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Nutrient-cycling and climate change in tropical forests

M. E. McGroddy and W. L. Silver

11.1 INTRODUCTION

Increased inputs of greenhouse gases have altered the composition of the atmosphere over the past 150 years (IPCC, 2001), resulting in shifts in temperature and precipitation around the globe. The scientific community has put an enormous effort into understanding the causes of these changes, and predicting future climate and the interactions between climate and the biosphere that may moderate or accelerate current trends. Most of the research on climate change, both ongoing and predicted, has focused on boreal and north temperate ecosystems where temperature shifts are predicted to be the largest (IPCC, 2001), and deep organic soils present the potential for a strong positive feedback to climate change (Vourlitis and Oechel, 1997; Oechel *et al.*, 1998; Hobbie *et al.*, 2002).

Tropical forests play an important role in the global carbon cycle, accounting for an estimated 43% of global net primary production, and storing over 25% of the C found in forest soils (Brown and Lugo, 1982; Melillo *et al.*, 1993). There has been considerable controversy over the potential effects of elevated CO_2 and climate change on productivity and C cycling in tropical forests (Körner, 1998; Silver, 1998; Chambers *et al.*, 2001; Chambers and Silver, 2004; Clark, 2004; Körner, 2004; Cramer *et al.*, 2004; Lewis *et al.*, 2004; Ometto *et al.*, 2005). Long-term forest inventory plots in Amazonia show increasing tree biomass over the past 50 years, coupled with parallel trends in tree recruitment and, to a lesser degree, mortality. While this has been suggested to result from increased atmospheric CO_2 concentrations (Phillips *et al.*, 1998; Baker *et al.*, 2004) it is equally possible that there are other causal factors—such as changes in disturbance regime or climate variation (Chambers and Silver, 2004; Lewis *et al.*, 2004). Greater productivity, whatever the ultimate cause, could slightly moderate the rate of increase of atmospheric CO_2 (i.e., Brown *et al.*, 1993; Wang and Polglase, 1995; McKane *et al.*, 1995; van Noordwijk *et al.*, 1997; Tian *et al.*, 1998; Körner 2004). Almost all efforts to model or predict the forest response to elevated atmospheric CO_2 and climate change are qualified by the caveat that nutrient limitations may restrict the ability of vegetation to respond with increased productivity (Lynch and St. Clair, 2004). The low C use efficiency of tropical trees has led to the hypothesis that productivity is likely to be limited by nutrients and/or water (Chambers *et al.*, 2004).

In attempting to understand the effects of predicted climate change and atmospheric CO_2 enrichment on nutrient-cycling in tropical forests and their implications for the future of these ecosystems we must keep in mind that atmospheric CO_2 concentrations have doubled over the past century and mean annual temperatures in most tropical forest regions have shown a strong warming trend over the past 40 years (Hulme *et al.*, 2001; Malhi and Wright, 2004). Inter-annual and multidecadal rainfall variability in the tropics is quite substantial and patterns in rainfall are less clear than those of temperature. Current measures of nutrient dynamics reflect a system that is already responding to climate changes. Long-lived perennial plants, adapted to fairly stable climates—such as those characteristic of tropical forest regions—may have limited plasticity to respond to the changes in atmospheric composition and climate they are experiencing. Thus, nutrient cycle processes dominated by plant physiology might have a limited range of responses while those dominated by microbes may be more rapidly and effectively shifting to match current conditions. Based on data from experimental manipulations we suggest that nutrient cycles in pre-industrial tropical forests may well have reflected more C-efficient physiological strategies with less C allocated to nutrient acquisition by plants (i.e., fine root biomass, root exudates including phosphatases and organic acids, mycorrhizal associations, etc.). Carbon conservation may have resulted in higher N mineralization rates, through N-based microbial metabolism. The combination of slightly cooler temperatures and reduced C inputs to below-ground processes might have resulted in lower rates of decomposition, P mineralization, and plant nutrient uptake.

Over the next century, mean annual temperature in tropical regions is predicted to increase anywhere from 1 to 5°C (IPCC, 2001; Hulme *et al.*, 2001; Lal *et al.*, 2002; Cramer *et al.*, 2004; Table 11.1). Tropical climates are generally characterized by warm temperatures with little seasonal variation in temperature (Holdridge, 1967). Near-constant warm temperatures throughout the year are likely to result in little temperature-related stress to organisms relative to that seen in temperate and boreal ecosystems, but may also make tropical systems particularly sensitive to even small

Table 11.1. Magnitude of predicted changes in regional climates in tropical regions. Data are from Cramer *et al.* (2004), based on output from four different climate models for the period 2081–2100 and are presented as anomalies relative to the period 1969–1998.

Region	Temperature (%)	Rainfall (%)
Neo-Tropics	+3 to +5.5	−17 to +8
Africa	+3.7 to +7.7	−17 to +10
Asia	+3.1 to +5.6	+7.5 to +23

changes in climate (Townsend *et al.*, 1992; Silver, 1998). Rainfall is more variable in tropical forests, ranging from 1 to 8 m/yr. Climate change induced patterns in precipitation are difficult to predict, and may vary significantly across regions within the tropics; this is in addition to predicted changes in the volume of rainfall changes in the seasonality or magnitude of rainfall events, which may also be important on the regional scale (IPCC, 2001; Lal *et al.*, 2001, 2002; Hulme *et al.*, 2001). Changes in precipitation that lead to increased drought, drenching rains, or soil saturation are likely to have a significant impact on tropical forest form and function. Approximately 42% of tropical forests currently experience significant drought during part of the year (Brown and Lugo, 1982). In these ecosystems, litterfall, decomposition, and nutrient uptake are synchronized with the timing and quantity of rainfall (Jaramillo and Sanford, 1995; Martinez-Yrizar, 1995). Changes in the frequency and severity of drought in seasonal and aseasonal forests will feed back on the amount and distribution of above- and below-ground NPP, nutrient mineralization rates, and the frequency and severity of fires (Mueller-Dombois and Goldammer, 1990).

In this chapter we discuss the potential effects of climate change on nutrient-cycling and explore the possibility for nutrient limitation to alter ecosystem response to elevated CO_2 and climate change. We briefly review the basic attributes of tropical soils, and then focus our analysis on soil phosphorus (P) and nitrogen (N), internal ecosystem fluxes (litterfall, decomposition, plant nutrient uptake), and C and N trace gas emissions. In tropical forests on highly weathered soils, P is thought to be the primary limiting nutrient to NPP, and thus the most likely to impact ecosystem response to global changes. In contrast, N is rarely thought to be limiting, but climate change coupled with increasing anthropogenic N deposition in tropical regions could have a significant impact on gaseous N losses, N leaching, and associated cation-leaching. We focus on short-term (less than 100 yr) effects of climate change on tropical forest biogeochemical cycling. Longer-term changes are more likely to include significant shifts in species composition and forest structure (Pimm and Sugden, 1994; Condit *et al.*, 1996; Bazzaz, 1998; Hilbert *et al.*, 2001; Enquist, 2002; McLaughlin *et al.*, 2002; Chambers and Silver, 2004; Jensen, 2004) confounding the effects of nutrient availability.

11.2 TROPICAL FOREST SOILS

The warm, and generally moist climate of the tropics combined with the lack of large-scale disruptions—such as the periodic glaciations of the boreal and temperate regions—has allowed soil development to continue undisturbed for millions of years. While most soil orders are represented in the tropics (Sanchez, 1976), the most common and extensive soil orders are the highly weathered Oxisols and Ultisols (McGill and Cole, 1981; Jordan, 1985; Vitousek and Sanford, 1986). These soils are generally characterized by fine textures, low charge density in the mineral fraction, and the dominance of variable, pH-dependent charge (Sanchez, 1976; Sollins *et al.*, 1988). Changes in precipitation can stimulate shifts in pH, which in turn affect cation and anion retention in soils. For example, dry-season irrigation in a moist forest in

Panama resulted in increased permanent charge and cation retention in surface soils (Yavitt and Wright, 2002).

With advanced weathering, most of the primary minerals in soils are absent, and Fe and Al oxides and hydroxides predominate. These minerals impart properties to soils that can decrease their nutrient-holding capacity in the mineral fraction, increase organic matter storage and associated nutrient retention, and lower pH (Uehara, 1995). In highly weathered tropical soils, organic coatings on mineral surfaces control a significant proportion of nutrient availability and cation exchange capacity (Tiessen *et al.*, 1994). Thus, factors that influence rates of production and decomposition can feed back on nutrient-cycling directly through mineralization of organically bound nutrients, and indirectly through changes in nutrient retention and storage associated with soil organic matter.

