Buttresses induced habitat heterogeneity increases nitrogen availability in tropical rainforests

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ABSTRACT

Role of buttresses as a physical support to trees is well known, however, information on how buttresses form habitat heterogeneity and increase availability of nitrogen (N) in tropical rainforests is not yet much known. This study reports consequence of buttresses induced habitat heterogeneity on build up and supply of mineral N in a tropical rainforest of the South Andaman Islands of India. Treatment included buttresses (upslope) and adjacent (flat) microhabitats. Mineral N (NH_4^+—N and NO_3^-—N) and microbial biomass carbon (MB-C) pools and mineral N supply rate (net nitrification and net soil N mineralization rates) were measured in both microhabitats for consecutive 12 months representing wet, post wet and dry seasons. Buttress microhabitats accumulated 7 t ha^{-1} yr^{-1} litters, which was 62% higher than adjacent microhabitats. The buttress microhabitats also had 13% more fine soil particles than adjacent microhabitats. Soil organic carbon (SOC), total N, mineral N and MB-C were 18%, 52%, 38% and 34%, respectively higher in the buttress than adjacent microhabitat. However, C/N ratio was lower in the buttress (18) than adjacent microhabitat (23). Net nitrification as well as net soil N mineralization rate was 45% and 44%, respectively higher in the buttress than adjacent microhabitat. High amount of rainfall during wet season reduced the net nitrification rate and NO_3^-—N pool, but increased NH_4^+—N pool; these phenomena probably protected mineral N from leaching losses and enhanced the habitat heterogeneity further. Net nitrification rate, net soil N mineralization rate and MB-C were inversely correlated to the rainfall amount. However, net soil N mineralization rate was positively correlated to MB-C. These observations suggest that buttresses accelerate nitrogen cycling at microhabitat scale and form habitat heterogeneity on a landscape scale (forest floor), which forms pockets of mineral N reserves and simultaneously increases supply of plant available N in the tropical rainforests.

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1. Introduction

Habitat heterogeneity is known to promote co-existence, maintain species diversity, increase productivity and bring stability to varied ecosystems (Gusewell et al., 2005; Jennifer et al., 2009; Townsend et al., 2008; Roy and Singh, 1994; Wright, 2002; Tang et al., 2011). Tree-buttresses, flared from the base of lateral roots of large trees, in addition to mechanical support, influence key ecological processes like carbon and nitrogen cycling in tropical rainforests (Wood et al., 2009). They accumulate litters, divert nutrient-rich stem flow (tree canopy wash), arrest fine soil particles by reducing overland flow generation and downslope transport of sediments (Herwitz, 1988), increase infiltration and maintain high soil moisture level even during dry season (Herwitz, 1988; Tang et al., 2011). The high soil moisture provides habitat to

soil-and litter-dependent fauna (Whitfield and Pierce, 2005) and promotes decomposition of the litters (Wood et al., 2009). Organic N in soils, resulted from the litter decomposition, undergo extracellular enzymatic oxidation and hydrolysis, which lead to simplification of complex proteins and allied compounds to NH_4^+—N (Gardner et al., 1989). The fine soil particles hold the NH_4^+—N on their surfaces and protect it from leaching losses (Pandey et al., 2000). Under favourable conditions NH_4^+—N is further oxidized to NO_3^+—N. Thus, root buttresses modify biogeochemical cycle and nutrient availability at a microhabitat scale and form habitat heterogeneity at a landscape scale in nutrient poor tropical rainforests (Sanchez and Logan, 1992; Pandey et al., 2007).

Rainfall amount is a major factor in tropical rainforests, which regulates seasonal availability of mineral N in the heterogeneous habitats (Pandey et al., 2007, 2009) through its influence on soil microbial activity (Powers, 1990). High amount of rainfall makes soil anaerobic, which kills aerobic and facultative microbes (Rinklebe and Langer, 2006) and probably thereby reduces net nitrification rates (Schuur and Matson, 2001; Pandey et al.,

2009). As a result NH_4^+—N accumulates particularly during wet season when amount of rainfall is high (Silver et al., 2001). In plants and microbes, NH_4^+—N assimilation generally exceeds NO_3^-—N assimilation due to the energy costs associated with NO_3^+—N reduction in tissues (Smirnoff and Stewart, 1985; Puri and Ashman, 1999; Silver et al., 2001). Function of root buttresses as a physical support to trees is well known (Ennos, 1993; Young and Perckoch, 1994). However, information on how buttresses induced landscape habitat heterogeneity influences soil N mineralization and microbial biomass carbon (MB-C) in tropical rainforests, to our knowledge, is yet unknown.

We hypothesized that buttresses would accelerate biological cycling of nitrogen at microhabitat scale and form habitat heterogeneity on a landscape (forest floor) scale, which would increase pool and supply of mineral N in tropical rainforests. However, pool and supply rate of mineral N would vary with season. To test these hypotheses we measured pools of mineral N (NH_4^+—N and NO_3^-—N) and microbial biomass carbon (MB-C), litter production and mineral N supply rate (net nitrification and net N mineralization rates) in the buttress and adjacent microhabitats in different seasons in the tropical rainforests of the South Andaman Islands of India.

2. Materials and methods

2.1. Study area

The study was conducted in the mountain tropical rainforests at Tirur, South Andaman Island, India (10°31′–13°42′N lat. and 92°14′–94°14′E long.). The soils at the study sites are Entisols (Dystric fluvisols, FAO) derived from sandstones. Climate is an equatorial humid tropical with mean monthly temperature of 23–30 °C and relative humidity 71–85%. About 10 years data (1995–2004) indicate that an average 3000 mm rainfall occurs in the study region with mean monthly variation of 300–500 mm during wet season (May–October), 100–200 mm during post-wet season (November–January) and <100 mm during dry season (February–April) (Pandey et al., 2007). Rainfall and temperature data for the study period are given in Fig. 1.

