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Sodium fertilization increases termites and enhances decomposition in an Amazonian forest

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Abstract. Added Na was used to determine whether litter decomposition and associated fungal biomass and termites are limited by Na availability in a lowland tropical rainforest at Yasuni, Ecuador. This is a partial test of the "sodium ecosystem respiration" (SER) hypothesis that posits Na is critical for consumers but not plants, that Na shortfall is more likely on highly weathered soils inland from oceanic aerosols, and that this shortfall results in decreased decomposer activity. We fertilized 4 × 4 m plots twice a month for a year with quantities of Na comparable to those falling on a coastal tropical rainforest. Decomposition rates of four substrates were consistently higher on +NaCl plots by up to 70% for cellulose, and 78%, 68%, and 29% for three woods of increasing percentage lignin. The density of termite workers averaged 17-fold higher on +NaCl plots; fungal biomass failed to differ. After controlling for temperature and precipitation, which co-limit gross primay productivity (GPP) and ecosystem respiration (ER), these results suggest that Na shortfall is an agent enhancing the storage of coarse woody debris in inland tropical forests.

Key words: biogeochemistry; brown food web; decomposition; ecosystem respiration; nutrient limitation; oceanic aerosols; precipitation; sodium; sodium ecosystem respiration (SER) hypothesis; tropical rainforest; Yasuni Ecological Research Station, Ecuador.

INTRODUCTION

There is a crucial need to better understand brown (or detrital) food webs given their role in ecosystem carbon dynamics (Moore et al. 2004, Coleman 2007, García-Palacios et al. 2013). Their structure shapes rates of plant-litter decomposition (Heneghan et al. 1999, Milton and Kaspari 2007), nutrient cycling (Seastedt 1984, Schneider et al. 2012*b*), and soil carbon stabilization (Mulder et al. 2011, Cotrufo et al. 2013). The activity of brown food webs is increasingly seen as constrained by biogeochemistry, particularly the availability of C, N, and P (Walker and Syers 1976, Hobbie and Vitousek 2000, Vitousek 2004, Wardle et al. 2004, Thingstad et al. 2005, Cleveland et al. 2006, Kaspari et al. 2008*a*, Kaspari 2012). Little is known about how the other more-than-20 biologically essential elements (Frausto da Silva and Williams 2001) regulate ecosystem respiration.

The sodium ecosystem respiration (SER) hypothesis posits that sodium (Na) limits the activity and abundance of organisms in brown food webs. Na has a unique biochemistry germane to the carbon cycle. Na is generally a plant toxin (NRC 2005), and terrestrial plants contain ~1.0 mg/kg (Marschner 1995, Taiz and Zeiger 1998). In contrast, decomposers—particularly fungi and animals—must accumulate Na to levels 100–1000-fold higher to remain viable (Cromack et al. 1977). Na concentrations in consumer tissues are highly conserved and tightly regulated (NRC 2005) even as Na is constantly excreted (N or P, in contrast, can be stored in a variety of inert molecules, Chapin et al. 1990). To gain access to the energy locked up in detritus, microbial and invertebrate consumers must first find sufficient quantities of Na. When Na is in short supply, the SER thus predicts decreased decomposition and herbivory relative to net primary productivity (NPP). Here we focus on the SER's prediction about gradients of decomposition.

Sodium concentrations vary geographically for a variety of reasons. At slow time scales magma flows

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and receding oceans enhance terrestrial Na (Jones and Hanson 1985). At faster time scales, anthropogenic inputs (e.g., irrigation, road salt) create a macro- and microgeography of Na. Intermediate are oceanic aerosols (where Na deposition decreases exponentially as one moves further inland, Stallard and Edmond 1981, NADP 2007). If aerosols significantly redistribute Na, then as one moves further inland and farther from oceans, Na shortfall should limit the activity not just of herbivores (Blair-West et al. 1968, Botkin et al. 1973, Arms et al. 1974, Simpson et al. 2006, Kaspari et al. 2008*b*) but of detritivores as well.

Inland tropical forests are an ideal test case for the SER, given their weathered soils and low sodium deposition. In an inland Peruvian rainforest we simulated urine deposition—a common point source of sodium—using a 0.5% NaCl solution applied to 0.25 m^2 plots seven times over two weeks (Kaspari et al. 2009); the +NaCl plots yielded more termites and 50% more cellulose decomposition. As rainfall along tropical coastlines is effectively dilute seawater (Stallard and Edmond 1981), the next step in testing SER would be to simulate such oceanic deposition far inland.

