

Evaluation of soil CO₂ production and transport in Duke Forest using a process-based modeling approach

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[1] Soil surface CO₂ efflux is an important component of the carbon cycle in terrestrial ecosystems. However, our understanding of mechanistic controls of soil CO₂ production and transport is greatly limited. A multilayer process-based soil CO₂ efflux model (PATCIS) was used to evaluate soil CO₂ production and transport in the Duke Forest. CO₂ production in the soil is the sum of root respiration and soil microbial respiration, and CO₂ transport in the soil mainly simulates gaseous diffusion. Simulated soil CO₂ efflux in the Duke Forest ranged from 5 g CO₂ m⁻² d⁻¹ in the winter to 25 g CO₂ m⁻² d⁻¹ in summer. Annual soil CO₂ efflux was 997 and 1211 g C m⁻² yr⁻¹ in 1997 and 1998, respectively. These simulations were consistent with the observed soil CO₂ efflux. Simulated root respiration contributed 53% to total soil respiration. Soil temperature had the dominant influence on soil CO₂ production and CO₂ efflux while soil moisture only regulated soil CO₂ efflux in the summer when soil moisture was very low. Soil CO₂ efflux was sensitive to the specific fine root respiratory rate and live fine root biomass. Elevated CO₂ increased annual soil CO₂ efflux by 26% in 1997 and 18% in 1998, due mainly to the enhanced live fine root biomass and litterfall. On a daily to yearly basis, CO₂ production is almost identical to CO₂ efflux, suggesting that CO₂ transport is not a critical process regulating daily and long-term soil surface CO₂ effluxes in the Duke Forest. We also developed a statistical model of soil CO₂ efflux with soil temperature and moisture. Daily soil CO₂ efflux estimation by the statistical model showed a similar pattern to the simulated soil CO₂ efflux, but the total annual CO₂ efflux was slightly lower. While the statistical model is simple, yet powerful, in simulating seasonal dynamics of soil CO₂ efflux, the process-based model has the potential to advance our mechanistic understanding of soil CO₂ efflux variations in the current and future worlds.

INDEX TERMS: 1615 Global Change: Biogeochemical processes (4805); 3210 Mathematical Geophysics: Modeling; 0300 Atmospheric Composition and Structure;

KEYWORDS: forest, modeling, soil moisture, soil CO₂ efflux, soil respiration, temperature

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1. Introduction

[2] Soil CO₂ efflux is an important component of the carbon cycle in terrestrial ecosystems. Soil carbon respired by terrestrial ecosystems contributes 68–100 Pg C yr⁻¹ to the atmosphere, only slightly less than the estimated global terrestrial gross primary productivity of 100–120 Pg C yr⁻¹ [Rustad *et al.*, 2000]. As atmospheric CO₂ concentration and global temperature continuously increase, more carbon will be respired from the soils [Schimel *et al.*, 1994; Schlesinger and Andrews, 2000]. Despite the global significance of soil CO₂ efflux, our understanding of the mechanistic controls of CO₂ production and transport in soil pores is greatly limited.

[3] Soil CO₂ production results from respiration of living roots and microbial decomposition of litter and soil organic matter (in this paper, we call the soil CO₂ production “soil

respiration” whereas soil CO₂ efflux is soil CO₂ release rate measured at soil surface) [Jenkinson *et al.*, 1991]. Soil CO₂ transport to the atmosphere is controlled by the rate of CO₂ production in the soil, the CO₂ concentration gradient between the soil and the atmosphere, soil physical properties, and environmental conditions [Carlyle and Than, 1988; Raich and Schlesinger, 1992]. Thus, measured soil CO₂ efflux from the soil surface is the result of these complex processes influenced by a number of factors.

[4] Relationships of soil CO₂ efflux with the environmental factors have been studied extensively. Regression analysis has been used to predict soil CO₂ efflux with soil temperature, soil moisture, and precipitation [e.g., Lloyd and Taylor, 1994; Epron *et al.*, 1999; Maier and Kress, 2000; Luo *et al.*, 2001a]. Soil CO₂ efflux in forest ecosystems generally increased exponentially with increasing temperature. For example, Tate *et al.* [1993] fitted an exponential equation and found that 87% of forest floor CO₂ efflux was explained by soil temperature. In environments with

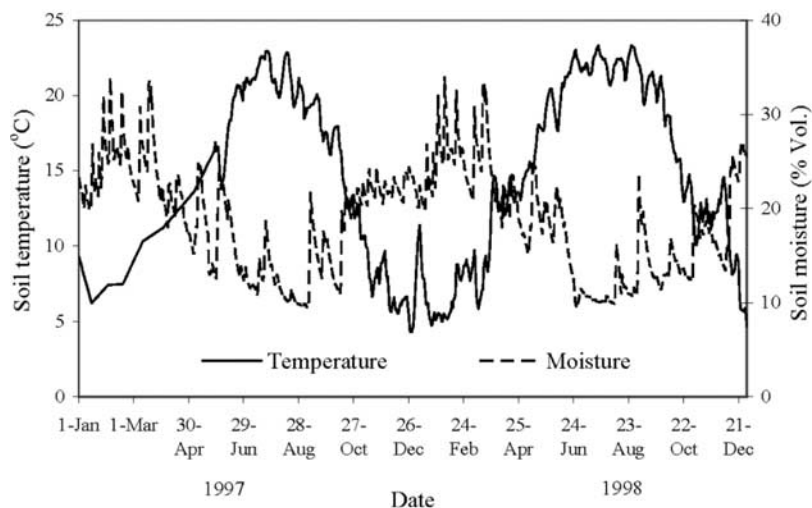


Figure 1. Measured soil temperature (5 cm) and soil moisture (0–30 cm) in 1997 and 1998 in the Duke Forest, North Carolina.

relatively stable temperatures or marked seasonal dry periods, soil CO₂ efflux can be reasonably well predicted using soil moisture [Holt *et al.*, 1990; Davidson *et al.*, 2000]. In addition to climatic factors, soil CO₂ efflux has been found to be positively related to root biomass [Ryan *et al.*, 1996; Thomas *et al.*, 2000], mycorrhizal associations [Rygielwicz and Andersen, 1994], and the size of soil carbon pools [Parton *et al.*, 1988]. While these studies suggested that soil CO₂ efflux is the result of several interactive processes regulated by numerous factors, it is imperative to develop process-based models to examine various aspects of soil CO₂ efflux.