Old tropical soils tend to have low, exchangeable P pools (Cross and Schlesinger, 1995). In terrestrial ecosystems, P is primarily derived from the weathering of parent material; ecosystem P pools—and especially the available P fraction—reach a maximum early in ecosystem development (Walker and Syers, 1976; Crews *et al.*, 1995). Phosphorus availability generally declines over geologic time as fresh weathering inputs diminish and losses remain constant or increase (Walker and Syers, 1976). Geochemical reactions with Fe and Al oxides provide an additional sink for P which can function as a loss from the perspective of the biota. If P becomes occluded with Fe and Al, it forms secondary minerals that may require hundreds to thousands of years to weather into plant-available forms (Walker and Syers, 1976; Tate, 1985; Stevenson and Cole, 1999). Supply of residual primary P through weathering usually occurs well below the surface layers of the soil where most of the active roots occur. The low total P pools, lack of primary mineral P, slow weathering of secondary P minerals, and low rates of P deposition provide the basis for potential P limitation to NPP in tropical forests (McGill and Cole, 1981; Galloway *et al.*, 1982; Vitousek, 1984; Vitousek and Sanford, 1986; Andreae *et al.*, 1990; Williams *et al.*, 1997).

However, the extent and importance of P limitation has recently come under scrutiny (Johnson *et al.*, 2003; Davidson *et al.*, 2004b; Chacon *et al.*, 2006), and some of the mechanisms proposed are likely to be sensitive to climate change. For example, P availability increases under short-term anaerobic conditions. Some humid tropical forest soils experience fluctuating redox in surface horizons due to rapid rates of oxygen consumption that exceed diffusive resupply (Silver *et al.*, 1999). As soil oxygen declines, oxidized Fe forms are reduced, releasing bound P and decreasing the bonding efficiency for new P (Peretyazhko and Sposito, 2005; Chacon *et al.*, 2006). Increased temperature and/or rainfall may result in more frequent anaerobic events in humid tropical soils, potentially increasing labile soil P pools (Silver *et al.* 1999). In contrast, increased drought in humid regions could enhance the proportion of oxidized Fe forms and decrease plant P availability through strong P sorption and occlusion.

Elevated CO_2 could indirectly impact soil P availability in a number of ways. Increased plant demand for P due to a CO_2 fertilization response could result in increased plant production of phosphatases and/or organic acids, resulting in increased mineralization of organically bound P. Additionally, increased plant produc-

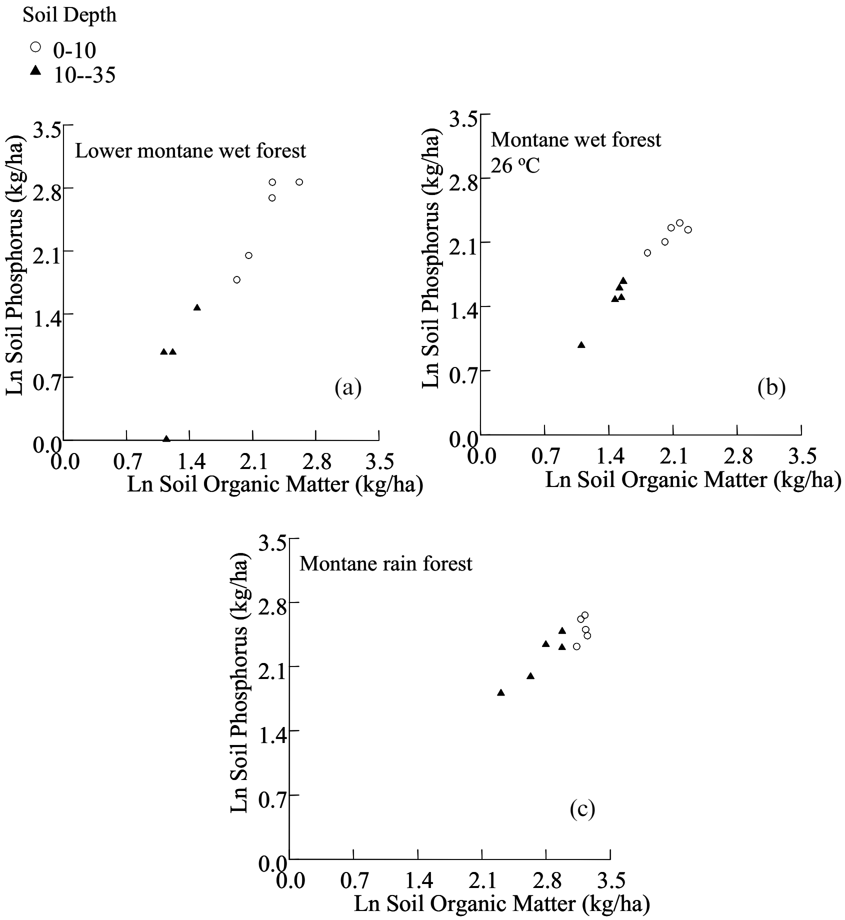

Figure 11.1. Relationships between soil organic matter content and exchangeable P in the 0–10- and 10–35-cm depths. Data are log-transformed and are from Silver *et al.* (1999). (a) For the lower montane wet forest $r_2 = 0.89$, $P < 0.01$; (b) for the montane wet forest $r_2 = 0.96$, $P < 0.01$; and (c) for the montane rain forest $r_2 = 0.82$, $P < 0.01$.

tion and soil organic matter density could result in decreased P sorption due to organic matter coating of Fe and Al oxide minerals (Lloyd *et al.*, 2001). At the landscape scale, soil organic matter was positively correlated with exchangeable P in soils along a rainfall and temperature gradient in a subtropical forest in Puerto Rico (Figure 11.1) and in a Bornean rainforest (Burghouts *et al.*, 1998). Similarly, labile P in mineral soils was strongly positively correlated with soil C pools along a localized soil texture gradient in moist tropical forest in Brazil (Figure 11.2). Elevated CO_2 or climate changes that decrease the mass of soil organic matter could indirectly impact soil P pools, and feed back to decrease NPP. It is also possible, however, that the strong correlations between P and soil organic matter along natural gradients result from other factors that affect soil P availability and in turn stimulate organic matter

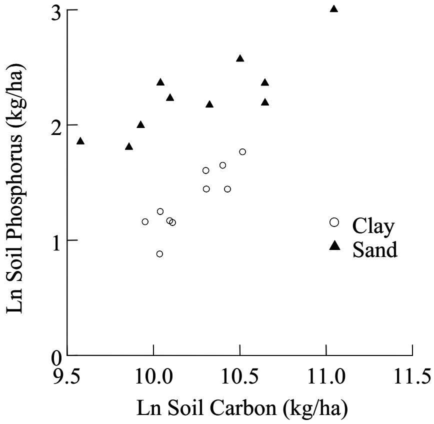

Figure 11.2. The relationship between total C and exchangeable P pools in sand and clay soils in a moist tropical forest in Brazil. Data are log-transformed and are taken from the 0–10-cm soil depth in Silver *et al.* (2000). For sandy soils, $r_2 = 0.71$, $P < 0.01$; for clay soils $r_2 = 0.77$, $P < 0.01$.

production and P content (Lloyd *et al.*, 2001). In the Brazilian forest, forest floor P content was positively correlated with forest floor C (Figure 11.3). This could indicate top-down control of the soil C and P relationship. Alternatively, fungal colonization of the forest floor may alter soil P concentrations (Lodge, 1993), leading to a narrow range of C : P ratios favorable during decay.

In contrast to many temperate ecosystems, tropical forests on highly weathered soils tend to have adequate to high N availability (Vitousek and Howarth, 1991). This is likely due both to N accumulation via N fixation over geological timescales (Riley

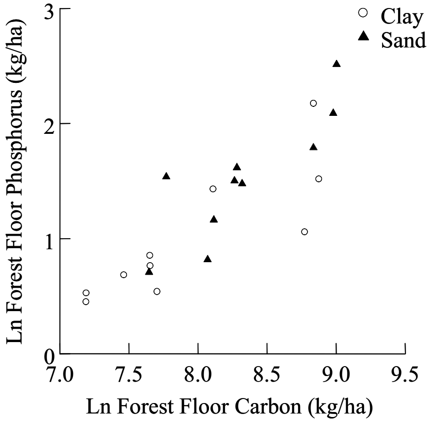

Figure 11.3. The relationship between forest floor C and forest floor P pools in sand and clay soils in a moist tropical forest in Brazil. Data are log-transformed and are from Silver *et al.* (2000). For sandy and clay soils combined, $r_2 = 0.71$, $P < 0.01$.

and Vitousek, 1995; Crews *et al.*, 2001), and internal N retention mechanisms that limit losses (Silver *et al.*, 2001, 2005b). Even when it is abundant, N-cycling in tropical forests can impact the availability of other nutrient cations and anions. Variable charge soils in high rainfall environments can experience ammonium and associated anion-leaching (Sollins *et al.*, 1988). High nitrification rates coupled with abundant rainfall can stimulate nitrate and associated cation-leaching from tropical soils (Silver and Vogt, 1993).

Factors that affect decomposition (see below) are likely to influence N mineralization rates. In temperate and boreal ecosystems, net N mineralization rates tend to increase with mean annual temperature and moisture, and generally increase with *in situ* warming (Rustad *et al.*, 2001). There have been few studies looking at soil N cycling in tropical forests in response to changes in temperature or moisture. In laboratory studies, net N mineralization rates were insensitive to temperature changes along a tropical montane forest elevation gradient (Marrs *et al.*, 1988), as were soils from a Colombian cloud forest (Cavelier *et al.*, 2000). In a recent review, Silver *et al.* (2006) found no apparent effect of temperature on net or gross N mineralization and nitrification rates along tropical elevation and temperature gradients.

