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Carbon isotope composition of ambient CO_2 and recycling: a matrix simulation model

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Abstract

The relationship between isotopic composition and concentration of ambient CO_2 in a canopy and its associated convective boundary layer was modeled. The model divides the canopy and convective boundary layer into several layers. Photosynthesis, respiration, and exchange between each layer can be simulated by matrix equations. This simulation can be used to calculate recycling; defined here as the amount of respired CO_2 re-fixed by photosynthesis relative to the total amount of respired CO_2. At steady state the matrix equations can be solved for the canopy and convective boundary layer CO_2 concentration and isotopic profile, which can be used to calculate a theoretical recycling index according to a previously developed equation. There is complete agreement between simulated and theoretical recycling indices for different exchange scenarios. Recycling indices from a simulation of gas exchange between a heterogeneous vegetation canopy and the troposphere also agreed with a more generalized form of the theoretical recycling equation developed here. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Carbon dioxide; Carbon-13; Convective boundary layer; Gas exchange; Recycling; Troposphere

1. Introduction

The cycling of matter, such as nutrients, contaminants and tracers, through ecological systems has been the focus of much study (e.g. Bunnell and Scoullar, 1975; Copping and Lorenzen, 1980). Ecologists have developed a number of tools to analyze cycling (e.g. Ulanowicz and Kay, 1991; Christensen and Pauly, 1992; Diffendorfer et al., 2001), as well as indices to quantify the amount of recycling of material that occurs. For example, Finn's (1976) well known cycling index (CI) is a general index that is used to quantify the efficiency of cycling of a nutrient through a multi-compartment food web. Plant eco-physiologists are frequently interested in a more limited aspect of the biological system, such as the interface between primary producers and the inorganic carbon pool. In that case, another index due to Finn, the cycling efficiency, RE_k, of a compartment k, comes closer to such interests. Finn defined RE_k as the fraction of the input to compartment k that is recycled. To put this in the context of the present paper, consider compartment k to be the

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autotroph compartment of a food web and the flux in question to be carbon. Then RE_k would be the ratio of input carbon (in photosynthesized CO_2) that has recently been respired (has not had a chance to mix with the general atmosphere) to the total carbon input. Some of the indices of carbon recycling developed by eco-physiologists are similar to Finn's RE_k index. These indices, however, hold a different history. This term became more commonly used by eco-physiologists with the advent of carbon-13 (^{13}C) abundance measurements in plant biomass. These measurements have been extremely useful in deciphering plant physiological and ecosystem processes. Carbon-13 abundance is expressed as a $\delta^{13}C$ value and given by the following equation:

$$\delta^{13}\mathrm{C} = \left[\frac{R_{\mathrm{SAMPLE}}}{R_{\mathrm{STANDARD}}} - 1\right] \times 10^3. \tag{1}$$

R represents the $^{13}C/^{12}C$ ratio of the sample in question or the standard. The standard commonly used to report $\delta^{13}C$ values is limestone from the Pee Dee formation in South Carolina. According to the equation above, carbon samples with negative $\delta^{13}C$ values would have less ^{13}C relative to the standard. Those with positive $\delta^{13}C$ values would have greater ^{13}C abundance relative to the standard.

There are at least three definitions of carbon recycling currently used by eco-physiologists. Vogel (1978), who first observed that vegetation in the understory of forests was isotopically depleted relative to that of the canopy, introduced the first definition. He measured the $\delta^{13}C$ values of respiratory CO_2 accumulated under upside down barrels and observed that this CO_2 was also isotopically depleted. Hence, he concluded that plants were utilizing isotopically depleted respired CO_2 during photosynthesis and called this process recycling. Several other investigators have also observed lower $\delta^{13}C$ in the plants from forest understory relative to those in the canopy (Medina and Minchin, 1980; Francey et al., 1985; Ehleringer et al., 1986; Sternberg et al., 1989; Medina et al., 1991; Broadmeadow et al., 1992; Brooks et al., 1997; Kruijt et al., 1997). Recycling here is ascribed to a specific tissue analyzed for $\delta^{13}C$ values. For example, if the $\delta^{13}C$ values of tropospheric and respired CO_2 are $-7.8‰$ and $-27‰$, respectively, the discrimination factor of photosynthesis is $-20‰$, and a tissue has a $\delta^{13}C$ value of $-34‰$, a mass balance equation can then be used to calculate the proportions of that tissue that came from tropospheric CO_2 and from respiration. This latter proportion has been previously designated as recycling. For the example given above, the mass balance equation would be:

$$\begin{aligned} -34‰ = {} & [(1-x)(-7.8‰ - 20‰)] \\ & + [x(-27‰ - 20‰)], \end{aligned} \tag{2}$$

where x is the proportion of respired CO_2, and for this case the solution is 0.32.

Further studies on the discrimination of ^{13}C by plant assimilation (Farquhar et al., 1982) indicated that discrimination could be altered depending on the ratio of CO_2 concentration internal and external to the leaf. It was also observed that there are several environmental factors, such as light levels and drought stress, which could affect this ratio and, therefore, the isotopic discrimination during photosynthesis (Farquhar et al., 1982). This research brought to light the possibility that ^{13}C depletion of plant tissue in forest understory biomass might not be caused by a source effect at all, but rather by an increased discrimination during photosynthesis due to low light levels (Francey et al., 1985; Ehleringer et al., 1986; Mulkey, 1986). In order to quantify how much of this phenomenon was caused by changes in discrimination and how much was due to a source effect, Sternberg et al. (1989) analyzed $\delta^{13}C$ values of plant tissue of an understory bamboo species (*Pharus latifolius* and *Streptochaeta sodiroana*) grown in the forest floor and under similar shady conditions but in a well ventilated shade house. Their measurements indicate that, for the particular species in this forest, about 30% of the decrease in $\delta^{13}C$ value was due to a source effect and about 70% was due to physiologically induced changes in the isotopic discrimination.

