

# Does Plant Litter Become More Recalcitrant Under Elevated Atmospheric CO<sub>2</sub> Levels?

B. Mohan KUMAR,<sup>1\*</sup> Kikuo HAIBARA<sup>2</sup> and Hiroto TODA<sup>2</sup>

<sup>1</sup>*College of Forestry, Kerala Agricultural University,  
KAU PO, Thrissur 680656, Kerala, India  
e-mail: bmkumar53@yahoo.co.uk*

<sup>2</sup>*Tokyo University of Agriculture and Technology (TUAT),  
3-5-8 Saiwaicho, Fuchu-shi, Tokyo 183-8509, Japan  
e-mail: kikuo@cc.tuat.ac.jp (\*author for correspondence)*

## Abstract

Increases in atmospheric CO<sub>2</sub> concentration exert several positive and negative effects on litter dynamics, but the net impact of climate change on litter decomposition and the carbon balance of the terrestrial ecosystem is yet unclear. The objective of this review is to summarize the current state of knowledge on litter dynamics under elevated CO<sub>2</sub> levels with a view to using it as a basis for mitigating the negative effects of rising anthropogenic CO<sub>2</sub> emissions. To understand the biogeochemical processes in response to elevated CO<sub>2</sub> levels, we propose a conceptual model illustrating the interactive effects of rising CO<sub>2</sub> levels on litter dynamics, which assumes that the expected positive effects on photosynthesis will be translated into higher detritus production. The general dilution of nitrogen within plant tissues grown under elevated CO<sub>2</sub> and the consequent N constraints on microbes, however, may have a strong feedback effect on photosynthetic efficiency through depressed nutrient mineralization. Again, a concomitant rise in the atmospheric temperature may accelerate the process of litter decomposition. Significant regional variations in litter production and decomposition rates are also probable in view of the changes in precipitation intensity/patterns and/or biodiversity changes associated with global warming. Gains in litter accumulation on the forest floor under elevated CO<sub>2</sub> levels may lead to increased carbon sequestration and could partially offset the negative effects of anthropogenic CO<sub>2</sub> emissions into the atmosphere.

**Key words:** Carbon accumulation, decomposers, global warming, litter dynamics, net primary productivity, substrate quality

## 1. Introduction

The concentration of CO<sub>2</sub> in the earth's atmosphere has increased since the beginning of slash-and-burn agriculture and in particular after the beginning of the industrial period. The current average annual increase is about 1.5 μL L<sup>-1</sup>, with a predicted doubling of pre-industrial concentrations by the end of the 21<sup>st</sup> century (IPCC, 2001). In 1995, the Intergovernmental Panel on Climate Change produced a 'business as usual' scenario which foresaw annual global emissions of CO<sub>2</sub> rising from 7.4 Pg C to 26 Pg C in the year 2100 along with significant increases in other green house gases (GHGs) including methane, nitrous oxide, hydrofluorocarbons, perfluorocarbons and sulphur hexafluoride (IPCC, 1996). The most important consequence of changing atmospheric composition is a pronounced warming of the global climate. Borehole measurements worldwide indicate a global surface

warming of around 1 °C during the last 500 years, with about half of this warming occurring in the 20th century. Climate experts also predict a global surface warming of 0.6 to 2.5 °C in the next 50 years and 1.4 to 5.8 °C by the end of the 21<sup>st</sup> century, with significant regional variations (IPCC, 1996).

Changes in atmospheric composition and the resultant increases in global temperatures are also associated with changes in precipitation intensity and/or distribution. With rising temperatures, global precipitation is expected to increase *a priori*, due to the greater rates of evaporation of sea surface water. Consistent with this, precipitation increased (2% to 20%) over land areas at high latitudes of the Northern Hemisphere between 1900 and 1994. However, a decrease in precipitation occurred gradually after the 1960s over the subtropics and the tropics from Africa to Indonesia (IPCC, 2001). Simulation models also project a climate change-induced increase in annual

precipitation in high and mid latitudes and most equatorial regions but a general decrease in the subtropics (Carter *et al.*, 2000). Lal *et al.* (2001), using a coupled atmosphere-ocean general circulation model (A-O GCM), predicted a 5% to 25% decline in winter rainfall and 10% to 15% increase in monsoon rainfall over South Asia during the 2080s. If these predictions are true, there may be increased drought occurrence during the dry months and more intense rainfall spells during the wet season, particularly in the tropics.

