Effect of increasing CO_2 on the terrestrial carbon cycle

David Schimel[a,1], Britton B. Stephens[b], and Joshua B. Fisher[a]

[a]Jet Propulsion Laboratory, California Institute of Technology, Pasadena, CA 91011; and [b]Earth Observing Laboratory, National Center for Atmospheric Research, Boulder, CO 80301

Edited* by Gregory P. Asner, Carnegie Institution for Science, Stanford, CA, and approved November 19, 2014 (received for review April 21, 2014)

Feedbacks from the terrestrial carbon cycle significantly affect future climate change. The CO_2 concentration dependence of global terrestrial carbon storage is one of the largest and most uncertain feedbacks. Theory predicts the CO_2 effect should have a tropical maximum, but a large terrestrial sink has been contradicted by analyses of atmospheric CO_2 that do not show large tropical uptake. Our results, however, show significant tropical uptake and, combining tropical and extratropical fluxes, suggest that up to 60% of the present-day terrestrial sink is caused by increasing atmospheric CO_2. This conclusion is consistent with a validated subset of atmospheric analyses, but uncertainty remains. Improved model diagnostics and new space-based observations can reduce the uncertainty of tropical and temperate zone carbon flux estimates. This analysis supports a significant feedback to future atmospheric CO_2 concentrations from carbon uptake in terrestrial ecosystems caused by rising atmospheric CO_2 concentrations. This feedback will have substantial tropical contributions, but the magnitude of future carbon uptake by tropical forests also depends on how they respond to climate change and requires their protection from deforestation.

climate feedback | carbon budget | tropics | atmospheric transport

In projections of future climate, the carbon cycle is second only to physical climate sensitivity itself in contributing uncertainty (1). Earth system model uncertainty has increased as more mechanisms have been incorporated into a growing number of increasingly sophisticated models. Terrestrial ecosystem feedbacks to atmospheric CO_2 concentration result from two mechanisms, direct effects of CO_2 on photosynthesis and effects of climate change on photosynthesis, respiration, and disturbance (2). The CO_2 effect, used here to describe the effect of increasing atmospheric CO_2 on terrestrial carbon storage by increasing photosynthetic rates, is also known as the β effect (3, 4). The effects of CO_2 on carbon uptake occur at the enyzmatic and stomatal scales but impact the global carbon cycle.

The CO_2 effect on terrestrial carbon storage is a key potential negative feedback to future climate, and in models of the present, it is the largest carbon cycle feedback (5, 6). In simulations of the next century, the CO_2 effect is four times larger than the climate effect on terrestrial carbon storage and twice as uncertain (4). Land use also creates large fluxes, but these are not driven by CO_2 or climate directly and so are not feedbacks. In models of the future, the biosphere operates as a net sink, reducing the climate impact of fossil fuel and deforestation emissions, until positive feedbacks from climate change [reduced productivity, increased respiration, or dieback (7)] and land use emissions exceed the CO_2 effect. The magnitude of this negative feedback is crucial to simulating future climate, but because observational constraints on the CO_2 effect are limited, the effects of CO_2 remain controversial. The effects of CO_2 are known mainly from small-scale experimental studies, ranging from single-leaf experiments through to ecosystem-scale experiments with a spatial scale of hundreds of meters (8), but predictions from theory of a large tropical effect of CO_2 have appeared to be inconsistent with global patterns of atmospheric CO_2 (6).

Photosynthesis increases with increasing CO_2 following a Michaelis–Menton curve, and this effect grows stronger at higher temperatures, implying, all else being equal, larger effects in warmer climates (9–11), especially in the tropics. Many factors control the relationship between increased photosynthetic rate and carbon storage, including how fixed carbon is allocated to plant tissues and soils with different residence times, the development of progressive nitrogen limitation, interactions with water or light limitation, and many other biological responses (12). Theory and experiments agree in suggesting a CO_2-driven net sink that should be roughly proportional to overall productivity (13) leading to a large sink in the tropics, a prediction that should be testable with global observations (11).

Materials and Methods

We develop a new framework for evaluating diverse estimates of terrestrial carbon feedbacks within the context of the global mass balance, and specifically focus on the impact of increasing CO_2 on terrestrial carbon uptake. The best-known terms in the global carbon cycle are the atmospheric concentration change, measured directly, the fossil plus cement emission rate, known from national statistical data, and ocean uptake, constrained by models and observations (6). Contrasting atmospheric and ecological evidence suggest very different carbon–climate futures, each supported by some evidence. If the land sink is dominated by northern midlatitudes, then it is likely due to recovery from land use and should saturate, or slow significantly, in the near future as forests mature. If the land sink is dominated by the tropics, it is likely due to a significant CO_2 effect leading to a continuing carbon uptake as CO_2 concentrations increase up to an unknown threshold.

Comparing bottom-up analyses and net fluxes from atmospheric approaches is surprisingly difficult. Many bottom-up analyses do not include all of the gross terms—for example, many forest-based estimates do not include growth in undisturbed forests or changes to soil storage. Top-down analyses have high uncertainty in regional fluxes, and are strongest when global patterns can be compared. We employ a new framework to test between the alternatives above, dividing carbon fluxes up between northern hemisphere extratropical and tropical plus southern hemisphere extratropical terms. We make use of a recent global carbon budget, results from

Significance

Feedbacks from terrestrial ecosystems to atmospheric CO_2 concentrations contribute the second-largest uncertainty to projections of future climate. These feedbacks, acting over huge regions and long periods of time, are extraordinarily difficult to observe and quantify directly. We evaluated in situ, atmospheric, and simulation estimates of the effect of CO_2 on carbon storage, subject to mass balance constraints. Multiple lines of evidence suggest significant tropical uptake for CO_2, approximately balancing net deforestation and confirming a substantial negative global feedback to atmospheric CO_2 and climate. This reconciles two approaches that have previously produced contradictory results. We provide a consistent explanation of the impacts of CO_2 on terrestrial carbon across the 12 orders of magnitude between plant stomata and the global carbon cycle.

