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The output and bio-cycling of Si in a tropical rain forest developed on young basalt flows (La Reunion Island)

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ABSTRACT

The importance of plant bio-cycling in the biogeochemical cycle of Si has been pointed out by recent studies. We analysed the litter and wood chemical composition of a lowland rainforest (Marelongue Reserve, Réunion Island, Indian ocean) not impacted by human activities, developed on a recent basalt flow dated ci 500 years. The amount of elements stored in the above ground biomass falls within the range of tropical forests developed on moderately fertile older soils with Ca, K, Mg and Si values respectively at 1458 kg ha⁻¹, 1506 kg ha⁻¹, 246 kg ha⁻¹ and 17 kg ha⁻¹. The estimated mineral uptake of the old trees gives a flux equivalent to $5 \pm 2\%$ of the elements returned to the soil with litterfall. The four species that contribute the most to the litterfall with 70% of the leaf fall represent only 45% of the annual Si bio cycling. The result demonstrates that species that are not highly productive in a rain forest could be significant for the bio-cycling of parent-rock elements such as Si. A mass balance calculation shows that the dissolved silicon (DSi) issued from the dissolution of basalt is 1.8 times the DSi from litterfall. Here, the biogeochemical cycle of Si is characterized by a limited contribution of the bio-cycling compartment compared to other cases reported for rainforests.

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1. Introduction

The roles of living organisms have long been identified in the global cycle of silica (Jones and Handreck, 1967; Aston, 1983). The biogeochemical cycle of silica has become a subject of increasing interest during the last years because of its interconnexion with the C cvcle and global change (Ittekot et al., 2006: Street-Perrott and Barker, 2008). It is well established that the source of silica in the streams is mainly due to soil chemical weathering (Dove, 1996; Sommer et al., 2006). A few studies (Bartoli, 1983; Alexandre et al., 1997; Markewitz and Richter, 1998; Meunier et al., 1999; Lucas, 2001; Derry et al., 2005) have shown that the biogeochemical cycle of Si, at the local scale, can be controlled by plant bio-cycling as it is well established for other nutrients such as Ca (Likens and Bormann, 1995). At the global scale, the effect of plants on controlling the output of dissolved silicon (DSi) to the coastal zones is still not well known because it is difficult to dissociate the effects of vegetation, lithology and runoff (Hartmann et al., 2010). In order to improve the prediction models of the global Si cycle, we need to better document the plant-soil interactions regarding Si (Laruelle et al., 2009).

Absorption of silica from a culture solution depends on plant species (Van der Vorm, 1980). Based on experiments of mono-species plantation developed on similar soils, Cornelis et al. (2010) show that bio-cycling depends on tree species. In greenhouse experiments, Henriet et al. (2008) show that the stock of Si in banana plantlets increases with the amount of weatherable minerals in soils. The plant cycling might thus depend on the weatherability of the parent-rock and/or the ability of the species to accumulate the parent-rock elements. In order to assess the role of plant Si bio-cycling at a global scale, more attention should be paid to tropical forests which are the major contributors to net primary production (NPP) of terrestrial ecosystems (Chapin and Eviner, 2003). The importance of bio-cycling in the weathering budget under tropical ecosystems is well demonstrated above old weathering mantle (Lucas et al., 1993) but the effects of weatherability and species diversity on the Si biogeochemical cycle are still poorly documented in rain forests.

In order to contribute to the knowledge of the impact of bio-cycling in rain forests, we will address here the following question: is the Si stored and recycled in a forest controlled by a few species which are Si accumulators or by species containing low concentration of Si but dominant regarding the productivity? We choose a forest developed on young basalt flow, which are known to weather rapidly (Louvat and Allègre, 1997). Besides, in young soils, nutrients issued from the parent material such as P, Ca, Mg, K, Si are at their maximum concentration but





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the vegetation production is limited by N (Walker and Syers 1976; Vitousek et al., 1993).

We also analyse the DSi from the throughfall and the DSi from the output i.e. the waters leaving the soil towards the streams; in order to evaluate the impact of Si bio-cycling in the budget of DSi. Indeed two possible scenarios are expected: either the bio-cycling is dominant over output and plants accelerate the weathering processess (Lucas et al., 1993; Meunier et al., 1999); or the Si bio-cycling is limited and the ecosystem is controlled by chemical weathering as so in the coniferous temperate forest described by Bartoli (1983).

