan et al. 2019; Macdonald et al. 2014; Parmenter and MacMahon 2009; Quaggiotto et al. 2019). For instance, Benninger et al. (2008) found increased nitrogen (N) and phosphorus (P) concentrations in the soil beneath decomposing Wild boar (*Sus scrofa*) carcasses. Towne (2000) found higher N concentrations at carcass sites after one year of decomposition. Likewise, Melis et al. (2007) found increased calcium (Ca) concentrations in the soil underneath European bison (*Bison bonasus*) carcasses. Such leakage of carrion fluid may positively affect plant growth in the close vicinity of decomposing carrion (Carter et al. 2007; Towne 2000).

However, animal bodies also contain a wide range of non-macro-elements, including elements that are essential for plants and animals, and some that are ecotoxic and may impede plant growth (Robinson et al. 2009). It has not been comprehensively examined how leakage of these elements influences soil elemental concentrations beneath carrion (Perrault and Forbes 2016). As a result, how multiple elements may contribute to carrion-driven local soil fertility and subsequent plant growth remain unknown.

In this study, we examined the leakage from carrion of a wide range of chemical elements, including essential and ecotoxic elements, and how this affected plant growth. We performed a controlled lab experiment in which we manipulated the duration of fluid leakage from the exact same carrion type—i.e. lab-raised mice (*Mus musculus*) -, measured a wide range of elemental concentrations (both essential and ecotoxic elements) in initially mineral-poor substrate below the carrion, and grew identical plants (F1 maize) in these substrates that were only affected by carrion fluid leakage to assess effects on plant growth, in the exact same habitat. We excluded scavenger activity to ensure that the source of leakage was controlled.

2 Material and Methods

We performed the experiment in three steps. First, we established 378 transparent plastic containers that were half filled with bare sand ("silver sand"), which is mineral-poor and does not by itself represent a suitable growing substrate to plants. Containers were covered with fine-meshed perforated plastic lids to exclude insects, and placed on worktables in a tunnel greenhouse at Wageningen University & Research Campus (see Fig. S1 for a schematic overview of the experimental design). We randomly assigned 360 of these containers to one of six treatments, in which carrion was placed and left to decompose for 14 to 24 days (six treatments with 60 replicates each). As carrion, we used identical frozen mice that were purchased at an online pet food store (www.animalfoodexpress.nl) in a single batch. The remaining 18 containers served as a control, i.e. received no carrion. Carrion was individually weighed before and after the decomposition period to calculate the weight decline per replicate, analyzed using a linear model.

Second, we took soil samples—5 cm of top soil directly beneath the carrion—from a selection of containers that we used in the previous step, for measuring the elemental concentrations in the substrate. The selection included, for each treatment, the eight containers with the highest and the eight with the lowest carrion weight loss. We also sampled 13 of the 18 control containers. We measured 23 elemental concentrations in total. N and carbon (C) were analyzed using the Dumas method (Shea and Watts 1939). For the other elements, samples were prepared with microwave digestion with 5 mL 65% nitric acid (HNO_3) and 2 mL 30% hydrogen peroxide (H_2O_2). We used inductively coupled plasma optical emission spectrometry (ICP-OES) to measure concentrations of nine elements (Van de Wiel 2003): aluminum (Al), Ca, iron (Fe), potassium (K), magnesium (Mg), sodium (Na), P, sulfur (S), and silicon (Si). We used inductively coupled plasma mass spectrometry (ICP-MS) to measure the concentration of twelve more elements (Van de Wiel 2003): chromium (Cr), manganese (Mn), Co, nickel (Ni), copper (Cu), zinc (Zn), arsenic (As), Se, strontium (Sr), molybdenum (Mo), cadmium (Cd), and lead (Pb). Four of these elements—Al, As, Cd, and Pb—are commonly assessed ecotoxic elements, while the other 18 elements are essential to plant and animal growth (e.g. Gasparik et al. 2004; Wenting et al. 2023). We used Mann–Whitney U tests to compare concentrations between carrion-treated and control substrates, and reported the median elemental concentrations and 25% and 75% quantiles, and test statistics per element.

