Land use change and nitrogen feedbacks constrain the trajectory of the land carbon sink

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[1] Our understanding of Earth's carbon climate system depends critically upon interactions between rising atmospheric CO₂, changing land use, and nitrogen limitation on vegetation growth. Using a global land model, we show how these factors interact locally to generate the global land carbon sink over the past 200 years. Nitrogen constraints were alleviated by N₂ fixation in the tropics and by atmospheric nitrogen deposition in extratropical regions. Nonlinear interactions between land use change and land carbon and nitrogen cycling originated from three major mechanisms: (i) a sink foregone that would have occurred without land use conversion; (ii) an accelerated response of secondary vegetation to CO₂ and nitrogen, and (iii) a compounded clearance loss from deforestation. Over time, these nonlinear effects have become increasingly important and reduce the present-day net carbon sink by ~40% or 0.4 PgC yr⁻¹. Citation: Gerber, S., L. O. Hedin, S. G. Keel, S. W. Pacala, and E. Shevliakova (2013), Land use change and nitrogen feedbacks constrain the trajectory of the land carbon sink, Geophys. Res. Lett., 40, 5218-5222, doi:10.1002/grl.50957.

1. Introduction

[2] The historical land carbon (C) budget offers a critical test of our ability to understand and forecast the global C cycle in a changing world [*Ballantyne et al.*, 2012]. Such determination has been difficult, however, as it demands the integration of several strongly interacting factors. First, human land use activities have long been seen as essential to the land C budget [*Arora and Boer*, 2010; *Houghton*, 1999; *Ramankutty and Foley*, 1999], but the history of land use transitions has only recently been determined with acceptable resolution [*Hurtt et al.*, 2006]. Second, land plants may increase biomass growth and sequester more C in response to elevated atmospheric CO₂ (i.e., CO₂ fertilization) [*Cernusak et al.*, 2013; *Norby et al.*, 2005]. Third, nutrient supply—in particular nitrogen (N)—can constrain both plant

CO₂ uptake and soil-atmosphere C exchange [*Gerber et al.*, 2010; *Jain et al.*, 2009; *Sokolov et al.*, 2008; *Thornton et al.*, 2007; *Zaehle et al.*, 2010].

[3] When combined, these three factors—land use transitions, CO₂, and N—can introduce complex feedbacks within the land C sink that are difficult to resolve using present-day models [Bonan and Levis, 2010; Pongratz et al., 2009; Strassmann et al., 2008; Zaehle et al., 2010]. For example, explicit consideration of C-N interactions in land models has shown not only that N can inhibit CO₂ uptake in land ecosystems [Gerber et al., 2010; Zaehle and Dalmonech, 2011] but also that the specific C-N interaction depends critically upon local land use transitions and disturbance [Churkina et al., 2007; Jain et al., 2013; Yang et al., 2010].

[4] Previous modeling studies have identified three broad mechanisms by which land use change (LUC) and response to forcing from climate, CO₂ and N deposition may generate nonlinear dynamics within the land C cycle: (i) Conversion of land to permanent agriculture (with limited capacity to store C) can forfeit the ability of the native ecosystem to sequester C in response to rising CO₂ and N deposition (C sink foregone) [Strassmann et al., 2008]; (ii) Ecosystems recovering from LUC and/or disturbance may sequester disproportionately more C by being more responsive to CO₂ and N deposition than undisturbed ecosystems (accelerated regrowth) [Churkina et al., 2007]; and (iii) Land clearance can trigger larger CO₂ emissions from ecosystems that historically have been exposed to increased CO₂ and N deposition and therefore contain greater C stores (compounded clearance loss) [Arora and Boer, 2010].

