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Linking ^{13}C-based estimates of land and ocean sinks with predictions of carbon storage from CO_2 fertilization of plant growth

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ABSTRACT

The residence times of carbon in plants, litter, and soils are required for partitioning land and ocean sinks using measurements of atmospheric $\delta^{13}CO_2$ and also for estimating terrestrial carbon storage in response to net primary production (NPP) stimulation by elevated levels of atmospheric CO_2. While ^{13}C-based calculations of the land sink decline with increasing estimates of terrestrial carbon residence times (through the fossil fuel-induced isotopic disequilibrium term in equations describing the global atmospheric budgets of $^{13}CO_2$ and CO_2), estimates of land sinks based on CO_2 fertilization of plant growth are directly proportional to carbon residence times. Here we used a single model of terrestrial carbon turnover, the Carnegie–Ames–Stanford Approach (CASA) biogeochemical model, to simultaneously estimate 1984–1990 terrestrial carbon storage using both approaches. Our goal was to identify the fraction of the $^{13}CO_2$-based land sink attributable to CO_2 fertilization. Uptake from CO_2 fertilization was calculated using a β factor of 0.46 to describe the response of NPP to increasing concentrations of atmospheric CO_2 from 1765 to 1990. Given commonly used parameters in the ^{13}C-based sink calculation and assuming a deforestation flux of 0.8 Pg C/yr, CO_2 fertilization accounts for 54% of the missing terrestrial carbon sink from 1984 to 1990. CO_2 fertilization can account for all of the missing terrestrial sink only when the terrestrial mean residence time (MRT) and the land isodisequilibrium forcing are greater than many recent estimates.

1. Introduction

Changes in atmospheric $^{13}CO_2$ provide a powerful constraint on land and ocean partitions of atmospheric sinks of CO_2. The constraint is based upon the relatively large difference in isotopic discrimination in atmospheric exchange of CO_2 by the terrestrial biosphere and oceans. In regions where C3 photosynthesis is dominant, strong discrimination against $^{13}CO_2$ during plant uptake leads to atmospheric enrichment (Lloyd and Farquhar, 1994). In contrast, the physical-chemical processes that regulate ocean exchange discriminate against $^{13}CO_2$ to a much lesser degree; thus, ocean sinks only minimally change the atmospheric ratio of $^{13}CO_2/^{12}CO_2$ (Tans et al., 1993; Inoue and Sugimura, 1985).

1.1. Calculating the terrestrial carbon sink

During the 1980s and early 1990s, the atmospheric ratio of $^{13}CO_2/^{12}CO_2$ (defined with respect

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to the Pee Dee Belemnite standard as $\delta^{13}CO_2$) decreased more slowly than could be explained by fossil fuel emissions, deforestation, and oceanic exchange alone (Francey et al., 1995; Ciais et al., 1995a; Ciais et al., 1995b). To explain this smaller than expected rate of decline in $\delta^{13}CO_2$, two classes of mechanisms were proposed: a terrestrial sink, which acts to increase atmospheric $\delta^{13}CO_2$; and terrestrial or oceanic isotopic disequilibria, which act to buffer change in atmospheric $\delta^{13}CO_2$ by re-introducing older carbon back into the atmosphere. Net uptake of carbon by the terrestrial biosphere acts to increase $\delta^{13}CO_2$ largely because of discrimination against $^{13}CO_2$ by the carbon assimilation enzyme, Rubisco (Farquhar et al., 1989). Thus, if net terrestrial uptake were to increase, the terrestrial biosphere would have a greater effect on slowing the rate of decline of atmospheric $\delta^{13}CO_2$.

Isotopic disequilibria arise from the finite period of time carbon spends on average in land and ocean reservoirs before returning to the atmosphere (Tans et al., 1993; Enting et al., 1995; Heimann and Maier-Reimer, 1996; Fung et al., 1997; Wittenberg and Esser, 1997). Because atmospheric $\delta^{13}CO_2$ has steadily decreased through time from fossil fuel emissions (the $^{13}CO_2$ Suess effect; Keeling et al., 1979), today's gross fluxes of carbon from land and ocean reservoirs to the atmosphere are comprised of carbon from the atmosphere of the past, and are thus enriched in $^{13}CO_2$ with respect to what gross fluxes would be were they allowed to reach steady state with the current atmosphere. The importance of this effect increases the longer carbon spends in either reservoir; thus, isotopic disequilibria (isodisequilibria) monotonically increase with the mean residence time (MRT) of carbon.