Last, we tested whether soil enriched by elemental leakage from carrion enhanced plant growth. This was done in a greenhouse at Radboud University in Aug-Oct 2021. We pregerminated F1 *Zea* maize seeds on vermiculite and sorted the sprouts by size after six days. Sprouts of the same size were potted in the carrion-treated and control substrates. The plants were watered every other day with rainwater until we harvested them after 44 days. Rainwater in Europe is rich in N (Stevenazzi et al. 2019), a commonly limiting element for plant growth (Ågren et al. 2012), hence we excluded N from further analysis and focused on the other elements. Insects entered the greenhouse and fed on some plants. To account for this source of variation, we scored the amount of insect damage for every plant before harvesting by five levels: plants (1) that died prematurely; (2) without insect damage; (3) with 0–30% insect damage; (4) with 30–70% insect damage; and (5) with more than 70% insect damage. We dried the harvested plants at 70 degrees Celsius for 48 h, and weighed them with a precision of four decimals to determine the plant biomass. We used a linear mixed-effects model with damage level as random factor to compare the biomass of the plants that grew on the carrion-treated substrates with the controls. We used R version 4.0.2 for all statistical analyses (R Core Team 2020).

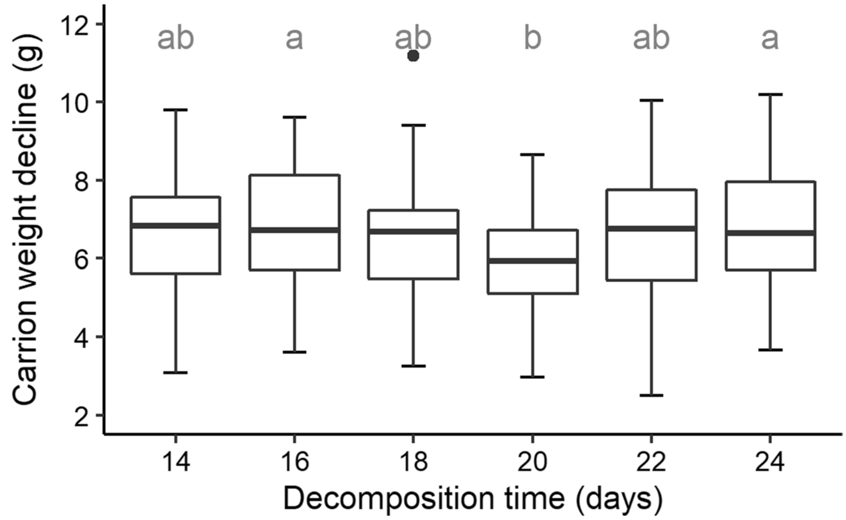

Fig. 1 Carrion weight decline after 14 to 24 days of decomposition time in a controlled experiment. The letters indicate significant differences between the median weight decline (see text for statistics)

3 Results and Discussion

We found no systematic decline in carrion weight loss over time (Fig. 1; linear model, df = 5, F = 2.903, p = 0.014). Likewise, there were no trends in elemental concentrations in the soil over time, implying that most leakage happened during the preceding 14 days. Therefore, we pooled the leakage-duration treatments and only focused on comparing the leakage versus control substrates. We found that the elemental concentrations were higher in soils with leakage than in the controls (Table 1). The median Mo concentration was even up to 16 times higher with leakage compared to the control (0.000175 and 0.000011 µg Kg^{-1}, respectively). All the 13 elements for which leakage elevated concentrations are essential and are moderately or highly mobile (Jigyasu et al. 2020). For none of the ecotoxic elements differences were significant. These