Nitrogen-cycling is likely to be sensitive to changes in precipitation, particularly at the arid or very wet extremes. In dry tropical forests, pulses of precipitation can result in rapid rates of N mineralization, nitrification, and nitric oxide emissions (Davidson *et al.*, 1993; Lodge *et al.*, 1994). In wet forests, increased precipitation can enhance element-leaching (Sollins and Radulovich, 1988), lower soil redox (Silver *et al.*, 1999), and lead to increased N losses via denitrification (Silver *et al.*, 2001). If increased precipitation lowers soil redox it could also decrease rates of nitrification, a strictly aerobic process, providing a potential negative feedback to cation-leaching and gaseous N losses.

Agricultural and urban development in the tropics is dramatically increasing the rate of N deposition to tropical ecosystems (Galloway *et al.*, 1994, 1995). Current N deposition theory argues that N-rich environments should experience large and rapid increases in N losses with N deposition (Aber *et al.*, 1989; Matson *et al.*, 1999). The interaction of N deposition and climate change, particularly increased duration or intensity of rainfall, could significantly increase nutrient losses from these ecosystems (Figure 11.4). Nitrogen fertilization in N-rich Hawaiian forests led to increased nitric oxide (NO) and nitrous oxide (N_2O) fluxes (Hall and Matson, 1999), and stimulated N-leaching (Lohse and Matson, 2005). Increased N-leaching could enhance cation and anion losses, leading to nutrient limitation to NPP. Nitrogen-leaching also pollutes streams and groundwater sources (Vitousek *et al.*, 1997). The interactions of N deposition, elevated CO_2, and climate change are poorly understood for tropical forests. This clearly should be a high priority for future research.

11.3 LITTER INPUTS

Alterations to the amount and timing of rainfall in tropical forests may significantly affect nutrient-cycling via litter production, although the relationship between climate

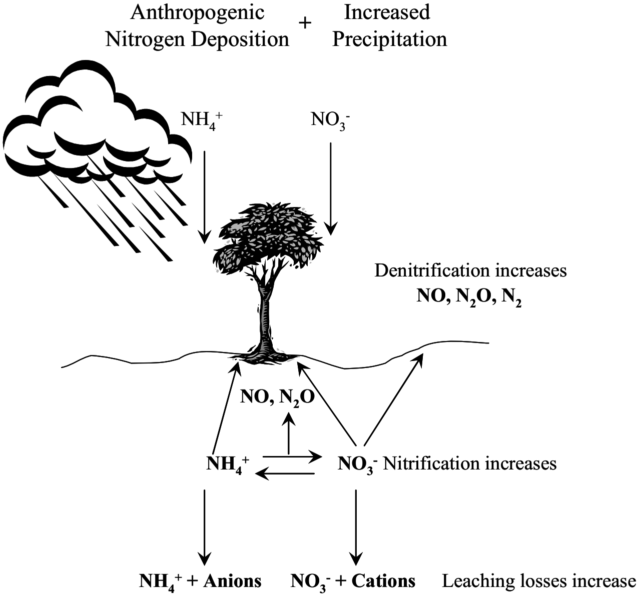

Figure 11.4. The potential effects of anthropogenic nitrogen deposition and increased precipitation in tropical forests. Increased inputs of ammonium could stimulate ammonium-leaching in variable charge soils, and lead to associated anion losses. Ammonium deposition could stimulate nitrification, enhancing nitric and nitrous oxide fluxes. Increased nitrate pools via nitrification or direct deposition could stimulate nitrate- and cation-leaching and denitrification. If soil redox declines with climate change, then nitrification rates could decrease, partially offsetting the effects of nitrogen deposition.

and litter dynamics is likely to be complex. Litter P concentrations have been found to correlate positively with rainfall seasonality and with inter-annual rainfall in moist and dry tropical rainforests (Read and Lawrence, 2003; Wood *et al.*, 2005), but not spatially along larger-scale elevation and rainfall gradients (Silver, 1998). The observed increase in litterfall P content during the wet season or wet years in seasonal environments may be due to increased soil P availability and/or decreased demand for the retranslocation of P during leaf senescence (Wood *et al.*, 2005). Similarly, there may be significant changes in plant P demand associated with seasonal phenological activity (Lal *et al.*, 2001). Although foliar N may increase per unit leaf mass with increasing precipitation (Wright *et al.*, 2001; Wright and Westoby, 2002; Santiago and Mulkey, 2005), leaf litter N concentrations do not appear to vary with precipitation in moist (Santiago and Mulkey, 2005; Read and Lawrence, 2003) or humid (Silver, 1998; Wood *et al.*, 2005) tropical forests. Elevated atmospheric CO_2 has also been shown in some cases to increase the litter C : N and C : P ratios, though again the effect is not consistent (Kanowski, 2001; Santiago and Mulkey, 2005).

Climate change impacts on litter inputs may also come from shifts in timing or amount of litterfall. In seasonal tropical forests, litterfall and nutrient uptake are synchronized to the annual patterns in precipitation (Jaramillo and Sanford, 1995).

Seasonality of litterfall has been shown to be negatively correlated to mean annual precipitation in gradient studies (Read and Lawrence 2003; Santiago and Mulkey, 2005). Shifts in the duration of the dry season may lead to temporal separation between plant demands and nutrient availability (Silver, 1998). Increased duration and severity of droughts may also lead to an increase in drought deciduousness, or a decrease in the leaf area index of the canopy (Nepstad *et al.*, 2002). This could decrease litter inputs and/or disrupt the synchronicity between nutrient inputs and plant demand (Lodge *et al.*, 1994). Over the long term, a shift to a significantly wetter or drier environment could lead to a species composition shift with associated changes in both litter quality and quantity (Condit, 1998; Santiago *et al.*, 2005).

Below-ground litter inputs are difficult to study and few data are available. Elevated CO_2 may increase allocation to root tissues in tropical forests if nutrients are limiting (Arnone and Körner, 1995), although this could be offset by increased root mortality and turnover. Thus far, the data from field and greenhouse experiments are very mixed (Norby and Jackson, 2000). At a global scale, there were no strong relationships between root turnover (below-ground NPP/fine root standing stocks) and temperature or precipitation in forested ecosystems (Gill and Jackson, 2000). In temperate forests, fine root growth cycles appear to be regulated by temperature, resulting in strong annual signals of productivity and mortality (Pregitzer *et al.*, 2000). In contrast, tropical soils experience little variation in soil temperature seasonally, suggesting that any patterns in turnover are more likely to be dominantly controlled by soil moisture, nutrient supply, or internal regulation of root : shoot ratios. Dry-season irrigation did not change overall root phenology in a moist tropical forest, but did alter the timing of root growth and mortality by increasing the longevity of new roots while simultaneously increasing the mortality of older roots (Yavitt and Wright, 2001).

11.4 DECOMPOSITION

Actual evapotranspiration is one of the strongest predictors of decomposition on a global scale (Aerts, 1997), although its explanatory power is quite weak ($r_2 = 0.14$). Regionally, the relationship between rainfall and decomposition appears even weaker. Using elevation gradient studies within tropical forests, Silver (1998) found no predictive relationship between rainfall and decomposition rates. A 50% reduction in precipitation reaching the forest floor had no effect on litter decomposition rates in a partial throughfall exclusion experiment in a moist forest in Amazonia (Nepstad *et al.*, 2002), and dry-season irrigation resulted in only a small increase in decomposition rates of the forest floor in a moist forest in Panama (Wieder and Wright, 1995). In Hawaii, leaves decayed faster in moist forests than in wet forests (Schuur, 2001), but a common substrate showed a weaker trend, suggesting an important interaction of plant characteristics with climate or site conditions. Given this, the direct effects of either an increase or a decrease in mean annual precipitation on decomposition would probably be quite small. There are, however, indirect effects of climate change that might significantly affect the rate of both decomposition and mineralization of essential nutrients. In tropical sites, litter chemistry and in particular C : P, lignin : P, C : N, and lignin : N ratios are often inversely related to decomposition rates (Ostertag and Hobbie, 1999; Hobbie and Vitousek, 2000). As discussed above, both decreased rainfall and/or elevated atmospheric CO_2 might lead to increased C : nutrient ratios in litter. Significant immobilization of nutrients during the early stages of decomposition is commonly observed in tropical forest ecosystems (Ostertag and Hobbie, 1999; McGroddy *et al.*, 2004; but see Kitayama *et al.*, 2004). Increased C : nutrient ratios in leaf litter could increase immobilization of nutrients in the microbial biomass during decomposition, could lower mineralization rates, and could reduce plant available nutrient pools.