[5] Mechanistic models have the potential to explain the temporal variation in soil CO₂ efflux and to predict soil CO₂ efflux in future climatic conditions. Several mechanistic models have been developed. For example, Ouyang and Boersma [1992] developed a mathematical model that consists of coupling movement and the transport of water, heat, and gases through the unsaturated soils. Šimůnek and Suarez [1993] constructed a model based on the relationship of the soil CO₂ efflux in terms of soil water potential, temperature, CO₂ concentration, depth in the soil, and time. Fang and Moncrieff [1999] built a process-based soil CO₂ efflux model (PATCIS) that includes one-dimensional water flow and multiphase transport of CO₂ as well as CO₂ production. This model considers decomposition rates for labile and resistant organic matter and separates roots into three different size classes. The model is intended to be a general one for simulation CO₂ efflux/soil respiration under most environmental conditions and was validated and applied to a mature slash pine plantation in Florida [Moncrieff and Fang, 1999].

[6] In this study we applied the modified PATCIS model to evaluate soil CO₂ production and transport in the Duke Forest in North Carolina. In the Duke Forest, an elevated CO₂ experiment using Free-Air CO₂ Enhancement (FACE) technique has been going on since August 1996. Soil CO₂ efflux, soil temperature, soil moisture, fine root biomass,

and soil organic matter have been measured at both ambient and elevated CO₂ treatments. Thus this experiment provided substantial data for us to evaluate variation of soil CO₂ efflux in a forest ecosystem, as well as the effect of elevated CO₂ on soil CO₂ efflux. Since statistical soil CO₂ efflux models are widely used in terrestrial carbon cycling studies, we also developed a statistical model of soil CO₂ efflux considering soil temperature and moisture. The estimation given by the statistical model was compared with the soil CO₂ efflux simulated by the process-based model PATCIS. We focused on the comparisons of soil CO₂ efflux with soil CO₂ production, root versus microbial respiration, the relative importance of the factors regulating CO₂ production and transport, and the influences of elevated CO₂ on soil CO₂ efflux.

2. Material and Methods

2.1. Site Description and Measurements

[7] The Duke Forest FACE experimental site is composed of six 30-m diameter plots in a loblolly pine (*Pinus taeda* L.) plantation in the Blackwood Division of the Duke Forest, North Carolina (35.6°N, 79.8°W). Three of the plots are exposed to the ambient CO₂ concentration plus 200 ppm while the other three are kept at ambient CO₂ as controls. The CO₂ fumigation began on 27 August 1996. Soil CO₂ efflux was measured approximately once a month using a field-portable infrared gas analyzer (IRGA) equipped with a soil respiration chamber between 12 pm and 4 pm [Andrews and Schlesinger, 2001]. The measured soil CO₂ efflux represented its daily maximum rates and was extrapolated to 24 hours by regression analysis with the soda lime measurements detailed by Andrews [1999]. The extrapolated daily total soil CO₂ efflux was used to compare with simulated soil CO₂ efflux. Soil temperature in the plots was measured and recorded every 30 min using a permanently installed thermocouple probe at 5 cm depth (Figure 1)

[Schafer *et al.*, 2002]. Volumetric soil moisture in the upper 30 cm of the soil profile was calculated using modified time domain reflectometry techniques that began on 23 May 1997 and were recorded every 30 min [Schafer *et al.*, 2002; Hui *et al.*, 2003]. Soil CO₂ concentration was measured in samples drawn from gas wells at 15, 30, 70, 100, and 200 cm depths [Andrews, 1999]. Soil temperature was measured at the time of gas analysis using a permanently installed thermocouple probe at these depths, and the data were used to develop the relationships of upper layer soil temperature with temperatures at other depths. Fine root biomass of live and dead roots was collected bi-monthly from June 1997 to November 1998 to a depth of 40 cm by *Mataamala and Schlesinger* [2000] and found mostly in the upper 30 cm of the soil profile. Soils are of the Enon Series, a low-fertility Ultic Alfisol derived from igneous rock, yielding a relative acidic (pH = 5.75), well-developed soil profile with mixed clay mineralogy. The site is homogeneous with respect to soil physical properties. The mean annual temperature is 15.5°C and mean annual precipitation is 1140 mm.

2.2. Model Structure

[8] We modified the PATCIS model to evaluate soil CO₂ production and transport at the Duke FACE site. PATCIS is a one-dimensional, multilayer, process-based soil CO₂ efflux/respiration model [Fang and Moncrieff, 1999]. In the model, gaseous diffusion and liquid phase dispersion are the major mechanisms governing the transport of CO₂. CO₂ production in the soil consists of respiration by plant live roots and decomposition of soil organic matter by microbes. CO₂ emission from the soil is considered to be the combined result of these two major processes. To account for the different effects of temperature and moisture on root and microbial respirations, we modified the program to allow separate parameter settings for root and microbial respiration. Data input method and structure of the program were also changed for easy of use. The model descriptions below mainly follow Fang and Moncrieff [1999]'s notations.

2.2.1. Production of CO₂ in the Soil

[9] The model defines the total CO₂ production in the soil as the combined respiration of living roots and heterotrophic microbial respiration and assumes that individual CO₂ processes are additive, thus

$$S = R_r + R_m, \quad (1)$$

$$R_r = r_r B, \quad (2a)$$

$$R_m = r_m M, \quad (2b)$$

$$r_r = r_{r0} f_r(T) f_r(W) f_r(O_2), \quad (3a)$$

$$r_m = r_{m0} f_m(T) f_m(W) f_m(O_2), \quad (3b)$$

where S is the CO₂ production rate in the soil and R_r and R_m are the rates of roots and microbial respiration, respectively.