2. Materials and methods

2.1. Study area

This study was conducted in a permanent plot of the Marelongue reserve, located on the flanks of an active volcano, the Piton de la Fournaise on the South East coast of La Réunion Island (Indian Ocean) (Fig. 1). La Réunion Island belongs to one of the 34 biodiversity "hot spots" of the world for conservation priorities (Myers et al., 2000; Myers, 2003). The lower corridor of the reserve is a tropical lowland rainforest growing on a 500-year-old basaltic flow (Bachelery, 1999). Information concerning this forest is provided by previous studies (Strasberg, 1995; Strasberg, 1996; Kirman et al., 2007). With 41 tree species/ha, its biodiversity is lower than in tropical continental forests with but provides us with a sufficient number of variables to evaluate the interspecific variation of Si. The average annual temperature and rainfall during the study period (August 2000-June 2002) were respectively 23 °C and 4200 mm (Météo France data base). The canopy trees with a diameter at breast height $(dbh) \ge 10 \text{ cm}$ were identified, mapped, measured and their total standing biomass was estimated to be 535 tha⁻¹. The aboveground biomass was estimated to be 451 tha⁻¹ of which 445 tha⁻¹ were woody biomass. The annual litterfall was estimated to be 7.6 t ha⁻¹ yr⁻¹, of which $5.3 \text{ tha}^{-1} \text{ yr}^{-1}$ were leaves. This case study can be justified as a good model ecosystem because the total standing biomass and litterfall production are consistent with data obtained from other tropical forests (Kirman et al., 2007).

Six species were largely dominant in terms of population size, biomass and contribution to litterfall amount and composition: *Nuxia verticilata* (NV), *Agarista salicifolia* (AS), *Labourdonnaisia callophyloides* (LC), *Doratoxylon apelatum* (DA), *Syzygium* sp. (SS) and *Antirhea borbonica* (AB). The complete list of species is given in Table 1. A large litter production period occurred during the warm and wet period from November to April. Only two species, *AS* and *Weinmannia tinctoria* (WT), seemed to have an opposite litterfall distribution, loosing their leaves during the dry period.

The soil of the Marelongue forest is a hyperskeletic abruptic Leptosol on continuous rock (Raunet, 1991; IUSS Working Group WRB, 2006). It is thin, on average 1-cm deep, and patchy. This is an average soil thickness which can be expected after 500-years-weathering of a basaltic rock (Minasny and McBratney, 1999). There is no organic layer at the surface. At the same time, the roughness of the soil surface allows roots to colonize deep volumes of parent-rocks.

2.2. Sampling

In order to better constrain the biogeochemical cycle at Marelongue, the compositions of litterfall and aboveground biomass were determined and compared to the compositions of the soil and parent-rock.

2.2.1. Litterfall and wood

During 2 years, litterfall was collected every 2 weeks in 40 small traps of 0.125 m^2 and in three larger nets of 2.3 m^2 distributed randomly over a surface of 5000 m². The total collection area covered 11.6 m². The coordinates of the 40 traps were mapped in the permanent plot. Upon collection, litterfall was separated into leaves, twigs and woody items,



Fig. 1. Location of the study area.

reproductive organs, orchids and undetermined items (Kirman et al., 2007). At each sampling date, the number of leaves was determined for each species and each trap and the contribution of the different species was calculated for each trap in percent of the total dry weight. Dead woods were collected along 2 transects of 50 m long and 1 m wide randomly chosen into the study plot. Bryophytes and ferns were grouped together because very few bryophytes and often only unidentifiable fern leaf fragments were collected.

All samples obtained after sorting were individually oven dried at 70 °C to constant weight and their dry weight recorded. Leaves of the main identified species were analyzed. In order to do so, and for each species, a mixture of leaves collected at different dates and from different traps was ground to powder. Wood of the 6 main species, contributing more than 84% to the total aboveground woody biomass (Kirman et al. 2007) was sampled and dried to constant weight.

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