Table 1 Elemental concentrations (µg Kg^{-1}) in soils with and without leakage of chemical elements from carrion, reported as 25% quantile—median—75% quantile. Test statistics from Mann–Whitney U tests are reported. Elements are in alphabetical order and p-values are adjusted using the step-down procedure of Heller and Gur (2011). * indicate the significant elements

Element	Carrion-treated substrate					Control substrate					Test statistics
Al	1.909	-	2.154	-	2.401	1.970	-	2.025	-	2.187	W = 569, p = 0.129
As	0.0014	-	0.0016	-	0.0018	0.00146	-	0.00151	-	0.00175	W = 602, p = 0.129
C	1882	-	2700	-	3787	1030	-	1520	-	2540	W = 427, p = 0.040*
Ca	0.280	-	0.334	-	0.413	0.276	-	0.286	-	0.321	W = 394, p = 0.026*
Cd	0.000027	-	0.000029	-	0.000034	0.000024	-	0.000027	-	0.000031	W = 467, p = 0.064
Co	0.0039	-	0.0044	-	0.0050	0.0035	-	0.0040	-	0.0044	W = 411, p = 0.034*
Cr	0.0050	-	0.0058	-	0.0067	0.0051	-	0.0052	-	0.0060	W = 519, p = 0.129
Cu	0.0027	-	0.0033	-	0.0046	0.0031	-	0.0035	-	0.0038	W = 643, p = 0.129
Fe	2.203	-	2.416	-	2.648	2.122	-	2.159	-	2.466	W = 436, p = 0.043*
K	0.293	-	0.338	-	0.392	0.266	-	0.290	-	0.334	W = 359, p = 0.012*
Mg	0.622	-	0.685	-	0.783	0.582	-	0.606	-	0.667	W = 409, p = 0.034*
Mn	0.020	-	0.023	-	0.026	0.0180	-	0.0192	-	0.0231	W = 413, p = 0.034*
Mo	0.000082	-	0.000175	-	0.000260	0.000010	-	0.000011	-	0.000020	W = 141, p < 0.001*
Na	0.242	-	0.253	-	0.261	0.203	-	0.220	-	0.227	W = 179, p < 0.001*
Ni	0.0090	-	0.0102	-	0.0120	0.0084	-	0.0087	-	0.0095	W = 356, p = 0.012*
P	0.691	-	0.710	-	0.724	0.670	-	0.688	-	0.692	W = 297, p = 0.002*
Pb	0.0035	-	0.0039	-	0.0042	0.0035	-	0.0038	-	0.0042	W = 619, p = 0.129
S	0.086	-	0.104	-	0.130	0.083	-	0.095	-	0.123	W = 529, p = 0.129
Se	0.0025	-	0.0028	-	0.0032	0.00236	-	0.00254	-	0.00273	W = 445, p = 0.047*
Si	0.589	-	0.647	-	0.722	0.622	-	0.655	-	0.680	W = 690, p = 0.532
Sr	0.0021	-	0.0023	-	0.0028	0.00206	-	0.00221	-	0.00239	W = 528, p = 0.129
Zn	0.021	-	0.028	-	0.033	0.0196	-	0.0213	-	0.0243	W = 376, p = 0.018*

findings extend those of previous studies to a much wider range of elements than considered so far (e.g. Barton et al. 2019; Quaggiotto et al. 2019). Our study should be considered as a first step towards a more comprehensive approach to investigate carrion-related nutrient fluxes.

Growth of maize was significantly higher on soils enriched with carrion fluid than on control soils (Fig. 2; linear mixed-effects model, df = 1, F = 11.489, $p < 0.001$), with plant biomass being up to nine times higher. Plant growth was not related to concentrations of any elements in particular (multiple regression with backward deletion, F = 2.593, $p = 0.057$). These results indicate that leakage of carrion fluid can enhance net local plant growth.