Author contributions: D.S. and B.B.S. designed research; D.S., B.B.S., and J.B.F. performed research; D.S., B.B.S., and J.B.F. analyzed data; and D.S., B.B.S., and J.B.F. wrote the paper.

The authors declare no conflict of interest.

*This Direct Submission article had a prearranged editor.

[1]To whom correspondence should be addressed. Email: dschimel@jpl.nasa.gov.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1407302112/-/DCSupplemental.

ECOLOGY

EARTH, ATMOSPHERIC, AND PLANETARY SCIENCES a comprehensive process model intercomparison (called TRENDY; *SI Text*) and results from two atmospheric studies [called TransCom and RECCAP (Regional Carbon Cycle Assessment and Processes); *SI Text*]. While these studies clearly contain information about the magnitude of the CO_2 effect, this has not been the focus of the literature on these studies. We also analyze related evidence from recent studies using in situ data constraining localized ecosystem sensitivity against our global conclusions. Finally, we show that the estimated CO_2 effect can be incorporated into the global carbon budget with consistency with other, better-known fluxes.

Results

Fig. 1 shows the modeled CO_2 effect on carbon uptake meridionally for the 2000s from a recent terrestrial model ensemble (Table S1). Global terrestrial simulations of the CO_2 effect show a strong tropical CO_2 effect and a strong global correlation between the CO_2 effect and gross photosynthetic rates (Fig. 1). The CO_2 effect is dominated by the tropics, consistent with theory, with additional uptake in forested northern midlatitudes and boreal latitudes. These ecosystem models still lack many processes that could ultimately affect the magnitude of the modeled CO_2 effect. The effects of residence time also influence this pattern, leading to a somewhat lower CO_2 effect uptake relative to GPP in the subtropics compared with forested regions.

Hickler et al. (9) showed that global modeled CO_2 effects agree with experimental data available in the midlatitudes and show greater relative enhancement of uptake in the tropics than the midlatitudes, and lower in the boreal, as a result of the modeled CO_2 effect's temperature dependence. Despite the theoretical (11, 13) and empirical (14) support for a CO_2 effect, the magnitude and even existence of this effect is uncertain because of apparent conflict between the prediction of models and empirical findings from atmospheric analyses. Analyses of atmospheric CO_2 patterns can be used to estimate carbon exchange between terrestrial ecosystems and the atmosphere, using inverse modeling techniques. Atmospheric inverse model ensemble results conflict with predictions of a tropical CO_2-driven sink and on average find strong northern and weak tropical uptake (15–18).

Inverse models estimate net carbon exchange, or the balance resulting from land use emissions and uptake in regrowing and established forests. This last term, uptake by established forests, may be the strongest signal of CO_2 effects, as it isolates the CO_2 effect in carbon uptake from that in regrowth. In 1990, as the likely physiological correlation between storage and photosynthesis, or gross primary productivity (GPP), was being established, Tans et al. (15) argued that atmospheric CO_2 signals could not be explained by a flux proportional to productivity (the CO_2 effect) and were best explained by a strong sink in the northern hemisphere midlatitudes, in effect falsifying the theoretical predictions of the CO_2 effect. They did note that the uncertainty (at that time) in tropical land use fluxes was so high that their assessment of a tropical sink was inconclusive (15). The combination of sparse observations and rapid vertical mixing make the tropical land "unseen" by the CO_2 network, such that tropical fluxes are estimated by the inversion systems as the residual from other better-constrained regions. Many inverse analyses and inversion ensemble means (16, 18, 19) show tropical net fluxes roughly equal to net deforestation (emission minus regrowth) leaving no room in the budget for an additional CO_2-driven storage increase.

The complete set of inverse model results, however, diverge on the tropical net flux (Tables S2 and S3). Stephens et al. (20) showed that filtering inverse models against an additional observational constraint, the vertical gradient of CO_2 in the northern hemisphere atmosphere, favored models with a more nearly neutral net flux, leaving room for a CO_2-driven storage increase. Despite this realization, and subsequent advances in the observing network (21) and inversion methodology, models continue to disagree about the relative partitioning of terrestrial uptake between the midlatitudes and low latitudes (18). The more recent models showed terrestrial fluxes spanning a 4.9 Pg C·y^{-1} range in northern minus tropical+southern partitioning with 6 of the 11 models giving near-zero net tropical exchange consistent with a strong CO_2 effect (ref. 18, Table S3). Few attempts have been made to reconcile the full range of evidence surrounding the CO_2 effect (22, 23), partly because such reconciliation requires integrating diverse methods and assumptions from disciplines such as plant physiology (11), forestry (24), dynamic global vegetation models (9), and atmospheric inverse and transport models (20). This reconciliation is crucial to constraining the magnitude of the feedback (22).

An additional, but circumstantial, line of evidence for a significant negative feedback in the carbon system comes from the increase over time of net terrestrial uptake (25–27). The land flux is estimated by the Global Carbon Project (GCP) (27) as the residual from atmospheric concentration data (25, 28), ocean models adjusted to match three observational constraints (29–31) and fossil fuel inventories (32). Before 1959, the ocean fluxes come from data-based estimates (33) and the atmospheric growth rate from ice and firn gas (34). The resulting net terrestrial flux has shifted from a small source to a sink >2 Pg C·y^{-1} from 1850 to 2012 (ref. 27, Fig. 2). The latter part of the trend (Fig. 2) shows increasing uptake, paralleling the acceleration of atmospheric CO_2 concentrations.