During recent years concern has also been growing among scientists and the general public about the possible impacts of future climate change on terrestrial ecosystems, especially with respect to plant growth, changes in biodiversity, distribution patterns of naturally growing tree species and the overall impact on carbon storage in the biosphere (Rasmussen *et al.*, 2002). With plant litter being both a sink as well as source of carbon and mineral nutrients, there has been profound interest in litter dynamics. Although it has been emphasized that changes in litter chemistry (reduction in litter N concentration and a concomitant increase in lignin levels) in an atmosphere with elevated CO<sub>2</sub> level, will reduce decomposition rates and release of N from organic materials (Norby *et al.*, 2001; Lindroth *et al.*, 2001), the ecological effects of increased CO<sub>2</sub> and global warming on litter dynamics are more complex and difficult to predict in view of the following:

- Plant responses (*e.g.*, photosynthesis, respiration, litter chemistry, etc.) vary with species and growth factors (Cuelemans, 1997; Mooney *et al.*, 1999).
- Individual processes in ecosystem biogeochemistry may oppose each other; hence laboratory and greenhouse experiments, often with single species and young seedlings cannot be directly extrapolated to mature ecosystems (Cuelemans, 1997; Van Breemen *et al.*, 1998; Mooney *et al.*, 1999).
- Anthropogenic N additions (Bobbink *et al.*, 1998) and the close link between C and N cycles and the potential for feedback among them (Tateno & Chapin, 1997) confound the effects of rising CO<sub>2</sub> levels.
- Few studies have compared the interactive effects of various GHGs (*e.g.*, CO<sub>2</sub>, O<sub>3</sub>, etc.) and rising temperature under altered soil moisture/nutrient regimes on ecosystem-level responses; and virtually none from the tropics. Recent free air CO<sub>2</sub> enrichment (FACE) studies in temperate regions (*e.g.*, Kasurinen *et al.*, 1999; Karnosky *et al.*, 1999; Olszyk *et al.*, 2001) and comparative analyses of elevated CO<sub>2</sub> on ecosystem processes (*e.g.*, Sowerby *et al.*, 2000; Norby *et al.*, 2001; Seneviratne, 2000; Ross *et al.*, 2003), however, have advanced knowledge in this respect; but clearly, more studies are needed for other ecosystems, and on the concomitant effects of rising temperature/alterd soil moisture regimes

and changing decomposer populations on litter dynamics.

In this paper we address questions relating to how litter dynamics and the associated nutrient turnover processes will be affected under changing atmospheric composition. Although previous reviewers have addressed aspects such as litter chemistry and/or soil microbial activity (*e.g.*, Zak *et al.*, 1993; Seneviratne, 2000; Norby *et al.*, 2001), the larger issue of how global warming would impact litter dynamics and nutrient cycling remains largely unanswered. The objective here is to summarize and analyze the recent trends in ecosystem research pertaining to litter dynamics under elevated CO<sub>2</sub> levels with a view to providing some new insights and indicating gaps in the existing knowledge base.

