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EDITORIAL

# Forest ecosystem responses to environmental changes: the key regulatory role of biogeochemical cycling

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## 1 Introduction

Forests cover ca. 42 million square kilometer in tropical, temperate, and boreal lands (ca. 30% of the land surface), store ca. 45% of terrestrial C, contribute ca. 50% of terrestrial net primary production, and harbor two thirds of terrestrial biodiversity (Bonan 2008; Purves and Pacala 2008; Xu et al. 2009). These forests not only provide timber and nontimber forest products, but more importantly, ecological services such as biodiversity and protection of watershed and soil resources and sequestration of C (Dixon et al. 1994; Chen et al. 2004a; Lamb et al. 2005; Purves and Pacala 2008). The N, P, and C interact in their biogeochemical cycles in ecosystems, and the stoichiometric balance is essential for maintaining forest ecosystem diversity, functioning, and stability (Wardle et al. 2004; Chen et al. 2005; Davidson et al. 2007). Environmental changes such as elevated atmospheric $CO_2$ and temperature, atmospheric N deposition, land-use change, and forest fires, have transformed much of the land surface on the earth in the past century (e.g., Wardle et al. 2004; Pan et al. 2008, 2009). It is essential to understand the ecosystem responses to these changes and the underlying processes regulating the responses (Dahlgren 2006). These environmental changes resulting mainly from anthropogenic activities have altered the biogeochemical cycles of C and N (Gruber and Galloway 2008). However, little is known about how the increased C and N by elevated $CO_2$ and N deposition and the loss of C and N by fires affect biogeochemical cycling of other elements (e.g., P; Gruber and Galloway 2008), how the interactions among C, N, and P cycles regulate forest ecosystem response to these changes, how the soil microbial community responds to these stoichiometry changes and mediate C, N, and P cycling processes under these changes, and how the aboveground and belowground processes are linked in response to these changes. In addition, impacts of interactions of these environmental changes on ecosystem processes are largely unknown (Knops et al. 2007; Gruber and Galloway 2008; He et al. 2009).

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## 2 Impacts of environmental changes on the belowground ecosystem processes

### 2.1 Elevated atmospheric $CO_2$

The global annual emissions of $CO_2$ have grown between 1970 and 2004 by about 80% and are projected to increase by 40–110% between 2000 and 2030 (IPCC 2007). Elevated atmospheric $CO_2$ leads to enhanced photosynthetic rate and growth and increased C inputs to the underground through root exudation and turnover and litterfall and affects ecosystem function and stability in the long term (Oren et al. 2001; Hyvönen et al. 2007; Lagomarsino et al. 2009). Elevated $CO_2$ alters nutrient concentrations of plant tissues and produces energy-rich but nutrient-poor litter with higher C:N ratios (Norby et al. 2001; Kurz-Besson et al. 2006). However, the effects of elevated $CO_2$ on litter decomposition are uncertain (Knops et al. 2007; Hyvönen et al. 2007). The impact of elevated $CO_2$ on the availability and turnover of soil P (particularly organic P) and its interactions with C and N is largely unknown. The elevated $CO_2$ may increase root exudation and then solubilization of soil P and tree P uptake (Delucia et al. 1997). Increased C:P ratios in organic substrates (leaf, root litters, etc.) induced by elevated $CO_2$ lead to the P limitation, which can in turn affect ecosystem responses to global climate changes (Hungate et al. 2003). Effects of elevated $CO_2$ on microbial biomass, activity, and composition are variable and far from predictable (e.g., Kao-Kniffin and Balser 2007). Recently, Austin et al. (2009) found that elevated $CO_2$ had no detectable effects on microbial community structure.