Process models suggest that CO_2 effects could explain a large part of this uptake: Models run with CO_2 effects independently mirror the observed trend, offset by about 1.2 Pg C·y^{-1}, possibly as a result of excluded climate and land use effects (Fig. 2). If this pattern of increase in the observed net sink were not occurring, it would falsify the CO_2 effect. This decadal pattern is highly suggestive of a negative feedback, but cannot be used quantitatively to constrain the process because the global signal also includes the effects of CO_2, climate, nitrogen and ozone deposition, nutrient cycle changes, and historical disturbance.

In Fig. 3, we synthesize a number of different lines of evidence within the constraints of the global carbon budget. Fig. 3 shows results from several community atmospheric inverse ensembles, plotted as northern extratropical versus tropical+southern land fluxes. Summed, these two terms comprise the total global

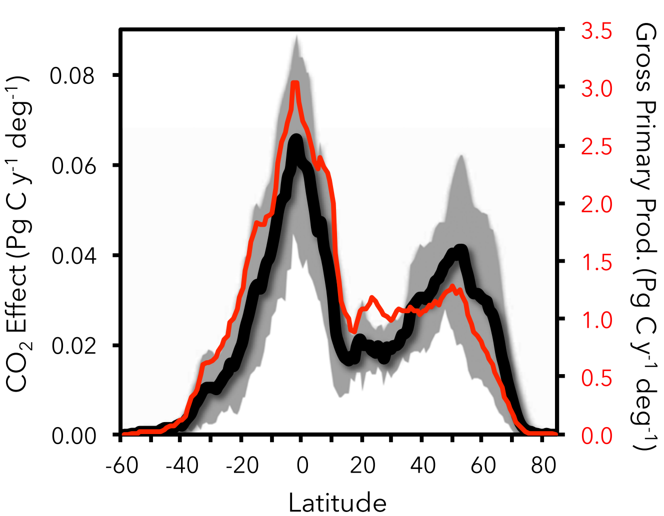

Fig. 1. Zonal sums of the CO_2 effect and gross primary productivity averaged over 2000–2010 from nine terrestrial biosphere models (see *SI Text*). The gray shaded area shows the multimodel SD around the multimodel mean CO_2 effect (thick black line). The red line shows the multimodel mean GPP, illustrating the strong correlation between GPP and enhanced storage (net biome production) due to CO_2 (the CO_2 effect); the sign convention is reversed here for clarity (normally, uptake is negative).

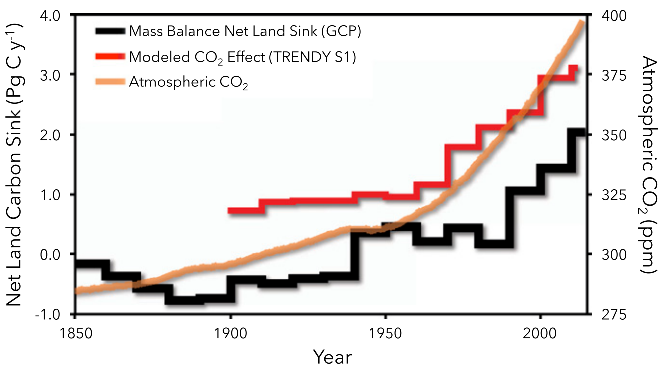

Fig. 2. Similarities in trend between atmospheric CO_2 concentration changes (orange), the net terrestrial sink from the Global Carbon Project (black), and the modeled CO_2 effect on net biome production from TRENDY (red) suggest that ecosystem responses to CO_2 have played a role in increasing land carbon uptake over the last 150 y. The TRENDY and GCP data were averaged to 10-y intervals. Sign convention as in Fig. 1.

terrestrial sink and so can be compared with the better-constrained global carbon budget estimate of the net land flux. Results in the upper left-hand quadrant correspond to dominance by land use effects, while the lower right-hand quadrant suggests a larger role for the CO_2 effect. Data that constrain tropical fluxes provide an indirect constraint on the global CO_2 effect.

The TransCom3 Level 2 (T3L2) study [red circles (16)] compared 12 model estimates for the period 1992–1996 using identical prior flux estimates, observational data, and inversion methodology to isolate the contribution of atmospheric transport errors. The RECCAP study (18) compared 11 inverse model estimates for the period 2001–2004 with differing prior constraints, data sets, and methodologies (purple squares). The T3L2 results diverge, spanning a range of 7.9 Pg C·y^{-1} in the difference between northern and tropical land fluxes (ref. 16, Table S2). This divergence is not random but rather is systematically dependent on differences in model representation of vertical mixing (20). The RECCAP results are more convergent, likely as a result of improvements in the representation of atmospheric transport by models, inversion methodology, and increased observations over the intervening period. Six of the RECCAP models suggest tropical uptake countering deforestation emissions completely or to within 0.6 Pg C·y^{-1}, while the remaining five show strong net tropical emissions of over 1.4 Pg C·y^{-1} (ref. 18, Table S3).