The second and third definition of recycling considers carbon recycling at the ecosystem level. Sternberg (1989) defined recycling (Φ_S) as the proportion of respired CO_2 re-fixed by photosynthesis relative to the total flux of respired CO_2. He derived a steady state (s.s.) model equation to determine the effect of respired CO_2 re-fixation by photosynthesis on the so-called "Keeling type" plot (Keeling, 1958, 1961). Normally, a mixture of respired CO_2 and tropospheric CO_2 should respect the relationship (Keeling, 1958, 1961):

$$\delta_E = \frac{C_A}{C_E}(\delta_A - \delta_R) + \delta_R. \tag{3}$$

The $\delta^{13}C$ values of CO_2 in the ecosystem, the troposphere, and of respiration are represented by δ_E, δ_A, and δ_R respectively. The CO_2 concentrations of the ecosystem and the troposphere are represented by C_E and C_A, respectively. Note that if δ_E values are plotted against $1/C_E$, the intercept of this linear relationship is the $\delta^{13}C$ value of respired CO_2. This relationship is extremely useful in determining the isotopic composition of respired CO_2 in terrestrial ecosystems, providing there is no refixation of respired CO_2 (Keeling, 1958, 1961; Sternberg et al., 1989, 1997; Lloyd et al., 1996; Buchmann and Ehleringer, 1998; Harwood et al., 1999 and several others). Sternberg's recycling equation (equation 14 in Sternberg, 1989) is given by:

$$\delta_E = \frac{C_A}{C_E}(\delta_A - \delta_R)(1 - \Phi_S) + \delta_R + \Phi_S \Delta_P, \tag{4}$$

where Δ_P is the photosynthetic fractionation during CO_2 assimilation by the vegetation. If there is no recycling ($\Phi_S = 0$), the above equation reverts to Keeling's original equation. A few investigators have used this relationship to derive forest recycling; values ranging from 7 to 40% were calculated (Sternberg, 1989; Broadmeadow et al., 1992; Flanagan and Varney, 1995; Sternberg et al., 1997). However, some of these results must be taken with caution, since there are problems with utilizing a linear regression of $\delta^{13}C$ value of ambient CO_2 (δ_E) versus the inverse of the ambient CO_2 concentration ($1/C_E$), and deriving recycling values from the slope and the intercept of this regression (Sternberg, 1997; Yakir and Sternberg, 2000). Further, there are also problems in using the assumptions of Eq. (4) on a heterogeneous vegetation structure, such as tropical forests. In these communities photosynthetic rates and fractionation, and the proportion of respired CO_2 can differ from one level of the vegetation to another, therefore violating the basic assumption of a well-mixed single compartment model used in deriving Eq. (4).

Eq. (4) was derived by a different method at a later date by Lloyd et al. (1996). Lloyd et al. (1996) proposed a new definition of recycling (Φ_L) to replace Φ_S. They defined Φ_L as the proportion of respired CO_2 assimilated relative to the total CO_2 fixed by the ecosystem. This same index was previously proposed by Schleser and Jayasekera (1985). Sternberg (1997), however, demonstrated that although these two recycling indices are related, they are recording different ecosystem processes and therefore one cannot replace the other. Presently, the issues of (1) which index to use, (2) how they are related to each other, and (3) how accurately Sternberg's theoretical equation measures recycling is still an open question. In this study we address the later question (3) by using a matrix compartment model that simulates CO_2 exchange between a vegetation stand and the troposphere, and derives a simulated value of recycling as previously defined by Sternberg (1989). The results of this simulation are compared with the previously developed theoretical recycling Eq. (4). In this model the vegetation and its associated convective boundary layer (c.b.l.) are divided into several horizontal layers. Simulation results for a heterogeneous multi-compartment vegetation stand are also compared with a s.s. theoretical equation developed here, which describes CO_2 exchange between a vertically heterogeneous vegetation stand and the troposphere.

2. Model

2.1. Steady state concentration equation

Compartment models of various types have a long history in ecology and, more generally, biology (e.g. Jacquez, 1972). In ecology, populations, trophic levels of an ecosystem, and carbon or nutrients in various depth classes of soils and lakes, have all been represented as discrete compartments. Here, similar to the last types of model, we use discrete compartments to represent carbon at different heights in the vegetation canopy and its associated c.b.l. Although height is a continuous property, discrete compartments are used to make it more amenable to computer simulation, but the following equations can also be written in a continuous integral form. The vegetation structure and the c.b.l. above are divided into 1 m^3 compartments. Consider a vegetation structure where the canopy occupies two compartments and the c.b.l. extends through the fourth compartment (Fig. 1). This may be much coarser than a realistic vegetation stand and its associated c.b.l., but is meant merely to illustrate the development of model equations. The CO_2 exchange rate between the center of two vertically neighboring compartments is represented by the following relationship:

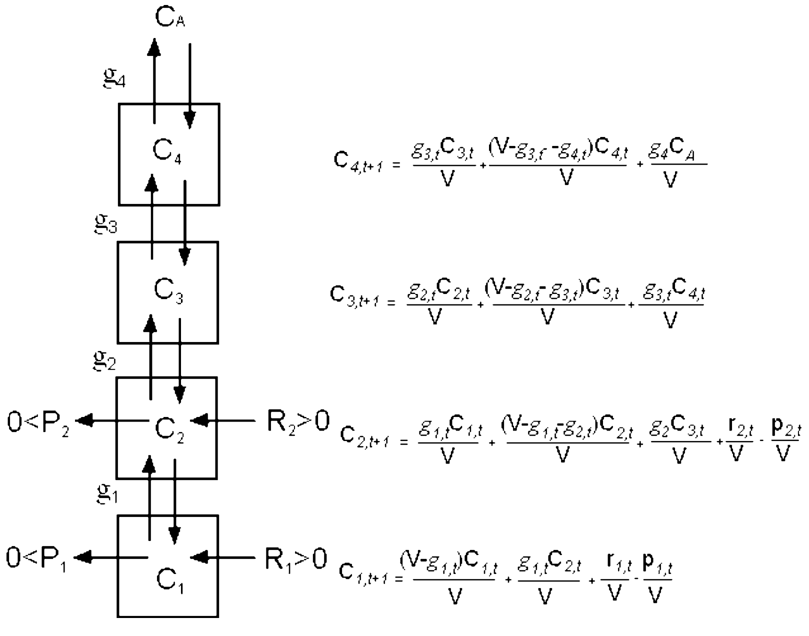
$$F = K \times \frac{\partial C}{\partial z} \tag{5}$$

where F (μmole m^{-2} s^{-1}) is the flux rate between the center of two consecutive compartments, K (mole m^{-1} s^{-1}) is the eddy diffusivity, and $\partial C/\partial z$ (μmole $mole^{-1}$ m^{-1}) is the concentration gradient over distance ∂z (1 m). If K is defined on the basis of turbulent exchange, however, the above equation is not descriptive of processes within the canopy, because eddies are large and coherent within the vegetation canopy (Raupach, 1988, 1989; Raupach et al., 1992).