Below-ground decomposition appears to be less sensitive to climate factors than above-ground litter, with tissue quality playing a key role in regulating the rate of decay (Silver and Miya, 2001). Matamala and Schlesinger (2000) found no effect of elevated CO_2 on root decomposition or tissue quality in a young temperate loblolly pine forest, though previous studies have found decreased root tissue N content under elevated CO_2 treatments (Crookshanks *et al.*, 1998).

11.5 NUTRIENT UPTAKE

Not surprisingly, the impact of climate change on below-ground ecology has received far less attention than above-ground effects. In order to stimulate more research, Norby and Jackson (2000) produced an excellent review of the data currently available on root responses to elevated CO_2 and climate changes. Plant uptake of essential nutrients is highly sensitive to soil temperature, moisture, and aeration, and thus is likely to be affected by climate change, but measured changes in nutrient uptake kinetics have not been strongly correlated with changes in productivity (Chapin, 1974; Bassirirad, 2000). The rate of plant nutrient uptake depends on the amount of active root surface, the movement of nutrients to the active root surface, nutrient availability, and the transport rate across membranes into both the root itself and finally into the xylem system. All of these factors may respond to climate change in ways that magnify or mitigate the impacts.

Tropical forests are often characterized by high below-ground biomass (Jackson *et al.*, 1996) and root turnover (Gill and Jackson, 2000; Trumbore *et al.*, 2006). Soil temperature and soil moisture both have the potential to affect root architecture and root growth (Gill and Jackson, 2000), and can be positively correlated to fine root length and root uptake (Bassirirad, 2000; Pregitzer *et al.*, 2000), though field studies have found phenological and other constraints often weaken these relationships (Fitter *et al.*, 1998). Under elevated CO_2 some species increased their below-ground biomass, suggesting that the additional available C is used to increase fine root volume and nutrient uptake, particularly in deciduous forests (Norby *et al.*, 1999). Other studies, however, have shown no effect or increased root mortality, resulting in higher turnover of fine root pools and no measurable change in stocks (Arnone *et al.*, 2000; Tingey *et al.*, 2000; Pregitzer *et al.*, 2000). Based on work with crop plants and the regulatory role of simple sugars on cell division, Pritchard and

Rogers (2000) suggested that under elevated CO_2 roots will be larger, more highly branched, but less efficient at nutrient and water uptake. They go on to suggest that this might amplify the impact of warmer, drier soil conditions predicted for some tropical regions—such as equatorial Africa.

Fine roots are only one component of plant uptake, and for P uptake, in particular, mycorrhizal associations are vital components (Bolan, 1991; Miyasaka and Habte, 2001). Mycorrhizal hyphae increase the amount of soil volume explored and exude phosphatases and organic acids to increase P uptake (Bolan, 1991). Mycorrhizal associations are ubiquitous in tropical forest soils, where up to 90% of tree species are thought to support associations with endomycorrhizae (Bolan, 1991). If elevated CO_2 increased C allocation below ground and, in particular, to mycorrhizal associations, this could in turn increase plant nutrient uptake. Studies thus far, however, have not found support for this (Fitter *et al.*, 2000; Zak *et al.*, 2000a; Gavito *et al.*, 2003; Staddon *et al.*, 2004). It appears that elevated CO_2 on its own has little or no impact on mycorrhizal infection rates or production of mycorrhizal tissue, at least under experimental conditions (Staddon and Fitter, 1998). Mycorrhizae do appear to respond positively to increased soil temperature, though most studies have been done on temperature ranges more typical of temperate regions (Braunberger *et al.*, 1997; Fitter *et al.*, 2000; Staddon *et al.*, 2004), and it is not clear if the relationship will continue to hold at the warmer temperatures typical of the tropics. Mycorrhizal infections are inversely related to soil P availability (Janos, 1983), and if plant P demand were to increase it could result in increased mycorrhizal infection rates. Responses of mycorrhizae to changes in soil temperature and moisture often appear to be species-specific; thus, any shift in climate that results in a significant shift in mycorrhizal community composition has potentially wide-reaching implications for nutrient cycles (Fitter *et al.*, 2000).

The nutrients held in the microbial biomass represent a small but very rapidly cycled pool. Though soil microbial communities are widely considered to be C-limited, recent work in highly weathered tropical sites suggests that microbial activity may be limited by P availability or co-limited by C and P (Cleveland *et al.*, 2002). As with plants, it is likely that microbial communities in highly weathered tropical soils are more limited by P than by N (Vitousek and Matson, 1988). The rate of mineralization of organically bound nutrients is closely linked to the rate of microbial activity and turnover of the microbial biomass. Field studies have found slightly positive, but highly variable responses in microbial biomass or microbial respiration to elevated atmospheric CO_2 in temperate forests (Zak *et al.*, 2000b). Under low-nutrient conditions, microbial immobilization of limiting nutrients increased in response to elevated CO_2 (Berntson and Bazzaz, 1997, 1998). This could lead to significant negative feedbacks to productivity in nutrient-limited ecosystems.

Drought may also strongly affect microbial biomass and activity including nutrient immobilization and mineralization. In seasonal tropical forests, microbial biomass and P pools have been found to increase in the dry season, presumably in response to decreased plant uptake (McGroddy *et al.*, submitted). As discussed above for litter inputs, there is a synchronous flush of nutrients released from the microbial biomass at the onset of the wet season in these seasonal forests, coinciding with the onset of new root growth and increased plant demand (Perrott *et al.*, 1990). In contrast, aseasonal tropical forests do not show intra-annual variations in microbial P pools (Yavitt and Wright, 1996; Luizão *et al.*, 1992). Shifts in the timing and length of dry seasons in seasonal forests and the introduction of drought into aseasonal forests could alter the competitive balance between microbial biomass and plant demand for nutrients. Drought or shifts in temperature can also lead to a shift in microbial community composition and function (Papatheodorou *et al.*, 2004; Sowerby *et al.*, 2005) with potential long-term effects on rates of nutrient-cycling and productivity. Several studies have shown the direct effects of elevated CO_2 on the composition and function of the microbial community, presumably through increased or altered carbon exudates into the rhizosphere, though this response may be moderated by soil nutrient or C availability (Zak *et al.*, 2000a).

11.6 TRACE GAS EMISSIONS

Tropical forests are important sources and sinks of greenhouse gases, particularly CO_2, N_2O, and methane (CH_4). The high NPP typical of moist and humid tropical forests is a significant component of the global C cycle (Melillo *et al.*, 1993; Clark *et al.*, 2003). Tropical forests also have the highest rates of soil respiration, which releases CO_2 back to the atmosphere (Raich and Schlesinger, 1992). Drought, fire, clearing, and disease—all factors that rapidly increase rates of tree mortality—can alter microbial activity or community structure, resulting in pulses of CO_2 and other greenhouse gases (Schimel and Gulledge, 1998). Methane is produced under anaerobic conditions and tropical forests have generally been considered a weak sink (Keller and Reiners, 1994; Steudler *et al.*, 1996). However, upland tropical forest soils have recently been identified as a significant source of CH_4 at local (Keller *et al.*, 1986; Silver *et al.*, 1999; Teh *et al.*, 2005) and regional (Frankenberg *et al.*, 2005) scales.

Humid tropical forests are the largest natural source of N_2O globally (Lashof and Ahuja, 1990). Nitrous oxide is produced via nitrification and denitrification. Factors that stimulate nitrification—such as the death of N-rich tissues and anthropogenic N deposition—can increase N_2O emissions (Hall and Matson, 1999; Silver *et al.*, 2005a); similarly, if soils become reduced, denitrification rates to N_2O and dinitrogen (N_2) may increase (Firestone *et al.*, 1980; Silver *et al.*, 2001). In the humid tropics, denitrification is likely to be the dominant source of N_2O emissions from soils. The potential effects of climate change on the ratio of $N_2O : N_2$ are poorly understood. Theory suggests that denitrification to N_2 is favored under low-NO_3^- and low-redox conditions, so it is possible that if increased rainfall and temperature lead to more strongly reducing conditions less NO_3^- will be available for denitrification and N_2 production will be favored. It is extremely difficult to accurately estimate N_2 fluxes from ecosystems, although this is an active area of research.

There have been few controlled experiments looking at the effects of climate changes on greenhouse gas production in tropical forests. Throughfall exclusion experiments—mimicking enhanced drought conditions—decreased N_2O emissions from seasonal forests in tropical Brazil (Cattanio *et al.*, 2002; Nepstad *et al.*, 2002;

Table 11.2. Summary of potential effects of climate change on nutrient cycling in tropical forests.