Roots are classified into three size classes according to the root diameter (0–1 mm, 1–2 mm, and >2 mm). Here r_r is the specific respiratory rate of the fine root and B is the root biomass of three size classes. Microbial decomposition matter includes aboveground litterfall, soil organic matter, and root litterfall. M is the amount of labile and resistant organic matter, r_m is the specific microbial decomposition rate, and r_{r0} and r_{m0} represents the maximum specific rates of root respiration and microbial decomposition under optimal conditions at 10°C (T_{10}). Different respiratory rates were specified for the three root size classes as well as for labile and resistant organic matter [Fang and Moncrieff, 1999]. Factors $f(T)$ and $f(W)$ are scaling factors reflecting the influence of soil temperature and soil moisture and defined as [Fang and Moncrieff, 1999]

$$f(T) = \exp\left(\frac{E}{RT} - \frac{T - T_{10}}{T_{10}}\right) \quad (4)$$

$$f(W) = 1 - \exp(-aW + c), \quad (5)$$

where E is the activation energy for respiration, in kJ mol⁻¹, R is the universal gas constant, T is temperature in K, a defines the maximal increase in the rate of soil respiration with soil moisture W , c is a constant, and $f(W)$ has a value between 0 and 1. Parameter values of E , a , and c can be specified differently for root and microbial respiration. The total CO₂ production, S_T , can be obtained by integrating equation (1) through the whole soil profile

$$S_T = \int_0^{z_l} S dz = \int_0^{z_l} r_r B dz + \int_0^{z_l} r_m M dz, \quad (6)$$

where Z_l is the depth of the lowest boundary in the soil.

2.2.2. Transport of CO₂ in the Soil

[10] One-dimensional CO₂ transport in both gas and liquid phases in the soil is expressed by a mass balance equation [Wood *et al.*, 1993; Fang and Moncrieff, 1999]. The CO₂ mass balance of an arbitrary volume below the surface is modeled as

$$\frac{\partial C_T}{\partial t} = -\frac{\partial}{\partial Z} (F_{dg} + F_{ag} + F_{dw} + F_{aw}) + S, \quad (7)$$

where C_T is the total CO₂ concentration in both gas and liquid phases; F_{dg} and F_{dw} are CO₂ fluxes caused by diffusion/dispersion in the gaseous and liquid phases of the soil, respectively; F_{ag} and F_{aw} are the fluxes resulting from gas convection and vertical water movement, respectively; and S is the CO₂ production rate defined in equation (1), whose magnitude may change with soil depth. Among these, F_{dg} is the most important and is defined [Šimůnek and Suarez, 1993; Fang and Moncrieff, 1999] as

$$F_{dg} = -D_{gs} \frac{\partial C_g}{\partial Z}, \quad (8)$$

where C_g is CO₂ concentration in the gas phase, and D_{gs} is the effective diffusion coefficient of CO₂ in the soil.

2.2.3. Model Inputs and Parameterization

[11] Input data for the model simulation include soil particle density, bulk density, live and dead fine root biomass, soil organic matter, soil temperature, and moisture, all at different depths. All inputs to the model were either directly measured at the study sites or derived from the literature. Simulations were conducted daily for the Duke Forest in 1997 and 1998. See Appendix A for a detailed description of the data sets and parameterization.

2.3. Statistical Model of Soil CO₂ Efflux

[12] We fitted soil CO₂ efflux with soil temperature and soil moisture using the following equation:

$$F_{CO_2} = F_0 \exp(bT)(1 - \exp(-cW + d)), \quad (9)$$

where F_{CO_2} is the extrapolated daily total soil CO₂ efflux from IRGA measurements ($\text{g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$); F_0 is the base CO₂ efflux when soil temperature is 0°C and soil moisture is not limiting; T is soil temperature (°C); and W is soil moisture (% Vol.). Here b , c , and d are parameters related to soil temperature and moisture. From equation (9), temperature sensitivity Q_{10} can be calculated as $Q_{10} = \exp(10b)$. Two moisture sensitivity values can be defined and calculated as: minimum soil moisture $W_0 = \frac{d}{c}$. When soil moisture is below W_0 , soil CO₂ efflux is 0; and limit-free soil moisture $W_f = \frac{(2 \ln(10) + d)}{c}$. When soil moisture is larger than W_f , soil CO₂ efflux is 99% higher than its maximum potential value, so soil moisture is not a limiting factor to soil CO₂ efflux. The monthly measured soil CO₂ efflux was used to develop the statistical model at the ambient and elevated CO₂ treatments. The model was then applied to daily soil temperature and moisture to estimate daily soil CO₂ efflux in 1997 and 1998. The estimations were compared to the soil CO₂ efflux simulated by the PATCIS model. Statistical analyses were conducted using SAS software (SAS Institute, Cary, North Carolina [Hui and Jiang, 1996]).

3. Results

3.1. Simulated Soil Surface CO₂ Efflux and Soil Respiration

[13] Simulated daily soil CO₂ efflux at the ambient CO₂ treatment increased from 4.5 $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ in January 1997 to the maximum value of 24.1 $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ in summer and decreased to 4.5 $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ in December 1997 at the Duke Forest FACE site (Figure 2a). In 1998, the maximum soil CO₂ efflux in summer was 26.3 $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$. The annual total soil CO₂ efflux was 997.4 $\text{g C m}^{-2} \text{ yr}^{-1}$ in 1997 and 1211.2 $\text{g C m}^{-2} \text{ yr}^{-1}$ in 1998. Simulated soil CO₂ production (i.e., soil respiration) was very similar to the soil CO₂ efflux in the Duke Forest. The difference between soil CO₂ efflux and soil respiration was mostly between -1.5 and +1.0 $\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ (Figure 2b). Annual total soil respiration in the Duke Forest was 996.8 $\text{g C m}^{-2} \text{ yr}^{-1}$ in 1997 and 1210.4 $\text{g C m}^{-2} \text{ yr}^{-1}$ in 1998. In both years, soil CO₂ efflux showed distinctive seasonal variation that was mainly controlled by soil temperature. Soil CO₂ efflux declined in July 1997 and in June 1998, was coincident with the lower moisture in those drought periods.