The above equation is modified to its integrated form:

$$F = G \times \Delta C \tag{6}$$

where ΔC is the carbon dioxide concentration difference between one compartment and a vertically adjacent compartment (μmole $mole^{-1}$), and G is aerodynamic conductivity (mole m^{-2} s^{-1}) between the two compartments. It is assumed here that each compartment is well mixed. However, G, as defined here, is not based on turbulence measurements, but is empirically defined. Several investigators have now derived in-canopy values of aerodynamic conductivity based on flux rates of water vapor or trace gases such as radon, nitrous oxides and methane (Legg and Long,



$$C_{4,t+1} = \frac{g_{3,t}C_{3,t}}{V} + \frac{(V-g_{3,t}-g_{4,t})C_{4,t}}{V} + \frac{g_4C_A}{V}$$

$$C_{3,t+1} = \frac{g_{2,t}C_{2,t}}{V} + \frac{(V-g_{2,t}-g_{3,t})C_{3,t}}{V} + \frac{g_{3,t}C_{4,t}}{V}$$

$$C_{2,t+1} = \frac{g_{1,t}C_{1,t}}{V} + \frac{(V-g_{1,t}-g_{2,t})C_{2,t}}{V} + \frac{g_2C_{3,t}}{V} + \frac{r_{2,t}}{V} - \frac{p_{2,t}}{V}$$

$$C_{1,t+1} = \frac{(V-g_{1,t})C_{1,t}}{V} + \frac{g_{1,t}C_{2,t}}{V} + \frac{r_{1,t}}{V} - \frac{p_{1,t}}{V}$$

Fig. 1. Compartmental exchange equations for a vegetation having the height of 2 m and having a convective boundary layer 2 m above the vegetation canopy.

1975; Trumbore et al., 1990; Leuning et al., 2000; and others). In the study of Trumbore et al. (1990), for example, night-time aerodynamic conductances were measured in the range of 0.024–0.28 mol m^{-2} s^{-1}. A good 1:1 relationship between radon and CO_2 conductances was observed in Trumbore et al. Even if negative values of conductance are measured, this will not affect the development of this model.

In the model developed here it is assumed that there is no net lateral exchange between horizontally neighboring compartments and that CO_2 leaving the c.b.l. to the troposphere will not return. In other words, CO_2 leaving the c.b.l. is diluted by an effectively infinite tropospheric pool of CO_2 at a much faster rate than it can be reassimilated by the c.b.l. The concentration profile of this system (Fig. 1) at time $t+1$ after a discrete time interval ($\Delta t = 1$ s) is given by the following matrix equation:

$$\begin{bmatrix} C_{1,t+1} \\ C_{2,t+1} \\ C_{3,t+1} \\ C_{4,t+1} \end{bmatrix} = \begin{bmatrix} \frac{V-g_{1,t}}{V} & \frac{g_{1,t}}{V} & 0 & 0 \\ \frac{g_{1,t}}{V} & \frac{V-g_{1,t}-g_{2,t}}{V} & \frac{g_{2,t}}{V} & 0 \\ 0 & \frac{g_{2,t}}{V} & \frac{V-g_{2,t}-g_{3,t}}{V} & \frac{g_{3,t}}{V} \\ 0 & 0 & \frac{g_{3,t}}{V} & \frac{V-g_{3,t}-g_{4,t}}{V} \end{bmatrix} \begin{bmatrix} C_{1,t} \\ C_{2,t} \\ C_{3,t} \\ C_{4,t} \end{bmatrix} + \begin{bmatrix} \frac{r_{1,t}}{V} \\ \frac{r_{2,t}}{V} \\ 0 \\ \frac{g_{4,t} \cdot C_A}{V} \end{bmatrix} - \begin{bmatrix} \frac{p_{1,t}}{V} \\ \frac{p_{2,t}}{V} \\ 0 \\ 0 \end{bmatrix} \tag{7}$$

where V is the molar volume of the compartments (about 44.64 moles at standard conditions for 1 m^3 compartment), $C_{i,t}$ represents the CO_2 concentration in the ith compartment for $i = 1,\ldots,4$ at time t, and $g_{i,t}$, $r_{i,t}$ and $p_{i,t}$ represent the product of aerodynamic conductance, respiratory and photosynthetic rates at time t with the time increment ($\Delta t = 1$ s) for each compartment i, respectively (i.e. $g_{i,t} = G_{i,t}\Delta t$, $r_{i,t} = R_{i,t}\Delta t$ and $p_{i,t} = P_{i,t}\Delta t$ where $G_{i,t}$, $R_{i,t}$, and $P_{i,t}$ represent the aerodynamic conductance between compartment i and $i+1$, respiratory rate and photosynthetic rate at compartment i, respectively). The above equation can be written as:

$$\overrightarrow{C_{t+1}} = \mathbf{A_t}\vec{C}_t + \vec{r}_t - \vec{p}_t \tag{8}$$

where $\mathbf{A}_t$, $\vec{C}_t$, $\vec{r}_t$, and $\vec{p}_t$represent the respective matrix and vectors of Eq. (7).