	Increased temperature	Altered rainfall (+/−)	Other effects	Research directions
Soil nutrient availability	Increase in mineralization rates for both N and P	+Increased P availability due to shift in redox conditions, increased N losses via nitrification, denitrification, and leaching	Increased soil organic matter due as a result of elevated CO_2 could increase nutrient retention capacity and organic coatings could decrease P sorption capacity	What is the impact of increases in nutrient deposition due to urbanization and intensification of agriculture in addition to climate shifts and elevated CO_2 in these systems?
Litter nutrient inputs and decomposition		Data show both + and − correlations between rainfall and litter nutrient concentrations Shifts in seasonality could decouple decomposition of litter from nutrient demand	Some evidence for increased C : nutrient ratios under elevated CO_2 potentially leading to decreased decomposition rates and/or increased nutrient immobilization during decomposition	What are the effects of climate change on below-ground nutrient inputs and decomposition?
Nutrient uptake	Root uptake kinetics are positively related to soil temperature. Mycorrhizal infection appears to be positively correlated to soil temperature	Stronger drought/dry-season dynamics may reduce fine root and microbial biomass in surface soils, thus reducing nutrient uptake	Shifts in relative and absolute below-ground plant biomass under elevated CO_2 appear to be species-specific, thus hard to predict in a diverse tropical forest	Are changes in nutrient uptake dynamics translated into shifts in net productivity?

(*continued*)

Table 11.2 (*cont.*)

	Increased temperature	Altered rainfall (+/−)	Other effects	Research directions
Trace gas emissions		N_2O emissions are sensitive to soil moisture conditions and have been found to positively correlate to rainfall. Under wet conditions upland tropical forests can switch from a slight sink to a net source of CH_4		Will trace gas dynamics in tropical forests under wetter and warmer conditions lead to positive feedbacks for the global climate?

Davidson *et al.*, 2004a). Similar results were found during an induced drought in a tropical megacosm experiment (van Haren *et al.*, 2005). Observational data along a tropical montane rainfall gradient showed increased N_2O emissions with increasing rainfall (Keller *et al.*, 1986) and decreased soil O_2 availability (Silver *et al.*, 1999).

11.7 SUMMARY AND FUTURE DIRECTIONS

In summary, nutrient-cycling in tropical forests is likely to be sensitive to current and future global changes, particularly changes in the amount and distribution of precipitation (Table 11.2). Existing research has focused on the effects of increased drought, which impacts P- and N-cycling primarily through changes in microbial processes and plant litter dynamics. From this review it is clear that predictions of the response of tropical forests to climate change and elevated atmospheric CO_2 are based primarily on extrapolation from other regions, observational changes along climate gradients, and a few direct experiments. Extrapolation from other regions—particularly, north temperate and boreal ecosystems—can be problematic because tropical forests: occur on highly weathered, P-limited soils; support very diverse microbial, plant, and animal communities; and have high mean annual temperatures with low temporal variability. Similarly, while climate gradient research can provide insights into systematic changes across plant communities and habitats (Silver, 1998; Schuur, 2001), they are generally poorly suited to explore climate changes within a given community or site. There have been some significant strides forward with the establishment of large-scale *in situ* manipulations in the tropics such as the throughfall exclusion experiment in eastern Amazonia (Nepstad *et al.*, 2002), and the irrigation of a seasonally dry forest in Panama (Wright, 1992; Yavitt and Wright, 1996). Clearly, more experimentation is needed to determine the sensitivity of tropical forest flora, fauna, and biogeochemical cycles to elevated CO_2 and climate change.

Future research should be designed to capture ecosystem responses within a realistic range of temperature and/or precipitation change, and over a long enough time interval to determine whether self-regulation or equilibration to a new condition occurs. As mentioned above, tropical regions are characterized by mean annual temperatures near the biological optimum. Under these conditions a small shift in temperature may have a stronger or different effect than a large increase in ecosystems that typically experience wide seasonal shifts in temperature. Collaborative research should be a key component of future climate change experiments, to better understand the linkages among population, community, and ecosystem processes. Consideration of other human impacts on the environment, such as land-use change, anthropogenic inputs such as N deposition, and invasive species will also improve our ability to predict future conditions.

11.8 REFERENCES

Aber, J. D., Nadelhoffer, K. J., Steudler, P., and Melillo, J. M. (1989) Nitrogen saturation in northern forest ecosystems. *BioScience* **39**, 378–386.

Aerts, R. (1997) Climate, leaf litter chemistry, and leaf litter decomposition in terrestrial ecosystems: A triangular relationship. *OIKOS* **79**, 439–449.

Andreae, M. O., Talbot, R. W., Beresheim, H., and Beecher, K. M. (1990) Precipitation chemistry in Central Amazonia. *Journal of Geophysical Research* **95**, 16987–16999.

Arnone III, J. A. and Körner, C. (1995) Soil and biomass carbon pools in model communities of tropical plants under elevated CO_2. *Oecologia* **104**, 61–71.

Arnone, J. A., Zaller, J. G., and Spehn, E. M. (2000) Dynamics of root systems in native grasslands: Effects of elevated atmospheric CO_2. *New Phytologist* **147**, 73–86.

Baker, T., Phillips, O. L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Higuchi, N., Killeen, T. J., Laurance, S. G. *et al.* (2004) Increasing biomass in Amazonian forest plots. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* **359**, 353–365.

Bassirirad, H. (2000) Kinetics of nutrient uptake by roots: Responses to global change. *New Phytologist* **147**, 155–169.

Bazzaz, F. A. (1998) Tropical forests in a future climate: Changes in biological diversity and impact on the global carbon cycle. *Climatic Change* **39**, 317–336.

Berntson, G. and Bazzaz, F. (1997) Nitrogen cycling in microcosms of yellow birch exposed to elevated CO_2: Simultaneous positive and negative below-ground feedbacks. *Global Change Biology* **3**, 247–258.

Berntson, G. and Bazzaz, F. (1998) Regenerating temperate forest mesocosms in elevated CO_2: Belowground growth and nitrogen cycling. *Oecologia* **113**, 115–125.

Bolan, N. S. (1991) A critical review on the role of mycorrhizal fungi in the uptake of phosphorus by plants. *Plant and Soil* **134**, 189–207.

Braunberger, P. G., Abbott, L. K., and Robson, A. D. (1997) The effect of rain in the dry-season on the formation of vesicular–arbuscular mycorrhizas in the growing season of annual clover-based pastures. *New Phytologist* **127**, 107–114.

Brown, S. and Lugo, A. E. (1982) The storage and production of organic matter in tropical forests and their role in the global carbon cycle. *Biotropica* **14**, 161–187.

Brown, S., Hall, C. A. S., Knabe, W., Raich, J., Trexler, M. C., and Woomer, P. (1993) Tropical forests: Their past, present and potential future in the terrestrial carbon budget. *Water Air and Soil Pollution* **70**, 71–94.

Burghouts, T. B. A., van Straalen, N. M., and Bruijnzeel, L. A. (1998) Spatial heterogeneity of element and litter turnover on a Bornean rain forest. *Journal of Tropical Ecology* **14**, 477–506.

Cattanio, J. H., Davidson, E. A., Nepstad, D. C., Verchot, L. V., and Ackerman, I. L. (2002) Unexpected results of a pilot throughfall exclusion experiment on soil emissions of CO_2, CH_4, N_2O, and NO in eastern Amazonia. *Biology and Fertility of Soils* **36**, 102–108.

Cavelier, J., Tanner, E., and Santamaria, J. (2000) Effect of water, temperature and fertilizers on soil nitrogen net transformations and tree growth in an elfin cloud forest of Colombia. *Journal of Tropical Ecology* **16**, 83–99.

Chacon, N., Silver, W. L., Dubinsky, E. A., and Cusack, D. F. (2006) Iron reduction and soil phosphorus solubilization in humid tropical forest soils: The roles of labile carbon pools and an electron shuttle compound. *Biogeochemistry* **78**, 67–84.

Chambers, J. Q. and Silver, W. L. (2004) Some aspects of ecophysiological and biogeochemical responses of tropical forests to atmospheric change. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* **359**, 463–476.

Chambers, J. Q., Higuchi N., Tribuzy, E. S., and Trumbore, S. E. (2001) Carbon sink for a century. *Nature* **410**, 429.

Chambers, J. Q., Tribuzy, E. S., Toledo, L. C., Crispim, B. F., Higuchi, N., dos Santos, J., Araújo, A. C., Kruijt, B., Nobre, A. D., and Trumbore, S. E. (2004) Respiration from a tropical forest ecosystem: Partitioning of sources and low carbon use efficiency. *Ecological Applications* **14**, S72–S88.

Chapin, F. S. (1974) Phosphate absorption capacity and acclimation potential in plants along a latitudinal gradient. *Science* **183**, 521–523.

Clark, D. A. (2004) Tropical forests and global warming: Slowing it down or speeding it up? *Frontiers in Ecology and the Environment* **2**, 73–80.

Clark, D. A., Piper, S. C., Keeling, C. D., and Clark, D. B. (2003) Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proceedings of the National Academy of Sciences* **100**, 5852–5857.

Cleveland, C. C., Townsend, A. R., and Schmidt, S. K. (2002) Phosphorus limitation of microbial processes in moist tropical forests: Evidence from short-term laboratory incubations and field studies. *Ecosystems* **5**, 680–691.

Condit, R. (1998) Ecological implications of changes in drought patterns: Shifts in forest composition in Panama. *Climatic Change* **39**, 413–427.

Condit, R., Hubbell, S. P., and Foster, R. B. (1996) Changes in a tropical forest with a shifting climate: Results from a 50 hectare permanent census plot at Barro Colorado Island in Panama. *Journal of Tropical Ecology* **12**, 231–256.

