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Aluminum cycling in a tropical montane forest ecosystem in southern Ecuador

Agnes Rehmus^a, Moritz Bigalke^{a,*}, Jens Boy^b, Carlos Valarezo^c, Wolfgang Wilcke^{a,d}

^a Institute of Geography, University of Bern, Hallerstr. 12, 3012 Bern, Switzerland

^b Institute of Soil Science, Leibniz Universität Hannover, Herrenhäuser Str. 2, 30419 Hannover, Germany

^c Dirección General de Investigaciones, Universidad Nacional de Loja, Ciudadela Universitaria Guillermo Falconí, sector La Argelia, Loja, Ecuador

^d Institute of Geography and Geoecology, Karlsruhe Institute of Technology (KIT), Reinhard-Baumeister-Platz 1, 76131 Karlsruhe, Germany

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ABSTRACT

Growth limitation induced by Al toxicity is believed to commonly occur in tropical forests, although a direct proof is frequently lacking. To test for the general assumption of Al toxicity, Al, Ca, and Mg concentrations in precipitation, throughfall, stemflow, organic layer leachate, mineral soil solutions, stream water, and the leaves of 17 native tree species were analyzed. We calculated Al fluxes and modeled Al speciation in the litter leachate and mineral soil solutions. We assessed potential AI toxicity based on soil base saturation, AI concentrations, Ca:Al and Mg:Al molar ratios and Al speciation in soil solution as well as Al concentrations and Ca:Al and Mg:Al molar ratios in tree leaves. High Al fluxes in litterfall (8.77 \pm 1.3 to 14.2 \pm 1.9 kg ha $^{-1-}$ yr^{-1} , mean \pm SE) indicated a high Al circulation through the ecosystem. The fraction of exchangeable and potentially plant-available Al in mineral soils was high, being a likely reason for a low root length density in the mineral soil. However, Al concentrations in all solutions were consistently below critical values and Ca:Al molar and the Ca²⁺:Al_{inorganic} molar ratios in the organic layer leachate and soil solutions were above 1, the suggested threshold for Al toxicity. Except for two Al-accumulating and one non-accumulating tree species, the Ca:Al molar ratios in tree leaves were above the Al toxicity threshold of 12.5. Our results demonstrate high Al cycling through the vegetation partly because of the presence of some Al accumulator plants. However, there was little indication of an Al toxicity risk in soil and of acute Al toxicity in plants likely reflecting that tree species are well adapted to the environmental conditions at our study site and thus hardly prone to Al toxicity.

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1. Introduction

Many plant species are sensitive to high concentrations of the phytotoxic Al^{3+} , $AlOH^{2+}$, or $AlOH_2^+$ and various other inorganic Al complexes which can occur in soil solutions at pH values < 5.5 (Alleoni et al., 2010; Delhaize and Ryan, 1995; Kabata-Pendias and Pendias, 2001; Macdonald and Martin, 1988). Aluminum phytotoxicity contributes to forest decline in temperate forests (Cronan, 1989; Farr et al., 2009; Godbold et al., 1988). In tropical montane forests, pH usually ranges between 4 and 5 and Al toxicity was suggested to contribute to low biomass production and slow

* Corresponding author.

E-mail addresses: agnes.rehmus@giub.unibe.ch (A. Rehmus),

moritz.bigalke@giub.unibe.ch (M. Bigalke), boy@ifbk.uni-hannover.de (I. Boy). cvalarezom@gmail.com (C. Valarezo), wolfgang.wilcke@kit.edu (W. Wilcke).

nutrient-cycling rates (Bruijnzeel, 2001; Bruijnzeel and Veneklaas, 1998: Hafkenscheid, 2000).

The Al fluxes in an ecosystem vary strongly depending on tree species (coniferous, deciduous), the climate conditions (temperate, tropical) and soil properties like texture, organic C concentrations, and pH (Table 1). Aluminum inputs depend on dust deposition and amount of precipitation. Our literature review revealed that the highest Al fluxes with litterfall occur in tropical environments while the highest Al fluxes in soil solution were reported in acidified temperate forests, because of locally low soil pH (Table 1).

The pH is the most important control of Al concentrations in soil solution and acid deposition is a main driver of Al fluxes in a forest (Mulder, 1988). Thus, seasonal acid deposition originating from Amazonian forest fires (Boy et al., 2008a) and the increasing NH⁺₄ deposition with subsequent nitrification already in the forest canopy and nitrate leaching through the ecosystem resulted in acidification of the organic layer leachate at our study site (Wilcke et al., 2013), which will probably also couple back to Al fluxes in the system.









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Table 1

Aluminum fluxes of bulk (BD) and dry deposition (DD), throughfall (TF), stemflow (SF), litterfall (LF), organic layer leachate (LL), mineral soil solution (SS), stream water (SW), and suspended particulate matter loss with stream water (PL) from the literature. * total litterfall (t $ha^{-1}yr^{-1}$) in parentheses, ** soil depth (m) in parentheses.