[5] A critical difficulty in analyzing these potentially nonlinear interactions is that they are the consequence of patterns of LUC occurring at small spatial scales ($< 1 \text{ km}^2$) far below the scale of the individual grid cells ($\sim 10^4 \text{ km}^2$) that limit the resolution of most land models. A second fundamental difficulty is that the N cycle displays highly transient behavior as vegetation and soils recover following a LUC event (Figure 1) and that the resulting dynamics is sensitive to local influences from climate, atmospheric N deposition, and biological N₂ fixation. As a result of these difficulties, models have greatly simplified these interactions by conjoining natural and recovering vegetation or by considering a single time-invariant land use class (aggregated secondary forest) [*Jain et al.*, 2013; *Yang et al.*, 2010] in addition to potential vegetation.

2. Modeling Setup

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[6] We here use a global land model that resolved subgrid land use transitions [*Shevliakova et al.*, 2009] and that can explicitly resolve C-N interactions as plants and soil recover

Additional supporting information may be found in the online version of this article.

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Figure 1. Emergence of N limitation in secondary succession. (a) Model scenarios illustrate how N limitation emerges during secondary regrowth in a forest (identified by purple, black versus green bars at the bottom of the graph), in response to different levels of N input and loss: high-N deposition (purple), low-N deposition (black), and high-DON losses (green). (b) The ability of biological N₂ fixation to supply external N when the internal N source is insufficient during forest regrowth. Fixation is highest during maximum plant growth in early succession, and thereafter depends on the specific scenario of N input and loss. The result is a transient successional feedback between rates of CO2 uptake, N2 fixation, and the plant-soil N cycle. The exact dynamics and the switches between N sufficiency and limitation depend on climate that influences growth and decomposition rates and on initial conditions. The final equilibrium of each scenario is identified by horizontal bars at the far right of the graph.

from land use effects over successional time (LM3V-N) [Gerber et al., 2010; Shevliakova et al., 2009]. We employ a novel approach of tracking within each grid cell transitions between individual tiles that represent the areal extent of different land use classes: primary vegetation (forest or grassland), secondary vegetation, pasture, and cropland. Further, secondary vegetation is tracked based on age/size structures that represent recovery from previous land use (see supporting information). The emergent C-N interactions therefore capture the consequence of land use history in addition to local biogeochemical, biotic, and climatic conditions. We illustrate in Figure 1 how, following a disturbance event, our model tracks the temporal evolution of CO₂ uptake and N limitation in response to the processes that govern the N balance: N deposition, biological N₂ fixation, and ecosystem N losses. The result is a transient successional feedback between CO₂ uptake, N₂ fixation, and the plant-soil N cycle.

[7] LM3V-N considers two critical feedbacks that govern the post-disturbance recovery of plant and soil C pools but that are rarely resolved dynamically within land models: First, N_2 fixation can enhance the CO₂ sink when N is limiting, as can occur during the period of rapid vegetation growth in early succession (Figure 1). The fixation response is substantial in tropical ecosystems where symbiotic N_2 fixers are abundant [*Hedin et al.*, 2009] but constrained where symbiotic fixers are absent or limited to early successional habitats [*Vitousek et al.*, 2002]. Second, we allow N losses via plant-unregulated pathways (e.g., leaching by dissolved organic N, DON, or volatilization of N by fire) to limit the retention and buildup of N at the ecosystem level [*Perakis and Hedin*, 2002]. While both mechanisms are essential for capturing interactions between CO₂ uptake, N limitation and LUC and are to some extent also considered in other models with N (e.g., fire loss in *Thornton et al.* [2007] and *Zaehle and Friend* [2010]; N fixation response to N demand in *Wang et al.* [2007] and *Fisher et al.* [2010]), their effect depends critically upon the specific dynamics by which they interact with the successional dynamics following LUC.