Tetramelus nudiflora R. Br., *Pterocymbium tinctorium* (Blanco) Merr., *Canarium euphyllum* Kurz., *Terminalia bialata* (Roxb.) Steud., *Persia insignis* (Blanford), *Pterocarpus dalbergioides* Roxb. ex DC were dominant tree species with root buttresses in the forests. Six stands (each ≈1 ha) in the forests similar in species structure were demarcated. Ten trees with similar buttress size, facing upslope, were selected in each stand for sampling. Adjacent to each tree buttress an area (plain) measuring 2×2 m in size was

selected as a control plot. Dimension of the buttresses was: length = 2.15 ± 0.67 m, width = 2.50 ± 0.89 m, and height = 1.87 ± 0.87 m. Thus each selected tree had two microhabitats i.e. buttress microhabitat and adjacent microhabitat. In total, there were six forest stands, and in each stand there were 10 buttress microhabitats and 10 adjacent microhabitats.

2.2. Soil sampling

Soils were sampled (0–15 cm depth) in both the microhabitats of each selected tree of all stands. Soils of the respective microhabitat were composited for a stand. The soil sampling was repeated for 12 months (May 2005–April 2006) in each microhabitat of all the stands. Thus, treatments included: two microhabitats (buttress microhabitat and adjacent microhabitat) and 12 months. Number of stands served as replicates. Pandey et al. (2007) found that seasonal variations in net N mineralization and net nitrification did not differ due to years. Therefore, we concluded that data for one year were sufficient to understand the effects of seasons and the microhabitats on net nitrification and net N-mineralization rates, pools of mineral N (NO_3^-—N and NH_4^+—N) and MB-C.

From each composited soil sample, plant material, such as fine roots, were removed by hand. Each composited soil sample was divided into two parts. One part in the field-moist condition was used for determination of mineral N (NO_3^-—N and NH_4^+—N), MB-C and soil moisture. The second part (field-moist) was used for assessing net N-mineralization rate. In October 2005, an additional part of the samples was utilized for analyses of physical and chemical characters of the soils.

2.3. Physico-chemical analyses of the soils

Air-dried soil samples were used for analyses of texture, bulk density, pH, organic C, and total N. Soil texture analysis was done using a hydrometer (Bouyoucos, 1962). Bulk density was determined by the core method (Grossman and Reinsch, 2002). Gravimetric soil water was estimated by drying 100 g soils in an oven (105 °C) until constant weight. Soil pH was measured with glass electrode (1:2, soil:water ratio). Organic C was estimated by Walkley and Black rapid titration method (Walkley and Black, 1934) and total N by microkjeldhal digestion method using a Kjel plus auto N analyzer (Jackson, 1958).

2.4. N-mineralization

Nitrogen-mineralization was measured by the buried bag technique (Eno, 1960) by incubating 150 g field-moist composited soil sample *in situ* at 0–15 cm depth for 15 days. Samples were transported to the laboratory within 3-h and analyzed for NO_3^-—N and NH_4^+—N within 6-h of collection. The NO_3^-—N and NH_4^+—N were measured in 2 M KCl extracts at the beginning and the end of the incubation (Bremner, 1965). Net N mineralization rate was calculated as: $(NO_3^-$—$N + NH_4^+$—N at $T_0) - (NO_3^-$—$N + NH_4^+$—N at $T_{15}) / T_{15} - T_0$, net nitrification rate as: $(NO_3^-$—N at $T_0) - (NO_3^-$—N at $T_{15}) / T_{15} - T_0$, and net ammonification rate as: $(NH_4^+$—N at $T_0) - (NH_4^+$—N at $T_{15}) / T_{15} - T_0$, where $T_{15} - T_0$ is the incubation time. All results are expressed on an oven-dry basis. Amount of N (kg ha^{-1} yr^{-1}) mineralized during the seasons was calculated using N mineralization rate (μg g^{-1} day^{-1}), soil bulk density and duration of the seasons.

2.5. Microbial biomass carbon (MB-C)

Soil microbial biomass C was estimated using a 24 h chloroform fumigation–extraction method (Vance et al., 1987). It was determined in the K_2SO_4 soil extracts of fumigated and unfumigated
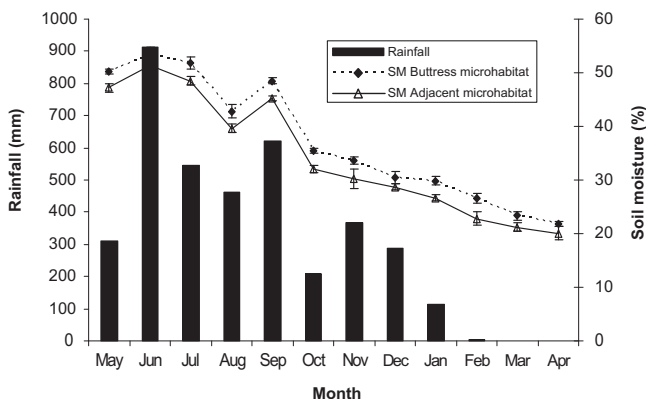

Fig. 1. Rainfall pattern and soil moisture in the soils under buttress and adjacent microhabitat in the mountain tropical rainforests of the South Andaman Islands of India.