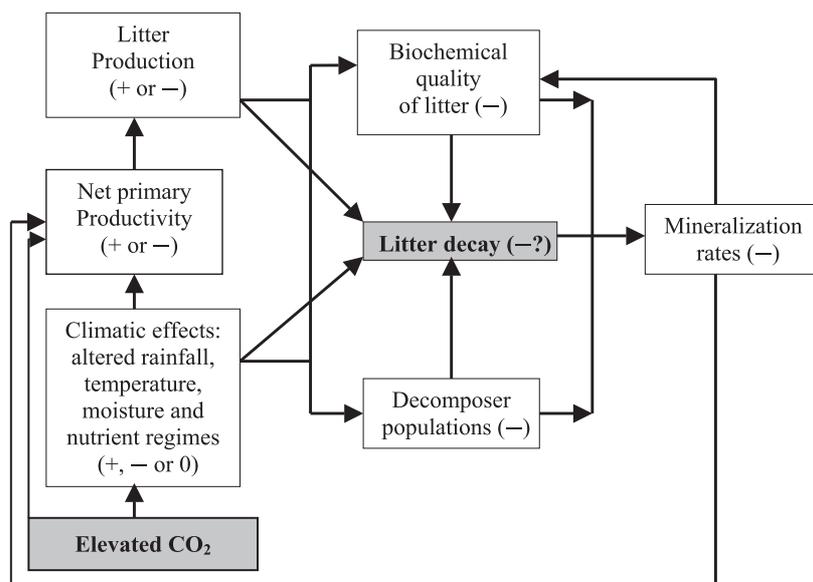
## 2. Climate-substrate-biota-interactive Litter Dynamics Model

In this article, we present a comprehensive view on litter dynamics, focusing on a conceptual model for interactions among environmental parameters, litter production, biochemical quality of litter and decomposer communities (Fig. 1). There are many state variables and driving functions in this model (the boxes and arrows, respectively), implying an intricate relationship characterised by positive, negative or neutral ('+', '-' or '0') feedback effects. The model predicts that litter production, decay and mineralization are deterministic outcomes of these interactions. That is, the linkages among climate, floristic attributes, substrate quality and biotic subsystems are major drivers of decay dynamics. The ensuing sections explain how each of these state variables/driving functions is altered under elevated CO<sub>2</sub> levels.

### 2.1 Net primary productivity

A large volume of literature exists on the impact of elevated CO<sub>2</sub> levels on photosynthesis and net primary productivity (NPP). Most of these could be rationalized based on two experimental paradigms, viz., the 'CO<sub>2</sub>-fertilization' and the 'litter quality' (negative feedback) hypotheses. The general consensus among proponents of the CO<sub>2</sub> fertilization hypothesis is that elevated CO<sub>2</sub> stimulates photosynthesis, and consequently NPP. Consistent with this, several workers reported increased plant growth associated with increased photosynthetic rates and decreased root respiration in response to elevated CO<sub>2</sub> levels (Koch & Mooney, 1996; Johnson *et al.*, 1998; Curtis & Wang, 1998; Mingkui & Woodard, 1998; Luan *et al.*, 1999; Olszyk *et al.*, 2001).

The consequent increase in forest productivity, notably in the mid-latitudes (Fan *et al.*, 1998) may increase labile C inputs into the soils (Finzi *et al.*, 2001), which in turn, may sustain NPP and/or stimulate soil carbon sequestration. Yet another positive impact of elevated CO<sub>2</sub> is reduced stomatal



**Fig. 1** Conceptual model of the feedback/feed forward effects of rising atmospheric CO<sub>2</sub> levels on litter dynamics (symbols: '+', '-' and '0' indicate positive, negative and neutral effects)

conductance of plants which results in higher water use efficiency. At the community level, this often results in decreased stand transpiration and higher soil water content (Körner, 2000) and can potentially stimulate photosynthetic production in water-limited ecosystems.

Conversely, the 'litter quality hypothesis' (McGuire *et al.*, 1995; Norby *et al.*, 2001) implies that changes in litter chemistry owing to CO<sub>2</sub> enrichment and the consequent slower decomposition, may have a 'seesaw' effect on soil N pool. Because plants are commonly N-limited in terrestrial ecosystems, and any tendency for increased CO<sub>2</sub> to decrease N availability may suppress primary productivity (Cotrufo *et al.*, 1998a; Norby & Cotrufo, 1998; Fahey *et al.*, 1998). Likewise, many authors reported that the effects of elevated CO<sub>2</sub> levels on NPP were not significant (Pérez-Soba *et al.*, 1995; Lippert *et al.*, 1997), or that the initial increase in NPP will not be sustained due to nutrient limitations (Comins & McMurtrie, 1993; Luo & Reynolds, 1999). Moreover, simulation experiments suggest that the initial increase in forest growth and NPP in response to doubling of atmospheric CO<sub>2</sub> concentrations may decline to original levels (*e.g.*, Comins & McMurtrie, 1993; Luo & Reynolds, 1999).