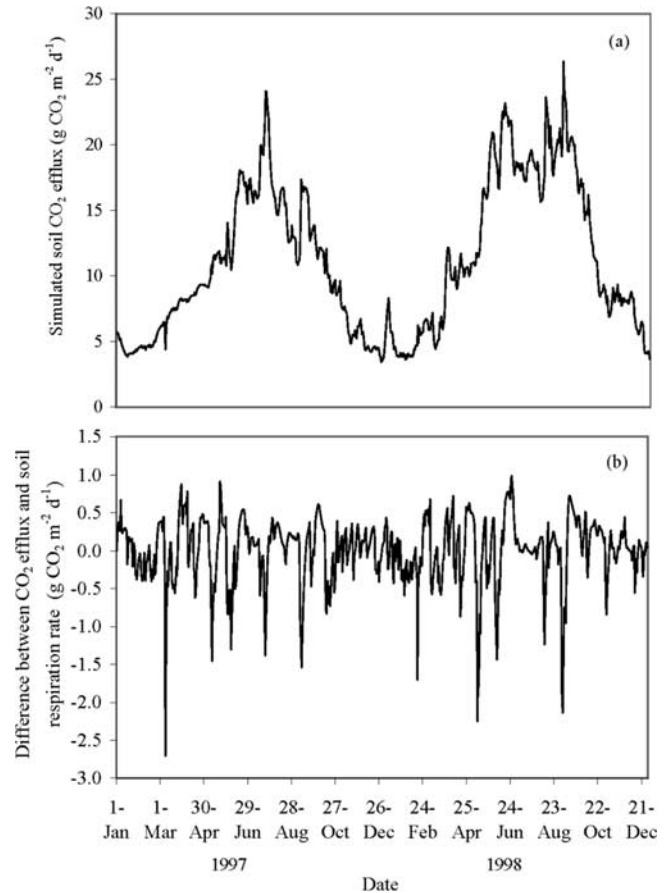


Figure 2. (a) Simulated soil CO₂ efflux and (b) the difference between CO₂ efflux and soil respiration at the ambient CO₂ treatment in the Duke Forest, North Carolina.

[14] Simulated soil CO₂ efflux fitted well with the observed soil CO₂ efflux during the winter and was slightly biased toward the measurements in summer (Figure 3a). Using this process-based model, 67% of the variation in observed soil CO₂ efflux was explained (Figure 3b). Estimated soil CO₂ efflux by the statistical model also showed strong seasonal variations, similar to the simulated soil CO₂ efflux (Figure 3a). In summer, the statistical estimation tracked the observed soil CO₂ efflux even better than the simulated value by PATCIS. Using only soil temperature and moisture, the statistical model explained 64% of the variation in observed soil CO₂ efflux. Temperature sensitivity Q_{10} was estimated as 2.66 at the ambient CO₂ treatment. Soil moisture showed “threshold” effects on soil CO₂ efflux. Minimum soil moisture W_0 and limit-free soil moisture W_f were estimated as 9.4% and 13.4%, respectively. When soil moisture was below 9.4%, the estimated soil CO₂ efflux was 0. A significant reduction of soil CO₂ efflux was found when soil moisture was between 13.4% and 9.4%. If soil moisture was larger than 13.4%, there was virtually no moisture limitation on soil CO₂ efflux.

3.2. Root Versus Microbial Respiration

[15] In the Duke Forest, root respiration contributed 53.3% of the total soil respiration (Table 1). Most of the

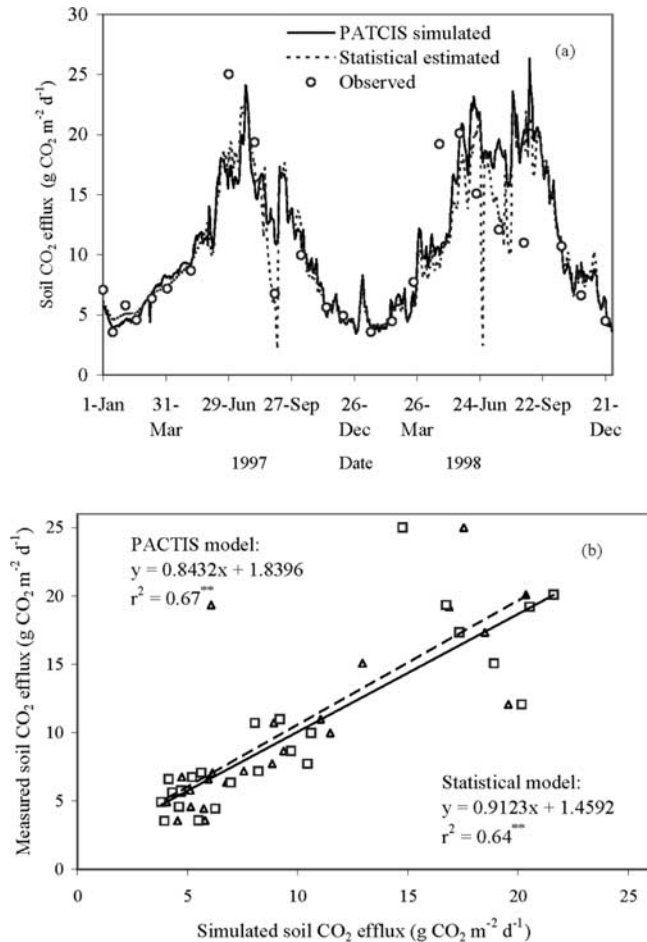


Figure 3. (a) Seasonal changes of soil CO₂ efflux simulated by PATCIS, estimated by the statistical model, and observed in 1997 and 1998 at the ambient CO₂ treatment in the Duke Forest, North Carolina. The statistical model of soil CO₂ efflux at the ambient CO₂ treatment is $F_{CO_2} = 2.466e^{0.098T} (1 - e^{(-1.135W+10.650)})$, $R^2 = 0.64$, $p < 0.001$. (b) Comparisons of modeled soil CO₂ efflux by PATCIS and by the statistical model with observed soil CO₂ efflux at the ambient CO₂ treatment. Solid line represents PATCIS and dashed line is for statistical model. Two asterisks represent significant at $\alpha = 0.01$ level.

soil CO₂ was produced in the top 30 cm of soil. Both root respiration and microbial respiration from the top two layers showed larger day-to-day variations, while respiration from other layers displayed a smooth seasonal change (Figure 4).