Both the T3L2 and the RECCAP results show negative correlations between northern extratropical and tropical+southern land fluxes (Fig. 3), as expected owing to the constraints on the total terrestrial uptake imposed by the lower uncertainties of fossil fuel and oceanic fluxes and the atmospheric growth rate in the inversion estimates. The light gray error band in Fig. 3 shows the constraint imposed by fixing the fossil fuel and ocean fluxes to those from the GCP (27) for the corresponding T3L2 and RECCAP periods. For any set of fossil fuel, ocean, and atmosphere constraints, a −1:1 correlation and uncertainty band in the residual land fluxes is imposed (see Fig. S1 for additional details). Estimates of net terrestrial uptake that lie outside of this uncertainty band are unlikely because they violate one or more of the better-known constraints. Models and observations spanning the period 1990–2010 suggest terrestrial fluxes of *ca.* −1 Pg C·y^{-1} in the northern extratropics and tropical+southern net fluxes of 0.0 Pg C·y^{-1} to −0.5 Pg C·y^{-1}. This requires sinks to balance the gross deforestation source of *ca.* 3 Pg C·y^{-1}. CO_2 fertilization in models and uptake in intact forests in inventories are in greater agreement with the mass balance results.

Evidence to support a gross tropical sink comes from the evaluation of transport models against an independent atmospheric observation. The mean and SD across the 12 TransCom models are shown by the large red cross in Fig. 3 (16). Stephens et al. (20), using an additional diagnostic test, showed that a subset of three of these models agreed most closely with annual mean vertical atmospheric CO_2 gradients in the north, and the mean and SD for these models is also shown in Fig. 3. The three models that best simulated the annual mean vertical gradient all showed reduced midlatitude and greater tropical uptake, consistent with a CO_2 effect, presumably resulting from better representation of vertical mixing and atmospheric transport. Smaller northern uptake (and so potentially higher tropical uptake) is also indicated by an analysis of the Total Carbon Column Observing Network, providing additional independent support (21).

Discussion

We can assess the consistency of bottom-up estimates with the top-down estimates from the atmosphere using forest and atmospheric data. Pan et al. (35) estimated fluxes associated with deforestation, regrowth of disturbed forests, and enhanced growth in intact forests. There are many estimates of local and regional forest uptake (e.g., refs. 36–38), but it is not possible to compare in situ to atmospheric estimates without global data; Pan et al. (35) is the most recent such complete compilation: Regional or deforestation-regrowth-only analyses are not subject to the mass balance constraint and so cannot be evaluated against atmospheric data. Recent attempts to reconcile tropical fluxes address part of the carbon budget and so cannot be directly integrated into our framework. The gross deforestation estimate lies well outside of the uncertainty bands implied by the GCP. Regrowth of disturbed forests only returns the estimate to the edge of the GCP uncertainty band for the RECCAP period. Including Pan et al.'s (35) estimate of uptake in intact forests, hypothesized to result from CO_2, brings the inventory-based budget within the GCP bounds and into reasonable agreement with the Stephens et al. (20) estimate.

Results for the CO_2 effect from a recent terrestrial ecosystem model ensemble are also shown in Fig. 3 (TRENDY) (39) and can add an additional constraint on the possible causes and magnitude of the CO_2 effect. The TRENDY results in Fig. 3 are shown broken down into fluxes responding to only climate and land use drivers (open blue triangles) and fluxes responding to climate, land use, and CO_2 effect drivers (closed blue triangles), with ellipses representing medians and SDs. Without the CO_2 effect, the median of the TRENDY models is well outside of the uncertainty bands implied by the GCP. Including the median CO_2 effect simulated by the TRENDY models produces a budget in agreement with independent global constraints. This effect is predicted to occur both in northern and tropical forests, with the combination bringing the TRENDY estimates into close agreement with both the Pan et al. (35) and Stephens et al. (20) estimates. Several models with extremely high sensitivity to CO_2 fall outside the GCP constraint.

Increases in plant growth in intact tropical forests, rather than just regrowth from deforestation, are required for consistency with the Stephens et al. (20) and GCP constraints. These increases may not be only due to CO_2, although it is considered the most likely hypothesis (35). One study at the La Selva field station in Costa Rica attempted to estimate the climate and CO_2-driven components of carbon uptake and estimated an increase of plant growth rate [net primary productivity (NPP)] (38) of 5.24 g C·m^{-2}·y^{-1}·y^{-1}. This increase was used to suggest that models and forest inventory studies were overestimating the tropical CO_2 sink. We found the ecosystem models in Fig. 3 that suggested a carbon sink of 1–2 Pg C y^{-1} showed changes in NPP that bracketed the 5 g C·m^2·y^{-1}·y^{-1} value, indicating that this acceleration of productivity is consistent with pantropical significant