There are only small changes in aerodynamic conductances and respiratory and photosynthetic rates over the several time increments specified here, so that the above equation can be simplified to:

$$\overrightarrow{C_{t+1}} = \mathbf{A}\vec{C}_t + \vec{r} - \vec{p}\,. \tag{9}$$

Eq. (9) can be put into a convenient form by subtracting $\vec{C}_t$ from both sides of the above equation:

$$\overrightarrow{C_{t+1}} - \vec{C}_t = \mathbf{A}'\vec{C}_t + \vec{r} - \vec{p}\,, \tag{10}$$

where $\mathbf{A}'$ is the matrix $\mathbf{A}$ in Eq. (9) minus the identity matrix. Observations of CO_2 concentration profiles indicate very little difference in concentration, $C_{i,t+1} - C_{i,t}$, from one second to

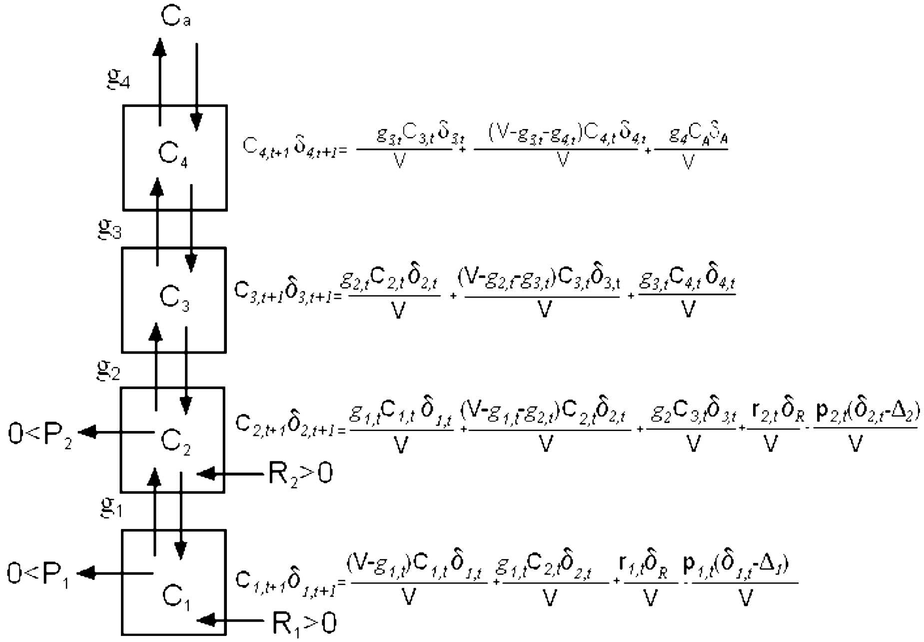


Fig. 2. Compartmental isotope mass balance equations for the vegetation profile described in Fig. 1.

another, ranging from 0.005 ppm at canopy level to 0.007 ppm at the forest understory level (Kruijt et al., 1997). Such values are very small compared to terms on the right-hand side of (10). This means that the terms on the left-hand side can be ignored or, equivalently, that the CO_2 concentration profile is always close to steady state and can be calculated as:

$$\vec{C}_t = (\mathbf{A}')^{-1}(\vec{p} - \vec{r}). \tag{11}$$

Similarly, a matrix equation can be developed for the isotope mass balance in the vegetation and c.b.l. profile (Fig. 2):

$$\mathbf{C}_{t+1}\overrightarrow{\delta_{t+1}} - \mathbf{C}_t\vec{\delta}_t = \mathbf{A}'\mathbf{C}_t\vec{\delta}_t + \mathbf{r}\vec{\delta}_r - \mathbf{p}(\vec{\delta}_t - \vec{\Delta}_t), \tag{12}$$

where $\mathbf{A}'$ is the same matrix as that of Eq. (11). $\mathbf{C}$, $\mathbf{r}$, and $\mathbf{p}$ represent square diagonal matrices having the same elements in the ith row and column as in the ith element of the $\vec{C}_t$, $\vec{r}$ and $\vec{p}$ vectors above, respectively. The isotopic discrimination during photosynthesis, the carbon isotope composition of ambient CO_2 in each cell, and the CO_2 source input (respiration and troposphere) for each cell are represented by vectors Δ_t, $\vec{\delta}_t$ and $\vec{\delta}_r$, respectively. By the same reasoning above, Eq. (12) can be transformed to solve for the s.s. isotopic composition of CO_2 in each cell:

$$\delta_t = (\mathbf{p} - \mathbf{A}'\mathbf{C}_t)^{-1}(\mathbf{r}\vec{\delta}_r + \mathbf{p}\vec{\Delta}) \tag{13}$$

3. Calculation of the proportion of respired CO_2 in each compartment

We can further develop Eq. (13) to calculate the proportion of respired CO_2 in each compartment. This is not merely a mass-balance problem, because any photosynthetic uptake will modify the isotopic composition of atmospheric and respired CO_2. Therefore, a mass balance equation using the original isotopic composition of atmospheric and respired CO_2 as end-members will not give the correct proportion. However, Eq. (13) developed in the previous section can simulate CO_2 exchange between the vegetation and the troposphere with the assumption that photosynthesis does not discriminate against one isotope or the other, i.e. $\Delta_i = 0$ for all i values. Therefore:

$$\overrightarrow{\delta'_t} = (\mathbf{p} - \mathbf{A}'\mathbf{C}_t)^{-1}(\mathbf{r}\overrightarrow{\delta_r}), \tag{14}$$

where $\vec{\delta'}$ is a vector in which the ith element is the $\delta^{13}C$ value of CO_2 in the ith compartment, under simulation conditions in which there is no photosynthetic discrimination. Note that this simulation will not differ from the simulation where fractionation is occurring in terms of the dynamics of gas exchange between the vegetation and the troposphere. The gas exchange simulation, which has no fractionation, can be used to calculate the proportion of respired CO_2 in each cell:

$$\alpha_i = (\delta'_i - \delta_A)/(\delta_r - \delta_A), \tag{15}$$

where α_i is the proportion of respired CO_2 in the ith compartment and the ith element of the percentage respired CO_2 vector, $\vec{\alpha}$. The above equations can be easily generalized to a canopy profile w meters above the soil and a c.b.l. extending L meters above the soil (Fig. 3). The following analysis will be based on this general canopy and boundary layer profile.