[8] We subjected the model to the following scenarios: (i) historical increase in CO_2 from 282 to 369 ppm [*Etheridge et al.*, 1998; *Keeling et al.*, 2009] combined with local climate from reanalysis data [*Sheffield et al.*, 2006] since 1950 (identified as + CO_2); (ii) historical land use transitions as gridded annual land conversions since 1500, including shifting cultivation and forestry [*Hurtt et al.*, 2006] (+LU). In both cases we prescribed either anthropogenic N deposition based on geographic source trends [*Dentener*, 2006]



Figure 2. Modeled changes in the land C sink between 1800 and 2000. The scenarios consider C-N interactions (red) versus the C cycle alone (orange) in the LM3V-N global land model. (a) Cumulative changes in the full model $(+CO_2 + LU + N)$, land use and $CO_2 (+CO_2 + LU)$, land use and N deposition (+LU+N), and land use alone (+LU). The black bar indicates the cumulative sink from ocean budgets (27) corrected for long-term C storage in wet/peat lands and wood products and caused by fire suppression (Tables S1–S3). The difference between (+LU) and $(+CO_2 + LU + N)$ simulations represents the "residual land sink." (b) Annual rates of land-atmosphere C exchange from our full model (+CO₂+LU+N; solid red and orange lines) compared against three independent records inferred from ¹³C/¹²C deconvolution of atmospheric CO_2 (dashed black line), ocean tracer deconvolution (solid black line), and ocean biogeochemistry models (gray area). The ocean model range was calculated from four broadly resolved models (1800-1990) and four comprehensive models (1948-2000) combined with a 5% uncertainty in fossil fuel emissions, using quadratic error propagation (supporting information).

 Table 1. C and N Net Uptake Into the Residual Terrestrial Sink

	Global	Tropics	Extratropics
Global cumulative residual C sink (PgC)	150	75	75
Residual C sink in primary and secondary vegetation	119	65	54
Cumulative N sink in primary and secondary vegetation (PgN)			
(a) Change in inputs (Δ)			
ΔDeposition	1.02	0	1.02
ΔFixation	2.10	1.63	0.48
(b) Change in losses			
ΔDIN	0.08	-0.17	0.26
ΔDON	0.01	0.01	0
Δ Fire volatilization	0.46	0.33	0.13
ΔBiomass removal	0.08	0.05	0.03
Net N accumulation in primary and secondary vegetation $(a - b)$	2.48	1.40	1.08

Detailed N and C budgets for nonagricultural land areas (primary and secondary vegetation) calculated as cumulative fluxes over the past 200 years. The "residual C sink" is the net C accumulation discounted for land use emissions, calculated as the difference between ($+LU+CO_2+N$) and (+LU) simulations.

(+N) or unpolluted background deposition. To evaluate N feedbacks in the land C system we compared simulations that coupled the C and N cycle (identified as C-N) versus the C cycle alone (C only).

3. Results and Discussion

3.1. Historical Land C and N Sink

[9] The full C-N model variant of LM3V-N considers all interacting factors (+CO₂+LU+N) and is capable of broadly recreating the historical land C sink (red line in Figures 2a and 2b). The predictions of the historical (1800-2005) cumulative land C loss and the modern (1980-2005) annual net C uptake (51 PgC and 0.9 PgC yr⁻¹, respectively) agree well with several independent estimates of the land C budget (Figure 2). First, the cumulative estimate coincides with reconstructions [Sabine et al., 2004] based on emission estimates adjusted for ocean uptake and atmospheric CO₂ increase and corrected for long-term C storage in wet/peat lands and wood products and caused by fire suppression (black bar in Figure 2a; supporting information and Tables S1-S3). Second, the results compare well against historical trends in land-atmosphere C exchange inferred from three types of independent records: ¹³C/¹²C deconvolution of atmospheric CO₂ [Joos and Bruno, 1998], analysis of oceanic tracers [Khatiwala et al., 2009], and ocean models [Enting et al., 1995; Sarmiento et al., 2010] (Figure 2b). The model recreates the broad secular pattern of these three records: a sustained low land C source before ~1950, a shift to C uptake in 1950–1960s, and a dramatic acceleration of C uptake over the past four decades. An abrupt peak in the historical forest to agriculture conversion estimates (Figure S2) leads to a large modeled land C source peaking in the 1950s (Figure 2b). The mismatch between 1930 and 1950 may have further been exacerbated by different time series available for ice core CO₂ data [Etheridge et al., 1998]: We have used the high-frequency spline-fitted CO₂ data to drive the model and to infer the land budget while ocean model uptake was calculated based on the low-frequency CO₂ series prior to 1950.