Neither model, however, considers the concomitant effects of rising temperature, O<sub>3</sub> and other GHGs. Clearly, the effects of elevated atmospheric CO<sub>2</sub> on ecosystems will not occur in isolation, but in the context of multiple environmental stresses (Gulke, 1999; McBride & Miller, 1999; Kumar, 2003) including herbivory (Coley, 1998). Regarding temperature effects, which are crucial and the focal theme of this discussion, warmer summer air temperatures due to global warming may be beneficial in the temperate latitudes, where the length of the growing season and

frost-free period would increase. Nonetheless, warmer temperatures exert negative effects in those regions where temperature and water stress limit NPP, and may cause early senescence of leaves. In the event of reduced summer rainfall in the tropics, as many GCM projections indicate, the photosynthetic efficiency will be further curtailed. Thus, it is likely that in a 'business as usual' scenario, the net ecosystem productivity (NEP) in most parts of the tropics and subtropics will be depressed, whereas there may be significant gains in the temperate zones. The predicted shifts in climate zones with global warming (IPCC, 2001), however, complicate this pattern.

## 2.2 Dinitrogen fixation

Nitrogen fixation is an energy-requiring process and derives its energy requirement from the oxidative metabolic pathway (Krebs cycle). The C skeletons required for converting N, fixed in the root nodules, into amino acids are also drawn from this pathway. Thus an increase in photosynthetic efficiency according to the CO<sub>2</sub>-fertilization model, following CO<sub>2</sub> enrichment, is likely to favour the biological nitrogen fixation (BNF) process. Conversely, any negative effects on photosynthesis owing to water and nutrient deficits may adversely affect it. The effects of rising CO<sub>2</sub> levels on BNF are, however, more complex, as concomitant changes in soil nitrogen release and environmental stresses exert positive or negative feedback controls on the photosynthetic/respiratory pathways and also on the activity of nitrogen fixing organisms. Experimental evidence available in this respect is not only scanty but also inconsistent. For example, Olszyk *et al.* (2001) found no significant effects of elevated CO<sub>2</sub> levels on autotrophic N fixation rates in a ponderosa pine ecosystem, whereas Temperton *et al.* (2003) reported consistently higher

nitrogenase activity in *Alnus glutinosa* grown under elevated CO<sub>2</sub> levels. Such variations in experimental results probably imply differences owing to the organisms involved and/or the method of assay used.

Many authors (Rygiewicz *et al.*, 2000; Staddon *et al.*, 1999; Olszyk *et al.*, 2001) also noted that elevated CO<sub>2</sub> increases mycorrhizal colonization, but in certain cases the response was transitory and dependent on P nutrition (Walker *et al.*, 1995). Overall, as the forests grow under elevated CO<sub>2</sub>, the fluxes of N and P in vegetation, microbes and soils are expected to increase, and a positive feedback to develop between elevated CO<sub>2</sub>, NPP and plant nutrient availability.

### 2.3 Litterfall production

The probable effects of elevated CO<sub>2</sub> levels and the consequent atmospheric warming on litterfall production can be summarized as follows. On the positive side, a large body of literature suggests that elevated CO<sub>2</sub> may increase plant photosynthesis, net primary production and thus, litter production. In consonance with this, in the Duke Forest FACE study, significant increases in loblolly pine leaf litterfall mass were observed (Allen *et al.*, 2000; Finzi *et al.*, 2001). In view of the limited nature and range of the experimental studies reported—mostly from the temperate zones—it is perhaps difficult to draw valid generalizations on the effects on litterfall production under increased CO<sub>2</sub> levels across the globe. Nevertheless, in view of the overwhelmingly positive effects of CO<sub>2</sub> enrichment on plant production owing to the warmer temperature in the temperate regions, increased N (biological and anthropogenic) and labile C inputs, it seems reasonable to assume that litter inputs may increase in the temperate ecosystems, but the picture in the tropics is still obscure.