Given the uncertainties underlying carbon pools and fluxes in tropical rainforests (Harmon et al. 1986, Chambers et al. 2000, Keller et al. 2004) the SER could provide a mechanism linking biogeochemistry to carbon flux. Here we report on a one-year NaCl fertilization of an Ecuadorian rainforest, 2000 km inland from oceanic aerosols, using NaCl in amounts that mirror deposition in a coastal tropical forest. We quantify the resulting decomposition rates of cellulose and woody substrates and the density of two decomposers—fungi (Lodge 1996) and termites (Heneghan et al. 1999)—the latter of which can account for half of total wood decomposition (Cornwell et al. 2009).

Methods

The experiment ran from June 2010 through May 2011 at the Yasuni Ecological Research Station in Ecuador (76°24′1.8″ W; 0°40′16.7″ S). Yasuni is an aseasonal lowland tropical rainforest (2900 mm annual rainfall, annual mean temperature 28°C, elevation 200–300 m above sea level). Located in the upper Amazon, it is bordered by the Tiputini River and is >2000 km from the aerosols of the Atlantic Ocean. Yasuni is a rolling mix of lowland and terre firme forest (Valencia et al. 2004). The soils are Udults that are well drained, kaolinitic, and rich in aluminum (Tuomisto 2003).

Experimental design

We set up 10 pairs of 4 × 4 m plots, marked with PVC posts, in old-growth forest. Pairs of plots were separated by 10 m; each pair was separated from the others by at least 20 m. Over the course of one year, plots were fertilized, twice monthly, with 6 L of water from the Tiputini River using backpack sprayers. Control plots received only river water (estimated by inductively coupled plasma [ICP] mass spectrometry to have a Na content of 0.955mg/L); +NaCl plots received a weak saline solution (9.2 g of NaCl/6 L of river water) that mimicked ~4 times the annual deposition in Puerto Rico ($35 kg \cdot ha^{-1} \cdot yr^{-1}$; NADP 2007). This regime simulated a 1-cm increase in annual rainfall.

Quantifying decomposers

We assayed fungal biomass soon after the beginning of the experiment. We used the Rossi Cholodny method (Moore-Landecker 1982) to quantify how hyphal biomass accumulated on a neutral surface over one month. In early July 2010, a month after the outset of fertilization, three glass microscope slides were randomly inserted into the litter of each plot. After a month the slides were air-dried, fixed with heat, rinsed, and stained with fluorescent calcofluor white M2R (Sigma Aldrich, St. Louis, Missouri, USA). Slides were digitally photographed with florescent microscopy and percentage area occupied by hyphae was used to estimate fungal biomass using ImageJ software (Schneider et al. 2012*a*).

We assayed termites using berlese funnels (Southwood 1978). We sampled at 2, 4, 26, and 52 weeks. Each time we sampled ~2 weeks after a fertilization so as not to measure the instantaneous response of termites to application of NaCl. All litter inside a 0.25-m^2 PVC quadrat, randomly placed inside the plot, was sifted through a 1-cm wire mesh Winkler eclector (a 40 cm diameter cloth tube, partitioned by wire mesh; the top of the tube is loaded with litter, the tube is shaken, and the siftate collected below) and extracted into 95% EtOH.

Quantifying chemistry

To determine the elemental composition of the litter + microbe matrix, we used the litter that had passed through the 1 cm mesh after invertebrate extraction. Ten-gram litter samples were dried at 50°C and analyzed for total N, total C, P, Ca, K, Mg, S, Fe, Zn, Cu, Mn, and Ni by the Oklahoma State Soil, Water, and Forage Analytical Laboratory (Stillwater, Oklahoma, USA) via a Spectro CirOs ICP spectrometer (Ametek, Kleve, Germany) using protocols in Robertson et al. (1999).

Quantifying decomposition

We quantified the effects of +NaCl fertilization on the decomposition of four carbon substrates. Cellulose paper, the most labile carbon, was placed out every two weeks for the first two months, and in the final two weeks of the experiment. In each case, two 11-cm disks of Whatman quantitative-grade filter paper were folded to form a half-circle, and pinned to mineral soil using a surveyor flag. Two replicates were placed randomly on each plot.