We presume that the enhanced plant growth on carrion-treated soils (Fig. 2) was the result of the net positive effect of all the evaluated elements combined (Table 1). Our experimental design, however, did not allow us to specify the magnitude of the impact on plants per element. We encourage future studies to comprehensively investigate which elements have strongest effects on plant growth.

By using rainwater, which is N-rich (Stevenazzi et al. 2019), we were able to eliminate N as a potential limiting factor for plant growth. It has been suggested that N is not likely to be the limiting factor for plant growth in many regions due to long-lasting N deposition (e.g. Siepel et al. 2019). Excessive N deposition results in skewed proportions between N and scarce essential elements, increasing the importance of carrion decomposition as potential high-quality source of these elements. We therefore consider our results to be relevant in natural systems, especially in systems with high N deposition.

Scavengers are a potential key determinant of elemental leakage from carrion, with the capacity to consume carrion before leakage can even occur (e.g. Gutiérrez-Cánovas et al. 2020; Wenting et al. 2022). However, in this controlled experiment, we did not include the effect of scavenger consumption in this experiment, nor other important aspects of carrion ecology such as carrion type and size (e.g. Moleón et al. 2015; 2017). Our results particularly apply to small carcasses such as mice but the effect might be different for larger carcasses, or under more natural circumstances. Moreover, our experimental design did not allow us to examine how long the elevated elemental concentrations in the soil will last. We encourage future studies to explore the importance of such aspects on elemental leakage of carrion fluid for a wide range of elements as we assessed here.

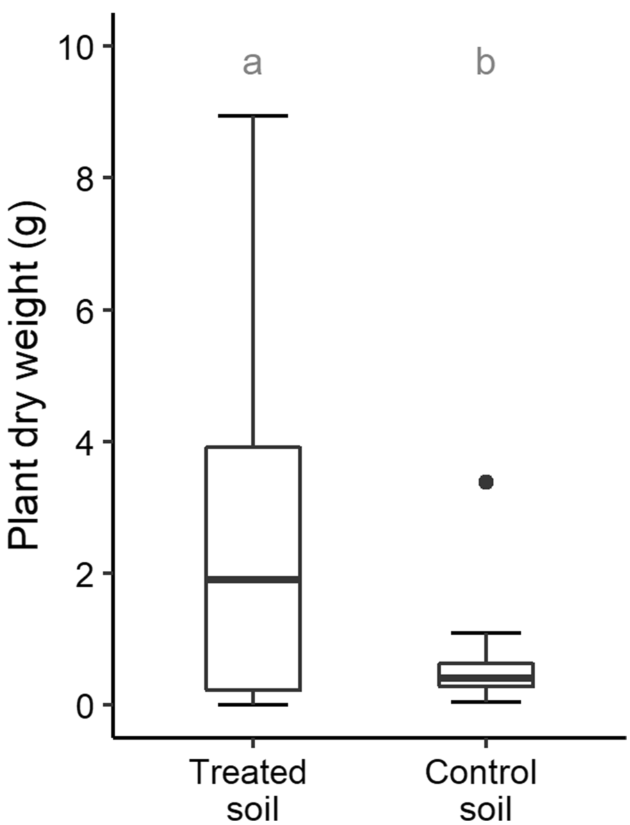

Fig. 2 Plant growth on substrates subject to nutrient leakage from carrion versus control substrates. The letters indicate significant differences between the median plant biomass (see text for test statistics)

4 Conclusions

In conclusion, leakage of carrion fluid affects at least 13 essential elemental concentrations in the soil underneath decomposing carrion. In the case of the mice carrion—as we used here -, these concentrations can enhance net plant growth. Our study must be considered as a first step towards a more comprehensive approach for investigating elemental leakage into the soil due to carrion decomposition.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42729-023-01430-0.

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Data Availability The data of used for this manuscript is available via Figshare: https://doi.org/10.6084/m9.figshare.22058870.

Declarations

Competing Interests The authors have no competing interest to declare that are relevant to the content of this article.

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