Cramer, W., Bondeau, A., Schaphoff, S., Lucht, W., Smith, B., and Stich, S. (2004) Tropical forests and the global carbon cycle: Impacts of atmospheric carbon dioxide, climate change and rate of deforestation. *Phil. Trans. R. Soc. London B* **359**, 331–343.

Crews, T. E., Kitayama, K., Fownes, J. H., Riley, R. H., Herbert, D. A., Mueller-Dombois, D., and Vitousek, P. M. (1995) Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. *Ecology* **76**, 1407–1424.

Crews, T. E., Kurina, L. M., and Vitousek, P. M. (2001). Organic matter and nitrogen accumulation and nitrogen fixation during early ecosystem development in Hawaii. *Biogeochemistry* **52**, 259–279.

Crookshanks, M., Taylor, G., and Broadmeadow, M. (1998) Elevated CO_2 and tree root growth: Contrasting responses in *Fraxinus excelsior*, *Quercus petraea* and *Pinus sylvestris*. *New Phytologist* **138**, 241–250.

Cross, A. F. and Schlesinger, W. H. (1995) A literature review and evaluation of the Hedley fractionation: Applications to the biogeochemical cycle of soil phosphorus in natural ecosystems. *Geoderma* **64**, 197–214.

Davidson, E. A., Matson, P. A., Vitousek, P. M., Riley, R., Dunkin, K., Garcia-Mendez, G., and Maass, J. M. (1993) Processes regulating soil emissions of NO and NO_2 in a seasonally dry tropical forest. *Ecology* **74**, 130–139.

Davidson, E. A., Ishida, F. Y., and Nepstad, D. C. (2004a) Effects of an experimental drought on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest. *Global Change Biology* **10**, 718–730.

Davidson, E. A., de Carvalho, C. J. R. Viera, I. C. G., Figueiredo, R. de O., Moutinho, P., Ishida, F. Y., dos Santos, M. T. P., Guerrero, J. B., Kalif, K., and Sabá, R. T. (2004b) Nitrogen and phosphorus limitation of biomass growth in tropical secondary forest. *Ecological Applications* **14**, S150–S163.

Enquist, C. A. F. (2002) Predicted regional impacts of climate change on the geographical distribution and diversity of tropical forests in Costa Rica. *Journal of Biogeography* **29**, 519–534.

Firestone, M. K., Firestone, R. B., and Tiedje, J. M. (1980) Nitrous-oxide from soil denitrification: Factors controlling its biological production. *Science* **208**, 749–751.

Fitter, A. H., Graves, J. D., Self, G. K., Brown, T. K., Bogie, D. S., and Taylor, K. (1998) Root production, turnover and respiration under two grassland types along an altitudinal gradient: Influence of temperature and solar radiation. *Oecologia* **114**, 20–30.

Fitter, A. H., Heinemeyer, A., and Staddon, P. L. (2000) The impact of elevated CO_2 and global climate change on arbuscular mycorrhizas: A myocentric approach. *New Phytologist* **147**, 179–187.

Frankenberg, C., Meirink, J. F., van Weele, M., Platt, U., and Wagner, T. (2005) Assessing methane emissions from global space-borne observations. *Science* **308**, 1010–1014.

Galloway, J. N., Likens, G. E., Keene, W. C., and Miller, J. M. (1982) The composition of precipitation in remote areas of the world. *Journal of Geophysical Research* **87**, 8771–8786.

Galloway, J. N., Levy, H., and Kashibhatla, P. S. (1994) Year 2020: Consequences of population growth and development on deposition of oxidized nitrogen. *Ambio* **23**, 120–123.

Galloway, J. N., Schlesinger, W. H., Levy II, H., Michaels, A., and Schnoor, J. L. (1995) Nitrogen fixation: Anthropogenic enhancement–environmental response. *Global Biogeochemical Cycles* **9**, 235–252.

Gavito, M. E., Schweiger, P., and Jakobsen, I. (2003) P uptake by arbuscular mycorrhizal hyphae: Effect of soil temperature and atmospheric CO_2 enrichment. *Global Change Biology* **9**, 106–116.

Gill, R. A. and Jackson, R. B. (2000) Global patterns of root turnover for terrestrial ecosystems. *New Phytologist* **147**, 13–31.

Hall, S. J. and Matson, P. A. (1999) Nitrogen oxide emissions after nitrogen additions in tropical forests. *Nature* **400**, 152–155.

Hilbert, D. W., Ostendorf, B., and Hopkins, M. S. (2001) Sensitivity of tropical forests to climate change in the humid tropics of north Queensland. *Australian Ecology* **26**, 590–603.

Hobbie, S. E. and Vitousek, P. M. (2000) Nutrient limitation of decomposition in Hawaiian forests. *Ecology* **81**, 1867–1877.

Hobbie, S. E., Nadelhoffer, K. J., and Hogberg, P. (2002) A synthesis: The role of nutrients as constraints on carbon balances in boreal and arctic regions. *Plant and Soil* **242**, 163–170.

Holdridge, L. R. (1967) *Life Zone Ecology* (206 pp.). Tropical Science Center, San Jose, Costa Rica.

Hulme, M., Doherty, R., Ngara, T., New, M., and Lister, D. (2001) African climate change: 1900–2100. *Climate Research* **17**, 145–168.

IPCC (2001) *Climatic Change 2001: The Scientific Basis*. Cambridge University Press, Cambridge, U.K.

Jackson, R. B., Canadell, J., Ehleringer, J. R., Mooney, H. A., Sala, O. E., and Schulze, E. D. (1996) A global analysis of root distributions for terrestrial biomes. *Oecologia* **108**, 389–411.

Janos, D. P. (1983) Tropical mycorrhizas, nutrient cycles and plant growth. In: S. L. Sutton, T. C. Whitemore, and Chadwick, A. C. (eds.), *Tropical Rain Forest: Ecology and Management* (pp. 327–345). Blackwell Scientific, Oxford, U.K.

Jaramillo, V. J. and Sanford Jr., R. L. (1995) Nutrient cycling in tropical deciduous forests. In: S. H. Bullock, H. A. Mooney, and E. Medina (eds.), *Seasonally Dry Tropical Forests* (pp. 346–361). Cambridge University Press, Cambridge, U.K.

Jensen, M. N. (2004) Climate warming shakes up species. *BioScience* **54**, 722–729.

Johnson, A. H., Frizano, J., and Vann, D. R. (2003) Biogeochemical implications of labile phosphorus in forest soils determined by the Hedley fractionation procedure. *Oecologia* **135**, 487–499.

Jordan, C. F. (1985) *Nutrient Cycling in Tropical Forest Ecosystems: Principles and Their Application in Management and Conservation*. John Wiley & Sons. New York.

Kanowski, J. (2001) Effects of elevated CO_2 on the foliar chemistry of seedlings of two rainforest trees from north-east Australia: Implications for folivorous marsupials. *Australian Ecology* **26**, 165–172.

Keller, M. and Reiners, W. A. (1994) Soil atmosphere exchange of nitrous oxide, nitric oxide, and methane under secondary succession of pasture to forest in the Atlantic lowlands of Costa Rica. *Global Biogeochemical Cycles* **8**, 399–410.

Keller, M., Kaplan, W. A., and Wofsy, S. C. (1986) Emissions of N_2O, CH_4, and CO_2 from tropical forest soils. *Journal of Geophysical Research* **91**, 11791–11802.

Kitayama, K., Aiba, S. I., Takyu, M., Majalap, N., and Wagai, R. (2004) Soil phosphorus fractionation and phosphorus-use efficiency of a Bornean tropical montane rain forest during soil aging with podzolization. *Ecosystems* **7**, 259–274.

Körner, C. (1998) Tropical forests in a CO_2-rich world. *Climatic Change* **39**, 297–315.

Körner, C. (2004) Through enhanced tree dynamics carbon dioxide enrichment may cause tropical forests to lose carbon. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* **359**, 493–498.

Lal, C. B., Annapurna, C., Raghubanshi, A. S., and Singh, J. S. (2001a) Foliar demand and resource economy of nutrients in dry tropical forest species. *Journal of Vegetation Science* **12**, 5–14.

Lal, M., Nozawa, T., Emori, S., Harasawa, H., Takahashi, K., Kimoto, M., Abe-Ouchi, A., Nakajima, T., Takemura T., and Numaguti, A. (2001b) Future climate change: Implications for Indian summer monsoon and its variability. *Current Science* **81**, 1196–1207.

Lal, M., Harasawa, H., and Takahashi, K. (2002) Future climate change and its impact over small island states. *Climate Research* **19**, 179–192.

Lashof, D. A. and Ahuja, D. R. (1990) Relative contributions of greenhouse gas emissions to global warming. *Nature* **344**, 529–531.

Lewis, S. L., Malhi, Y., and Phillips, O. L. (2004) Fingerprinting the impacts of global change on tropical forests. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* **359**, 437–462.