Table 1. Contributions of Root and Microbial Respiration to Total Soil Respiration

Layer	Thickness, m	Root Respiration, %	Microbial Respiration, %
1	0.05	5.7	24.6
2	0.10	39.5	10.6
3	0.15	3.0	3.0
4	0.40	3.0	3.8
5	0.30	2.1	2.4
6	1.00	0.0	2.3
Total		53.3	46.7

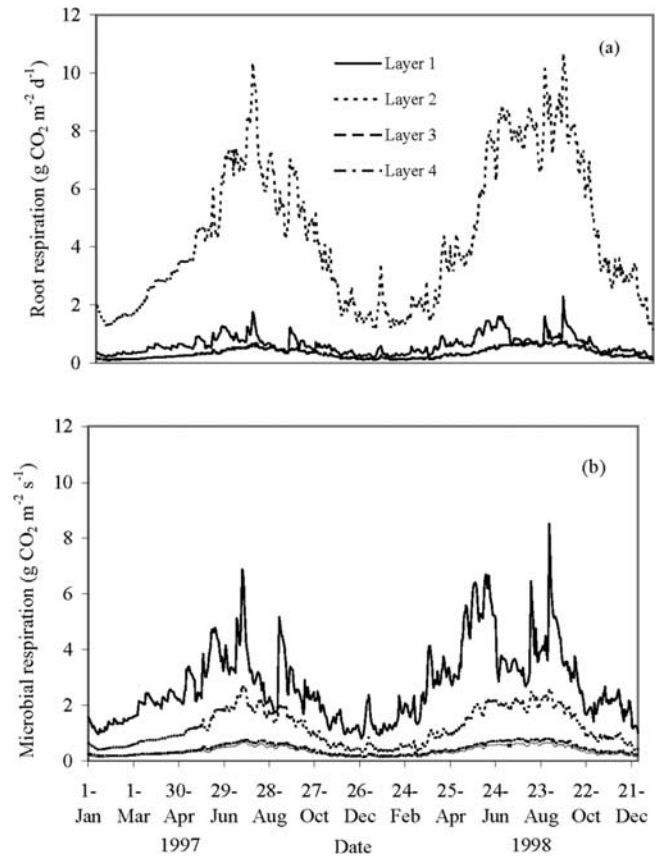


Figure 4. Seasonal change of simulated (a) root respiration and (b) soil microbial respiration at different layers at the ambient CO₂ treatment in the Duke Forest, North Carolina. Root respiration and soil microbial respiration at layers 5 and 6 are small and relatively constant (not shown in the figure).

Annual total soil CO₂ efflux in 1998 was increased by 21.4% compared with that in 1997, but the ratio of root respiration to total soil respiration did not change within these 2 years. While there was no difference of mean root contribution to total soil respiration between 1997 and 1998, root contribution to total respiration showed a seasonal change ranging from 48% in winter to 56% in summer 1997 and 58% in summer 1998.

3.3. Factors Influencing Soil CO₂ Efflux and Soil Respiration

[16] We did the sensitivity analysis to identify important factors on soil CO₂ efflux and soil respiration in the Duke Forest. Soil temperature proved to be one of the most important factors regulating soil CO₂ efflux (Table 2). Changes in soil CO₂ efflux caused by temperature changes were larger in summer than in winter (Figure 5a). Live fine root biomass and its specific respiratory rate contributed largely to the total soil CO₂ efflux. Another sensitive factor was soil moisture. The enhancement of soil CO₂ efflux by soil moisture was relatively constant throughout the year compared to that caused by soil temperature (Figure 5b). Compared to the change of activation energy of microbial

Table 2. Sensitivity Analysis of the Annual CO₂ Efflux to a ±10% Change in Model Inputs and Parameter Values

Variable or Parameter	+10%	-10%
Soil temperature	+16.1	-13.7
Soil moisture	+4.6	-4.7
Activation energy for roots, >20°C, $E_1 = 83.0$; 10°–20°C, $E_2 = 85.0$; <10°C, $E_3 = 100.0$ kJ mol ⁻¹	+4.7	-4.1
Activation energy for microbes, >20°C, $E_1 = 78.2$; 10°–20°C, $E_2 = 79.3$; <10°C, $E_3 = 94.9$ kJ mol ⁻¹	+2.8	-2.6
Moisture parameter for roots, $a = 11$, $c = 0.11$ for mineral soil; $a = 5$, $c = 0.12$ for litter soil	+2.1	-2.4
Moisture parameter for microbes, $a = 15$, $c = 0.11$ for mineral soil; $a = 7.5$, $c = 0.15$ for litter soil	+1.5	-1.7
Optimal specific fine root respiratory rate	+5.2	-5.2
Optimal specific organic-matter decomposition rate	+3.5	-3.7
Soil particle density	-0.1	+0.7
Soil bulk density	-0.8	-0.2
Soil organic matter	+3.4	-3.4
Aboveground litter fall and root litter	+1.3	-1.3
Live fine root biomass	+5.3	-5.3

respiration, soil CO₂ efflux was more sensitive to the change in activation energy of root respiration. Other factors such as soil bulk density had less influence on soil CO₂ efflux.

3.4. CO₂ Effects on Soil CO₂ Efflux in the Duke Forest

[17] Simulated soil CO₂ efflux at the elevated CO₂ treatment showed seasonal change similar to soil CO₂ efflux at the ambient CO₂ treatment, but was higher most of time, especially in early spring and summer (Figure 6). In general, elevated CO₂ increased soil CO₂ efflux by 21.9% in 2 years (i.e., 25.9% in 1997 and 17.6% in 1998); 10.1% increase was contributed by the increase in root respiration and 11.8% by the increase in soil microbial respiration. The annual total soil CO₂ efflux was estimated as 1268.1 and 1426.2 g C m⁻² yr⁻¹ at the elevated CO₂ treatments in 1997 and 1998, respectively.

[18] Simulated soil CO₂ efflux by PATCIS at the elevated CO₂ treatment fitted well with the measured value with $r^2 = 0.86$ (Figures 7a and 7b). Estimated soil CO₂ efflux by the statistical model also displayed a similar seasonal pattern as that of PATCIS (Figure 7a). Large enhancements in soil CO₂ efflux by elevated CO₂ occurred in summer. The annual CO₂ efflux was estimated as 1226 g C m⁻² yr⁻¹ in 1997 and 1348 g C m⁻² yr⁻¹ in 1998. Using only soil temperature and moisture, the statistical model explained 86% of the variation in observed soil CO₂ efflux at the elevated CO₂ treatment (Figure 7b). Temperature sensitivity Q_{10} at the elevated CO₂ treatment was estimated as 2.77. Minimum soil moisture W_0 and limit-free soil moisture W_f at the elevated CO₂ treatment were estimated as 9.9% and 11.7%, respectively. Compared to the ambient CO₂ treatment, the range of W_f and W_0 was smaller; soil CO₂ efflux was less sensitive to soil moisture at the elevated CO₂ treatment. Soil moisture did not show much influence when its value was larger than 11.7%. Less summer drought effect on soil CO₂ efflux was found at the elevated CO₂ treatment.