The three other substrates—Balsa (genus *Ochroma*) and woods locally known as Seike (henceforth "H2") and Sandi (henceforth "H1")—were purchased from a Quito lumber mill and hewn into 1.5 × 3 × 10 cm blocks. They were placed in the litter for six sequential two-month periods. Wood was pre-weighed and affixed to aluminum tags, with two replicates of each wood type placed randomly in each plot and marked with a PVC surveyor flag. Analysis of three samples of each yielded significant differences in percentage lignin (H2, 19.3%; H1, 14.8%; Balsa, 9.9%; Kruskal Wallis $\chi^2 = 7.2$, $P < 0.05$), percentage P (H2, 0.009%; H1, 0.067%; Balsa, 0.023%; $\chi^2 = 7.2$, $P < 0.05$), and percentage Na (H2, 0.002%; H1, 0.007%; Balsa, 0.007%; $\chi^2 = 6.1$, $P < 0.05$), with percentage N indistinguishable (H2 0.33%, H1 0.55%, Balsa, 0.47%). In all cases, decomposition was quantified by mass loss of substrate after drying at 50°C. A replicate consisted of the mean mass loss of a substrate on a plot.

Statistics

Chemistry, fungal biomass, and termite densities were compared across +NaCl and control plots using Kruskal Wallis tests, given their nonnormal distributions. Decomposition data fit assumptions of normality and were analyzed using repeated-measures ANOVA to evaluate the effects of +NaCl treatments, time, and their interaction (SAS 2006).

RESULTS

Litter chemistry varied through the course of the experiment. Litter residuum (the fragments passing through a 1 cm sieve) doubled from month 2 to month 12 (707 to 1370 ml, Kruskal Wallis $\chi^2 = 16$, $P < 0.0001$), as did the concentrations of all 12 elements tested (percentage N, C, P, Ca, K, Mg, S, Fe, Zn, Cu, Mn, and Ni), from a 44% increase in Mg (0.09% vs. 0.13%, $\chi^2 = 19$, $P < 0.0001$) to a 246% increase in Zn (21.4 vs. 52.8 ppm, $\chi^2 = 29$, $P < 0.0001$). However, only Na increased with +NaCl fertilization. After four months and four twice-monthly fertilizations, litter from +NaCl plots had 48% more Na (0.0094% vs. 0.0064%, $\chi^2 = 9.6$, $P = 0.0019$). After 12 months and 24 fertilizations, +NaCl plots had 32% more Na (0.020% vs. 0.015%, $\chi^2 = 11.2$, $P = 0.0008$).

Fungal biomass, recorded as area occupied by hyphae on glass microscope slides, averaged 51% higher on +NaCl plots (6.7% vs. 4.4%) but failed to differ significantly after two months of fertilization ($\chi^2 = 1.12$, $P = 0.29$; Fig. 1). Termite densities, however, averaged 16-fold higher on +NaCl plots over the course of the experiment (0.25 vs. 4.2 termites per 0.25m^2, $\chi^2 = 6.4$, $P = 0.0112$; Fig. 1)

All four carbon-rich substrates decomposed more rapidly on +NaCl plots and did so consistently over time (Fig. 2). Cellulose mass loss, evaluated over 14-day windows, averaged 7–70% higher on +NaCl plots (Fig. 2; repeated-measures ANOVA $F_{1,18} = 4.3$, treatment $P = 0.052$) and was consistently higher on +NaCl plots (interaction $F_{4,72} = 0.6$, $P = 0.67$; Table 1) despite varying three-fold over time ($F_{4,72} = 10.1$, time $P < 0.0001$).

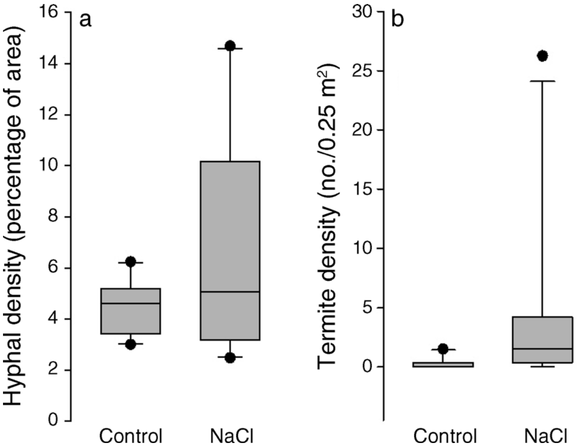

FIG. 1. Fungal biomass and termite density results from a year-long experiment in an old-growth forest at the Yasuni Ecological Research Station in Ecuador. The box and whisker plots contrast decomposer responses to twice-monthly watering of 4 × 4 m plots—10 receiving water, and 10 receiving a dilute NaCl solution—over one year. The horizontal lines of the box represent the median and 25th and 75th percentiles, whiskers are the 10th and 90th percentiles, and solid black circles are minima and maxima. (a) Fungal hyphal densities come from slides that were left in the litter for 30 days beginning at month 2; (b) termite densities describe the plot averages from litter samples harvested at weeks 2, 4, 26, and 52.