Since isodisequilibria and terrestrial sinks have the same effect on atmosphere $\delta^{13}CO_2$, they compete with each other with respect to explaining the atmospheric $\delta^{13}CO_2$ trend. If isodisequilibria are large, a terrestrial sink is not necessary to explain the $\delta^{13}CO_2$ observations; thus, the oceans must be invoked to account for the current rate of increase in atmospheric CO_2. If isodisequilibria are small, however, the situation is reversed. The practical implications of this are that with increasing estimates of the magnitude of the isodisequilibria forcing, the terrestrial sink (as calculated using ^{13}C) will decrease.

Because our estimates of the partition between the land and ocean sinks are so sensitive to the magnitude of either the land or ocean isodisequilibria, it is critical we get them right (Fung et al., 1997). However, by selecting a value for the terrestrial isodisequilibrium, we are in point of fact making an a priori estimate of residence times of terrestrial carbon. In modeling studies of the terrestrial carbon cycle that have looked at responses of the sink to increases in net primary production (NPP), the MRT is of central importance (Taylor and Lloyd, 1992; Friedlingstein et al., 1995; Thompson et al., 1996; Townsend et al., 1996). The longer the delay between the sequestration and release of carbon, the more carbon can be stored for a given increase in NPP. This means that the terrestrial carbon sink calculated by the NPP-sink relationship method is directly proportional to the MRT (Taylor and Lloyd, 1992).

The ^{13}C methodology, which uses the turnover time to calculate an isodisequilibrium, and the NPP-sink methodology, which used the turnover time to calculate the sensitivity of the sink to a given increase in NPP, are complementary. With a reasonable understanding of terrestrial carbon residence times, the magnitude of other components of the ^{13}C atmospheric budget, and the rate of change of NPP under elevated levels of atmospheric CO_2, it is possible to calculate the net land sink using the ^{13}C method and the component of this sink that is driven by CO_2 fertilization.

1.2. *The importance of CO_2 fertilization*

Identifying the contribution of CO_2 fertilization, nitrogen deposition, and climate variability to the land sink is a critical prerequisite for assessing the sustainability of this sink over the next century. We focus on the contribution of CO_2 fertilization of plant growth to ^{13}C-based estimates of the land sink because of the relatively well-characterized response of NPP to elevated levels of atmospheric CO_2. A standard means of describing the sensitivity of NPP to elevated CO_2 is given by the logarithmic β relation:

$$P_1 = P_0\left[1 + \beta \ln\left(\frac{C_1}{C_0}\right)\right], \quad (1)$$

where C_0 is the initial CO_2 concentration, C_1 is the enhanced CO_2 concentration, P_0 is the initial

NPP of the plant under C_0, and P_1 is the enhanced NPP under C_1. In a review of 58 studies on the effects of elevated CO_2 on trees, Wullschleger et al. (1995) found on average a 32% increase in NPP in response to a doubling of atmospheric CO_2. In eq. (1) this response corresponds to a β of 0.46. Many of the trees considered in this analysis, however, were relatively young and were grown at temperatures that exceeded those in their natural habitat (Wullschleger et al., 1995). Few long-term data exist for the response of natural ecosystems to elevated CO_2; this is especially the case for forest ecosystems (Amthor and Koch, 1996).

Studies investigating carbon sequestration from CO_2 fertilization have typically examined cumulative C storage over the last two centuries (Goudriaan and Ketner, 1984; Polgase and Wang, 1992; Kirschbaum, 1993; Gifford, 1995; Post et al., 1997; Bruno and Joos, 1997) or even steady state responses of the terrestrial carbon storage to a doubling of atmospheric CO_2 (Melillo et al., 1993; VEMAP members, 1995). In contrast, many studies of land and ocean sinks using the ^{13}C method have focused on changes during the last two decades when accurate measurements of atmospheric and oceanic $\delta^{13}C$ are available (Quay et al., 1992; Francey et al., 1985; Keeling et al., 1995; Trolier et al., 1996).