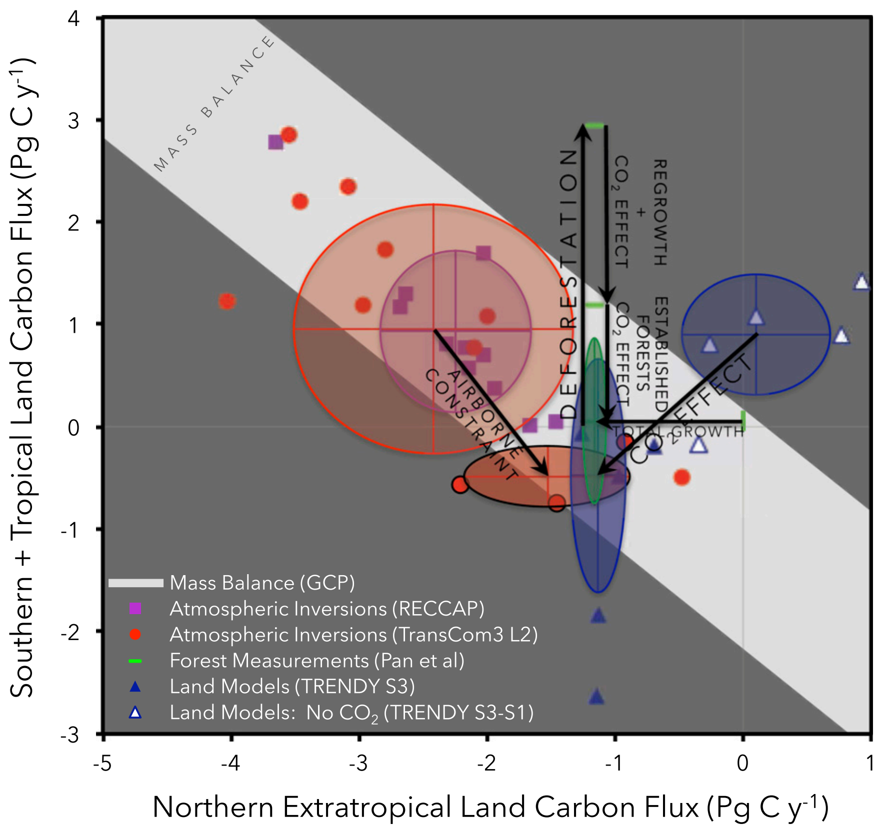

Fig. 3. Comparison of independent carbon flux estimates. Atmospheric inverse results from the T3L2 and RECCAP intercomparison experiments show that across models, northern extratropical and tropical+southern fluxes are anticorrelated (since the models are also constrained by the atmospheric growth rate and tight fossil fuel and ocean flux estimates). The light gray region shows the corresponding constraints from GCP for 1992–2004, with the upper edge corresponding to the GCP estimate for the RECCAP period (2001–2004), +0.9 Pg C·y^{-1} uncertainty, and the lower edge corresponding to the GCP estimate for the T3L2 period (1992–1996), −0.9 Pg C·y^{-1} uncertainty. Although GCP shows a long-term increasing terrestrial sink (Fig. 2), shorter-term fluctuations result in the average sink for 1992–1996 being larger than for 2001–2004 (27). The upper red circle shows the mean and SD of the T3L2 results as reported by Gurney et al. (16), while the lower shows the mean and SD of the three models selected by the additional vertical gradient constraint in Stephens et al. (20). The green ellipse shows the estimates and uncertainty ranges from the Pan et al. (35) global forest inventory-based study for the period 1990–2007. The upward black vector shows the gross deforestation flux from Pan et al. (35), reduced, first, by regrowth (upper downward vector) and then by fluxes in intact forests (lower downward vector, potentially CO_2 effect fluxes). Pan et al. (35) do not partition northern land components but estimate a net flux there of −1.1 Pg C·y^{-1}, which is indicated by the horizontal black vector. The vertical vectors have been spread slightly for clarity. The solid blue triangles show process model estimates for the period 1990–2007 (TRENDY: see *SI Text*) including the simulated CO_2 effect, climate effect, and land use fluxes. The open blue triangles show the same models excluding the CO_2 effect flux. Blue ellipses show median and uncertainty with and without the CO_2 effect, and the diagonal vector shows the additional impact of including CO_2 effects T3L2, RECCAP, and TRENDY results are all presented here partitioned by the TransCom/RECCAP regions (see *SI Text*).

net carbon storage. Models that generate a tropical+southern >1 Pg C·y^{-1} sink are not falsified by observed in situ fluxes.

The results shown in Fig. 3 combine estimates over varying time periods: T3L2 from 1992 to 1996, RECCAP from 2001 to 2004, TRENDY from 1990 to 2007, Pan et al. (35) from 1990 to 2007, and GCP from 1992 to 2004. Interannual variations in terrestrial carbon uptake are known to be large. The 5-y and 4-y periods represented by T3L2 and RECCAP are likely to average over much of this variability, but to address concerns about interannual variability, we have used the TRENDY output and GCP results, which are both available on an annual basis, to examine comparisons on time periods matched to either of the Pan et al. (35) decadal estimates or the shorter T3L2 or RECCAP periods. As shown in Fig. S1, all of these finer time periods support the conclusions from Fig. 3 that a significant CO_2 effect is needed to bring the TRENDY and Pan fluxes into agreement with a validated subset of atmospheric inversions and the global carbon budget constraints.

Within the range of extant atmospheric inversions, a subset allow a significant CO_2 effect, and this is a simple explanation for the bulk of nonatmospheric information. This set of results converge to better define the tropical carbon budget, and also provide increasing support for the CO_2 effect, showing that (*i*) estimates of the CO_2 effect "fit" within the GCP carbon mass balance allowing the effect to be included in a consistent global carbon budget; (*ii*) the estimated magnitude of the CO_2 effect is consistent with a vetted subset of atmospheric inverse models; (*iii*) the magnitude of the CO_2 effect is also consistent with in situ estimated uptake in intact forests, and with observed long-term changes to productivity; (*iv*) simulation results omitting CO_2 effects mostly lie outside the mass balance constraint but converge within when the effect is included; and (*v*) the time history of the residual terrestrial sink is suggestive of a significant CO_2 effect.

As Fig. 3 shows, atmospheric inversions constrained by airborne data, bottom-up inventories, and prognostic models are broadly consistent in terms of their net land sinks and latitudinal partitioning. It is not possible to rigorously merge these flux estimates, because of the different time periods covered and different processes considered, but we report our best estimate for the 1990–2007 average global terrestrial carbon cycle in Table 1. First, the GCP (27) estimates of the global fossil fuel source, atmospheric growth rate, and oceanic sink over this period together require a net terrestrial sink of -1.1 ± 0.6 Pg C·y^{-1}.

