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A MODEL TO ESTIMATE CARBON DIOXIDE RECYCLING IN FORESTS USING $^{13}C/^{12}C$ RATIOS AND CONCENTRATIONS OF AMBIENT CARBON DIOXIDE

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ABSTRACT

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Carbon dioxide from respiration of forest litter can be dissipated in two ways; photosynthesis and turbulent mixing with the atmosphere. Because there is a discrimination against $^{13}CO_2$ associated with photosynthesis and none for turbulent mixing, different relationships between carbon isotope ratios and concentrations of ambient forest carbon dioxide will occur, depending on which process is responsible for the dissipation of carbon dioxide. A steady-state model predicting the relationship between ambient forest CO_2 concentrations and $\delta^{13}C$ values as a function of the proportion of respired CO_2 reabsorbed by photosynthesis is presented here. Comparisons of the predictions of this model with data collected in a tropical moist forest in Barro Colorado Island (Republic of Panama) show that about 7-8% of the respired carbon dioxide is recycled via photosynthesis.

INTRODUCTION

Recent investigations indicate that deforestation of tropical regions can be an important component of the reported increase in atmospheric carbon dioxide concentration (Woodwell et al., 1983). A large part of the carbon in tropical forests is in structural materials. Burning and biologically degrading this structural material releases carbon dioxide back into the atmosphere. Recently much has been learned about the dynamic interaction between tropical forests and the global atmospheric CO_2 pool (Wofsy et al., 1988). It is now well documented that ground respiration in tropical forests can be quite variable but often quite high (see compilation of Goreau and de Mello, 1985). One question that immediately comes to mind is whether respired carbon dioxide is largely refixed by photosynthesis of forest vegetation, or released to the global atmospheric system. Papers concerning the carbon budget of tropical forests have

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been in relation to temporal and altitudinal variations of carbon dioxide concentration (Lemon et al., 1970; Allen et al., 1972; Aoki et al., 1975; Wofsy et al., 1988). Extensive measurements have been made on the carbon dioxide concentration gradient across the canopy of agricultural crops as well as across canopy levels in temperate and tropical forests (see Baumgartner, 1969, for a review). These measurements do not indicate the amount of respired carbon dioxide refixed by photosynthesis. Schleser and Jayasekera (1985) determined that about 5% of respired carbon dioxide contributed to the total photosynthetic carbon dioxide uptake in a temperate beech forest, by analyzing carbon isotope ratios of leaf tissues. Implicit in their methods, however, are certain assumptions about the physiological state of leaves and assimilatory performance of trees. A previous publication demonstrated that plants in a tropical moist forest are capable of fixing respired carbon dioxide (Sternberg et al., 1989), but did not quantify the extent of respired carbon dioxide fixation. In this paper a steady-state model is developed which quantifies the proportion of respired carbon dioxide fixed by photosynthesis and the proportion lost to the atmosphere by turbulent mixing using previously reported direct measurements of ambient carbon dioxide concentration and carbon isotope ratios. This model is based on the fact that photosynthesis results in a preferential uptake of $^{12}CO_2$ and turbulent mixing does not. Therefore different relationships between carbon dioxide concentration and carbon isotope ratios for these two different dissipation processes will occur.

BACKGROUND ON STABLE ISOTOPES

Carbon, one of the major components incorporated into plant biomass, is present in the biosphere in two stable forms: carbon-12 (about 98.89%) and carbon-13 (about 1.11%) (Hoefs, 1973). The isotope with the greater amount of neutrons (carbon-13) is the heavier of the two. Atmospheric carbon dioxide can be found either as a molecule containing the carbon-13 atom or the carbon-12 atom. Because it is extremely hard to measure absolute abundances of stable isotopes, they are usually measured relative to a standard. The usual standard for the expression of carbon isotope ratios is the carbonate from the Pedee Belemnite formation in South Carolina. Carbon isotope ratios are expressed in δ units according to the formula

$$\delta^{13}C‰ = \left[\frac{R_{\mathrm{sample}}}{R_{\mathrm{standard}}} - 1\right]1000 \tag{1}$$

where R is the $^{13}C/^{12}C$ ratio of the sample and standard, respectively. When $\delta^{13}C$ values are less than 0, the sample has less ^{13}C than the standard, while $\delta^{13}C$ values greater than 0 indicate a greater amount of ^{13}C than the standard. The precision with which $\delta^{13}C$ values can be measured is ±0.2‰.