1.3. Our approach

In this paper, we will use a single model of terrestrial carbon turnover to simultaneously estimate terrestrial carbon uptake using both atmospheric $\delta^{13}CO_2$ measurements and estimated increases in NPP driven by increasing atmospheric CO_2. For the CO_2 fertilization calculation we apply a globally uniform β of 0.46 that we assume is a reasonable upper bound for the stimulation of NPP by elevated levels of atmospheric CO_2. We use impulse response functions from the CASA (Carnegie–Ames–Stanford Approach) biogeochemical model (Thompson and Randerson, 1998) to calculate, from 1984 to 1990, the MRT of carbon, the terrestrial $\delta^{13}C$ isodisequilibrium forcing, and increased plant growth from CO_2 fertilization. In a series of additional simulations we adjust the rate constants for carbon decay in the terrestrial biosphere to examine the sensitivity of these two approaches to a range of terrestrial carbon residence times. We will show that commonly used values for the fossil fuel-induced terrestrial isodisequilibrium forcing in the ^{13}C-based sink calculation limit the fraction of total land uptake attributable to elevated levels of atmospheric CO_2.

2. Methods

2.1. The global carbon budget

The ^{13}C constraint is described by the following two equations which can be solved to obtain the ocean and land sinks (Tans et al., 1993; Francey et al., 1995). The equation for the atmospheric CO_2 budget is:

$$\frac{d(C_t^a)}{dt} = F_t^f + F_t^{def} + N_t^b + N_t^o \quad (2)$$

where $d(C_t^a)/dt$ is the rate of change of atmospheric CO_2, F_t^f is the fossil fuel release, F_t^{def} is the balance between deforestation and forest regrowth, N_t^b is the net land sink (apart from deforestation and regrowth), and N_t^o is the net ocean sink. The equation for the atmospheric $^{13}CO_2$ budget expressed in δ notation is given by:

$$\begin{aligned}\frac{d(C_t^a\delta_t^a)}{dt} &= \delta_t^a \frac{d(C_t^a)}{dt} + C_t^a \frac{d(\delta_t^a)}{dt} \\ &\approx F_t^f\delta_t^f + F_t^{def}\delta_t^{def} + N_t^b(\delta_t^a + \varepsilon_t^{ab}) \\ &\quad + N_t^o(\delta_t^a + \varepsilon_t^{ao}) + G_t^b D_t^b + G_t^o D_t^o, \quad (3)\end{aligned}$$

where the rate of change of the atmosphere's isotopic composition through time is given by fossil fuel and deforestation releases, isotopic exchange associated with net land and ocean uptake, and two terms that describe forcing from land ($G_t^b D_t^b$) and ocean ($G_t^a D_t^o$) isodisequilibria. δ_t^a, δ_t^f, and δ_t^{def} are the isotopic composition of CO_2 in the atmosphere, and CO_2 fluxes from fossil fuels and deforestation. ε_t^{ab} and ε_t^{ao} are the discrimination effects associated with CO_2 exchange between the atmosphere and land and between the atmosphere and oceans. The isotopic disequilibria terms are the product of the gross (one way) land-atmosphere and ocean-atmosphere fluxes (G_t^b and G_t^o) and the difference between the isotopic value of this flux and the value that would be expected if the gross fluxes were in steady state with the current atmospheric isotopic composition (D_t^b and D_t^o). Mean values for the parameters in eqs. (2) and (3) for the period of 1984 to 1990

are given in Table 1. While G_t^b formally represents total ecosystem respiration, we assume (for purposes of simplicity) that all carbon used for plant respiration was fixed within the previous year. With this assumption, we can allow G_t^b to be approximated by heterotrophic respiration (equal to NPP in steady state) because plant respiration will have a negligible impact on the disequilibrium forcing. The extent to which plants store and reuse starches and other compounds in maintenance and growth respiration over periods longer than one year is not well characterized for many species, and is likely to significantly impact the isodisequilibrium forcing discussed here.