### 2.2 Atmospheric N deposition

Total N deposition is estimated to be nearly twofold greater by 2050 compared with deposition in the early 1990s due to continuous emissions of increased anthropogenic N on a global scale (Galloway et al. 2004). Atmospheric N deposition is known to be responsible for reduced plant diversity in natural and seminatural ecosystems (Phoenix et al. 2006). Atmospheric N deposition may initially increase N availability, N mineralization, and nitrification and thus, forest growth in the N-limiting areas (Aber et al. 1998; Horswill et al. 2008). Chronic N deposition can cause nutrient imbalances, acidification, base cation depletion, nitrate leaching, and water pollution (Aber et al. 1998; Horswill et al. 2008). At the later stage of N deposition, mineralization rate may decrease (Aber et al. 1998) and nutrient (e.g., P) limitation becomes a constraint to additional increases in productivity. Atmospheric N deposition modifies elemental composition of plant tissues, litters, and soil by decreasing C:N ratios and increasing N:P ratios (Månsson and Falkengren-Grerup 2003; Horswill et al. 2008) and lignin content (Knops et al. 2007), but impacts of N deposition on decomposition of litter is uncertain (e.g., Manning et al. 2008). The enhanced N availability induced by continued N deposition will increase P demand, which favors depletion of inorganic P. The availability and turnover of organic P will become important and may regulate the effects of atmospheric N deposition. Some temperate forests have moved from N limitation to P limitation due to N deposition (e.g., Akselsson et al. 2008). Atmospheric N deposition modifies soil microbial communities by direct effects on substrate quality and soil chemistry (e.g., acidification) and indirect effects by changing plant species composition and then affecting soil microbial community. Frey et al. (2004) found that N deposition decreased active fungal biomass and altered the pattern of microbial substrate use. But Waldrop et al. (2004) showed that response of microbial community to N deposition is ecosystem specific.

### 2.3 Forest fire

Fire profoundly modifies the terrestrial cycle of ca. 40% of land surface on the earth (Alexis et al. 2007) and plays an important ecological role in shaping natural rainforest ecosystems. Impacts of fire on soil depend upon its intensity, frequency, forest type, the slope, and fuel load (Knicker 2007). In general, immediate impacts of fire are the loss of C and N as gases and particulates into atmosphere from the ecosystem, while P remains in soil (Hungate et al. 2003; Carter and Foster 2004: Alexis et al. 2007). Some work has also shown that low intensity fire may have minor effects (e.g., Knicker 2007). Fire can increase immediate N availability (increases in $NO_3^-$-N and/or $NH_4^+$-N; Carter and Foster 2004). However, little is known about the impacts of fires on the amount and nature of soil P. Fires may increase P availability (Carter and Foster 2004). Changes in stoichiometry (i.e., decreased C:P and N:P ratios) induced by fires can have significant impacts on the soil P cycling and the interactions of biogeochemical cycles of C and N, which is still largely unknown. Further, the long-term impacts of these stoichiometric changes on the aboveground forest growth and productivity, species composition, and the belowground microbial community composition and activity have not been studied. In particular, in P-limiting forests, the increased P availability and the decreased N:P ratio resulting from the forest fire may encourage the growth of P-demanding species, which could not grow well previously and further change soil microbial community composition. Fire alters the soil microbial community structure in the short-term primarily through heat-induced microbial mortality. Over the long-term, fire may modify soil community by altering plant community composition via plant-induced changes in the soil environment (Hart et

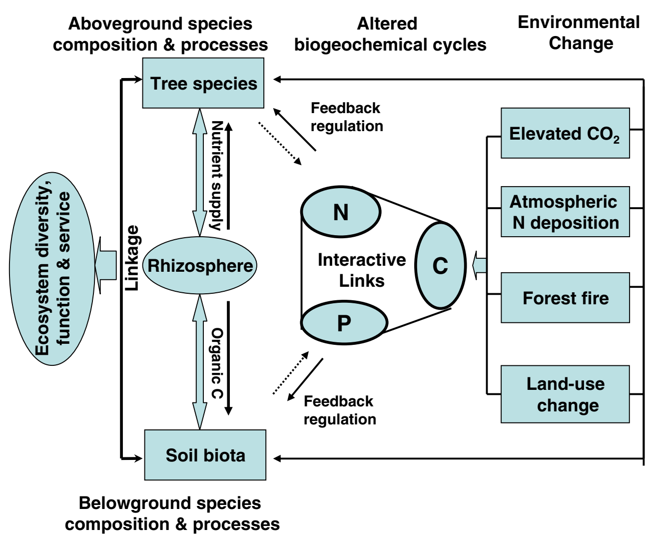


**Fig. 1** Hypothetical framework on the impacts of environmental changes (elevated atmospheric $CO_2$ and N deposition, fires, and land-use change) on forest ecosystem processes and regulation of the ecosystem responses to the environmental changes

al. 2005). Bacteria are more resistant to fire than fungi (González-Pérez et al. 2004). Repeated burning significantly reduced fungal biomass and mycorrhizal abundance and modified the fungal community structure (Hart et al. 2005).