### 2.4 Litter chemistry

The central hypothesis of litter dynamics is that N and lignin control the decay process (Melillo *et al.*, 1982; Kumar & Deepu, 1992; Cadisch & Giller, 1997 and many others). Lignin is recalcitrant to enzyme degradation, and its intimate association with cellulose fibers results in masking of a large fraction of carbohydrate, which otherwise would be accessible to microbes (Gessner & Chauvet, 1994). Likewise, polyphenolics (*e.g.*, tannins) form resistant complexes with proteins (Hättenschwiler & Vitousek, 2000), directly inhibiting microbial growth and activity (Swift *et al.*, 1979). Hence, the lignin and polyphenol contents of litter are often regarded as inverse indexes of carbon availability to decomposers, and thereby decay rates (McClougherty & Berg, 1987; Berg, 2000; Kumar & Goh, 2000).

It has generally been assumed that rising atmospheric CO<sub>2</sub> concentrations will increase the concentration of carbon-based secondary or structural compounds in plant tissues. Increased biomass productivity also may lead to a concomitant reduction in

N concentrations (dilution effect). Consistent with this, several workers (see reviews by Koricheva *et al.*, 1998; Norby *et al.*, 2001) noted that CO<sub>2</sub> enrichment increased levels of tannins and starch in litter, but decreased foliar levels of N, and the magnitude of such variations were dependent on both plant species and resource availability (*e.g.*, light, nutrients).

However, lack of consistent evidence with respect to the changes in litter chemistry obscures this pattern. For instance, in certain cases, starch levels in CO<sub>2</sub> enriched foliage showed no consistent increase over those in unenriched foliage (Peñuelas & Estiarte, 1998). Some authors also observed that chemical composition of green leaves and leaf litter were unaffected by elevated CO<sub>2</sub> (*e.g.*, Finzi *et al.*, 2001; Olszyk *et al.*, 2001). Naturally senesced litter often changes in C/N as a result of variations in CO<sub>2</sub> levels (Norby *et al.*, 2001). Differences among species were also prominent in some cases. For example, Lindroth *et al.* (2001) found that condensed tannins for carbon-based metabolites derived from the shikimic acid pathway increased in response to enriched atmospheric CO<sub>2</sub> in birch (*Betula papyrifera*) leaves, but there was little response in aspen (*Populus tremuloides*).

In addition, studies on the impact of elevated CO<sub>2</sub> on litter chemistry have excluded the coarse litter fraction, which constitutes a significant part of forest litter, and may be of interest in the context of carbon accumulation in terrestrial ecosystems (Mackensen & Bauhus, 1999). Presumably, the lignin/polyphenol contents of coarse fractions may show a greater degree of variability in response to elevated CO<sub>2</sub> than foliage litter, but to our knowledge, no previous studies have examined the effects of rising atmospheric CO<sub>2</sub> levels on either the chemical composition or decomposition rates of coarse litter.

### 2.5 Resorption efficiency

Based on experimental evidence on the chemistry of fresh foliage, it can be deduced that lower N levels will be characteristic of leaf litter under elevated CO<sub>2</sub> levels. It is, however, debatable whether the N of fresh leaves accurately predicts the N content of litter or, indeed, its subsequent decomposition rate (Norby *et al.*, 2001) – because resorption plays a pivotal role in determining the N concentration of leaf litter, and thereby the soil N pool. An increase in resorption prior to senescence generally tends to decrease the N concentration of litter and increase the residence time of litter.