$\delta^{13}C$ values of atmospheric carbon dioxide are on the average about −8.00 (Gleason and Kyser, 1984). This indicates that the carbon dioxide in the atmosphere is to a large part in equilibrium with the carbonate pool of ocean water. Plants during the process of photosynthesis absorb carbon dioxide from the atmosphere and incorporate carbon into photosynthates. Plants however incorporate carbon-12 at a faster rate than carbon-13 (O'Leary, 1981). The process of unequal incorporation of two isotopes into a final product is called isotopic fractionation. There are several steps during photosynthesis where isotopic fractionation can occur during conversion of one metabolite to another. As a result of these fractionations, $\delta^{13}C$ values of plant materials, with the exception of C_4 and CAM plants, are considerably more negative than values of atmospheric carbon dioxide ranging from −20 to −36‰ (O'Leary, 1981).

Several investigators have now observed that the $\delta^{13}C$ values of plants in the lower levels of temperate and tropical forests are lower relative to those of plants in the upper canopy. One environmental factor responsible for this phenomenon is the effect of respired carbon dioxide input at the lower levels of the forest (Vogel, 1978; Medina and Minchin, 1980; Schleser and Jayasekera, 1985; Medina et al., 1986; Sternberg et al., 1989). Plant litter with isotope ratios ranging from −23 to −36‰ is undergoing decomposition. Another component of respired carbon dioxide is plant respiration with $\delta^{13}C$ values in the same range as that of plant litter. Because the carbon isotope ratio of respired carbon dioxide closely matches the isotope ratio of its substrate there should be a significant amount of carbon dioxide input with $\delta^{13}C$ values ranging from −23 to −36‰ into the forest air. This respired carbon dioxide will mix with the atmospheric carbon dioxide having a $\delta^{13}C$ value of about −8‰. Thus isotope ratios of carbon dioxide available for plant photosynthesis are actually proportional to the amount of mixing between respired and atmospheric carbon dioxide, and most likely less than −8‰.

Another factor influencing the decrease in $\delta^{13}C$ values of understory plants in the lower levels of light in the understory. This is explained by the principle that photosynthetic isotopic discrimination against $^{13}CO_2$ increases when there is ample carbon dioxide available relative to the photosynthetic flux. This relationship is expressed by the equation developed by Farquhar et al. (1982). Several instances where discrimination against carbon-13 is diminished or increased with changing environmental effects have been demonstrated. Most relevant is the demonstration that low light levels can increase the discrimination against carbon-13 by photosynthesis (Mulkey, 1986). The crucial test to quantify how each of these factors is important in determining $\delta^{13}C$ values of understory plants has been actual measurements of $\delta^{13}C$ values of ambient CO_2 throughout the day at different levels in a forest. Measurements at Barro Colorado Island (Panama) indicate that respired carbon dioxide can contribute up to 70% of the lower carbon isotope ratios of forest understory plants

(Sternberg et al., 1989). Measurements of $\delta^{13}C$ values and concentrations of ambient carbon dioxide in Barro Colorado Island can also be used to investigate the carbon budget of this forest.

Only three publications report on the carbon isotope ratios of ambient carbon dioxide in forests and only two of these report $\delta^{13}C$ values in conjunction with concentrations of ambient forest carbon dioxide. The first study involved placing barrels over forest soil and sampling carbon dioxide accumulated after a period of time (Vogel, 1978). Results of this research indicate that there is a significant input of isotopically light respired carbon dioxide into the forest. The experimental procedure adopted by Vogel (1978), however, does not indicate whether there is a rapid mixing of respired and atmospheric carbon dioxide. The second publication reports on the abundance and isotopic composition of carbon dioxide at lower levels of a Lagostrobus forest in Tasmania (Francey et al., 1985). These results indicate that although at a lower level of the forest there is a greater amount of isotopically light carbon dioxide, the difference is rather small and would be of little consequence to the carbon isotope ratios of understory plants. The third publication, and the one to be closely examined here, reports on the concentrations and $\delta^{13}C$ values of ambient CO_2 from a tropical moist forest at Barro Colorado Island, Panama (Sternberg et al., 1989). In this study, ampules of air about 150 ml in volume were sampled at three heights (0.5, 1.0 and 25.0 m above the forest floor) during the dry season and wet season over a period of several days (Sternberg et al., 1989). Samples were collected from 0800 to 1300 h (Sternberg et al., 1989). This particular time period was chosen because it is the period of greatest change in photosynthetic rates as well as the period of greatest photosynthetic activity (Sternberg et al., 1989). Both CO_2 concentration and $\delta^{13}C$ values were determined as described in Sternberg et al. (1989). Significant differences were observed in the carbon isotope ratios of carbon dioxide at lower levels in the forest relative to the canopy. $\delta^{13}C$ values were on the average -8.9 ± 0.3 (SEM), -10.6 ± 0.3 and -11.4 ± 0.4‰ with a concentration of 348.7 ± 3.5, 374.6 ± 6.3 and 388.9 ± 9.4 ppm at 25, 1, and 0.5 m above the soil, respectively, showing that respired carbon dioxide can comprise up to 18% of the carbon dioxide at lower levels of the forest (Sternberg et al., 1989). Surprisingly, no trends in $\delta^{13}C$ values and concentrations were observed between wet and dry season, nor between different times of the day when photosynthetic shifts are the greatest (Sternberg et al., 1989). The differences in observation between measurements of Francey et al. (1985) and of Sternberg et al. (1989) is not surprising since forests differ greatly in their soil respiratory flux (Goreau and de Mello, 1985).