4. Discussion

4.1. Model Comparison and Uncertainty in Modeling Soil CO₂ Efflux

[19] Modeling is an important tool to estimate, predict, and probe the mechanisms underlying soil CO₂ efflux. In this study, we evaluated two types of models, which are the simple statistical model and the process-oriented produc-

tion-transport model, to examine soil CO₂ efflux. The statistical model estimated seasonal patterns and the annual totals of soil CO₂ efflux, which were similar to those simulated by the production-transport model PATCIS. However, the statistical model does not incorporate any process knowledge and thereby lacks the power to understand mechanisms of soil respiration processes. In comparison, the production-transport model provides extra explanatory power by incorporating processes of root respiration and microbial decomposition of litter and soil organic matter. Thus the model PATCIS can be used to investigate relative contributions of root and microbial components to total soil

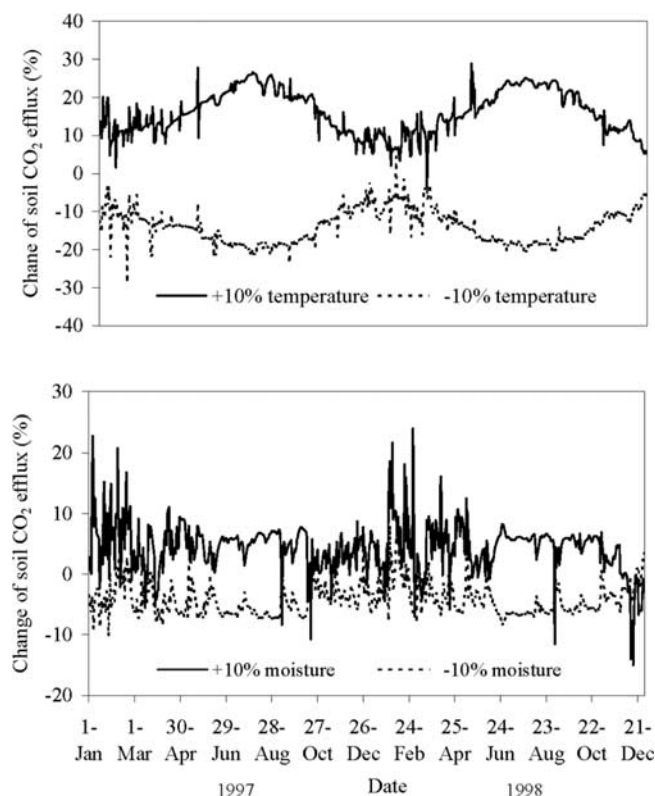


Figure 5. Change of simulated soil CO₂ efflux (%) when (a) soil temperature or (b) soil moisture was changed by 10% at the ambient CO₂ treatment in the Duke Forest, North Carolina.

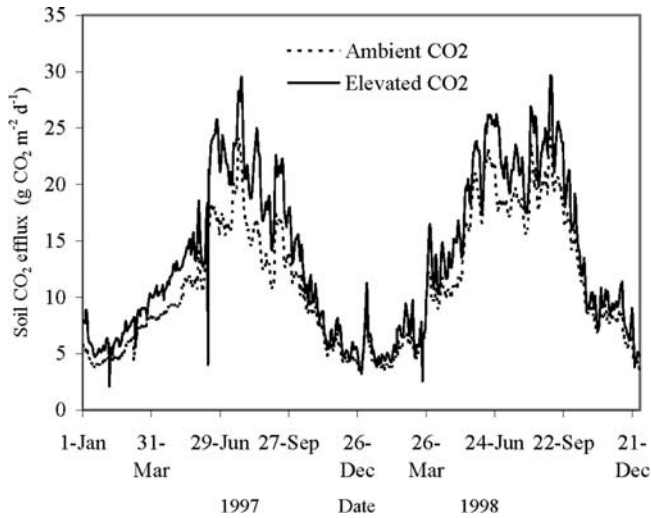


Figure 6. Comparison of simulated soil CO₂ efflux by PATCIS at the elevated CO₂ treatment with that at the ambient CO₂ treatments in the Duke Forest, North Carolina.

respiration, and to examine the mechanisms of increased soil CO₂ efflux at the elevated CO₂. The modeling study with PACTIS indicates, for example, that root respiration contributed 53% of the total respiration in the Duke Forest. Elevated CO₂ enhanced soil CO₂ efflux by 22%, nearly equally contributed by the increases in root respiration and microbial respiration. In spite of the fact that such simulated results might bear great uncertainty, integration of process-based modeling with experimental studies would be an effective approach to advance our understanding of soil respiration processes.

[20] Indeed, uncertainty in model simulations could result from several sources, including model structure, model parameter values, and accuracy of data that are used for model parameterization and validation. First, since a model is an abstraction of reality, uncertainty in modeling results usually decreases as the model structure more closely represents the reality. Second, modeling results also vary greatly with parameter values. Accurate estimation of parameter values will help reduce uncertainty in model simulations. Third, experimental data bear great variability due to spatial and temporal heterogeneities, instrumental accuracy, and other random errors. The variability in experimental data will be introduced into modeling studies to cause uncertainty in simulated results. In our study, for example, the PATCIS model was calibrated against data of root biomass and the specific root respiratory rate, which were measured on separated and washed roots in solution. The measured specific root respiratory rate may or may not accurately represent the rate of intact roots. Thus, simulated root respiration using the model that was calibrated by those data sets could be highly uncertain. However, by conducting a sensitivity analysis, we have identified key parameters in regulating soil respiration. Those parameters include specific fine root respiratory rate, live fine root biomass, and temperature parameter for root respiration. Future data collection on those processes with high accuracy will reduce uncertainty in model estimations.