2.2. *Impulse–response functions*

Impulse–response (or Green's) functions allow efficient description of the movement of carbon in complex, multiple-pool models (Joos et al., 1996). These functions characterize the turnover of carbon in a model, and can be used to predict the sequestration rate of a given model under a given rate of increase in NPP. They can also be used to calculate the fossil fuel-induced isodisequilibrium. The impulse–response function of a terrestrial biogeochemical model is the probability density function of carbon release as a function of residence time. It is denoted as ϕ_τ^b

$$\phi_\tau^b = \frac{\Phi_\tau^b}{\sum_{\tau=0}^{\infty} \Phi_\tau^b}, \tag{4}$$

where τ is the time since the carbon was sequestered and Φ_τ^b is the amount of carbon in the initial impulse that is respired at time τ. The usage of ϕ_τ^b and the details of its derivation with respect to terrestrial carbon models is described by Thompson and Randerson (1998), but note that the integral of ϕ_τ^b over τ from 0 to ∞, by definition, always equals 1. The MRT of the model can be calculated as the first moment of ϕ_τ^b with τ:

$$\bar{\tau} = \sum_{\tau=0}^{\infty} \phi_\tau^b \tau \tag{5}$$

where $\bar{\tau}$ is the MRT of the model, i.e., the time

Table 1. *Global carbon budget parameters: 1984–1990 average values*

Parameter	Description	Mean value: 1984–1990	Refs.
C_t^a	carbon mass of atmosphere	740 Pg C	Francey et al. (1995)
$\frac{d(C_t^a)}{dt}$	atmospheric growth rate	3.5 Pg C yr^{-1}	Conway et al. (1994)
$\frac{d(\delta_t^a)}{dt}$	atmospheric $^{13}C/^{12}C$ rate of change	-0.025‰ yr^{-1}	Francey et al. (1995)
F_t^f	rate of fossil fuel emissions	5.7 Pg C yr^{-1}	Boden et al. (1995)
F_t^{def}	rate of deforestation	0.8 Pg C yr^{-1}	Houghton (1996)
δ_t^a	atmosphere $^{13}C/^{12}C$ composition	-7.7‰	Francey et al. (1995)
δ_t^f	$^{13}C/^{12}C$ of fossil fuel emissions	-27.2‰	Andres et al. (1995)
ε_t^{ao}	discrimination in air-sea transfer	-1.8‰	Tans et al. (1993)
ε_t^{ab}	discrimination in photosynthesis	-18.0‰	Tans et al. (1993)
δ_t^{def}	$^{13}C/^{12}C$ of the deforestation flux	-25.0‰	Fung et al. (1997)
D_t^o	ocean ^{13}C disequilibrium	0.54‰	Tans et al. (1993), Fung et al. (1997)
G_t^o	annual sea to air transfer of C	90 Pg C yr^{-1}	Tans et al. (1993), Fung et al. (1997)
G_t^b	land net primary production (NPP)	$\sim$60 Pg C yr^{-1}	Field et al. (1998)
D_t^b	terrestrial $\delta^{13}C$ disequilibrium	allowed to vary in simulations (eq. (6))	Thompson & Randerson (1998)
N_t^o	net flux into oceans	solved for (eq. (2) and (3))	
N_t^b	net flux into terrestrial ecosystems	solved for (eq. (2) and (3))	

required, on average, for a given parcel of carbon to pass through the system. The isotopic disequilibrium can be calculated using the discrete form of ϕ^b_τ, as well as δ^a_t and ε^{ab}_t, as follows:

$$D^b_t = -(\delta^a_t + \varepsilon^{ab}_t) + \sum_{\tau=0}^{\infty} (\delta^a_{t-\tau} + \varepsilon^{ab}_{t-\tau})\phi^b_\tau. \quad (6)$$

The second term on the right is the convolution integral of the impulse response function, ϕ^b_τ, and the $\delta^{13}C$ of atmospheric CO_2 sequestered some time $(t-\tau)$ in the past, offset by discrimination $(\delta^a_{t-\tau} + \varepsilon^{ab}_{t-\tau})$.