GAS MIXING MODELS

Two models predicting the relationship between $\delta^{13}C$ values and concentrations of ambient forest carbon dioxide will be presented. The simplest model explaining the mixing of two isotopically distinct gases is expressed by the following equation

$$[\delta^{13}C_F - \delta^{13}C_R]\,[CO_2]_F = [\delta^{13}C_A - \delta^{13}C_R]\,[CO_2]_A \tag{2}$$

where $[CO_2]_F$, $[CO_2]_A$ represent the CO_2 concentrations in forest air and the atmosphere, respectively; $\delta^{13}C_F$, $\delta^{13}C_R$, and $\delta^{13}C_A$ represent the $\delta^{13}C$ values of forest, respired and atmospheric carbon dioxide, respectively. This equation can be simplified to the following

$$\delta^{13}C_F = \frac{[CO_2]_A}{[CO_2]_F}\,(\delta^{13}C_A - \delta^{13}C_R) + \delta^{13}C_R \tag{3}$$

as reported by Keeling, (1961). Thus the relationship between carbon isotope ratios and the inverse of the carbon dioxide concentration is linear, having an intercept at the $\delta^{13}C$ value of respiratory carbon dioxide, and predicts a $\delta^{13}C$ value equal to atmospheric carbon dioxide at the carbon dioxide concentration of forest air equal to atmospheric concentration. Measurements of $\delta^{13}C$ values and concentration of forest air (Francey et al., 1985; Sternberg et al., 1989) and air from well-ventilated and open areas (Keeling, 1961) fit quite well with this simplistic model. This model, however, does not consider all carbon dioxide fluxes present in the forest environment and assumes a closed system; an unrealistic assumption. According to this model, the carbon dioxide concentration in the forest air will be ever increasing with time and a constant input of respired carbon dioxide. However, as previously mentioned, concentration and carbon isotope ratios of ambient forest carbon dioxide at Barro Colorado Island stayed constant throughout the sampling period, roughly from about 0800 to 1300 h, the period of time where there is the greatest shift in photosynthetic rates and the greatest photosynthetic rates (Sternberg et al., 1989).

Since both the carbon dioxide concentration and isotope ratio of forest air did not change significantly throughout the day, carbon dioxide fluxes are causing a steady state in both concentrations and isotope ratios. Here I develop a steady-state model to explain the relationship between CO_2 concentrations and isotope ratios in ambient forest air. The steady-state equation expressing the change in carbon dioxide concentration with regard to different carbon dioxide fluxes is as follows

$$0 = V\frac{d[CO_2]_F}{dT} = J_R + J_A - J_D - J_P \tag{4}$$

where $d[CO_2]_F/dT$ is the change in carbon dioxide concentration of forest air through time; J_R, J_A, J_D and J_P are the respiratory, atmospheric fluxes of carbon dioxide into and out of the forest, and the flux of carbon dioxide out of ambient forest air via photosynthesis, respectively; V is the unit volume considered.