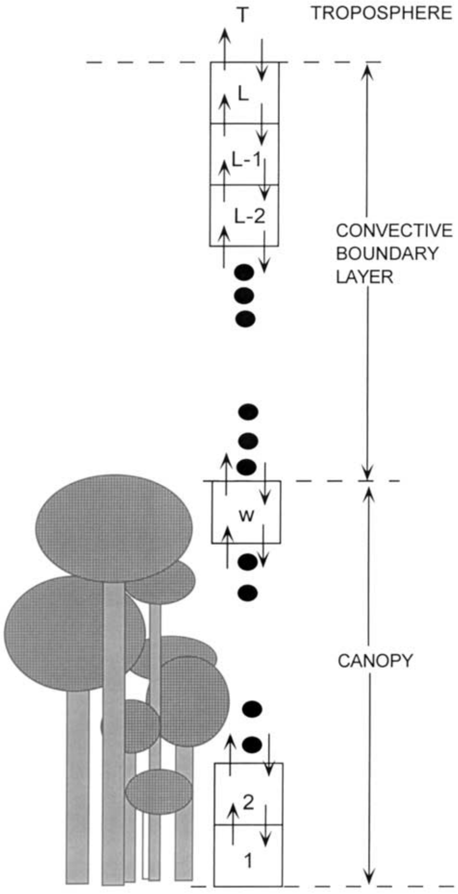


Fig. 3. A generalized compartmental profile for a vegetation w meters tall and having a convective boundary layer L meters high.

Given the proportion of respired CO_2 in each compartment, it is now easy to calculate from the matrix model an index that is equivalent to recycling as defined by Sternberg (1989) (see R_2 in Eqs. (6) and (7)).

$$\Phi^* = \frac{\vec{P}\circ\vec{\alpha}}{\vec{P}\circ\vec{\alpha} + G_w(C_w\alpha_w - C_{w+1}\alpha_{w+1})} \tag{16}$$

where $\vec{P}$ is the photosynthetic rate vector; i.e. the ith element of this vector is the photosynthetic rate in the ith compartment. Eq. (16) is the ratio of respired CO_2 taken up by photosynthesis, i.e. the dot product of the photosynthesis and proportion of respired CO_2 vector, over that of total CO_2 leaving the canopy either by photosynthesis ($\vec{P}\circ\vec{\alpha}$) or by turbulent mixing with the air above the canopy $[G_w(C_w\alpha_w - C_{w+1}\alpha_{w+1})]$. Note that this index takes into account the respired CO_2 that leaves the canopy and returns. Hereafter, this index will be referred to as the simulated recycling index. We can also determine the recycling index previously proposed by Lloyd et al. (1996) as:

$$\Phi_L = \frac{\vec{P}\circ\vec{\alpha}}{\vec{P}\circ\vec{u}} \tag{17}$$

where $\vec{u}$ is a vector of dimension L with all of its element equal to 1.

4. Simulation and comparison with theoretical recycling Eq. (4)

Exchange between a one-layer vegetation stand (1 m tall), having its c.b.l. extending 4 m above soil level, and tropospheric CO_2 can be simulated with this model and the simulated recycling index as defined by Eq. (16) can be calculated. These results can then be compared with the recycling index calculated with Sternberg's (1989) s.s. theoretical Eq. (4). A matrix manipulation program MATLAB© was chosen to simulate CO_2 exchange between the troposphere and the vegeta-

Table 1
Results of the model simulation of gas exchange between a vegetation occupying one compartment, its c.b.l. occupying the next three compartments and the troposphere

Comp.	Given parameters				Calculated parameters at s.s.				
	G	P	R	Δ	C_i	$\delta^{13}C$	α	Φ^*	Φ_s
1	1	14	9.1	20	359.8	−7.2	0.049	0.0750	0.0750
2	2	0	0	0	364.7	−7.5	0.025		
3	3	0	0	0	367.1	−7.6	0.013		
4	4	0	0	0	368.8	−7.7	0.006		
Troposphere	–	–	–	–	370.0	−7.8	0		

Given parameters are aerodynamic conductance (G), photosynthetic rates on a per compartment basis (P), respiratory rates on a per compartment basis (R), and isotopic discrimination during photosynthesis (Δ). The simulation program calculates: the s.s. CO_2 concentration at each compartment (C_i), the $\delta^{13}C$ value of CO_2 at each compartment, the percentage of respired CO_2 in each compartment, and a simulated (Φ^*) and a theoretical value (Φ_s) of respired CO_2 recycling.

tion stand and its associated c.b.l. This simulation is realistic in terms of the magnitude of the aerodynamic conductances normally encountered in vegetation stands and their c.b.l. (Table 1), but unrealistic in terms of height and the early day dynamics of the c.b.l. Nevertheless, it will serve to illustrate some key conceptual aspects of recycling. Tropospheric CO_2 is assumed to have a concentration of 370 ppm and a $\delta^{13}C$ value of -7.8‰. Any CO_2 entering the c.b.l. from the troposphere will have the concentration and isotopic identity of tropospheric CO_2 because CO_2 that leaves the c.b.l. is assumed to lose its isotopic identity by being rapidly diluted in an effectively infinite tropospheric CO_2 pool. It is also assumed here that the $\delta^{13}C$ value of CO_2 from respiration throughout the canopy is -27.0‰ and that photosynthetic fractionation is 20‰.

The program performs 20 simulations by choosing 20 random values of photosynthesis within the limits of 0–50 µmoles/compartment s and 20 random values of respiratory rates within the limits of 0–10 µmoles/compartment s for the vegetation stand. A small constant is added to the respiration rate (0.1) to avoid division by zero in the simulation. The simulation program constructs matrix $\mathbf{A}'$ in Eq. (11) for the particular aerodynamic conductance values and calculates the steady state CO_2 concentration profile ($\vec{C}_t$) for each set of randomly chosen photosynthetic and respiratory rate values. The program then constructs matrices for the s.s. Eq. (13) and calculates the s.s. $\delta^{13}C$ values of CO_2 in each compartment with fractionation and without fractionation as per Eqs. (13) and (14), respectively. The results of the latter are then used to calculate the proportion of respired CO_2 in each compartment and the simulated recycling index (Φ^*) according to Eqs. (15) and (16), respectively. The simulated recycling index is then compared with the theoretical recycling index from Eq. (4), which is calculated at the last part of the program using the concentration of tropospheric CO_2, the s.s. CO_2 concentration of the vegetation canopy (C_1), the isotopic composition of tropospheric, respired, and ecosystem CO_2, and the photosynthetic fractionation by the vegetation.