Lloyd, J., Bird, M. I., Veenendaal, E. M., and Kruijt, B. (2001) Should phosphorus availability be constraining moist tropical forest responses to increasing CO_2 concentrations? In: E. D. Schulze (ed.), *Global Biogeochemical Cycles in the Climate System* (pp. 95–114). Academic Press, San Diego.

Lodge, D. (1993) Nutrient cycling by fungi in wet tropical forests. In: S. Isaac, J. C. Frankland, R. Watling, and A. J. S. Whalley (eds.), *Aspects of Tropical Mycology*. Cambridge University Press, Cambridge, U.K.

Lodge, D. J., McDowell, W. H., and McSwiney, C. P. (1994) The importance of nutrient pulses in tropical forests. *Trends in Ecology and Evolution* **9**, 384–387.

Lohse, K. A. and Matson, P. (2005) Consequences of nitrogen additions for soil losses from wet tropical forests. *Ecological Applications* **15**, 1629–1648.

Luizão, R. C. C., Bonde, T. A., and Rosswell, T. (1992) Seasonal variation of soil microbial biomass: The effects of clearfelling a tropical rainforest and establishment of a pasture in the central Amazon. *Soil Biology and Biochemistry* **24**, 805–813.

Lynch, J. P. and St. Clair, S. B. (2004) Mineral stress: The missing link in understanding how global climate change will affect plants in real world soils. *Field Crops Research* **90**, 101–115.

Malhi, Y. and Wright, J. (2004) Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* **359**, 311–329.

Marrs, R. H., Proctor, J., Heaney, A., and Mountford, M. D. (1988) Changes in soil nitrogen-mineralization and nitrification along an altitudinal transect in tropical rain forest in Costa Rica. *Journal of Ecology* **76**, 466–482.

Martinez-Yrizar, A. (1995) Biomass distribution and primary productivity of tropical dry forests. In: S. H. Bullock, H. A. Mooney, and E. Medina (eds.), *Seasonally Dry Tropical Forest* (pp. 326–345). Cambridge University Press, Cambridge U.K.

Matamala, R. and Schlesinger, W. H. (2000) Effects of elevated atmospheric CO_2 on fine root production and activity in an intact temperate forest ecosystem. *Global Change Biology* **6**, 967–979.

Matson, P. A., McDowell, W. H., Townsend, A. R., and Vitousek, P. M. (1999) The globalization of N deposition: Ecosystem consequences in tropical environments. *Biogeochemistry* **46**, 67–83.

McGill, W. B. and Cole, C. V. (1981) Comparative aspects of cycling of organic C, N, S and P through soil organic matter. *Geoderma* **26**, 267–286.

McGroddy, M. E., Silver, W. L., and de Oliveira, R. C. (2004) The effect of phosphorus availability on decomposition dynamics in a seasonal lowland Amazonian forest. *Ecosystems* **7**, 172–179.

McKane, R. B., Rastetter, E. B., Melillo, J. M., Shaver, G. R., Hopkinson, C. S., Fernandes, D. N., Skole, D. L., and Chomentowski, W. H. (1995) Effects of global change on carbon storage in tropical forests of South America. *Global Biogeochemical Cycles* **9**, 329–350.

McLaughlin, J. F., Hellmand, J. J., Boggs, C. L., and Ehrlich, P. R.. (2002) Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences of the United States of America* **99**, 6070–6074.

Melillo, J. M., McGuire, A. D., Kicklighter, D. W., Moore III, B., Vörösmarty, C. J., and Schloss, A. L. (1993) Global climate change and terrestrial net primary production. *Nature* **363**, 234–240.

Miyasaka, S. C. and Habte, M. (2001) Plant mechanisms and mycorrhizal symbioses to increase phosphorus uptake efficiency. *Communications in Soil Science and Plant Analysis* **32**, 1101–1147.

Mueller-Dombois, D. and Goldammer, J. (1990) Fire in tropical ecosystems and global environmental change: An introduction. In: J. Goldammer (ed.), *Fire in the Tropical Biota: Ecosystem Processes and Global Challenges* (pp. 1–10). Springer-Verlag, Berlin.

Nepstad, D. C., Moutinho, P., Dias-Filho, M. B., Davidson, E., Cardinot, G., Markewitz, D., Figueiredo, R., Vianna, N., Chambers, J., Ray, D. *et al.* (2002) The effects of partial throughfall exclusion on canopy processes, aboveground production and biogeochemistry of an Amazon forest. *Journal of Geophysical Research*, doi:10.1029/2001JD000360.

Norby, R. J. and Jackson, R. B. (2000) Root dynamics and global change: Seeking an ecosystem perspective. *New Phytologist* **147**, 3–12.

Norby, R. J., Wullschleger, S. D., Gunderson, C. A., Johnson, D. W., and Ceulemans, R. (1999) Tree responses to rising CO_2: Implications for the future forest. *Plant, Cell and Environment* **22**, 683–714.

Oechel, W. C., Vourlitis, G. L., and Hastings, S. J. (1998) The effects of water table manipulation on the net CO_2 flux of wet sedge tundra ecosystems. *Global Change Biology* **4**, 77–90.

Ometto, J. P. H. B., Nobre, A. D., Rocha, H. R., Artaxo, P., and Martinelli, L. A. (2005) Amazonia and the modern carbon cycle: Lessons learned. *Oecologia* **143**, 483–500.

Ostertag, R. and Hobbie, S. E. (1999) Early stages of root and leaf decomposition in Hawaiian forests: Effects of nutrient availability. *Oecologia* **121**, 564–573.

Papatheodorou, E. M., Stamou, G. P., and Giannotaki, A. (2004) Response of soil chemical and biological variables to small and large scale changes in climatic factors. *Pedobiologia* **48**, 329–338.

Peretyazhko, T. and Sposito, G. (2005) Iron(III) reduction and phosphorous solubilization in humid tropical forest soils. *Geochimica et Cosmochimica Acta* **69**, 3643–3652.

Perrott, K. W., Sarathchandra, S. U., and Waller, J. E. (1990) Seasonal storage and release of phosphorus and potassium by organic matter and the microbial biomass in a high-producing pastoral soil. *Australian Journal of Soil Research* **28**, 593–608.

Phillips, O. L., Malhi, Y., Higuchi, N., Laurence, L. F., Nuñez, V. P., Vasqueth, M. R., Laurence, S. G., Ferreira, L. V., Stern, M., Brown, S., and Grace, J. (1998) Changes in the carbon balance of tropical forests: Evidence from long-term plots. *Science* **282**, 439–442.

Pimm, S. L. and Sugden, A. M. (1994) Tropical diversity and global change. *Science* **263**, 933–934.

Pregitzer, K. S., King, J. S., Burton, A. J., and Brown, S. E. (2000) Responses of tree fine roots to temperature. *New Phytologist* **147**, 105–115.

Pritchard, S. G. and Rogers, H. H. (2000) Spatial and temporal deployment of crop roots in CO_2-enriched environments. *New Phytologist* **147**, 55–71.

Raich, J. W. and Schlesinger, W. H. (1992) The global carbon dioxide flux in soil respiration and relationship to vegetation and climate. *Tellus* **44B**, 81–99.

Read, L. and Lawrence, D. (2003) Litter nutrient dynamics during succession in dry tropical forests of the Yucatan: Regional and seasonal effects. *Ecosystems* **6**, 747–761.

Riley, R. H. and Vitousek, P. M. (1995) Nutrient dynamics and nitrogen trace gas flux during ecosystem development in montane rain forest. *Ecology* **76**, 292–304.

Rustad, L., Campbell, J., Marion, G., Norby, R., Mitchell, M., Hartley, A., Cornelissen, J. Gurevitch, J. and GCTE-NEWS (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* **126**, 543–562.

Sanchez, P. A. (1976) *Properties and Management of Soils in the Tropics*. John Wiley & Sons, New York.

Santiago, L. S. and Mulkey, S. S. (2005) Leaf productivity along a precipitation gradient in lowland Panama: Patterns from leaf to ecosystem. *Trees—Structure and Function* **19**, 349–356.

Santiago, L. S., Schuur, E. A., and Silvera, K. (2005) Nutrient cycling and plant–soil feedbacks along a precipitation gradient in lowland Panama. *Journal of Tropical Ecology* **21**, 461–470.

Schimel, J. P. and Gulledge, J. (1998) Microbial community structure and global trace gases. *Global Change Biology* **4**, 745–758.

Schuur, E. A. G. (2001) The effect of water on decomposition dynamics in mesic to wet Hawaiian montane forests. *Ecosystems* **4**, 259–273.

Silver, W. L. (1998) The potential effects of elevated CO_2 and climate change on tropical forest soils and biogeochemical cycling. *Climatic Change* **39**, 337–361.

Silver, W. L. and Miya, R. (2001) Global patterns in root decomposition: Comparisons of climate and litter quality effects. *Oecologia* **129**, 407–419.

Silver, W. L. and Vogt, K. A. (1993) Fine root dynamics following single and multiple disturbances in a subtropical wet forest ecosystem. *Journal of Ecology* **8**, 729–738.

Silver, W. L., Lugo, A. E., and Keller, M. (1999) Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils. *Biogeochemistry* **44**, 301–328.