Since the concentration of ^{13}C in ambient CO_2 is small, the steady-state equation relating the change in $\delta^{13}C$ values of ambient CO_2 relative to different CO_2 fluxes can be approximated by

$$0 = V\frac{d\delta^{13}C_F}{dT} = J_R\delta^{13}C_R + J_A\delta^{13}C_A - J_D\delta^{13}C_F - J_P(\delta^{13}C_F - E) \tag{5}$$

where $\delta^{13}C/dT$ is the change in $\delta^{13}C$ values of ambient CO_2 in the forest through time, E is the photosynthetic discrimination factor, and the other terms are as previously defined. These equations can be merged and the following equation expressing the steady-state relationship between carbon isotope ratios of forest air and different carbon dioxide fluxes is derived

$$\delta^{13}C_F = \frac{J_R}{J_P + J_D}(\delta^{13}C_R - \delta^{13}C_A) + \delta^{13}C_A + \frac{J_P}{J_P + J_D}E \tag{6}$$

Since $J_P + J_D = J_R + J_A$ (see eq. 4), this equation can be simplified to

$$\delta^{13}C_F = R_1(\delta^{13}C_R - \delta^{13}C_A) + \delta^{13}C_A + R_2E \tag{7}$$

where R_1 is the respiratory flux of carbon dioxide relative to the total flux of carbon dioxide into the forest and R_2 is the uptake of carbon dioxide via photosynthesis relative to the total loss of carbon dioxide from the forest. According to this equation, the carbon isotope ratios of forest air will be entirely determined by the relative fluxes of respiration and photosynthesis. If the relative flux via photosynthesis is the same as the relative respiratory flux, then the steady-state $\delta^{13}C$ values of forest air will approach $\delta^{13}C$ values of atmospheric carbon dioxide depending on the difference between $\delta^{13}C_R$ and E, and on R_1. If, however, the relative photosynthetic flux is less than the relative respiratory flux, the $\delta^{13}C$ values of forest air would decrease and approach $\delta^{13}C$ values of respiratory carbon dioxide.

We can further develop this steady-state model and incorporate carbon dioxide concentrations into eq. 7 after one assumption and a definition. The assumption is that carbon dioxide flux from the forest to the atmosphere and from the atmosphere to the forest occurs not by diffusion, but by turbulent mixing. Thus there is a certain amount of bulk air exchange between forest air and atmosphere. This bulk exchange parameter is defined here as J_E (for example: liters of air exchanged between the forest air and atmosphere). Further it is assumed that the bulk volume of air leaving the forest and the volume of air entering the forest from the atmosphere are the same and equal to J_E. Thus, the carbon dioxide flux entering the forest from the atmosphere (J_A) and leaving the forest to the atmosphere (J_D) can be expressed by the following terms, $J_E\,[CO_2]_A$ and $J_E[CO_2]_F$, respectively. Inserting these terms into the R_1 value of eq. 7, the following is derived

$$R_1=\frac{J_R}{J_R+J_A}=\frac{J_R}{J_R+J_E[CO_2]_A} \tag{8}$$

The photosynthetic flux can be defined relative to the respiratory flux by a factor k such that $J_P=kJ_R$. For example, when $k=1$, the photosynthetic flux is equal to the respiratory flux. Since the carbon dioxide concentration is not changing, eq. 4 can be solved for J_E which is equal to $(J_R-kJ_R)/([CO_2]_F-[CO_2]_A)$ and this expression is substituted in eq. 8, and simplified to

$$R_1=\frac{1}{1+\frac{(1-k)}{\Delta CO_2}[CO_2]_A} \tag{9}$$

where ΔCO_2 is the carbon dioxide gradient $([CO_2]_F-[CO_2]_A)$. Since $J_P=kJ_R$ then $R_2=kR_1$, and eq. 9 becomes

$$R_2=\frac{k}{1+\frac{(1-k)}{\Delta CO_2}[CO_2]_A} \tag{10}$$

This equation can be solved for k

$$k=\frac{R_2[CO_2]_F}{R_2[CO_2]_A+\Delta CO_2} \tag{11}$$

For the same reason that $R_2=kR_1$, eq. 7 can also be solved for k giving the following expression

$$k=\frac{R_2(\delta^{13}C_R-\delta^{13}C_A)}{\delta^{13}C_F-\delta^{13}C_A-R_2E} \tag{12}$$

Thus, two expressions for k are given, one based on CO_2 concentration and one based on $\delta^{13}C$ value. Merging eqs. 11 and 12, the following equation is derived

$$\frac{R_2[CO_2]_F}{R_2[CO_2]_A+\Delta CO_2}=\frac{R_2(\delta^{13}C_R-\delta^{13}C_A)}{\delta^{13}C_F-\delta^{13}C_A-R_2E} \tag{13}$$

which is simplified to

$$\delta^{13}C_F=\frac{[CO_2]_A}{[CO_2]_F}(\delta^{13}C_A-\delta^{13}C_R)(1-R_2)+\delta^{13}C_R+R_2E \tag{14}$$

It is easily recognized that this equation has similar characteristics to eq. 3, relating the $\delta^{13}C$ values of CO_2 from forest air to the inverse of CO_2 concentrations of ambient forest air. In fact, when the photosynthetic uptake of respired carbon dioxide is small relative to the loss of CO_2 via turbulent mixing (when R_2 approaches 0), eq. 14 is reduced to eq. 3.