5. Results of comparison

A comparison of 20 simulations, in which photosynthetic and respiratory rates were randomly chosen within the limitations imposed by the program, shows a perfect fit between the simulated and theoretical recycling indices (Fig. 4). Parameters for a specific example (Table 1) indicate a CO_2 profile with decreasing concentrations from the troposphere to the canopy and an increase in $\delta^{13}C$ values from the troposphere to the canopy. With regards to the perfect fit observed in Fig. 4, there are two points in the discussion between Lloyd et al. (1997) and Sternberg (1997) that need further clarification. First, Lloyd et al. (1996, 1997) stated that Sternberg's theoretical equation should be calculated with the isotopic composition and concentration of CO_2 entering the canopy rather than tropospheric CO_2. In the model presented here this would refer to CO_2 in the compartment just above the canopy (i.e. C_{w+1}, and δ_{w+1}). Sternberg (1989, 1997) reasoned, alternatively, that the theoretical equation should be calculated using tropospheric CO_2, since the modification of isotopic composition of ambient CO_2 in the vegetation stand is ultimately determined by photosynthesis and turbulent mixing acting on a mixture of the two sources: tropospheric and respired CO_2. The end-members of this mixing model should therefore be respired and tropospheric CO_2 as originally suggested (Sternberg 1989). A comparison (Fig. 4) of simulated recycling indices with those calculated using the theoretical Eq. (4), but with concentrations and isotopic composition of the CO_2 from the compartment just above the canopy ($w+1$), as suggested by Lloyd et al. (1996, 1997), shows a large discrepancy between the two measures, with theoretical recycling values much lower than simulated values. No such discrepancy is observed when tropospheric CO_2 values are used in the place of C_A and δ_A on Eq. (4).

The second aspect that needs further clarification is the relationship between Φ_S and Φ_L. Lloyd et al. (1997) indicated that a comparison between Φ_L and Φ_S cannot be done, because Sternberg's recycling index does not take into account CO_2 that leaves the vegetation canopy and re-enters the canopy, whereas their index does. The compartment model presented here considers CO_2 both leaving the canopy and re-entering the vegetation (see Eq. (16)), yet there is complete agreement with simulated and theoretical recycling indices (Fig. 4). The basis for this discussion needs to be examined. When Sternberg (1989) first developed his model equation, he assumed that CO_2 leaving the vegetation canopy becomes diluted by an effectively infinitely large tropospheric pool at a rate that is orders of magnitude faster than its rate of re-entry to the canopy. The compartment model developed here assumes that this occurs only at the boundary between the c.b.l. and the troposphere; i.e. CO_2 leaves the last compartment

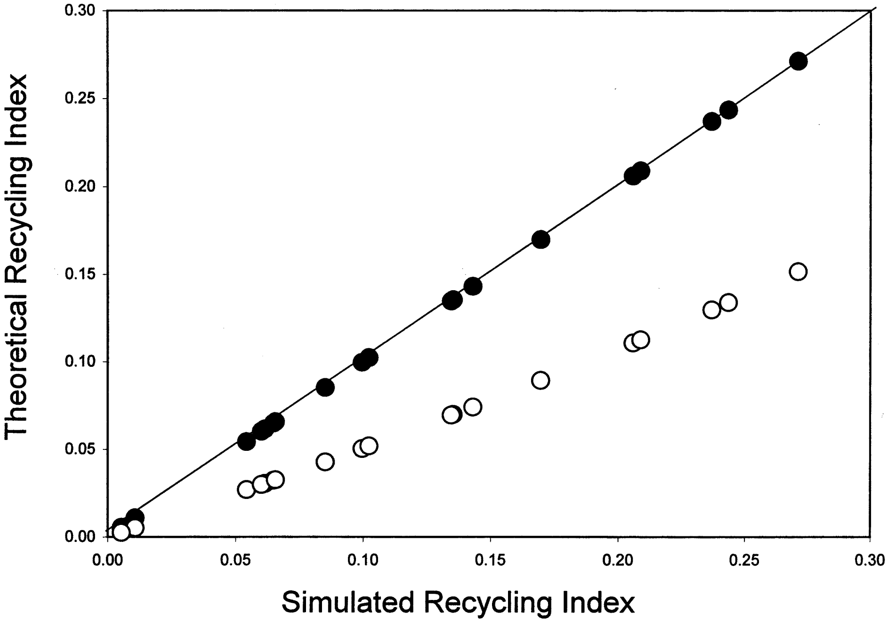


Fig. 4. The relationship between theoretical (calculated with Eq. (4)) and simulated recycling indices for a homogeneous 1 m tall vegetation modeled here as occupying only one compartment. Full circles represent values of theoretical recycling indices using the $\delta^{13}C$ value and concentration of tropospheric CO_2. Empty circles represent values of theoretical recycling indices using $\delta^{13}C$ and concentrations of the CO_2 from the compartment just above the canopy (compartment 3 for this analysis).

of the c.b.l. (compartment L) and its completely diluted by tropospheric CO_2, so that any eddy entering the c.b.l. from the troposphere has the concentration and isotopic identity of tropospheric CO_2. The aerodynamic conductance between the vegetation canopy and troposphere is observed at the canopy edge for the initial model (Sternberg, 1989), and is the overall aerodynamic conductance from the canopy to the troposphere for the model presented here. Regardless, the value of the aerodynamic conductance is irrelevant for Sternberg's theoretical equation (Eq. (4)) relating CO_2 isotope ratios and concentration to recycling, because aerodynamic conductance is cancelled out of the final equation.

Lloyd et al. (1996) estimated recycling in two forests, using aerodynamic conductances measured a few meters above the vegetation canopy, with Sternberg's (1989) definition of recycling index based on CO_2 fluxes, and showed that recycling values were very low. Sternberg (1997) indicated that if one is going to calculate Φ_S using flux measurements rather than isotope and concentration measurements, one should use aerodynamic conductances at the level where the probability of CO_2 returning to the vegetation canopy is negligible. Lloyd et al. (1997) rightly pointed out that this would give even lower recycling values. In fact, both propositions are wrong. According to the model presented here, conductance from the canopy through several layers of the c.b.l. and to the troposphere represents conductance in series. In order to derive the true flux of CO_2 from the vegetation to the troposphere, the overall conductance (Γ) from the canopy to the troposphere should be calculated with the following equation according to the analogy with electrical circuits:

$$\Gamma = \frac{1}{\sum_{i=w}^{L} \frac{1}{G_i}} \tag{18}$$

where Γ is the aerodynamic conductance from the canopy to the troposphere. Calculation of recycling based on flux rates can be done with the following equation, as Lloyd et al. (1996) attempted, but using the more correct value from Eq. (18), rather than the erroneous conductance value used by Lloyd et al. (1996).

$$\Phi_s = \frac{\sum_{i=1}^{w} P_i}{\Gamma C_w + \sum_{i=1}^{w} P_i}. \tag{19}$$

There is a complete agreement between the recycling index calculated by flux measurements (Eq. (19)) and by the isotopic/concentration equation (Eq. (4)) using actual values from the specific simulation shown on Table 1. The discrete summation sign is used in Eq. (18) to compare with a computer simulation, but an integral form of this equation can be used as well.