Terrestrial carbon uptake, N^b_t, driven by increasing levels of NPP (P^b_t) can be estimated using the following relation:

$$N^b_t = P^b_t - \sum_{\tau=0}^{\infty} P^b_{t-\tau}\phi^b_\tau. \quad (7)$$

In the case of CO_2 fertilization, P^b_t is described by eq. (1). To examine the consequences of changing the turnover time of the system, ϕ^b_τ must first be converted to the decay function of the system (Thompson and Randerson, 1998). The decay function is formally defined as:

$$k^b_\tau = \frac{\Phi^b_\tau}{\Psi^b_t}, \quad (8)$$

where Ψ^b_τ is the distribution of steady state carbon storage as a function of age, but it can also be defined in terms of ϕ^b_τ:

$$k^b_\tau = \frac{\phi^b_\tau}{1 - \sum_{i=0}^{\tau-1} \phi^b_i}. \quad (9)$$

The decay function is multiplied by some scaling factor (to adjust the carbon residence times of the system), the same at all values of τ, and then re-transformed into ϕ^b_τ using:

$$\phi^b_\tau = k^b_\tau \prod_{i=0}^{\tau-1} (1 - k^b_i). \quad (10)$$

The new ϕ^b_τ can then be used in eq. (7) to calculate the CO_2 fertilization sink for the modified carbon residence times and in eq. (6) to calculate the corresponding value of the terrestrial isodisequilibrium. Note that this method works only if all values of k^b_τ are less than 1.0.

2.3. *Description of simulations*

Annual time series of $\delta^{13}CO_2$ from 1765 to 1990 were constructed from a cubic spline interpolation of measurements from Friedli et al. (1986), Keeling et al. (1989), and Francey et al. (1995). For CO_2 we used the standard spline fit (1765–1990) of ice core and atmospheric measurements constructed by Enting et al. (1994).

We used the CASA terrestrial biogeochemical model (Potter et al., 1993; Randerson et al., 1996) to generate 400-year impulse response functions of global annual heterotrophic respiration (Φ^b_τ) and total carbon stocks (Ψ^b_τ; living biomass + litter + soil organic matter). We constructed a carbon decay vector, k^b_τ, using eq. (8). In a series of simulations, we multiplied the carbon decay vector, k^b_τ, by a scalar between 0.1 and 2.0 to span a wide range of terrestrial MRTs. For each simulation we reconstructed ϕ^b_τ from k^b_τ using eq. (10), and then calculated the MRT (eq. (5)) and the land isodisequilibrium (eq. (6)). For each simulation, we estimated carbon uptake from CO_2 fertilization of plant growth for each year in the period from 1984 to 1990 using eq. (7) with NPP prescribed from eq. (1). NPP was assumed to be in steady state at 54 Pg C yr^{-1} (P^b_0) at the beginning of the simulation in 1765.

The land isodisequilibrium from each of these simulations was then used to calculate the ^{13}C-based net land sink from 1984 to 1990 according to eqs. (2) and (3) with parameter values given in Table 1.

3. Results

CO_2 fertilization of plant growth accounts for 54% of the ^{13}C-based land sink from 1984 to 1990 using a β value of 0.46, predictions of terrestrial carbon residence times from the CASA model, and values for terms in the global carbon budget listed in Table 1. We estimate the global terrestrial $\delta^{13}C$ disequilibrium to be 0.30‰ for NPP and the terrestrial disequilibrium forcing term to be 18 Pg C‰.