The mass loss of three species of wood, measured over two-month windows, was also consistently higher on +NaCl plots (Table 1; treatment $P < 0.0009$, time × trt $P = 0.97$; Fig. 2). Low-lignin Balsa lost mass 9% to 78% faster on +NaCl plots; the intermediate-lignin H1 wood lost mass 22–68% faster; and the high-lignin H2 wood lost mass 17%–29% faster. The period of lowest mass loss varied among the wood types (month 6, 12, and 1, respectively) generating a significant time × wood interaction ($P < 0.0001$).

DISCUSSION

The SER (sodium ecosystem respiration) hypothesis predicts that consumers facing Na shortfall conserve existing supplies by decreasing metabolic rate (and hence density and/or activity). Conversely, ample supplies of ecosystem Na should promote individual activity and abundance. Here, in a year-long experiment at Yasuni Ecological Research Station (Ecuador), we have shown that supplemented Na in an inland lowland rainforest, added in concentrations 4 times the quantities falling as rain on tropical islands, increased the density and/or activity of at least one decomposer (termites). Moreover, it enhanced decomposition rates of carbon-rich substrates consistently over the course of a year. These results provide the strongest evidence yet (Kaspari et al. 2008*b*, 2009) that Na shortfalls promote carbon storage in inland tropical ecosystems.

Tropical forests are estimated to store 30% of Earth's soil carbon (Jobbágy and Jackson 2000). Most global models of the carbon cycle assume co-limitation of water and solar energy (Lieth 1975, Meentemeyer 1978, Gholz et al. 2000) and correctly predict high carbon flux in

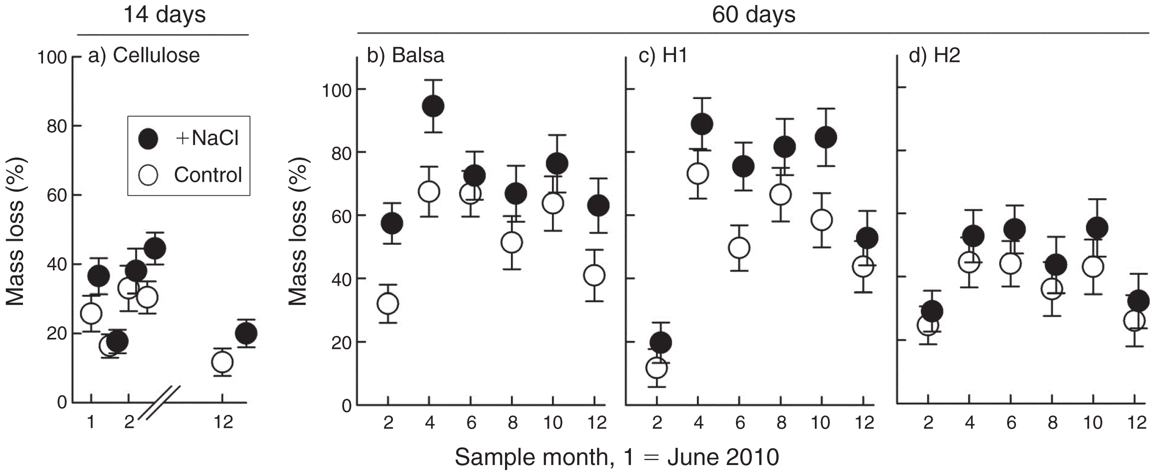

FIG. 2. Decomposition rates (least-squares means ± 2 SE) of four substrates, (a) cellulose, (b) balsa wood (low in lignin), (c) H1 (intermediate lignin), and (d) H2 (high lignin) over the year-long experiment (June 2010–May 2011). Substrate density and percentage of lignin increase from left to right. Cellulose filter paper was placed out over five two-week windows; the three types of wood were placed out for six two-month windows.