		Al fluxes (kg ha ^{-1} yr ^{-1})								
Reference	Ecosystem	BD	DD	TF	SF	LF*	LL	SS**	SW	PL
Current study	Tropical montane forest, Ecuador	0.2	0.2	0.5	0.01	11.4 (10.0)	5.0	10.19 (0.15), 6.02 (0.30)	0.18	28.8
Likens (2013)	Northern hardwood forest, USA	< 0.01							2.79	1.38
Rustad and Cronan (1995)	Northern red spruce forest, USA	0.2		0.06	0.03	0.65	2.1		2.6	
Berg and Gerstberger (2004)	Deciduous forest, Germany					0.98 (5.45)				
Matzner et al. (2004)	Deciduous forest, Germany							2.4 (0.6)		
Berg and Gerstberger (2004)	Coniferous forest, Germany					1.2 (2.14)				
Matzner et al. (2004)	Coniferous forest, Germany							17.2–26.9		
								(0.2-0.9)		
Matzner (1989)	Temperate forest, Germany	1.2	0.9-1.3	1.6-2.9				17.6-52.7 (0.9)		
Cornu et al. (1998)	Tropical lowland rainforest, Brazil	1.4		0.6	0.03	2.62		3.7 (0.4)		
Mayer et al. (2000)	Rain forest, Brazil	5.2		3.2				26.5-43.5		
								(0.1-1)		
Hafkenscheid (2000)	Tropical montane forest, Jamaica					1.50-5.22	1.9-4.9	16.1-35.1		
						(6.47-6.16)		(0.05-0.14)		
Gerold (2008)	Tropical montane forest, Bolivia					15.5 (12.2)				
Bergamini et al. (2011)	Atlantic rain forest, Brazil					11.2-9.69				
						(6.37-3.01)				
Moraes et al. (1999)	Atlantic rain forest, Brazil					5.3 (6.31)				
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A hydroponic experiment with saplings of three different tree species typical for the south Ecuadorian montane forests has shown that Al toxicity thresholds (EC10 values) are between 126 and 376 µM Al in solution (Rehmus et al., 2014). However, knowledge of Al concentrations in soil solutions alone is not sufficient to judge the threat of Al toxicity, because Al speciation is crucial for toxic effects (Alleoni et al., 2010). If the solid Al pool is limited, which is particularly the case in the organic layer compared to the mineral soil, ligand complexation in the solid and dissolved phases leads to detoxification of Al^{3+} . Several studies demonstrated an alleviation of Al toxicity by the formation of organo-Al complexes with dissolved organic matter in solution (Alleoni et al., 2010; Drabek et al., 2005; Hernandez-Soriano et al., 2013; Vieira et al., 2009) and in the solid organic matter (Álvarez et al., 2012; Eimil-Fraga et al., 2015). At our study site, most nutrients are stored in the thick organic layers (Wilcke et al., 2002) where also 51 to 76% of the fine root length is located (Soethe et al., 2006). Previous studies showed that depending on dissolved organic matter concentrations, 97% to almost 100% of the Al in organic layer solution is organically bound in complexes and nontoxic (Wullaert et al., 2013).

A variety of indices based on chemical composition of the soil solid phase, soil solution, and plant tissue can be used to estimate Al stress of an ecosystem (Álvarez et al., 2005). One commonly used approach to estimate the threat of Al stress to plants is the Ca:Al molar ratio in plant tissue and soil solution and the base saturation of the soil (Cronan and Grigal, 1995), because the Ca-Al antagonism may disturb the Ca nutrition at high Al concentrations (Rengel, 1992). According to Cronan and Grigal (1995), indices for a 50% risk of adverse impacts on tree growth induced by Al stress are a Ca²⁺:Al_{inorganic} (sum of inorganic Al species) molar ratio of ≤1.0 in soil solution, a Ca:Al molar ratio of ≤ 12.5 in the foliar tissue, and a soil base saturation $\leq 15\%$ of the effective cation-exchange capacity (ECEC). Aluminum can also affect the Mg nutrition of plants (Kidd and Proctor, 2000; Kinraide, 2003). Reduced Mg concentrations in needles of Picea abies (L.) H.Karst. in an in-situ experiment with elevated Al concentrations (up to 500 μ M) in soil solution were revealed by De Wit et al. (2010). In a previous hydroponic experiment, impaired Mg translocation to the leaves and possibly reduced photosynthesis was suggested as a reason for reduced shoot biomass production under Al stress (Rehmus et al., 2015).

We analyzed Al fluxes and cycling in a tropical mountain forest in southern Ecuador and tested soil, soil solution and plant leaves for indications of Al toxicity to answer the following questions: 1. Is Al cycling enhanced in tropical montane forests because of acid soils and elevated litterfall production?

2. Do toxicity indicators point at negative effects of Al on plant growth?



Fig. 1. Schematic illustration of Al fluxes (kg ha⁻¹ yr⁻¹) in bulk (BD) and dry deposition (DD), throughfall (TF), litterfall (LF), stemflow (SF), organic layer leachate (LL), soil solution in the 0.15 (SS15) and 0.3 (SS30) m soil depths, and stream water (SW), and the Al canopy (CB) and dissolved Al catchment budgets (WB) for an approximately 9-ha large water catchment under tropical montane rain forest in southern Ecuador. Shown are arithmetic means of annual values (\pm SE) from 1998 to 2003 (n = 5), in case of soil solutions from 2000 to 2003 (n = 3).



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