The simulations with varying terrestrial carbon MRTs demonstrate the contrasting sensitivity of the ^{13}C and NPP-sink methods to estimates of carbon turnover (Fig. 1). Terrestrial uptake from CO_2 fertilization increases nearly linearly with estimates of the MRT from 0.5 Pg C/yr at 7 years to 2.6 Pg C/yr at 57 years (Fig. 1a). In contrast, the ^{13}C-based land sink decreases with estimates

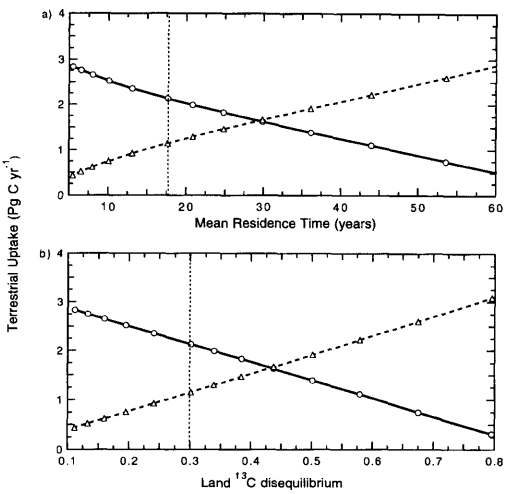

Fig. 1. (a) Land uptake from NPP stimulation by elevated levels of atmospheric CO_2 increases with estimates of the MRT of terrestrial carbon (triangles and dashed line; mean values are given for the 1984–1990 period). In contrast, the net land sink calculated from measurements of atmospheric $\delta^{13}CO_2$ decreases with estimates of the MRT (solid line). Predictions based on carbon residence times from the CASA model are denoted by the vertical dotted line. (b) The sink estimates shown in Fig. 1a are also given as a function of the fossil fuel-induced terrestrial isodisequilibrium. The isodisequilibrium term is calculated as a monotonically increasing (but non linear) function of the terrestrial MRT (see eq. (6), Subsections 2.1, and 2.2 for details).

of the terrestrial MRT from 2.8 Pg C/yr at 7 years to 0.7 Pg C/yr at 57 years.

The two methods yield the same prediction of carbon uptake (CO_2 fertilization comprises all of the net land sink) for a MRT of 29 years and $\delta^{13}C$ terrestrial isodisequilibrium of 0.44‰ (Fig. 1). Assuming the parameter values we used here for the global carbon budget are correct (Table 1), the two approaches are incompatible for estimates of the terrestrial MRT greater than 29 years. That is, for MRTs greater than 29 years, the total uptake from CO_2 fertilization exceeds the ^{13}C based estimate of the net land sink (Fig. 1, Table 2).

Significant uncertainty is associated with several of the parameters required for the ^{13}C sink calculation, most notably the ocean isodisequilibrium. If the ocean isodisequilibrium forcing is greater than the estimate we used, then the net land sink will be smaller, with CO_2 fertilization representing a proportionally greater fraction. For example, if we adopt an ocean isotopic disequilibrium forcing of 52 Pg C‰ (higher than the 48.6 Pg C‰ value that was our standard, but comparable to estimates by Joos and Bruno (1998) and Heimann and Maier-Reimer (1996) for the 1980s), the contribution of CO_2 fertilization would approach 60%. In contrast, if we have overestimated photosynthetic discrimination, and instead use a value of 14.8‰ (lower than the 18.0‰ value that was our standard, but closer to estimates that include C4 photosynthesis by Lloyd and Farquhar (1994) and Fung

Table 2. *Land and ocean sinks calculated for a range of terrestrial carbon residence times*

	Terrestrial mean residence time (years)	Fossil fuel-induced land disequilibrium D_t^b (‰)	Contribution of CO_2 fert. to the ^{13}C land sink (%)	CO_2 fertilization sink (Pg C/yr)	^{13}C land sink, N_t^b (Pg C/yr)	^{13}C ocean sink, N_t^o (Pg C/yr)
	43.99	0.58	200.2	2.22	1.11	1.89
	36.16	0.50	137.9	1.92	1.39	1.61
	29.87	0.44	102.3	1.67	1.63	1.37
	24.86	0.38	80.0	1.46	1.83	1.17
	20.87	0.34	65.0	1.29	1.99	1.01
CASA est.:	17.70	0.30	53.9	1.15	2.13	0.87
	13.12	0.24	39.2	0.92	2.35	0.65
	10.09	0.19	29.8	0.75	2.52	0.48
	8.02	0.16	23.4	0.62	2.65	0.35
	6.56	0.13	18.9	0.52	2.75	0.25
	5.49	0.11	15.5	0.44	2.83	0.17

et al. (1997)), land uptake increases and the contribution of CO_2 fertilization drops to 43%.