Table 1. **The global carbon budget for 1990–2007, updated and inclusive with all terrestrial fluxes attributed to processes or regions**

Carbon budget component	Flux (1990–2007) Average annual flux, Pg C·y^{-1}	Uncertainty, Pg C·y^{-1}	Source
Atmospheric increase (AI)	3.6	0.4	GCP
Fossil plus cement (FpC)	6.9	0.1	GCP
Tropical gross deforestation (TGD)	2.9	0.5	(35)
Ocean uptake (OU)	−2.3	0.5	GCP
Tropical regrowth after deforestation (TRD)	−1.6	0.5	(35)
Northern extratropical uptake (all processes) (NEU)	−1.2	0.1	combined
Tropical plus southern CO_2 effect uptake (TpS)	−1.4	0.4	combined

This table combines the GCP 2013 carbon budget with the additional flux estimates derived in this paper. This budget has a residual error of 0.3 Pg C·y^{-1}, within the uncertainty of the total budget (1 Pg C·y^{-1}). The values in the NEU and TpS rows are weighted means of Pan et al. (35) and TRENDY estimates (see *SI Text*). Note that most carbon budgets (e.g., GCP) include a terrestrial term estimated by difference and so sum to zero. Budget summary: AI = FpC + TGF + OU + TRD + NEU + TpS + *residual (uncertainty)*; 3.6 = 6.9 + 2.9–2.3–1.6–1.2–1.4 + *0.3 (1.0)*.

We partition this net sink into the CO_2 effect and all other processes, and into northern extratropical or tropical+southern regions. Our resulting best estimate of the tropical+southern CO_2 effect is −1.4 ± 0.4 Pg C·y^{-1}. This is an upper-bound estimate on the absolute magnitude of the tropical+southern CO_2 effect, as the observed estimate (35) no doubt adds effects of other changes to light, water, and nutrients to the CO_2 effect.

For the northern extratropics, where nitrogen deposition and air pollution, climate, and historical land use also all affect carbon uptake, and Pan et al. (35) did not partition the inventory estimates, we must rely on the prognostic models. The TRENDY models estimate a northern extratropical CO_2 effect of −1.1 ± 0.4 Pg C·y^{-1} (median of nine models, S1 experiment). Combined, we estimate a global effect of −2.5 ± 0.6 Pg C·y^{-1}. The median global CO_2 effect simulated by the TRENDY models over the 1990–2007 time period is −2.6 ± 1.0. Fig. 3 shows models with very high sensitivity to CO_2 lie well outside the mass balance constraint.

As a check, if we assume that the Stephens et al. (20) estimate of the net tropical+southern atmospheric flux is correct and representative of the full decade at roughly −0.5 Pg C·y^{-1}, and further assume that Pan et al.'s (35) 1990–1999 deforestation and regrowth numbers are correct, this yields an uptake in intact forest of −0.8 Pg C·y^{-1}, within the uncertainty of the other Pan et al. (35) and TRENDY estimates; this analysis cannot be done more formally, as the inverse model results and atmospheric constraint (vertical profiles) do not span the entire Pan et al. (35) period.

Conclusions

The CO_2 effect likely acts as a significant negative feedback in today's global carbon cycle, absorbing up to 30% of fossil fuel CO_2 emissions. Uncertainty in the strength of this effect contributes significant variability to projections of future atmospheric CO_2 concentrations. Process models, forest inventories, forest NPP time series (38) and a data-constrained subset of atmospheric inverse models lead to a carbon budget consistent with a significant CO_2 effect. Further, assuming uptake due to the global CO_2 effect of −2.5 Pg C·y^{-1} (text above) and total land sinks of −4.2 Pg C·y^{-1} (Table 1), this implies that up to 60% of current terrestrial sinks are due to this single feedback. For reasons stated above, this is likely an upper bound, as the atmospheric and forest inventory data include fluxes not due to the CO_2 effect. Including estimates for these new process-specific gross fluxes in the GCP (27) global carbon budget results in a bottom-up budget including the CO_2 effect estimated as described above (Table 1 and *SI Text*). This budget is not forced to balance by the traditional "residual terrestrial flux" and so does not sum to zero but rather (encouragingly) balances within the uncertainty of the other fluxes.

All of the evidence suggests that the CO_2 effect is a significant feedback in the climate system, except for that from a group of inverse models that do not agree between themselves. To refine the quantification of the CO_2 effect (Fig. 3), it is critical to reduce the remaining uncertainty in inverse model partitioning of tropical versus northern flux estimates. Inverse studies should be designed so they span long enough for robust comparison of atmospheric to biomass results. Atmospheric analyses need to produce and archive posterior atmospheric CO_2 concentrations for comparison with observations (20). Models need improved numerical representation of northern extratropical atmospheric convection to reduce uncertainty in inverse estimates (20).

Recent studies show significant but highly variable carbon uptake in the tropics (40), and this year-to-year variability may be increasing (41). Long-term trends in climate will also produce carbon storage trends that must be estimated. The high variability (40–42) implies that observations and inverse analyses must span a period of years sufficient to average over short-term climate-driven variability. Standardizing time periods, or producing all estimates on an annual basis, is essential to allow integrative analysis.

Further reductions in uncertainty require reducing the persistent disagreement between inverse estimates of tropical versus midlatitude uptake. Comparing posterior concentration fields from atmospheric inversions to observations has not become routine, and posterior concentrations were not archived in the RECCAP study (18). Given the importance of assessing modeled meridional partitioning, saving posterior concentration fields and comparing them to observations should be a high priority. New atmospheric measurements of tropospheric vertical profiles, in particular in the tropics (where data are sparse), are needed. Isotopic measurements may also help: An early study using ^{13}C had results consistent with ours, but could not distinguish between an overestimate of deforestation or the existence of a large sink (43).