How do the average concentrations and isotope ratio measurements in Barro Colorado Island fit the proposed model, and what can it indicate about the proportion of respiratory carbon dioxide consumed by photosynthesis in the forest? In order to test these data with the steady-state model developed here, one must choose several parameters related to the steady-state equation, namely E the photosynthetic fractionation factor, $\delta^{13}C_R$ and $\delta^{13}C_A$, the $\delta^{13}C$ values of respiratory and atmospheric carbon dioxide, respectively and atmospheric CO_2 concentration $[CO_2]_A$. For E, the value of 22.8‰ is chosen, a high discrimination factor, but not unexpected for the high relative humidity and low light intensities encountered in tropical moist forests. The estimation of this fractionation factor is based on measurements of carbon isotope ratios of three species of plants (*Hirtella triandra, Trichilia cipo, Tetragastris panamensis*) grown in the forest understory (1 m above the soil level) with the average $\delta^{13}C$ value of −33.4‰ having ambient CO_2 with the average $\delta^{13}C$ value of −10.6‰ (−10.6‰ + 33.4‰ = 22.8‰; Sternberg et al., 1989). For $\delta^{13}C$ values and concentrations of atmospheric carbon dioxide, the values of −8‰ (Gleason and Kyser, 1984) and 330 ppm (a commonly observed CO_2 concentration) are chosen. In a previous publication the $\delta^{13}C$ value of respired carbon dioxide was extrapolated to −28.3‰ (Sternberg et al., 1989). For this extrapolation, however, we had to make the assumption that photosynthesis was not influencing the concentration and $\delta^{13}C$ values of ambient forest carbon dioxide, which is exactly what I wish to test here. Thus the estimation of $\delta^{13}C_R$ must be independent of this assumption. There are two sources of respired CO_2 during the day, the major one being leaf litter decomposition and the minor component being respiration by the non-photosynthetic plant parts (Baumgartner, 1969; Allen et al., 1972). Measurements of leaf material for three species of plants growing throughout different heights in the forest ranged from the average of −30.0‰ for plant material collected 10 m or more above the forest soil to −33.4‰ for heights of 1 m (Sternberg et al., 1989). Under the assumption that the major input of litter in this forest is coming from the upper levels of the forest (Medina et al., 1986), it is estimated that litter decomposing in the forest floor has a $\delta^{13}C$ value of −30‰. Since carbon dioxide from respiration has $\delta^{13}C$ values similar to its substrate (Jacobson et al., 1970), the respired carbon dioxide will have a $\delta^{13}C$ value of −30‰. The $\delta^{13}C$ value of CO_2 from respiration of non-photosynthetic plant parts should be similar to that of leaf litter and have little effect on the $\delta^{13}C$ values of total respired carbon dioxide. Further evaluation of this model with experimental data, however, will require accurate measurement of the carbon isotope ratio of respired carbon dioxide.

The best fit for the relationship between $\delta^{13}C$ values and the inverse concentration of ambient CO_2 from three different heights in the Barro Colorado Island forest is presented in Fig. 1 ($\delta^{13}C_F = 6703\ (1/[CO_2]_F - 28.3‰, r^2 = 0.69, P < 0.01$; Sternberg et al., 1989). In addition the loci of points for different values of R_2 and the chosen values of E, $\delta^{13}C_A$ and $\delta^{13}C_R$ are presented in the