6. Deriving s.s. theoretical equation for a vertically heterogeneous vegetation

The previous recycling model (Sternberg, 1989) assumed that the vegetation occupies one well mixed compartment exchanging with the tropospheric CO_2. It was therefore possible to conclude that recycling could be defined by the equation:

$$\Phi_s = \frac{P_w}{P_w + \Gamma C_w}. \tag{20}$$

The reason is that recycling is partly a function of the proportion of respired CO_2 in the vegetation compartment (α_w) and described by the following equation if the vegetation occupies only one well mixed compartment (i.e. $w = 1$):

$$\Phi_s = \frac{P_w \alpha_w}{P_w \alpha_w + \Gamma C_w \alpha_w}. \tag{21}$$

The proportion of respired CO_2 in the vegetation compartment in Eq. (21) is canceled out to give Eq. (20). However, as pointed out in previous discussions (Lloyd et al., 1996, 1997; Sternberg, 1997), a tropical forest, for example, is not a well mixed compartment. Isotopic composition of ambient CO_2, CO_2 concentration, proportion of respired CO_2, photosynthetic fluxes and associated discrimination factors can differ significantly from one level of the vegetation to another. Therefore, the simplification of Eq. (21) to Eq. (20) cannot be done for this type of vegetation. Here, a more general form of the s.s. recycling equation is derived, which can be used to calculate recycling for vegetation occupying more than one compartment, each having different properties. Consider the initial situation previously described by Fig. 3: the vegetation extends through compartment w and the c.b.l. extends to compartment L. By mass balance at s.s.

$$\sum_{i=1}^{w} R_i + \Gamma C_{\mathrm{A}} = \Gamma C_w + \sum_{i=1}^{w} P_i. \tag{22}$$

Likewise for the s.s. condition the equation for isotopic composition of CO_2 is approximated by the following equation:

$$\delta_{\mathrm{r}} \sum_{i=1}^{w} R_i + \Gamma C_{\mathrm{A}} \delta_{\mathrm{A}} = \Gamma C_w \delta_w + \sum_{i=1}^{w} P_i(\delta_i - \Delta_i). \tag{23}$$

Merging Eqs. (22) and (23) and using the same algebraic manipulation as previously (Sternberg, 1989), the following equation is derived:

$$\frac{\delta_w \Gamma C_w + \sum_{i=1}^{w} P_i \delta_i}{\Gamma C_w + \sum_{i=1}^{w} P_i} = \frac{\sum_{i=1}^{w} R_i}{\Gamma C_w + \sum_{i=1}^{w} P_i}(\delta_{\mathrm{R}} - \delta_{\mathrm{A}}) + \delta_{\mathrm{A}} + \frac{\sum_{i=1}^{w} P_i \Delta_i}{\Gamma C_w + \sum_{i=1}^{w} P_i}. \tag{24}$$

The average isotopic composition of ambient CO_2 and photosynthetic discrimination weighted to the photosynthetic rate at each compartment is defined as

$$\hat{\delta} = \frac{\sum_{i=1}^{w} P_i \delta_i}{\sum_{i=1}^{w} P_i} \quad \text{and} \quad \hat{\Delta} = \frac{\sum_{i=1}^{w} P_i \Delta_i}{\sum_{i=1}^{w} P_i}. \tag{25}$$

When these weighted averages are inserted into Eq. (24), the following equation is derived:

$$\frac{\delta_w \Gamma C_w + \hat{\delta} \sum_{i=1}^{w} P_i}{\Gamma C_w + \sum_{i=1}^{w} P_i} = \frac{\sum_{i=1}^{w} R_i}{\Gamma C_w + \sum_{i=1}^{w} P_i} \times (\delta_{\mathrm{R}} - \delta_{\mathrm{A}}) + \delta_{\mathrm{A}} + \frac{\hat{\Delta} \sum_{i=1}^{w} P_i}{\Gamma C_w + \sum_{i=1}^{w} P_i} \tag{26}$$

which simplifies to:

$$(1 - R_2)\delta_w + R_2 \hat{\delta} = R_1(\delta_{\mathrm{R}} - \delta_{\mathrm{A}}) + \delta_{\mathrm{A}} + R_2 \hat{\Delta}. \tag{27}$$

R_2 as defined by Sternberg (1989), is the amount of CO_2 leaving the vegetation by photosynthesis relative to the total amount of CO_2 leaving the vegetation (equivalent to Eq. (20)), and R_1 is the amount of CO_2 given off by respiration relative to the amount of CO_2 entering the vegetation (Sternberg, 1989). Sternberg (1989) defined R_2 as recycling, but this definition is only true for a well-mixed one-compartment vegetation model. The above equation is reduced to the following equation by algebraic manipulations similar to that done in Sternberg (1989):

$$(1 - R_2)\delta_w + R_2 \hat{\delta} = \frac{C_A}{C_w}(\delta_{\mathrm{R}} - \delta_{\mathrm{A}})(1 - R_2) + \delta_{\mathrm{R}} + R_2 \hat{\Delta}. \tag{28}$$

