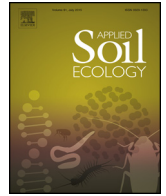




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Short communication

# First evidence that the sodium ecosystem respiration (SER) hypothesis may also hold for a coastal tropical rainforest



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## ABSTRACT

The sodium (Na) respiration hypothesis (SER) states that low Na availability limits the activity and density of soil organisms and therefore plays an important role in decomposition processes of tropical forest soils. Support for this hypothesis was found in several studies reporting higher decomposition rates attributed to higher densities of macro-invertebrates after sodium chloride (NaCl) additions. However, it was also suggested that high doses of NaCl might make organic material unpalatable or even toxic for microbes. Most of these studies were conducted in inland tropical rainforests, where atmospheric deposition of Na is low compared to coastal areas and therefore Na limitation may be more severe. We assessed how treating standardized organic material with different NaCl concentrations affects decomposition rates in a coastal primary rainforest on the island of Borneo. For this purpose, we established a multi-factorial short-term (7 days) decomposition experiment in which we incubated cotton cloths (standard organic material). The cloths were treated with 0%, 0.5%, 1%, 2.5% or 5% NaCl solutions and either provided access for all soil decomposer communities (no mesh) or excluded macro-invertebrates >2 mm (metal mesh). The cloths were placed in the mineral soil and on top of the litter layer. We found higher decomposition in the mineral soil compared to the top of the litter layer. Decomposition rates of cloths treated with 5% NaCl were significantly higher compared to all other cloths, which provides first evidence that the SER might also hold for coastal systems. In addition, we found higher decomposition for the meshed than the non-meshed cloths suggesting that macro-invertebrates either “grazed” on the smaller invertebrates/microbes or that the smaller soil fauna was more efficient in exploiting NaCl when macro-invertebrates were absent. Overall our findings suggest that Na may also control the activity of soil organisms in coastal tropical forest ecosystems.

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## 1. Introduction

Sodium (Na) is only found in small quantities in plants, but is essential for fungi and animals to remain viable (Cromack et al., 1977). According to the “sodium ecosystem respiration” (SER) hypothesis, Na limits the activity and abundance of organisms in the brown food web (NRC 2005; Kaspari et al., 2014): If a shortage in Na exists, decomposition processes are limited as the densities and activities of invertebrates and microbes are reduced (see also

Kaspari et al., 2009). Several authors assessed the SER hypothesis by studying decomposition processes as well as soil fauna and microbial community responses in inland tropical and sub-tropical forest soils (e.g., Kaspari et al., 2009, 2014; Clay et al., 2014, 2015; Ott et al., 2014; Jia et al., 2015), where a shortage of Na is assumed (see also Doughthy et al., 2016). Kaspari et al. (2009, 2014) and Clay et al. (2015) generally found higher decomposition of organic materials (wood, filter paper) when “fertilizing” with NaCl solutions (0.05–0.1% NaCl) in inland tropical forest soils. The increases in decomposition were partially attributed to higher densities of macro-invertebrates (termites, ants) detected on the NaCl treated plots. Also Jia et al. (2015), who conducted a litterbag experiment (tree leaf-litter) with different NaCl solutions (0.005%,

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0.05%, 0.5%) in an inland subtropical forest in China, found increasing decomposition with increasing NaCl concentrations when all invertebrates had access. However, when macro- and meso-invertebrates were excluded, decomposition was lower in the bags treated with 0.5% NaCl solution compared to the control bags. This led the authors to conclude that microbes experienced Na-toxicity.

Although some of these studies provide strong evidence for the SER hypothesis, the role of NaCl in controlling decomposition processes in tropical forests is still not very well understood as the study by Jia et al. (2015) shows. In addition, all studies were conducted in inland tropical forests with the exception of Clay et al. (2015), who compared NaCl controlled decomposition in both inland and coastal forests. Generally, coastal tropical forests are thought to be less Na limited due to their proximity to oceans (Kaspari et al., 2009; Doughthy et al., 2016), yet the importance of Na for decomposition within these soils is not well explored. A study by Kaspari et al. (2008) showed that macro-invertebrates (ants) did not respond positively to NaCl bait in coastal forests, but did in forests at larger distances inland. However, they did not assess the role of smaller soil invertebrates and microbes within these systems. For this reason we set out to learn more about the affinity of Na for the soil fauna and microbes in a coastal primary rainforest with highly weathered soils in Borneo. We conducted a short-term (7 days) multi-factorial experiment, in which we used standard organic material (cotton cloths) treated with different NaCl solutions (0%, 0.5%, 1%, 2.5%, 5%). Half the cloths were enclosed in metal mesh bags to exclude soil macro-fauna (>2 mm; Lavelle et al., 2003), while the others remained uncovered (access for all soil decomposers). Cloths were incubated in the mineral soil and on top of the litter layer. Based on the SER hypothesis we expected that increasing Na availability would lead to higher cotton cloth decomposition also in coastal forest soils. According to Jia et al. (2015), we expected slower decomposition of the meshed cloths compared to the non-meshed cloths due to reduced microbial activity at higher Na concentrations (lower “palatability” of cotton cloth). Further, we expected higher decomposition within the mineral soil compared to the top of the litter layer.