4. Discussion

4.1. *The contribution of CO_2 fertilization to the terrestrial sink*

Several lines of evidence suggest that CO_2 fertilization drives only a limited fraction of the terrestrial sink and that our estimate of 54% is an upper bound. As previously mentioned, the β factor of 0.46 we used is the mean from 58 controlled exposure studies of young trees (Wullschleger et al., 1993). Experimental studies on intact ecosystems suggest that when natural feedbacks from species competition and limiting nutrients are included, the NPP response to elevated CO_2 is lower than previous reports for single species experiments conducted in growth chambers and in the laboratory (Mooney et al., 1998). The β value from the mean of intact ecosystem studies is approximately 0.2 (Mooney et al., 1998), less than half of the value used here to represent the sensitivity of NPP to elevated levels of CO_2. With a β of 0.2, the contribution of CO_2 fertilization to the net land sink is only 23%.

Evidence at the global scale for a limited role of CO_2 fertilization comes from single deconvolution analyses and constraints on the latitudinal distribution of the land sink from measurements of the meridional gradient of atmospheric CO_2, $^{13}CO_2$, and O_2. In single deconvolution studies, the history of the net land flux is obtained as the residual between ice core measurements of atmospheric CO_2, model estimates of ocean uptake, and fossil fuel inputs over the last several centuries (Sarmiento et al., 1995). The net release of CO_2 from deforestation and regrowth over this period can then be subtracted from the net land flux to obtain uptake by the sum of all other processes within the terrestrial biosphere, including CO_2 fertilization (Houghton, 1993). This flux, referred to as the terrestrial sink, is the same as N_t^b described above. In a number of single deconvolution estimates, the temporal dynamics of the terrestrial sink cannot be adequately explained by linear or logarithmic responses of NPP to elevated levels of atmospheric CO_2 (Enting and Mansbridge, 1987; Enting, 1992; Friedlingstein et al., 1995; Bruno and Joos, 1997). Both Bruno and Joos (1997) and Friedlingstein et al. (1995) find that if CO_2 fertilization were allowed to explain all of the missing sink during the decade of the 1980s, then uptake from CO_2 fertilization far exceeds estimates of the terrestrial sink for periods earlier in the century. Thompson et al. (1996) derived the changes in NPP required to match a single deconvolution estimate of the sink from Houghton (1995). In the Thompson et al. analysis, the minimum NPP increase sufficient to explain the land sink was 20% from 1880 to 1990 (in this analysis NPP increases were allowed to occur in all biomes). This cumulative increase amounts to a β of 0.9, roughly 2 times the observed mean from enrichment experiments conducted in growth chambers. If terrestrial uptake is confined to specific geographic regions or biomes, even greater NPP increases are required to explain the sink (Thompson et al., 1996).

Additional evidence for a limited role of CO_2 fertilization comes from analyses of the meridional gradient of CO_2, $^{13}CO_2$, and O_2 that put a large fraction of the net land sink at mid and high latitudes of the northern hemisphere (Tans et al., 1990; Ciais et al, 1995; Keeling et al., 1996). In these regions, forest regrowth from harvesting can account for only part of the net uptake (Houghton, 1996). Other mechanisms are required to explain the remainder, including changes in other forms of disturbance and increases in NPP. For the case of changing NPP, high rates of increase are required over the last few decades to maintain sinks in these regions because of the relatively low sink potential in temperate and boreal ecosystems as compared with the tropics (Taylor and Lloyd, 1992; Thompson et al., 1996). Consequently, the required β values would be even higher than for the case in which NPP increases occur in all biomes. Satellite measurements showing increases in NDVI north of 35°N (Myneni et al., 1997), increases in high northern latitude amplitudes of the seasonal cycle of CO_2 (Keeling et al., 1996; Randerson et al., 1997), and patterns of nitrogen deposition from fossil fuel combustion (Townsend et al., 1996; Holland et al., 1997) are also consistent with rapid increases in NPP in mid- and high-latitude regions.