[21] We intended to use the PATCIS model to evaluate relative importance of production and transport processes in determining soil CO₂ efflux and regulating its temporal patterns. We found that daily CO₂ efflux rates at the soil surface were almost identical to the daily CO₂ production rates over the 2 years, indicating that the CO₂ transport process did not play much of a role in regulating soil CO₂ efflux in the Duke Forest at the daily and annual timescales. This result was probably due to the fact that the PATCIS model simulates carbon processes at a daily time interval. It is yet to be evaluated whether the transport process plays a more important role in regulating soil CO₂ efflux at hourly

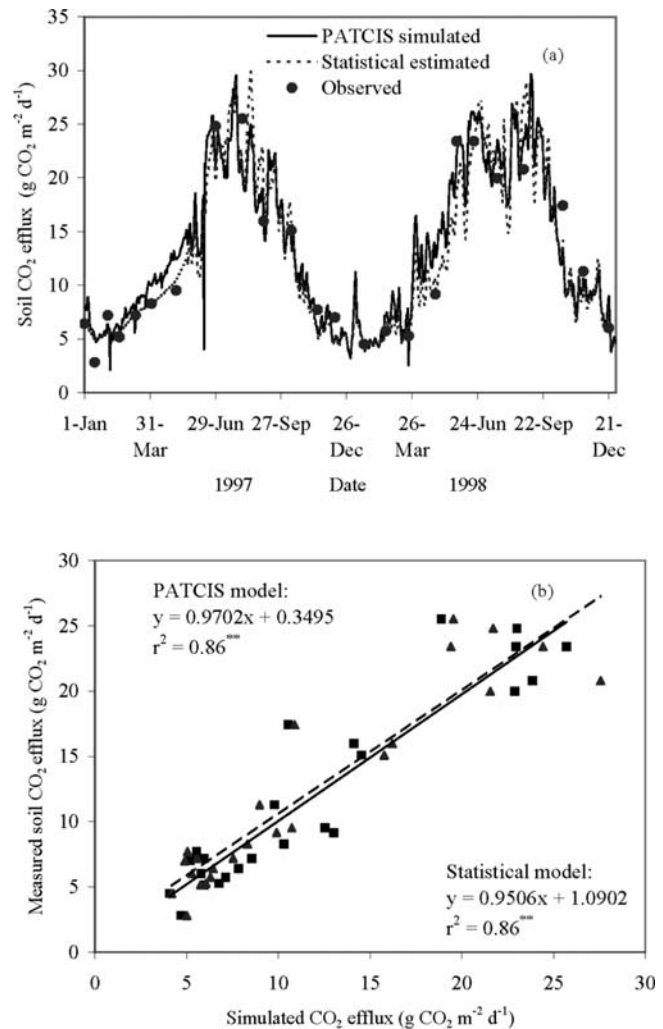


Figure 7. (a) Seasonal changes of soil CO₂ efflux simulated by PATCIS, estimated by the statistical model, and observed at the elevated CO₂ treatment in 1997 and 1998 in the Duke Forest, North Carolina. The statistical model of soil CO₂ efflux at the elevated CO₂ treatment is $F_{CO_2} = 2.616e^{0.1018T} (1 - e^{(-2.666W+26.554)})$, $R^2 = 0.86$, $p < 0.001$. (b) Comparisons of modeled soil CO₂ efflux by PATCIS and the statistical model with observed soil CO₂ efflux. Solid line represents PATCIS and dashed line is for statistical model. Two asterisks represent significant at $\alpha = 0.01$ level.

or even shorter timescales, especially after perturbation events such as rainfall.

4.2. Soil CO₂ Efflux in the Duke Forest

[22] The simulated annual soil CO₂ efflux by PATCIS was 997 and 1211 g C m⁻² yr⁻¹ in 1997 and 1998, respectively, consistent with our statistical model estimations (983 and 1102 g C m⁻² yr⁻¹ in 1997 and 1998, respectively). At the same Duke Forest site, *DeLucia et al.* [1999] reported that annual CO₂ efflux was 1066 g C m⁻² yr⁻¹ in 1997 and 928 g C m⁻² yr⁻¹ in 1998. The higher estimate of annual CO₂ efflux in 1998 in this study was mainly caused by the higher daily soil CO₂ efflux estimated in late summer (Figure 3a). During this period, both PATCIS and the statistical model displayed peaks of soil CO₂ efflux, but only one measurement was made that did not show a higher soil CO₂ efflux. Considering higher soil CO₂ efflux in summer, more frequent measurements would be desirable. Given the uncertainty of the measurements and the model, these values provide a possible range of soil CO₂ efflux in the Duke Forest. The results are also comparable to other studies. *Maier and Kress* [2000] found that annual CO₂ efflux was 1263 g C m⁻² yr⁻¹ in a nearby loblolly pine forest. Wide ranges of annual CO₂ efflux in forest ecosystems were reported by *Janssens et al.* [2001] and *Trumbore* [2000]. Compared to other studies, both process-based and statistical models provided reasonable estimates of soil CO₂ efflux in the Duke Forest.

4.3. Influence of Environmental Factors on Soil CO₂ Efflux and Soil Respiration

[23] As expected, soil temperature played the most important role in regulating soil CO₂ production and soil CO₂ efflux, since no seasonal variation of live and dead fine root biomass was found in the Duke Forest [*Matamala and Schlesinger*, 2000]. Only in summer, when the temperature was high and the soil moisture was low, did soil moisture instead of soil temperature regulate soil CO₂ efflux and decrease soil CO₂ efflux (see Figures 1 and 2a). Statistical model results quantified the limit-free soil moisture as $W_f = 13.4\%$ and the minimum soil moisture $W_0 = 9.4\%$ at the ambient CO₂ treatment. Since soil moisture on most of the days was higher than 13.4%, soil CO₂ efflux was mainly dominated by soil temperature in the Duke Forest. However, due to the fact that lower moisture occurred in summer when potential soil CO₂ efflux was higher, the limitation due to soil moisture during this period could have had remarkable influence on annual total soil CO₂ efflux estimations.

4.4. Effects of Elevated CO₂ on Soil CO₂ Efflux

[24] We estimated that soil CO₂ efflux at the elevated CO₂ treatment was 18–26% higher than at the ambient CO₂ treatment by PATCIS. While no significant differences of temperature and soil moisture were found between the ambient and the elevated CO₂ treatments [*Andrews*, 1999], the increases in soil CO₂ efflux were mainly due to the increases in root respiration and decomposition of litterfall [*Luo et al.*, 2001b]. Large enhancement of stimulated soil CO₂ efflux was observed in the summer of 1997 (Figure 6), but less stimulation was observed in 1998 due to a smaller increase in fine

live root biomass at the elevated CO₂ in 1998 compared to that in 1997. The differences of CO₂ efflux at the elevated and ambient CO₂ treatments reflected differences in the production of CO₂ by roots and microbes, and not by the differences in CO₂ diffusivity. The statistical model showed that Q_{10} was slightly enhanced by elevated CO₂. Soil CO₂ efflux was less sensitive to soil moisture at the elevated CO₂ treatment, as the limit-free soil moisture $W_f = 11.7\%$ was lower than that at the ambient CO₂ treatment. Annual soil CO₂ efflux was enhanced by 22–25%, which was comparable to that by PATCIS.