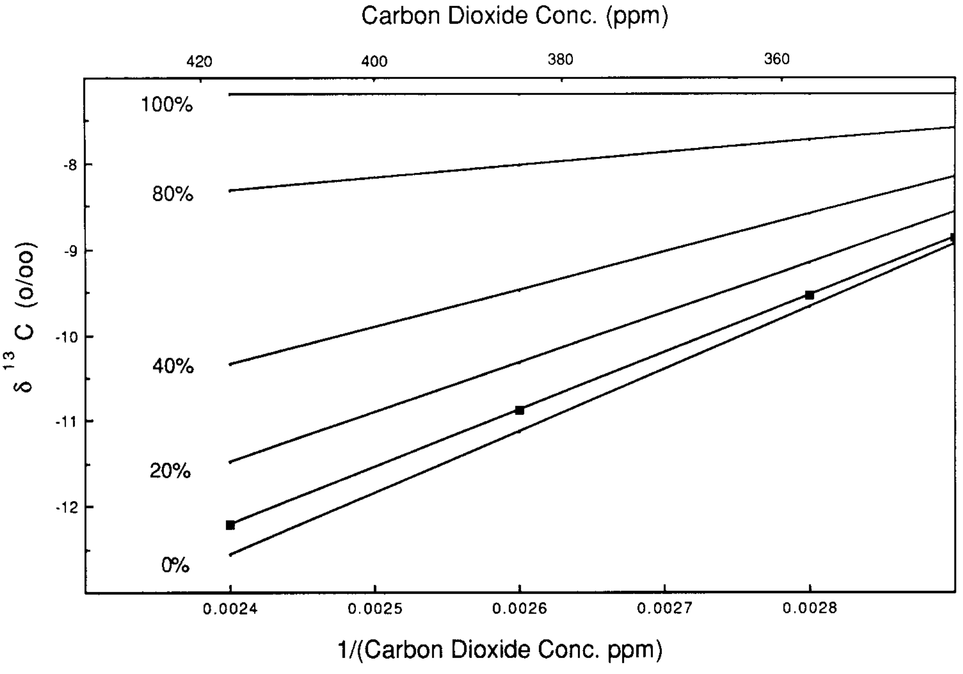

Fig. 1. Relationship between $\delta^{13}C$ values and inverse concentration of ambient carbon dioxide of forest air for different degrees of carbon dioxide recycling. The photosynthetic discrimination factor and $\delta^{13}C$ values of respired carbon dioxide were chosen as described in the text. Also shown in the best fit linear regression (line intersecting square symbols) to $\delta^{13}C$ values and inverse CO_2 concentration measurements from ambient forest CO_2 at Barro Colorado Island (Republic of Panama; Sternberg et al., 1989).

same figure. The predictions of the model as shown on this figure and eq. 14 are that at steady state, the relationship between $\delta^{13}C$ values and the inverse of CO_2 concentration will be linear for any particular photosynthetic flux. However a higher photosynthetic flux will cause the 0 intercept of this linear regression to be higher, and the slope to be lower. It has been generally assumed that the 0 intercept of the line described by plotting $\delta^{13}C$ values versus inverse CO_2 concentrations of ambient CO_2 reflects the $\delta^{13}C$ values of respired CO_2. As is shown here, this is not the case. The intercept of the above relationship is a function of the $\delta^{13}C$ values of respired CO_2, the extent of CO_2 recycling, and the fractionation factor E. The average values for measurements taken at Barro Colorado Island lie on a line described where there is only a small percentage of photosynthetic uptake of respired CO_2 (between 0 and 10%). Using the best fit equation for the Barro Colorado Island data and eq. 14, it is possible to calculate the percentage of respired carbon dioxide refixed by photosynthesis based on both the slope and intercept of this equation. For the slope

$$6703 = 7260(1 - R_2) \qquad (15)$$

and solved for R_2 which gives a value of 7.7%. For the intercept the following equation is developed

$$-28.3‰ = -30‰ + R_2(-22.8‰) \tag{16}$$

which gives a value of 7.4% for R_2. These results are very similar to the 5% recycling observed for a temperate forest by Schleser and Jayasekera (1985).

CONCLUSIONS

Two models predicting the relationship between $\delta^{13}C$ values and concentration of ambient carbon dioxide were presented – a simple closed system model and a more complex steady-state model assuming four different fluxes of carbon dioxide into and out of the forest ambient. Predictions of the latter model are that when turbulent air mixing is the only dissipator of carbon dioxide from the forest, the relationship between carbon isotope ratios and the inverse of its concentration is identical to the simple closed system model. On the other hand, a higher photosynthetic flux will cause a higher 0 intercept and a lower slope for this relationship. Plotting $\delta^{13}C$ values and concentration of ambient carbon dioxide from a tropical moist forest at Barro Colorado Island along with the predictions of this model indicates only 7–8% photosynthetic uptake of respired carbon dioxide.

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