Resorption efficiency in senescing leaves is presumably under environmental control; *i.e.*, more efficient under conditions of CO<sub>2</sub> enrichment (Cotrufo *et al.*, 1998b; Coûteaux *et al.*, 1999) and less efficient under high soil fertility (Jamaludheen & Kumar, 1999). Here again, however, scientific opinion is divided, just as in many other aspects relating to CO<sub>2</sub> enrichment and biogeochemistry. Some authors (*e.g.*, Aerts &

Chapin, 2000; Heerwaarden *et al.*, 2003) suggest that resorption efficiency is not very responsive to changes in nutrient supply, while others (Lindroth *et al.*, 2001; Finzi *et al.*, 2001) argue that resorption efficiency is not affected by CO<sub>2</sub> enrichment.

Yet another complicating factor is that, in many ecosystems N availability has increased during recent decades due to enhanced atmospheric N deposition (Bobbink *et al.*, 1998). It can, therefore, be rationalized that if global warming enhances soil N concentrations, it will probably result in lower resorption efficiency, and therefore, more N available for microbial and plant growth. As a result, if resorption efficiencies decline, then the effects of CO<sub>2</sub> on N levels in green leaves may not carry over to leaf litter; i.e., the 'litter quality hypothesis' will not be supported. Resorption, however involves changes not just in N, but in dry matter as well, and the resulting N concentration in litter is determined by changes in both N content and dry matter content (Norby *et al.*, 2001). Also, more efficient retranslocation is expected in the twigs and branches in view of their greater longevity, not to mention the improbability of their 'early senescence,' as in the case of foliage.

## 2.6 Litter decay

While changes in litter chemistry in an atmosphere of elevated CO<sub>2</sub> (i.e., lower N and higher lignin/polyphenol concentrations in foliage of plants) will decelerate decomposition, increased atmospheric N inputs may offset any potential negative effects on litter decay owing to intrinsically lower litter N concentrations. Although not strictly comparable, Norby *et al.* (2001) observed that across a database covering 33 herbaceous plants and 48 woody species, neither the mass loss nor respiration rates from leaf litter produced under elevated CO<sub>2</sub> showed any consistent pattern or differences. Likewise, Finzi *et al.* (2001) reported that the rate of mass loss was unaffected by 'litter type' (i.e., whether the litter was produced under ambient or elevated CO<sub>2</sub> levels); and 'site' of decomposition (i.e., whether the litter was decomposed in the ambient or elevated CO<sub>2</sub> plots). It should be noted that these studies did not consider variations in soil moisture availability and/or decomposer populations, which usually co-vary with atmospheric CO<sub>2</sub> levels in the natural environment. Yet, it can be argued that the net effect of rising CO<sub>2</sub> levels on decay rates owing to changes in microbial N availability under 'steady state' conditions (no concomitant variations in temperature and moisture regimes, as predicted by the climate models) is modest. Having stated, there could still be potential effects of increasing lignin/polyphenol content, in particular in the coarse litter fractions that is likely to contribute more to litterfall production as NPP increases.

## 2.7 Soil moisture and temperature

The direct effects of abiotic factors such as tem-

perature and moisture on the decomposition process are well documented. That is, within a threshold, microbial activity increases exponentially with temperature, and as a result, high temperatures are likely to hasten decomposition (Kumar & Goh, 2000; Seneviratne, 2000). However, the temperature effect on the decay process is moderated by litter/soil moisture content. Potential moisture limitations as a result of global warming in the tropics can restrict microbial activity of soils. Many authors have also reported higher relative loss of litter mass during the rainy season than during the dry season (Facelli & Pickett, 1991; Thönnissen *et al.*, 2000; Vucetich *et al.*, 2000), implying a proximate control of summer moisture on litter decomposition. Therefore, if the global warming process reduces summer precipitation rates in the tropics/subtropics, as predicted in the GCMs, then litter decay will in all probability be adversely affected.