4.2. *A standard metric*

The use of a standard metric that combines NPP and MRT information may allow us to

avoid confusion in comparing the isotopic forcing of the atmosphere as predicted by terrestrial carbon models. The product of primary production and the MRT is well suited for this purpose (Taylor and Lloyd, 1992). This quantity represents the potential of a system to store or release carbon in response to a perturbation of primary production from any given mechanism. For the version of the CASA model used here we obtain a value of ~ 60 Pg C/yr $\times$ 17.8 years, or 1068 Pg C. This "sink potential" can also be calculated for each location in a model. With CASA, the relative global distribution would be equivalent to the map of the sink shown in Plate 2c of Thompson et al. (1996).

For terrestrial carbon models that start with gross primary production (GPP), the equivalent metric is the product of GPP and the MRT. The MRT in this case will be lower than one based on NPP because it includes plant respiration. For example, the sink potential of the GPP-referenced Emanuel et al. (1981) model is 1751 Pg C, consisting of the product of a GPP of 113 Pg C/yr and a MRT of 15.5 years (as calculated in Thompson and Randerson (1998)). Consequently, ^{13}C sink calculations by Enting et al. (1993) and Francey et al. (1995) (based on the Emanuel et al. (1981) model) use a larger terrestrial isodisequilibrium forcing term for the 1980s than what is predicted by CASA (26.5 Pg C‰ versus 18 Pg C‰).

4.3. *Uncertainties in rates of terrestrial carbon turnover*

Our ability to use ^{13}C as a tool for assessing ocean and land sinks depends critically on our understanding of residence times of carbon in the terrestrial biosphere. The same applies to our ability to predict carbon storage in response to perturbations of net primary productivity such as CO_2 fertilization (examined in this paper), nitrogen deposition, or climate change. Is the MRT of carbon in the terrestrial biosphere 10 years, 20 years, or 40 years? Much of the uncertainty in our understanding of terrestrial carbon residence times is associated with processes that occur prior to the decomposition of root and leaf litter in the soil and on the soil surface. Specifically, carbon residence times depend critically on the age of living biomass, allocation, disturbance (including fire frequency, harvesting, and insect outbreaks), species composition (and hence tissue quality), and the covariance of residence times with NPP across landscapes and biomes. Because we have only a limited understanding of how many of these processes vary within and across biomes, they are represented only crudely in the current suite of terrestrial biogeochemical models.

4.4. *Other land isotopic disequilibria*

Isodisequilibria can also occur if discrimination in terrestrial ecosystems changes over time. Human modification of terrestrial ecosystems that may have induced changes in discrimination over the last century include deforestation and land use change, and in particular conversions between C3 and C4 ecosystems (Townsend et al., 1995; VanDam et al., 1997). Other modifications that may change ecosystem discrimination include elevated levels of atmospheric CO_2, invasive species, and increased inputs of nitrogen from fertilizers and atmospheric deposition. The impact of these changes in discrimination would also be mediated through carbon turnover dynamics in terrestrial ecosystems, though the sign and magnitude of the isodisequilibria may be different from the one generated from the fossil fuel-induced decrease in $\delta^{13}CO_2$.

5. Conclusions

Many recent studies of ^{13}C use a value for the terrestrial isodisequilibrium forcing that implies only a limited contribution of CO_2 fertilization to the terrestrial carbon sink. In contrast many model simulations of terrestrial carbon uptake from CO_2 fertilization and other perturbations to NPP may or may not be consistent with ^{13}C-based sink calculations. To improve future predictions of atmospheric concentrations of CO_2, these two types of approaches should be checked for consistency and integrated. More generally, the functioning of the biosphere should be considered concurrently with the oceans and atmosphere; the next step is to use a single, calibrated model of terrestrial carbon residence times to calculate net exchange from ^{13}C measurements, CO_2 fertilization, and disturbance/forest regrowth.

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