[10] Third, LM3V-N recreates the increase in strength of the land C sink observed on a decadal time scale between 1980 and 2005 (Figure S3). Fourth, the model reasonably predicts the observed geographical pattern of a strong Northern Hemisphere C sink (0.7 PgC yr⁻¹), a weaker tropical sink (0.4 PgC yr⁻¹), and a negligible Southern Hemisphere sink (<0.1 PgC yr⁻¹, Figure S3).

[11] In contrast, if we ignore N feedbacks by considering the C-only model (+CO₂+LU), we overestimate the current land C sink by 0.6 PgC yr⁻¹ and cumulative land uptake by as much as 57 PgC and (Figure 2). This discrepancy in land C uptake between the C-N versus C-only models intensified in recent decades and remained exceptionally high between 1980 and 2005 (Figure 2b).

[12] We next examined the historical influence of each factor individually. LUC alone (disallowing changes in CO2, climate, and N deposition) caused a loss of 198 PgC from land over the entire record (+LU in Figure 2a). In this scenario, N limitation has little impact on the simulated land use C loss. Inclusion of N deposition (+LU+N) diminished this loss term starting in the 1940s when fossil fuel burning brought about large-scale atmospheric N pollution. Further, inclusion of the CO_2 increase (+ CO_2 +LU+N) induced a substantial C uptake by vegetation and soils, which in turn transformed the land biosphere into a net C sink after ~1960. The quantity of C sequestered by land after discounting C emitted by land conversion-referred to as the residual C sink-increased steadily throughout the historical period (difference between full model and +LU in Figure 2a). C sequestered by plants and soil in non-agricultural ecosystems (i.e., that contain either primary or secondary vegetation; Table 1) is similar in tropical (65 PgC) and extratropical (54 PgC) regions, with the ratio of C sequestered in vegetation versus soil higher in tropical compared to extratropical regions (0.55 versus 0.26).

[13] Our findings do not support the idea of a static land N cycle, but instead imply that the land biosphere possesses considerable capacity to adjust the N balance to CO₂ fertilization. We summarize in Table 1 the sources of new N that have supported the historical land C sink: anthropogenic N deposition (1.0 PgN) and biological N₂ fixation (2.1 PgN). The tropical C sink was largely supported by increased N₂ fixation (1.6 PgN) in response to enhanced vegetation N demand. In contrast, the extratropical sink was mainly created by N deposition downwind of industrialized regions (1.0 PgN), with fixation playing a minor role (0.48 PgN;



Figure 3. Cumulative magnitude of the nonadditive C sink (*v*) from land use and CO_2 effect. We calculate terms of nonlinear interaction between land use transitions (+LU) and environmental change (combined effect of CO_2 and N deposition; + CO_2 +N) based the C-N scenario of LM3V-N. The total nonlinear effect (black line) is the sum of a C *sink foregone* in agricultural land (red line), an *accelerated regrowth* vegetation sink after disturbance (blue line), and a *compounded clearance loss* following disturbance (green line, see supporting information for specific calculations).

Figure S4). Elevated N deposition was partly offset by increased hydrological and gaseous N losses (sum quantity expressed as "DIN" in Table 1) from temperate regions that experienced N saturation [Ågren et al., 2001]. Fire contributed a small but nonnegligible change to the tropical N cycle (0.33 PgN). Overall, we obtained a terrestrial uptake efficiency of 48 PgC per Pg N accumulated across the entire biosphere.