Silver, W. L., Neff, J., McGroddy, M., Veldkamp, E., Keller, M., and Cosme, R. (2000) Effects of soil texture on belowground carbon and nutrient storage in a lowland Amazonian forest ecosystem. *Ecosystems* **3**, 193–209.

Silver, W. L., Herman, D. J., and Firestone, M. K. (2001) Dissimilatory nitrate reduction to ammonium in upland tropical forest soils. *Ecology* **82**, 2410–2416.

Silver, W. L., Thompson, A. W., McGroddy, M. E., Varner, R. K., Dias, J. D., Silva, H., Crill, P. M., and Keller, M. (2005a) Fine root dynamics and trace gas fluxes in two lowland tropical forest soils. *Global Change Biology* **11**, 290–306.

Silver, W. L., Thompson, A. W., Reich, A., Ewel, J. J., and Firestone, M. K. (2005b) Nitrogen cycling in tropical plantation forests: Potential controls on nitrogen retention. *Ecological Applications* **15**, 1604–1614.

Silver, W. L., Thompson, A. W., Herman, D. J., and Firestone, M. K. (2006) In: L. S. Hamilton and P. Bubb (eds.), *Forests in the Mist: Science for Conserving and Managing Tropical Montane Cloud Forests*. University of Hawaii Press, Honolulu, HI.

Sollins, P. and Radulovich, R. (1988) Effects of soil physical structure on solute transport in a weathered tropical soil. *Soil Science Society of America Journal* **52**, 1168–1173.

Sollins, P., Robertson, G. P., and Uehara, G. (1988) Nutrient mobility in variable- and permanent-charge soils. *Biogeochemistry* **6**, 181–199.

Sowerby, A., Emmett, B., Beier, C., Tietema, A., Penuelas, J., Estiarte, M., van Meeteren, M. J. M., Hughes, S., and Freeman, C. (2005) Microbial community changes in heathland soil communities along a geographical gradient: Interaction with climate change manipulations. *Soil Biology and Biochemistry* **37**, 1805–1813.

Staddon, P. L. and Fitter, A. H. (1998) Does elevated atmospheric carbon dioxide affect arbuscular mycorrhizas? *Trends in Ecology and Evolution* **13**, 455–458.

Staddon, P. L., Gregersen, R., and Jakobsen, I. (2004) The response of two *Glomus* mycorrhizal fungi and a fine endophyte to elevated atmospheric CO_2, soil warming and drought. *Global Change Biology* **10**, 1909–1921.

Steudler, P. A., Melillo, J. M., Feigl, B. J., Neill, C., Piccolo, M. C., and Cerri, C. C. (1996) Consequences of forest-to-pasture conversion on CH_4 fluxes in the Brazilian Amazon Basin. *Journal of Geophysical Research* **101**, 18547–18554.

Stevenson, F. J. and Cole, C. V. (1999) The phosphorus cycle. In: F. J. Stevenson and C. V. Cole (eds.), *Cycles of Soil: Carbon, Nitrogen, Phosphorus, Sulfur, Micronutrients* (2nd Edn.). John Wiley & Sons, New York.

Tate, K. R. (1985) Soil phosphorus. In: D. Vaughn and R. E. Malcolm (eds.), *Soil Organic Matter and Biological Activity* (Developments in Plant and Soil Sciences Series). Marinus Nijhoff/Dr. W. Junk, Boston.

Teh, Y. A., Silver, W. L., and Conrad, M. E. (2005) Oxygen effects on methane production and oxidation in humid tropical forest soils. *Global Change Biology* **11**, 1283–1297.

Tian, H. J., Melillo, J. M., Kicklighter, D. W., McGuire, A. D., Helfrich III, J. V. K., Moore III, B., and Vörösmarty, C. J. (1998) Effect of interannual climate variability on carbon storage in Amazonian ecosystems. *Nature* **396**, 664–667.

Tiessen, H., Cuevas, E., and Chacon, P. (1994) The role of soil organic matter in sustaining soil fertility. *Nature* **371**, 783–785.

Tingey, D. T., Phillips, D. L., and Johnson, M. G. (2000) Elevated CO_2 and conifer roots: Effects on growth, life span and turnover. *New Phytologist* **147**, 87–103.

Townsend, A. R., Vitousek, P. M., and Holland, E. A. (1992) Tropical soils could dominate the short-term carbon cycle feedbacks to increased global temperatures. *Climatic Change* **22**, 293–303.

Trumbore, S., Salazar da Costa, E., Nepstad, D. C., de Camargo, P. B., Martinelli, L. A., Ray, D., Restom, T., and Silver, W. (2006) Dynamics of fine root carbon in Amazonian tropical ecosystems and the contribution of roots to soil respiration. *Global Change Biology* **12**, 217–229.

Uehara, G. (1995) Management of isoelectric soils of the humid tropics. In: R. Lal, J. Kimble, E. Levine and B. A. Stewart (eds.), *Soil Management and the Greenhouse Effect: Advances in Soil Science* (pp. 271–278). CRC Press, Boca Raton, FL.

van Haren, J. L. M., Handley, L. L., Biel, K. Y., Kudeyarov, V. N., McLain, J. E. T., Martens, D. A., and Colodner, D. C. (2005) Drought-induced nitrous oxide flux dynamics in an enclosed tropical forest. *Global Change Biology* **11**, 1247–1257.

van Noordwijk, M., Cerri, C., Woomer, P. L., Nugroho, K., and Bernoux, M. (1997) Soil carbon dynamics in the humid tropical forest zone. *Geoderma* **79**, 187–225.

Vitousek, P. M. (1984) Litterfall, nutrient cycling and nutrient limitation in tropical forests. *Ecology* **65**, 285–298.

Vitousek, P. M. and Howarth, R. W. (1991) Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry* **13**, 87–115.

Vitousek, P. M. and Matson, P. A. (1988) Nitrogen transformations in a range of tropical forest soils. *Soil Biology and Biochemistry* **20**, 361–367.

Vitousek, P. M. and Sanford Jr., R. L. (1986) Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics* **17**, 137–167.

Vitousek, P. M., Aber, J., Howart, R. W., Likens, G. E., Matson, P. A., Schindler, D. W., Schlesinger, W. H., and Tilman, G. D. (1997) Human alteration of the global nitrogen cycle: Causes and consequences. *Issues in Ecology* **1**, 1–15.

Vourlitis, G. L. and Oechel, W. C. (1997) Landscape-scale CO_2, H_2O vapor and energy flux of moist–wet coastal tundra ecosystems over two growing seasons. *Journal of Ecology* **85**, 575–590.

Walker, T. W. and Syers, J. K. (1976) The fate of phosphorus during pedogenesis. *Geoderma* **15**, 1–19.

Wang, Y. P. and Polglase, P. J. (1995) Carbon balance in the tundra, boreal forest and humid tropical forest during climate-change: Scaling-up from leaf physiology and soil carbon dynamics. *Plant, Cell and the Environment* **18**, 1226–1244.

Wieder, R. K. and Wright, S. J. (1995) Tropical forest litter dynamics and dry season irrigation on Barro-Colorado Island, Panama. *Ecology* **76**, 1971–1979.

Williams, M. R., Fisher, T. R., and Melack, J. H. (1997) Chemical composition and deposition of rain in the central Amazon, Brazil. *Atmospheric Environment* **31**, 207–217.

Wood, T. E., Lawrence, D., and Clark, D. A. (2005) Variation in leaf litter nutrients of a Costa Rican rain forest is related to precipitation. *Biogeochemistry* **73**, 417–437.

Wright, I. J. and Westoby, M. (2002) Leaves at low versus high rainfall: Coordination of structure, lifespan and physiology. *New Phytologist* **155**, 403–416.

Wright, I. J., Reich, P. B., and Westoby, M. (2001) Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology* **15**, 423–434.

Wright, S. J. (1992) Seasonal drought, soil fertility and the species density of tropical forest plant communities. *Trends in Ecology and Evolution* **7**, 260–263.

Yavitt, J. B. and Wright, S. J. (1996) Temporal patterns of soil nutrients in a Panamanian moist forest revealed by ion-exchange resin and experimental irrigation. *Plant and Soil* **183**, 117–129.

Yavitt, J. B. and Wright, S. J. (2001) Drought and irrigation effects on fine root dynamics in a tropical moist forest, Panama. *Biotropica* **33**, 421–434.

Yavitt, J. B. and Wright, S. J. (2002) Charge characteristics of soil in a lowland tropical moist forest in Panama in response to dry-season irrigation. *Australian Journal of Soil Research* **40**, 269–281.

Zak, D. R., Pregitzer, K. S., Curtis, P. S., and Holmes, W. E. (2000a) Atmospheric CO_2 and the composition and function of soil microbial communities. *Ecological Applications* **10**, 47–59.

Zak, D. R., Pregitzer, K. S., King, J. S., and Homes, W. E. (2000b) Elevated atmospheric CO_2, fine roots and the response of soil microorganisms: A review and hypothesis. *New Phytologist* **147**, 201–222.