[25] Experimental report of soil CO₂ efflux at the elevated CO₂ treatments in an intact forest ecosystem was still rare. *Hamilton et al.* [2002] reported a 27% increase in soil CO₂ efflux by elevated CO₂ in the Duke Forest, but the contribution to this increase was not clear. Growing young loblolly pine trees in open-top chambers, *Thomas et al.* [2000] found that soil CO₂ efflux was increased by elevated CO₂ by 23% in the first year and 13% in the second year, due to increases in fine root biomass. An even larger increase of 35% at the elevated CO₂ chambers was reported in a 3-year study of ponderosa pine trees [*Vose et al.*, 1997]. Soil CO₂ effluxes in California grasslands [*Luo et al.*, 1996], in a sunflower soil [*Hui et al.*, 2001], and in a short grass steppe [*Pendall et al.*, 2003] were also increased by elevated CO₂ treatments. While most studies showed enhanced soil CO₂ efflux caused by elevated CO₂, but the relative contributions of root respiration and microbial respiration to the increase are still in debate [*Zak et al.*, 2000]. As showed in this study, increases in fine root respiration and litterfall decomposition could lead to an enhancement of soil CO₂ efflux. In the long-term, decomposition of dead root and soil organic matter may also add to the increase of soil CO₂ efflux at the elevated CO₂ treatment.

5. Conclusions

[26] By evaluating a process-based soil CO₂ efflux model (PATCIS) and a statistical model, we demonstrated that seasonal variations in soil CO₂ efflux at both the ambient CO₂ and the elevated CO₂ treatments in the Duke Forest can be well simulated. Annual soil CO₂ efflux was estimated by PATCIS as 997 and 1211 g C m⁻² yr⁻¹ in 1997 and 1998, respectively. Elevated CO₂ increased soil CO₂ efflux by 18–26% in the Duke Forest. The enhancements of soil CO₂ efflux were mainly through root respiration which in turn was caused by increased fine root biomass, and microbial respiration through increased aboveground litterfall. Soil CO₂ efflux was regulated mainly by soil temperature. Soil moisture influenced soil CO₂ efflux only when its value was below the limit-free soil moisture. Modeling results also showed that on a daily basis, soil CO₂ efflux was very close to the production of CO₂ in the soil. The CO₂ transport process may not be an important constraint for surface CO₂ efflux. This modeling study has shown the value of a process-based model in interpreting temporal variability of and elevated CO₂ effect on soil CO₂ efflux in a forest ecosystem.

Appendix A: Inputs and Parameterization of PATCIS Model

[27] We divided the forest floor and the mineral soil into 6 layers (Table 1) to simulate soil respiration at different

depths. Soil bulk density of 1.07 g cm^{-3} was used for the top organic layer [Matamala and Schlesinger, 2000], 1.10 g cm^{-3} for layer 2, and 1.3 g cm^{-3} for mineral soil layers [Hacks et al., 2000; Glinski and Stepniewski, 1985]. Soil particle density of 2.65 g cm^{-3} was used for mineral soil layers [Glinski and Stepniewski, 1985]. Soil organic matter [Schlesinger and Lichter, 2001], root biomass [Matamala and Schlesinger, 2000], and litterfall [Allen et al., 2000] were measured in the Duke Forest and have been published by the investigators. Most of the measurements were conducted at certain time intervals. Data on days between the measurements were interpolated linearly using the measured data. Activation energy for root and microbial respiration and other parameters were adopted from Moncrieff and Fang [1999] with some modifications (Table 2). Optimal fine root (<1 mm) specific respiratory rate at 10°C , an important parameter for root respiration, was set as $1.74 \times 10^{-4} \text{ mg CO}_2 \text{ g}^{-1} \text{ DM s}^{-1}$ (i.e., $0.0625 \text{ g g}^{-1} \text{ hr}^{-1}$) for loblolly pine [Luo et al., 2001b]. This value was between the measured values of 1.39×10^{-4} in November and $2.20 \times 10^{-4} \text{ mg CO}_2 \text{ g}^{-1} \text{ DM s}^{-1}$ in May at the same Duke Forest site [Matamala and Schlesinger, 2000]. Specific respiratory rate of roots 1–2 mm and >2 mm in diameter was set to 8.7×10^{-5} and $1.74 \times 10^{-5} \text{ mg CO}_2 \text{ g}^{-1} \text{ DM s}^{-1}$, respectively. Values of specific decomposition rate at 10°C were set to 1.80×10^{-5} , 1.80×10^{-6} , and $1.76 \times 10^{-5} \text{ mg CO}_2 \text{ g}^{-1} \text{ DM s}^{-1}$ for above-ground litterfall, soil organic matter, and root litter, respectively, based on the experimental and model results [Luan et al., 1999; Matamala and Schlesinger, 2000; Luo et al., 2001b].

[28] At the elevated CO₂ treatment, we used the same specific root respiration rates, as experimental results showed that specific root respiratory rates did not increase at elevated CO₂ treatment in the Duke Forest [Matamala and Schlesinger, 2000]. Because loblolly pine litter C:N ratio, fine root turnover, and microbial biomass C and N were not significantly affected by elevated CO₂ in the Duke Forest [Allen et al., 2000; Finzi and Schlesinger, 2003], we used same specific decomposition rate as at the ambient CO₂ treatment. However, significant differences for total mass and carbon content of the forest floor and in the top mineral soil were found between the ambient and the elevated CO₂ treatments [Schlesinger and Lichter, 2001]. A significant increase of 37.8% of live fine roots at the elevated CO₂ treatment versus ambient treatment was found during the 2 years of CO₂ fumigation [Matamala and Schlesinger, 2000]. A significant increase in loblolly pine leaf litterfall mass was also revealed at the elevated CO₂ treatment [Allen et al., 2000]. We modified the model inputs to reflect these changes at the elevated CO₂ treatment. Soil temperature and moisture measured at the elevated CO₂ treatment were used in model simulation.

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