



Response of the N and P cycles of an old-growth montane forest in Ecuador to experimental low-level N and P amendments

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ARTICLE INFO

Article history:

Received 3 March 2010

Received in revised form 6 July 2010

Accepted 13 July 2010

Keywords:

Tropical montane forest

Nutrient cycle

Leaching losses

N deposition

P deposition

Environmental change

ABSTRACT

Atmospheric nitrogen (N) and phosphorus (P) depositions are expected to increase in the tropics as a consequence of increasing human activities in the next decades. In the literature, it is frequently assumed that tropical montane forests are N-limited, while tropical lowland forests are P-limited. In a low-level N and P addition experiment, we determined the short-term response of N and P cycles in a north Andean montane forest on Palaeozoic shists and metasandstones at an elevation of 2100 m a.s.l. to increased N and P inputs. We evaluated experimental N, P and N + P additions (50 kg ha⁻¹ yr⁻¹ of N, 10 kg ha⁻¹ yr⁻¹ of P and 50 kg + 10 kg ha⁻¹ yr⁻¹ of N and P, respectively) and an untreated control in a fourfold replicated randomized block design. We collected litter leachate, mineral soil solution (0.15 and 0.30 m depths), throughfall and litterfall before the treatment began (August 2007) until 16 months after the first nutrient application (April 2009). Less than 10 and 1% of the applied N and P, respectively, leached below the organic layer which contained almost all roots and no significant leaching losses of N and P occurred to below 0.15 m mineral soil depth. Deposited N and P from the atmosphere in dry and wet form were retained in the canopy of the control treatment using a canopy budget model. Nitrogen and P retention by the canopy were reduced and N and P fluxes in throughfall and litterfall increased in their respective treatments. The increase in N and P fluxes in throughfall after fertilization was equivalent to 2.5% of the applied N and 2% of the applied P. The fluxes of N and P in litterfall were up to 15% and 3%, respectively, higher in the N and N + P than in the control treatments. We conclude that the expected elevated N and P deposition in the tropics will be retained in the ecosystem, at least in the short term and hence, N and P concentrations in stream water will not increase. Our results suggest that in the studied tropical montane forest ecosystem on Palaeozoic bedrock, N and P are co-limiting the growth of organisms in the canopy and organic layer.

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1. Introduction

Atmospheric nitrogen (N) enters ecosystems in particulate, gaseous or dissolved inorganic and organic forms. Furthermore, biological N₂ fixation converts atmospheric N₂ to reactive N species introduced into the ecosystems (Galloway et al., 2004, 2008). Human activities can alter the N supply to forest soils mainly via elevated N concentrations in rainfall. The greatest future increase in N deposition from the atmosphere to land surface is expected in tropical areas (Galloway et al., 2004; Phoenix et al., 2006). The main reasons for increased N deposition are increasing biomass burning (Da Rocha et al., 2005; Fabian et al., 2005), increasing use of N fertil-

izers in agriculture and a higher fossil fuel consumption (Galloway et al., 2004, 2008). Increasing N deposition from the atmosphere can lead to soil acidification and consequently reduced availability of phosphorus (P) and base metals (Matson et al., 1999), NH₄⁺ and NO₃⁻ leaching, emissions of NO (which regulates the production of tropospheric ozone and is a precursor of nitric acid) and N₂O (which is a greenhouse gas, Matson et al., 1999; Koehler et al., 2009).

Phosphorus is deposited to ecosystems predominantly (82%) in the form of mineral aerosol dust (Pett-Ridge, 2009), but also includes aerosol P from biomass burning (5%) and biogenic materials such as pollen and spores (12%; Mahowald et al., 2005, 2008). Anthropogenic disturbance like slash-and-burn activities can lead to a total P loss of 36 kg ha⁻¹ in Amazonia, through emission of P to the atmosphere during the burning activities and through subsequent wind and water erosion of ash (Kauffman et al., 1993). More frequent forest fires are expected in Amazonia because of intensi-

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fied land clearing (Cochrane and Laurance, 2008), which might be further enhanced by climate change (reduced precipitation with subsequent forest dieback, Cochrane and Barber, 2009). Emitted and wind-eroded P is transported with the trade winds to the Equatorial Andes.

It is frequently assumed that N limits plant production on young soils since N is accumulated from the atmosphere and P limits plant production on old soils, since P gradually becomes unavailable during soil genesis (Walker and Syers, 1976). Since tropical lowland forests mainly grow on old soils and tropical montane forests on young soils, Tanner et al. (1998) speculated that lowland forests are P-limited while montane forests are N-limited. Vitousek (1982, 1984) reported that tropical lowland forests—which mainly occur on “old” soils—showed a low N use efficiency whereas the P and calcium (Ca) use efficiencies were high. In contrast, tropical montane forests were frequently characterized by a higher N use efficiency. Nutrient use efficiency for trees is defined as the amount of biomass produced per unit of assimilated nutrient. For practical measurements, this can be approximated as the amount of biomass lost per unit of nutrient lost.

The model of Walker and Syers (1976) was tested and confirmed in fertilization experiments in Hawaii on differently aged soils (Vitousek et al., 1993; Herbert and Fownes, 1995; Vitousek and Farrington, 1997; Harrington et al., 2001). However, there is a number of studies showing that tropical montane forests on young soils respond to N (Tanner et al., 1990, 1992; Cavelier et al., 2000) and P fertilization (Tanner et al., 1990; Cavelier et al., 2000) with increased growth. Similar results were reported for a dry tropical lowland forest in Yucatan, Mexico (Campo and Vazquez-Yanes, 2004). In contrast, stem growth in tropical lowland forest of Borneo on old soils did neither respond to N nor to P addition (Mirmanto et al., 1999).