## 2.8 Species diversity and litter decomposition

### 2.8.1 Microbiological changes

Theoretically, rates of ecosystem processes increase linearly with species richness if all species contribute substantially and in unique ways to a given process (Johnson *et al.*, 1996). By extension, microbial and meso-faunal richness and diversity can lead to increased decomposition of litter and organic matter. Changes in the global environment, however, have altered biological diversity at all organizational levels, ranging from genetic diversity within populations to the diversity of ecosystems (Chapin *et al.*, 2000), and the effects are likely to be more potent in the future. Loss of species diversity has functional consequences in terms of litter decay because the number and kinds of species determine the organizational traits that influence any ecosystem process (Hooper & Vitousek, 1997). Previous investigations (Salonius, 1981) showed that microbial species richness increased organic matter decomposition, although others found no predictable relationships between number of organisms and the decay rates (e.g., Wardle *et al.*, 1997; Chihara *et al.*, 2000). Chapin *et al.* (2000) explained such variations in experimental results to be on account of the differential sensitivity of ecosystem processes to species richness vis a vis other components of diversity such as evenness, composition or interactions, or to the strong dependence of ecosystem processes on one or a few species.

Microbial responses to elevated CO<sub>2</sub> in complex natural ecosystems are also less understood (Kampichler *et al.*, 1998). Some workers (e.g., Lamborg *et al.*, 1983; O'Neill, 1994) thought that direct effects of elevated CO<sub>2</sub> concentrations on soil organisms were improbable because CO<sub>2</sub> concentrations in soils were already 10 to 50 times greater than in the atmosphere. Zak *et al.* (2000), however, concluded that the response of soil microorganisms to elevated CO<sub>2</sub> is highly variable. Consistent with this,

published results show a range of responses from no marked increase in the soil microbial biomass with elevated CO<sub>2</sub> (Runion *et al.*, 1994; Kampichler *et al.*, 1998) to significantly greater levels of microbial biomass (Diaz *et al.*, 1993; Sowerby *et al.*, 2000) or activity (Ebersberger *et al.*, 2003). Higher metabolic activity in the soil was rationalized on account of the extra C entering the soil through greater fine root turnover and higher rhizodeposition (Rogers *et al.*, 1994).

Although changes in microbial communities in response to rising CO<sub>2</sub> levels are certain, it is yet unclear whether such changes will result in increased or decreased decay rates. This is partly because of a lack of sufficient evidence regarding species changes consequent to global warming and the variable influence of individual organisms on the decomposition process. Also, most information on soil microbial response to elevated CO<sub>2</sub> originates from short-term experiments and/or experiments with disturbed soil (Hu *et al.*, 1999). Extrapolation of these results to mature ecosystems and to longer time scales is rather risky.

### 2.8.2 Changes in invertebrates and vascular flora

The vast majority of the soil organisms are heterotrophs (*e.g.*, soil invertebrates, such as earthworms, termites and the microarthropods) and any changes in their population dynamics will certainly affect organic matter decomposition (Lavelle *et al.*, 1997). Climate change has the potential to drastically alter the diversity attributes (richness, evenness) of these organisms, besides that of higher plants (Thomas *et al.*, 2004). While changes in the structure of the soil invertebrate fauna have a direct impact on litter decomposition, changes in the floristic composition exert a countervailing influence on decomposition, through changes in litter chemistry, relative proportion of different litter fractions and the amount of root exudates production. Indeed, a large body of literature indicates that litter/organic matter decomposition is dependent on factors such as origin of the litter (*i.e.*, from C3 or C4 plants; Kemp *et al.*, 1994; Ball & Drake, 1997; Ross *et al.*, 2003), composition of plant tissues (roots and shoots; Rogers *et al.*, 1994; Johnson *et al.*, 1998; Allen *et al.*, 2000; Olszyk *et al.*, 2001), relative proportions of coarse and fine litter, and root exudates (Ebersberger *et al.*, 2003). Floristic changes alter most or all these parameters, and could bring about substantial changes in the population size and diversity and functions of food web biota in litter and soil.