## 2. Material and methods

Our study was conducted in Lambir Hills National Park (4°12' N, 114°02' E) approximately 25 km south of Miri, Sarawak, on the island of Borneo. This remnant primary rainforest (6949 ha) mainly consists of mixed dipterocarp trees and is located at 465 m above sea level, 13.7 km from the coast (Gomyo, 2010). Annual temperature is 25.9°C (2000–2007) and annual precipitation 2650 mm (2000–2008; Gomyo, 2010). Annual Na deposition through precipitation amounts to 6.8 kg ha<sup>-1</sup> (Gomyo, 2010). We established three 10 × 10 m plots (blocks) divided into 100 1 × 1 m subplots with distance between the blocks exceeding 500 m. Parent materials underlying the plots are tertiary sedimentary rocks (sandstone and/or shale; Tan et al., 2009). The soils are classified as Ultisols, which are typical for both inland and coastal rain forests worldwide (Brady and Weil, 2016) and cover roughly

8% of the ice-free land area (FAO, 2015). Ultisols are generally low in base saturation and the carbon (C), nitrogen (N) and phosphorus (P) contents are correlated with the amount of clay contained within the soils (Ishizuka et al., 1998). The soil properties measured for the 0–10 cm topsoil in the long term ecological research plot in Lambir Hill National Park are the following: organic C: 1.0% (0.9–1.2%) [mean (range), n = 487], total N: 0.10% (0.09–0.10%), C:N ratio: 9.65 (9–13), total P: 67 ppm (27–108), available P: 1.6 ppm (1–2 ppm; Tan et al., 2009). For exchangeable cations (neutral NH<sub>4</sub>OOCCH<sub>3</sub>, in cmol<sub>c</sub> kg<sup>-1</sup>) the following values have been measured: calcium 0.26 (0.20–0.36)/magnesium 0.18 (0.1–0.26)/potassium 0.13 (0.08–0.04)/Na 0.07 (0.06–0.13), total exchangeable bases: 0.65 (0.48–0.83), cation exchange capacity: 7.23 (5.72–7.64; Tan et al., 2009). Average pH is 4.46 (4.3–4.8) and average base saturation 8.9% (6–13%; Tan et al., 2009). We used 100% unbleached cotton cloth (Daniel Jenny & Co., Haslen, Switzerland; for specifications see Risch et al., 2007) as standard organic material. Each cloth was 17 × 10.5 cm (width × depth) with a 1.5 cm strip marked at the middle (4.5–6 cm). Half of the cloths were sewed inside stainless steel metal mesh bags (1 × 1 mm; Sala Ferramenta SA, Biasca, Switzerland; hereafter called “Mesh”), the other half remained without mesh. The mesh excluded macro-invertebrates >2 mm (see classification by Lavelle et al., 2003). Yoshima et al. (2013) sampled soil and litter macro-invertebrates in 2008 within the “crane plot” where our three plots were located. In addition, they collected invertebrates in the “canopy biology plot” which is located at roughly 500 m distance from the “crane plot”. The dominant macro-invertebrate groups in both the litter layer and mineral soil are ants (*Formicidae*) and termites (*Isoptera*), but also spiders (*Aranea*) and isopods (*Isopoda*) are found in high numbers (Yoshima et al., 2013). In addition, worms (*Oligochaeta*) are quite frequent in the mineral soil (Yoshima et al., 2013).

We soaked all cloths in Milli-Q water (Advantage A10, Merck Millipore) to saturate the fabric for 24 h and then put them into one of the following NaCl solutions: 0%, 0.5%, 1%, 2.5%, 5% NaCl (p.a. VWR 1.06404; hereafter called “Treatment”) for 24 h. Thereafter, the cloths were dried at 35 °C for 48 h. Half of the cloths were assigned for vertical incubation in the mineral soil, the other half for horizontal incubation on top of the litter layer (hereafter called “Location”). We used five replicates each, thus a total of 300 cloths (3 blocks × 5 Treatment × 2 Mesh × 2 Location × 5 replicates). The 100 cloths incubated within a block were randomly assigned to one of the 1 × 1 m subplots. For details on the insertion of mineral soil cloths please see Risch et al. (2007). To correct, for cotton cloth strength loss due to insertion (mineral soil only) we inserted an additional three control replicates per treatment with and without mesh and immediately removed them (90 cloths; 3 blocks × 5 Treatment × 2 Mesh × 1 Location × 3 replicates). Cloths incubated on top of the litter layer were held in place with steel ground staples (Forestry Suppliers, Jackson MS, USA).

The experiment started on March 5 and the cloths were retrieved on March 12, 2015 (7 days incubation). Such a short incubation time is optimal in moist and warm climate, where decomposition is fast. Upon retrieval of the cloth, we gently removed soil from each cloth (mesh) surface, placed each cloth into

**Table 1**

Initial NaCl concentrations for each of our NaCl treatments with and without mesh prior to incubation into soil. Values represent means with standard errors in parentheses.

Treatment Target % NaCl	Initial NaCl conc. without mesh (mmol Cl <sup>-</sup> /kg cotton cloth)	Initial NaCl conc. with mesh (mmol Cl <sup>-</sup> /kg cotton cloth)
0.0%	4.5 (1.1)	1.6 (0.5)
0.5%	146 (32.1)	116 (26.5)
1.0%	175 (43.6)	378 (69.6)
2.5%	416 (106)	869 (66.0)
5.0%	1329 (306)	1569 (333)

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