Besides response of growth to fertilizer application, also the response of a number of other biogeochemical processes was reported in the literature. In early- and late-succession dry tropical lowland forests in Mexico, Solis and Campo (2004) observed increased N mineralisation and nitrification after N, P and N+P fertilization. Furthermore, N and P fluxes with litterfall increased, while in the early-succession forest, 15 and 30% of added N and P, respectively, were microbially immobilized (Campo et al., 2007). Campo et al. (2007) concluded that in dry tropical forests, fertilization with N and/or P reduced N and P limitation since they measured increased N and P fluxes to the soil by litterfall after two years in plots treated with N and P, respectively. In a 6 yr-old secondary forest in Amazonia growing on degraded pastures where repeated fires and other N losses occurred, plants took up 20% of 100 kg ha⁻¹ applied N and 10% of 50 kg ha⁻¹ applied P which was determined as the fraction not recovered in the soil. No changes were detected in soil inorganic N and soil microbial biomass N concentrations, or litter decomposition rates but more than twice as many arthropod individuals (excluding ants) were encountered in P and N+P plots than in the control plots (Davidson et al., 2004).

In summary, the type of nutrient limitation in tropical forests remains unclear and the biogeochemical responses to fertilizer applications are complex. Furthermore, it is possible that different compartments of the forest such as the canopy, the soil organic layer or the mineral soil show different nutrient limitations (Kaspari et al., 2008; Hedin et al., 2009). Recently, Kaspari et al. (2008) showed that in a tropical lowland forest in Panama, N influenced tree reproduction, P and potassium (K) the decomposition rate of cellulose and P and at least one micronutrient the rate of leaf litter decomposition. In the same forest, Barron et al. (2009) reported that molybdenum (Mo), a cofactor in the N₂-fixing enzyme nitrogenase, limited N₂ fixation by free-living heterotrophic bacteria in soils. In the Andean tropical montane forest in Ecuador, an incubation experiment showed that manganese

(Mn), zinc (Zn) and Ca were immobilized after adding a specific nutrient solution to soils. The mineralisation of sulfur (S) was found to be too slow to satisfy plants needs. The results therefore, suggested that S, Mn, Zn and Ca might contribute to limit plant growth (Wilcke et al., 2002). Boy et al. (2008a) showed that N and Mn deposited to the Andean tropical montane forest in Ecuador are largely retained in the canopy. Furthermore, additional Ca and Mg input into the Andean tropical montane forest by Sahara dust surprisingly changed the Ca and magnesium (Mg) budgets from loss to retention, suggesting that the additionally available Ca and Mg was used by the ecosystem possibly as the consequence of the input of another unknown limiting element which enhanced nutrient uptake in general (Boy and Wilcke, 2008). The differential nutrient requirements of the complex mixture of taxa and even ecosystem strata together with the temporal variation in nutrient requirements e.g., during different phenological stages of vascular plants might therefore result in a positive response of tropical forest to the amendment of any essential mineral nutrient.

Our overall goal was to assess short-term effects of elevated N and P depositions on N and P cycling in the Andean tropical montane forest by adding N and P at low levels to an old-growth forest. We hypothesized that (i) the forest is N-limited, that therefore (ii) added N remains in the aboveground cycle between soil organic layer and vegetation while (iii) added P is mainly abiotically retained by adsorption to soil minerals and little recycled in the ecosystem.

2. Materials and methods

2.1. Study area

The studied forest belongs to the Reserva Biologica San Francisco (RBSF) and is located in southern Ecuador on the eastern slope of the Cordillera Real of the Andes (i.e. the eastern cordillera) at an altitude between 2020 and 2120 m above sea level (a.s.l.) (3°59'S, 79°05'W), in the deeply incised valley of the Rio San Francisco draining to the Amazon. The vegetation at the study site can be classified as “evergreen lower montane forest” according to Homeier et al. (2008). Mean canopy height at the study site is about 12–14 m. The estimated crown radius for canopy trees is between 2 and 4 m, some of the biggest trees may reach 5–6 m. In the study area, more than 280 tree species have been identified so far with Lauraceae, Melastomataceae and Rubiaceae as the most abundant plant families (Homeier and Werner, 2007). *Graffenrieda emarginata* Triana (Melastomataceae) is the most abundant tree species with a diameter at breast height ≥ 10 cm. The 4-yr mean annual rainfall (2004–2008) ranged between 2527 \pm standard deviation, SD 400 and 2611 \pm 397 mm at two rainfall gauging stations (Wullaert et al., 2009). Rainfall has a unimodal distribution with a maximum between April and September and without a pronounced dry season (Fleischbein et al., 2005, 2006). Annual bulk N and P depositions with rainfall were 9.5–10 and 0.64–1.1 kg ha⁻¹ yr⁻¹, respectively, between 1998 and 2003 (Boy et al., 2008a). Mean annual temperature at 1950 m is 15.2 °C. The coldest months are June and July with a mean temperature of 14.4 °C; the warmest month is November with a mean temperature of 16.1 °C (Bendix et al., 2008). The soil is a Stagnic Cambisol (Hyperdystric, Chromic) (IUSS Working Group WRB, 2007) developed from Palaeozoic phyllites, quartzites and metasandstones.

2.2. Experimental design

Our study was conducted in the framework of the interdisciplinary NUTrient Manipulation EXperiment (NUMEX). The study site was located on the upper slope near a major ridge and has

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