### 2.4 Land-use change

Land-use change is a global phenomenon in response to changes in political, social, economic, or environmental conditions (Rudel et al. 2005) and the consequences of land-use change have been widely recognized (e.g., Rudel et al. 2005; Chen et al. 2008; de Chazal and Rounsevell 2009; Lu et al. 2009; Pan et al. 2009). These include its potential effects on carbon sequestration, soil quality, long-term sustainability, and the water and environmental quality (e.g., Fahey and Jackson 1997; Rudel et al. 2005; Richards et al. 2007; Macdonald et al. 2009). The impact of land-use changes on the ecosystem processes depends mainly on plant species and associated management practices (e.g., Chen et al. 2008; Chen and Xu 2008; Pan et al. 2008, 2009). It has been reported that land-use change from grassland to plantation forest enhanced the availability of soil P and other nutrients (e.g., Chen et al. 2000; Chen et al. 2003), while other studies suggested that land-use change from native forest to plantation forest decreased C and N availability (e.g., Chen et al. 2004b; Burton et al. 2007; Xu et al. 2008). Shifts in C and nutrient availability and balance would affect soil microbial community composition and functioning (Chen et al. 2004a, b; He et al. 2005; Macdonald et al. 2009). Land-use change is also a key driver of biodiversity change (e.g., Fischlin et al. 2007; de Chazal and Rounsevell 2009). Complex interactions of land-use change and other environmental changes make it difficult to estimate its effects on ecosystem biodiversity and function when the land-use change effects are examined alone.

## 3 Biogeochemical cycling regulates ecosystem responses to the environmental changes

Biogeochemical cycling processes play a vital role in the establishment or degradation of forests by regulating the natural and human impacts on forest ecosystems across a wide range of spatial and temporal scales (Wardle et al. 2004; Dahlgren 2006). Impacts of environmental changes on the interactions of C, N, and P biogeochemical cycles, and the role of these biogeochemical processes in regulating ecosystem responses to environmental changes are largely unknown. Here, we put forward the hypothetical framework (Fig. 1) in an attempt to elucidate impacts of environmental changes and biogeochemical regulation of ecosystem responses to these changes. Elevated $CO_2$ and atmospheric N deposition decrease relative P availability by increasing C and N inputs to the forest ecosystem, respectively. This results in increases in C:P and N:P ratios in soil organic substrates and altered biogeochemical cycles of C, N, and P, which may lead to the shift in the soil microbial community composition and function and thus, the aboveground species composition and growth and then regulate ecosystem responses to the elevated $CO_2$ and the N deposition. Fire causes losses of soil C and N but P remains. This leads to an increase in relative P availability by decreasing C:P and N:P ratios and changes in the chemical nature of soil organic P. This may cause changes in soil microbial community composition and activity and the aboveground forest growth and species composition. Land-use change, as previously discussed, also leads to the shifts in soil C and nutrient availability and stoichiometric balance, which in turn will affect soil microbial community composition and function and then the aboveground ecosystem processes.

In conclusion, ongoing natural and anthropogenic environmental changes such as increased atmospheric $CO_2$ and N deposition, fires, and land-use change have significantly impacts on the belowground ecosystem processes, and the forest ecosystem responses to the environmental change are likely to be regulated by interactive biogeochemical cycling processes. The environmental changes frequently occur at the same time and the interactions among these changes are very complicated. The mechanisms involved in the biogeochemical regulation of ecosystem responses to the environmental changes are largely unknown and warrant a detailed study using multiple disciplinary approaches, including soil chemistry, microbial ecology, plant physiology, and molecular biology.

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