The apparent CO_2-driven sink also increases the priority of experimental manipulations in tropical forests to confirm the sensitivity of tropical forests to increasing CO_2. Estimates of gross deforestation are beginning to converge (44–46); reconciling inventory and atmospheric estimates requires robust estimates of all fluxes. Satellite CO_2 measurements provide vastly higher density of observations but, because of cloud cover, remain sparser in the tropics than elsewhere. The Orbiting Carbon Observatory 2 (OCO-2), just launched, with its vastly higher sampling density, may aid in partitioning fluxes meridionally, while even denser and more frequent sampling of concentrations using data from a geostationary sensor is likely required to separate fluxes in intact versus deforested regions (47, 48).

The balance of evidence from in situ, inventory, simulation, and atmospheric studies provides support for a long-hypothesized negative feedback to CO_2 from the terrestrial biosphere that is distributed spatially as theory predicts. Terrestrial sinks dominate over land use and climate sources in the present, but the effects of climate are likely to grow over the next decades. This implies a potential transition, influenced by climate and land use trends, when climate effects exceed CO_2 effects and other sinks, leading to an enhanced growth rate of CO_2. Accurately forecasting when this transition might occur requires improved quantification of all of the feedback sensitivities. The CO_2 effect cannot absorb the majority of fossil fuel emissions, but carbon uptake in response to increasing CO_2 is a crucial global ecosystem service. The future tropical balance of deforestation and climate sources and regrowth and CO_2 sinks will only remain a robust feature of the global carbon cycle if the vast tropical forests are protected from destruction.

ACKNOWLEDGMENTS. We thank the TRENDY modelers: Stephen Sitch, Chris Huntingford, Ben Poulter, Anders Ahlström, Mark Lomas, Peter Levy, Sam Levis, Sönke Zaehle, Nicolas Viovy, and Ning Zeng, and the RECCAP modelers: Philippe Peylin, Frederic Chevallier, Rachel Law, Peter Rayner, Andy Jacobson, Wouter Peters, Christian Roedenbeck, Prabir Patra, Kazutaka Yamada, Kevin Gurney, and Yosuke Niwa, for sharing their results, with particular thanks to Philippe Peylin for regridding and making results available. Michael Keller and Sassan Saatchi provided insights into forest inventories. We thank the students and faculty of the Niwot Ridge Flux course for years of stimulating discussion, Munish Sikka for data processing, and Chip Miller, Stan Sander, Riley Duren, Kevin Bowman, Duane Waliser, and the Jet Propulsion Laboratory (JPL) Carbon-Climate Initiative for support, valuable discussions, and feedback. The research carried out at the JPL, California Institute of Technology, was under a contract with the National Aeronautics and Space Administration. Government sponsorship is acknowledged and was supported by JPL's Carbon and Climate Initiative. The National Center for Atmospheric Research is sponsored by the National Science Foundation.