### 2.9 Nitrogen limitation of microbial decomposition

Studies on the effects of increased CO<sub>2</sub> on soil microbes have made the implicit assumption that CO<sub>2</sub> enrichment enhances C input for microbial biomass and activity, underscoring the premise that soil microbes are C-limited (Hu *et al.*, 2001). They further suggest that CO<sub>2</sub> enrichment in the atmosphere can

exacerbate N constraints on microbes and suppress microbial use of soil C (Kaye & Hart, 1997; Wang & Bakken, 1997). That is, a decrease in N availability due to increased CO<sub>2</sub>, suppresses microbial decomposition, owing to increased competition for N between plants and microbes. The increased C availability under elevated CO<sub>2</sub> would also boost microbial biomass, in turn, leading to nutrient immobilization and constrained plant responses (Diaz *et al.*, 1993). Conversely, Zak *et al.* (1993) and Ebersberger *et al.* (2003) reported increased N mineralization of native organic matter, resulting in higher N availability to plants. The specific response, however, would depend on a complex set of factors such as litter quality, the amount of litter inputs and changes in decomposer populations in response to altered temperature/moisture regimes.

## 3. Conclusions

Little is known about the interactions between decomposition dynamics of litter across different ecosystems and rising levels of atmospheric CO<sub>2</sub>. Decomposition drivers such as chemical attributes of litter, precipitation/temperature regimes and decomposer populations, often vary with one another and with increasing CO<sub>2</sub> levels, making such interactions intricate. Understanding the nature of these interactions is, nevertheless, crucial to providing a scientific foundation for evaluating the impacts of climate change on various aspects of SOM dynamics and nutrient cycling, including the effects of litter/green manure addition on soil nutrient dynamics. Thus research (both experimental studies and simulation modeling to characterize ecosystem responses) is needed on all fronts and in particular on tropical ecosystems.

Regarding the effects of elevated CO<sub>2</sub> levels on NEP, it is reasonable to assume that NEP will increase and at least a part of the extra C fixed in response to enhanced CO<sub>2</sub> levels will also be allocated below ground. Concomitant floristic changes, changes in resource availability (*e.g.*, moisture and nutrients) and/or abiotic factors (*e.g.*, temperature) can, however, alter the NEP and biomass allocation strategies. It is, therefore, difficult to extrapolate the short-term responses to changes in CO<sub>2</sub>/temperature of individual ecosystem processes, such as photosynthesis and respiration to whole ecosystems, and a comprehensive understanding of the response to global warming remains elusive.

The consequences of CO<sub>2</sub> enrichment for plant chemical composition and decomposer communities are also of immense interest. As regards to the effects of CO<sub>2</sub> enrichment on litter chemistry, there are two predominant notions. The first is that litter lignin/polyphenol levels would increase and N levels would decline under elevated CO<sub>2</sub> levels, leading to a negative impact on decomposition. Experimental evidence

mainly from temperate regions, however, has been mixed, probably depending on several factors such as species, experimental conditions and litter chemistry. The second is, as many workers have indicated, that the observed chemical changes in litter have been largely transitory in nature and there would be little or no change in litter chemistry under elevated CO<sub>2</sub> levels in the long run. It can then be argued that decay rates under elevated CO<sub>2</sub> environment would predominantly be determined by factors other than chemical attributes, such as changes in temperature/moisture levels and/or decomposer populations.

In view of the complex nature of ecosystem processes and inconsistencies in experimental results on various aspects of atmospheric CO<sub>2</sub> enrichment and litter dynamics, it is perhaps difficult to predict whether litter decomposition would increase or decrease and what potential effects of this would be on sequestration of the extra carbon fixed in the photosynthetic process. It can be parsimoniously argued that litter inputs in temperate regions might increase following the stimulation of NPP, but decay rates may decline owing to changes in litter chemistry (e.g., lignin/polyphenol concentrations). Consequently, the net amount of litter and carbon accumulating on the forest floor may increase. As regards to the tropics, the picture is still hazy, but assuming that environmental stresses (especially for moisture) would amplify, litter production may decline. The enhanced CO<sub>2</sub> levels would favor production of high C and low N litter. This coupled with the strong negative effects of global warming on soil fauna and flora probably would lower decay rates. Thus, modest increases in the amount of litter remaining on the tropical forest floor could be anticipated, provided ecosystem integrity were maintained.

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