Note that the right side of this equation is similar to the original recycling Eq. (4) in this paper (and equation 14 in Sternberg, 1989) describing recycling for a vegetation stand occupying only one compartment. R_2, as explained previously, for a multiple compartment heterogeneous vegetation stand is not truly recycling. Recycling, however, can be defined by the following equation:

$$\Phi_{\mathrm{S}} = \frac{1}{\left(\frac{1}{R_2} - 1\right)\frac{\alpha_w}{\hat{\alpha}} + 1}, \tag{29}$$

where α_w and $\hat{\alpha}$ are the proportion of respired CO_2 in the last compartment at the canopy of the vegetation and the photosynthesis weighted average proportion of respired CO_2 through out the canopy, respectively. Eq. (28) can therefore be expanded to a generalized recycling equation:

$$\left[1 - \frac{\Phi_{\mathrm{S}} \alpha_w}{\hat{\alpha} + \Phi_{\mathrm{S}}(\alpha_w - \hat{\alpha})}\right]\delta_w + \frac{\Phi_{\mathrm{S}} \alpha_w}{\hat{\alpha} + \Phi_{\mathrm{S}}(\alpha_w - \hat{\alpha})}\hat{\delta} = \frac{C_{\mathrm{A}}}{C_w}(\delta_{\mathrm{A}} - \delta_{\mathrm{R}})\left[1 - \frac{\Phi_{\mathrm{S}} \alpha_w}{\hat{\alpha} + \Phi_{\mathrm{S}}(\alpha_w - \hat{\alpha})}\right] + \delta_{\mathrm{R}} + \frac{\Phi_{\mathrm{S}} \alpha_w}{\hat{\alpha} + \Phi_{\mathrm{S}}(\alpha_w - \hat{\alpha})}\hat{\Delta}. \tag{30}$$

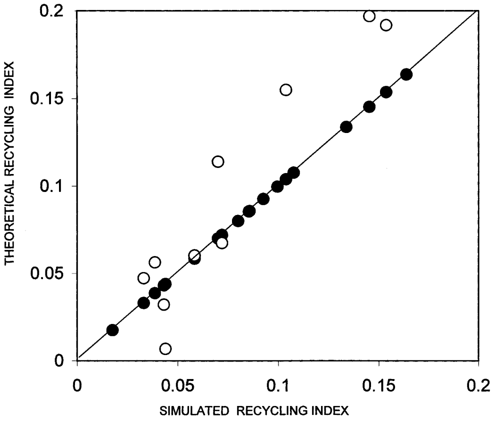


Fig. 5. The relationship between theoretical and simulated recycling indices in a vertically heterogeneous vegetation having the height of 2 m and modeled as occupying two compartments. Full circles represent theoretical recycling values using photosynthesis weighted isotope ratios and concentration of carbon dioxide, discrimination, and proportion of respired CO_2 on Eq. (30). Empty circles represent theoretical recycling indices using Eq. (4) with average $\delta^{13}C$ and concentration values of CO_2 from the two vegetation compartments. Many of the recycling values calculated using these averages were off scale and not shown here.

The above equation collapses to the original one compartment Eq. (4) when applied to a well-mixed one-compartment vegetation stand, because $\alpha_w = \hat{\alpha}$, $\delta_w = \hat{\delta}$, and $\Delta_w = \hat{\Delta}$. Eq. (30) will also collapse to the original Keeling Eq. (3) when there is no recycling, i.e. $\Phi_S = 0$.

7. Comparison between the simulated and theoretical recycling indices for multi-compartmental heterogeneous vegetation

Recycling is calculated by a program similar to that used for the single compartment simulation. Theoretical and simulated recycling values for two compartment heterogeneous vegetation show a perfect agreement (Fig. 5). Parameters for a specific example are shown on Table 2. Unlike the single compartment simulation, recycling here cannot simply be calculated on the basis of conductance to the troposphere with Eq. (20).

When the vegetation canopy is heterogeneous, it has been previously suggested to consider the vegetation as one compartment and to scale values of isotopic composition and concentration of CO_2 in the canopy, and total net ecosystem fractionation, by averaging these values over the height occupied by the canopy (Lloyd et al., 1996). A comparison between simulated and theoretical values using a one-compartment equation with averaged isotopic composition and concentration of canopy CO_2, and fractionation shows a poor relationship (Fig. 5). As demonstrated on Eq. (30), scaling of these parameters relative to the photosynthetic rate at each level of the vegetation canopy and consideration of the exchange between the canopy edge and the c.b.l. gives the correct recycling indices. In tropical forests photosynthetic rates in the understory, where ambient CO_2 has a higher concentration and ^{12}C abundance is much lower compared to canopy levels. Therefore, photosynthetic weighted parameters

Table 2
Calculations for a simulation where a vertically heterogeneous vegetation occupies the first two compartments and the c.b.l. occupies the next two compartments

Comp.	Given parameters				Calculated parameters at s.s.				
	G	P	R	Δ	C_i	$\delta^{13}C$	α	Φ^*	Φ_s
1	1	10	9.1	22	348.6	−6.6	0.053	0.105	0.105
2	2	19	1	19	349.5	−6.7	0.005		
3	3	0	0	0	359.0	−7.2	0.014		
4	4	0	0	0	365.3	−7.5	0.006		
Troposphere	–	–	–	–	370.0	−7.8	0		

Symbols for the parameters are given in Table 1.

$\hat{\delta}$, $\hat{\Delta}$, and $\hat{\alpha}$ would probably be well approximated by values observed in the canopy.

8. Conclusions

Computer simulations of CO_2 exchange between vegetation and the troposphere agree with a previously developed theoretical equation relating concentration and isotopic composition of ambient and tropospheric gases to recycling. A generalized recycling equation applicable to vertically heterogeneous vegetation stands with differences in parameters, such as photosynthesis, isotopic fractionation, and others was developed. This equation collapses to the previously developed single one-compartment model equation when no such differences in the above parameters are observed on the vegetation profile. This equation, as well as the single one-compartment model equation, will collapse to a Keeling type mixing model equation when there is no recycling. With a homogeneous one-compartment equation it is possible to calculate recycling at s.s. only with the knowledge of isotopic composition of tropospheric, respiratory and ambient CO_2, the concentration of tropospheric and ambient CO_2, and the isotopic discrimination by ecosystem assimilation. With a heterogeneous multi-compartment vegetation, it is necessary to know in addition to the above factors, the relative amount of photosynthesis in each compartment and the associated fractionation factor as well as non-biotic processes associated with CO_2 exchange between compartments. Therefore measuring recycling in this latter case may prove to be more challenging. Relative amounts of photosynthesis in each compartment, however, can be estimated based on leaf area indices as well as light intensity in each compartment. Conductance profiles in the canopy can be measured using natural available soil derived trace gases such as radon (Trumbore et al., 1990), methane (Leuning et al., 2000), or by fumigation experiments with nitrous oxides (Legg, 1975; Legg and Long, 1975).

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