1. Bodman RW, et al. (2013) Uncertainty in temperature projections reduced using carbon cycle and climate observations. *Nat Clim Change* 3:725–729.
2. Friedlingstein P, et al. (2006) Climate–carbon cycle feedback analysis: Results from the C4MIP model intercomparison. *J Clim* 19:3337–3353.
3. Keeling CD (1973) The carbon dioxide cycle: Reservoir models to depict the exchange of atmospheric carbon dioxide with the oceans and land plants. *Chemistry of the Lower Atmosphere*, ed Rasool SI (Plenum Press, New York), pp 251–329.
4. Gregory JM, Jones CD, Cadule P, Friedlingstein P (2009) Quantifying carbon cycle feedbacks. *J Clim* 22:5232–5250.
5. Friend AD, et al. (2014) Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO_2. *Proc Natl Acad Sci USA* 111(9):3280–3285.
6. Ciais P, et al. (2013) Carbon and other biogeochemical cycles. *Climate Change 2013. The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, eds Stocker TF, et al. (Cambridge Univ Press, New York), pp 465–570.
7. Cox PM, et al. (2013) Sensitivity of tropical carbon to climate change constrained by carbon dioxide variability. *Nature* 494(7437):341–344.
8. Luo Y, Hui D, Zhang D (2006) Elevated CO_2 stimulates net accumulations of carbon and nitrogen in land ecosystems: A meta-analysis. *Ecology* 87(1):53–63.
9. Hickler T, et al. (2008) CO_2 fertilization in temperate FACE experiments not representative of boreal and tropical forests. *Glob Change Biol* 14:1531–1542.
10. Mooney HA, et al. (1991) Predicting ecosystem responses to elevated CO_2 concentrations. *Bioscience* 41(2):96–104.
11. Lloyd J, Farquhar GD (2008) Effects of rising temperatures and [CO_2] on the physiology of tropical forest trees. *Philos Trans R Soc Lond B Biol Sci* 363(1498):1811–1817.
12. Zaehle, et al. (2014) Evaluation of 11 terrestrial carbon–nitrogen cycle models against observations from two temperate Free-Air CO_2 Enrichment studies. *New Phytol* 202(3):803–822.
13. Taylor JA, Lloyd J (1992) Sources and sinks of atmospheric CO_2. *Aust J Bot* 40(5): 407–418.
14. Norby RJ, et al. (2005) Forest response to elevated CO_2 is conserved across a broad range of productivity. *Proc Natl Acad Sci USA* 102(50):18052–18056.
15. Tans PP, Fung IY, Takahashi T (1990) Observational contrains on the global atmospheric CO_2 budget. *Science* 247(4949):1431–1438.
16. Gurney KR, et al. (2004) Transcom 3 Inversion Intercomparison: Control results for the estimation of seasonal carbon sources and sinks. *Global Biogeochem Cycles* 18:GB1010.
17. Jacobson AR, et al. (2007) A joint atmosphere-ocean inversion for surface fluxes of carbon dioxide: 2. Regional results. *Global Biogeochem Cycles* 21:GB1020.
18. Peylin P, et al. (2013) Global atmospheric carbon budget: Results from an ensemble of atmospheric CO_2 inversions. *Biogeosciences* 10:6699–6720.
19. Deng F, et al. (2013) Nested inversion of the North America carbon flux with forest stand age constraint. *Biogeosciences* 10:5335–5348.
20. Stephens BB, et al. (2007) Weak northern and strong tropical land carbon uptake from vertical profiles of atmospheric CO_2. *Science* 316(5832):1732–1735.
21. Yang Z, et al. (2007) New constraints on Northern Hemisphere growing season net flux. *Geophys Res Lett* 34:L12807.
22. Enting IG, Rayner PJ, Ciais P (2012) Carbon cycle uncertainty in REgional Carbon Cycle Assessment and Processes (RECCAP). *Biogeosciences* 9:2889–2904.
23. Houghton RA (2003) Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850–2000. *Tellus Ser B* 55:378–390.
24. Goodale CL, et al. (2002) Forest carbon sinks in the Northern Hemisphere. *Ecol Appl* 12:891–899.
25. Ballantyne AP, Alden CB, Miller JB, Tans PP, White JWC (2012) Increase in observed net carbon dioxide uptake by land and oceans during the past 50 years. *Nature* 488(7409): 70–72.
26. Sarmiento JL, et al. (2010) Trends and regional distributions of land and ocean carbon sinks. *Biogeosciences* 7:2351–2367.
27. Le Quéré C, et al. (2014) Global carbon budget 2013. *Earth Syst. Sci. Data* 6:235–263.
28. Keeling CD, et al. (2001) *Exchanges of Atmospheric CO_2 and $^{13}CO_2$ with the Terrestrial Biosphere and Oceans from 1978 to 2000. I. Global Aspects* (Scripps Inst Oceanogr, San Diego), SIO Ref Ser 01-06.
29. McNeil BI, Matear RJ, Key RM, Bullister JL, Sarmiento JL (2003) Anthropogenic CO_2 uptake by the ocean based on the global chlorofluorocarbon data set. *Science* 299(5604): 235–239.
30. Mikaloff Fletcher SE, et al. (2006) Inverse estimates of anthropogenic CO_2 uptake, transport, and storage by the oceans. *Global Biogeochem Cycles* 20:GB2002.
31. Manning AC, Keeling RF (2006) Global oceanic and land biotic carbon sinks from the Scripps atmospheric oxygen flask sampling network. *Tellus Ser B* 58:95–116.
32. Boden TA, Marland G, Andres RJ (2008) *Global, Regional, and National Fossil-Fuel CO_2 Emissions* (Oak Ridge Natl Lab, Oak Ridge, TN). Available at cdiac.ornl. Accessed March 2014.
33. Khatiwala S, et al. (2013) Global ocean storage of anthropogenic carbon. *Biogeosciences* 10:2169–2191.
34. MacFarling Meure C, et al. (2006) Law Dome CO_2, CH_4 and N_2O ice core records extended to 2000 years BP. *Geophys Res Lett* 33:L14810.
35. Pan Y, et al. (2011) A large and persistent carbon sink in the world's forests. *Science* 333(6045):988–993.
36. Lewis SL, et al. (2009) Increasing carbon storage in intact African tropical forests. *Nature* 457(7232):1003–1006.
37. Phillips OL, et al. (2009) Drought sensitivity of the Amazon rainforest. *Science* 323(5919):1344–1347.
38. Clark DA, Clark DB, Oberbauer SF (2013) Field-quantified responses of tropical rainforest aboveground productivity to increasing CO_2 and climatic stress, 1997–2009, *J Geophys Res* 118:783–794.
39. Piao S, et al. (2013) Evaluation of terrestrial carbon cycle models for their response to climate variability and to CO_2 trends. *Glob Change Biol* 19(7):2117–2132.
40. Gatti LV, et al. (2014) Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements. *Nature* 506(7486):76–80.
41. Wang X, et al. (2014) A two-fold increase of carbon cycle sensitivity to tropical temperature variations. *Nature* 506(7487):212–215.
42. Fisher JB, et al. (2013) African tropical rainforest net carbon dioxide fluxes in the twentieth century. *Philos Trans R Soc Lond B Biol Sci* 368(1625):20120376.
43. Townsend AR, Asner GP, Tans PP, White WC (2002) Land use effects on atmospheric ^{13}C imply a sizable terrestrial CO_2 sink in tropical latitudes. *Geophys Res Lett* 29(10).
44. Tollefson J (2012) Scientists publish consensus statement on deforestation emissions. *Nat News Blog* Dec 4. Available at blogs.nature.com/news/2012/12/scientists-publish-consensus-statement-on-deforestation-emissions.html. Accessed March 1, 2014.
45. Harris N, Brown S, Hagen S, Baccini A, Houghton R (2012) *Progress Toward a Consensus on Carbon Emissions from Tropical Deforestation: Policy Brief* (Meridian Inst, Washington, DC).
46. Baccini A, et al. (2012) Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. *Nat Clim Change* 2:(182–185).
47. Crisp D, DeCola PL, Miller CE (2008) NASA Orbiting Carbon Observatory: Measuring the column averaged carbon dioxide mole fraction from space. *J Appl Remote Sens* 2(1):023508.
48. Duren RM, Miller CE (2012) Measuring the carbon emissions of megacities. *Nat Clim Change* 2:560–562.