tropical ecosystems. Such tropical models can leave up to 40% of variation in decomposition rates unexplained (Powers et al. 2009). Biogeochemical limitation of gross primary production (GPP) and ecosystem respiration (ER) is increasingly used as a means to plug this explanatory gap (Walker and Syers 1976, Hobbie and Vitousek 2000, Vitousek 2004, Wardle et al. 2004, Thingstad et al. 2005, Cleveland et al. 2006, Kaspari et al. 2008*a*, Kaspari 2012). Our experiment enhanced decomposition in amounts comparable to those found when N, P, and K were applied to a Panama rainforest (Kaspari et al. 2008*a*). Converting our percentage mass loss values to k (the fraction of remaining litter $= e^{-kt}$, where t is expressed as fraction of a year; Harmon et al. 1999) shows that Yasuni's NaCl fertilization enhanced the average cellulose decomposition by 26% ($n = 6$, control $k_1 = 7.2$, +NaCl $k = 9.1$); compared to Panama's 49% increase in decomposition on +P plots and 30% increase on +K plots (Kaspari et al. 2008*a*). Yasuni's NaCl fertilization enhanced the decomposition rate of three types of wood from 76% for low-lignin balsa ($n = 6$, control $k = 5.0$, +NaCl $k = 8.7$) to 74% for intermediate-lignin H1 (control $k = 4.8$, +NaCl $k = 8.3$), to 32% for high-lignin H2 (control $k = 2.9$, +NaCl $k = 3.74$). These values are comparable to or exceed the 30% increase in leaf-litter decomposition on +P plots in Panama (Kaspari et al. 2008*a*). However, unlike N, P, and K, adding NaCl is unlikely to promote both GPP and ER (Luo 2007, Kaspari and Yanoviak 2008). Na is scarcely used in plants, but is essential for consumers (Frausto da Silva and Williams 2001). Moreover, Na shortfall in inland ecosystems has generated a variety of adaptations that allow consumers to find and exploit patchy sources of Na (like urine and clay licks; Blair-West et al. 1968, Arms et al. 1974, Simpson et al. 2006). Plants, in contrast, would not suffer, and may even benefit (through decreased consumer pressure) from low quantities of ecosystem Na.

Caveats and future work

First, we added Na as the compound NaCl; we did not control for the action of Cl. However, we doubt that Cl was the active ingredient enhancing decomposition. A previous experiment in a Peru rainforest showed NaCl and Na_3PO_4 equally enhanced decomposition compared to a water control, and that a common consumer, ants, uniformly preferred compounds with Na, and not Cl (Kaspari et al. 2009).

Second, we provide evidence for Na shortfall limiting the decomposition of coarse woody debris, but the factors regulating the metabolism of large soil carbon pools remain poorly understood (Gleixner et al. 2002, Davidson and Janssens 2006, Grandy and Neff 2008). The SER remains to be tested belowground.

Finally, even in the relatively fast-paced tropics, a one-year experiment will not capture all the long-term consequences of changing biogeochemistry. For example, if accumulating Na displaces cations of Ca, Mg, and

TABLE 1. Repeated-measures ANOVA results analyzing the response of three substrates to fertilization by NaCl.

Effect	df	*F*	*P*
Treatment, trt	1	12.3	0.0009
Wood	2	11.2	0.0001
Trt × Wood	2	0.57	0.5682
Error	51		
Time	5	29.6	0.0001
Time × Trt	5	0.2	0.9783
Time × Wood	10	3.7	0.0001
Time × Trt × Wood	10	0.8	0.7529
Error (Time)	255		

K from exchange microsites, this may make them unavailable to plants (Jackson and Jobbágy 2005) and slow GPP. However, after one year we saw no evidence for a changing balance of cations on +NaCl plots. Likewise, increases in shredders like termites may ultimately result in more predators to absorb this increase (Swift et al. 1979, Moore et al. 1988, Milton and Kaspari 2007) leading to ecosystem acclimation (Luo and Zhou 2006). Longer fertilization experiments will help address these scenarios.

Here we suggest that the lack of Na may enhance terrestrial carbon storage. Given the quantity of carbon in terrestrial soils (Amundson 2001, Davidson and Janssens 2006), even small changes in ER may have large effects on atmospheric CO_2. Low levels of Na deposition, likely of little direct consequences to plants, enhanced decomposition in this study; low-levels of Na delivery by hurricanes, to otherwise Na-impoverished ecosystems, have a similar potential to enhance ER. Aerosol deposition of Na and other marine ions peak during tropical storms (Miller et al. 2008, Mullaugh et al. 2012). Moreover, anecdotal accounts from New England suggest hurricanes can deposit Na far inland. For example, the Harvard Forest archives contain passages describing 19th-century hurricanes that struck New England: "Everything was concreted with a fine salt" and "Pastures ruined by salt spray, and whole of trees and vegetables so blighted and changed to appear as though they had been burned"; David Foster, *personal communication*. If the frequency and power of tropical storms increases with temperature (Emanuel 2005) the SER hypothesis may provide another mechanism generating positive feedback between global temperatures and ecosystem respiration.

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