3.2. Interactive Effects of the C Sink With Land Use

[14] Our analysis explicitly considers the interactive effects of CO₂, LUC, and N on the cumulative C sink, and therefore allows us to quantify the potential existence of nonlinear interactions over time. We estimated the nonlinear component (v) of the land-atmosphere C flux (F) by comparing the combined effects of all factors (+CO₂+LU+N) versus the sum of LUC effects and biogeochemical factors (+LU versus +CO₂+N) in partial models (Figure S5):

$$v = F(+CO_2 + LU + N) - F(+LU) - F(+CO_2 + N).$$

[15] We found a substantial and accelerating nonlinear effect (Figure 3) in which the interaction between LUC, CO₂, and N deposition reduced the C sink by 22 PgC over the historical record. By calculating accumulation and removal of C across land use categories (natural vegetation, secondary vegetation, pasture, and cropland), we can decompose this nonlinear effect into the three specific mechanisms discussed earlier-sink foregone, accelerated regrowth, and compounded clearance loss (Figure 3 and supporting information). Regrowing secondary vegetation has a positive effect on CO₂ fertilization, in contrast to recent simulations [Jain et al., 2013]. Consideration of successional dynamics during land use recovery allows us to resolve the transient behavior of N dynamics, showing periods of high-N supply and diminished N limitation (Figure 1) combined with up-regulated N fixation at early recovery stages. A transient N sufficiency originating from land use disturbance is in alignment with the long-term trend in nitrate export at the Hubbard Brook Experimental Forest [Bernal et al., 2012]. The resulting N-induced accelerated regrowth ultimately enhanced the land C sink in secondary compared to primary vegetation (Figure 4). In contrast, the C sink foregone and compounded clearance loss acted to diminish the sink over time. The combined effect of all three terms has been to repress the current day land C sink by as much as $40\% (0.4 \text{ PgC yr}^{-1})$ compared to the purely additive/linear scenario (see Table S4 for recent nonlinear fluxes).

4. Conclusions

[16] Most broadly, our results suggest that, over the anthropocene, the land C sink has been strongly influenced by biogeochemical feedbacks between LUC and the coupled cycles of C and N. Our findings differ from models based on either potential vegetation alone [Sokolov et al., 2008; Thornton et al., 2007] or time-invariant vegetation classes [Churkina et al., 2007; Jain et al., 2013; Yang et al., 2010], in that our ability to resolve land use disturbance and successional dynamics allows us to identify and quantify specific mechanism that cause nonlinear interactions in the land C sink. We conclude that the combined effects of three mechanisms—sink foregone, accelerated regrowth, and compounded clearance loss—are increasingly influencing the trajectory of the land C sink. As a result, the land

biosphere is experiencing accelerating constraints on the C sink. Most global models do not consider local interactions between CO_2 uptake, N limitation, and land use recovery, foregoing the potential for nonlinear interactions. Our results call for more detailed representation of land use recovery in global land models by considering the successional dynamics of C and N cycles.

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References

- Ågren, G., E. Bosatta, and A. Magill (2001), Combining theory and experiment to understand effects of inorganic nitrogen on litter decomposition, *Oecologia*, 128(1), 94–98, doi:10.1007/s004420100646.
- Arora, V. K., and G. J. Boer (2010), Uncertainties in the 20th century carbon budget associated with land use change, *Global Change Biol.*, 16(12), 3327–3348, doi:10.1111/j.1365-2486.2010.02202.x.
- Ballantyne, A. P., C. B. Alden, J. B. Miller, P. P. Tans, and J. W. C. White (2012), Increase in observed net carbon dioxide uptake by land and oceans during the past 50 years, *Nature*, 488(7409), 70–72, doi:10.1038/ nature11299.
- Bernal, S., L. O. Hedin, G. E. Likens, S. Gerber, and D. C. Buso (2012), Complex response of the forest nitrogen cycle to climate change, *Proc. Natl. Acad. Sci. U. S. A.*, 109, 3406–3411, doi:10.1073/pnas.1121448109.
- Bonan, G. B., and S. Levis (2010), Quantifying carbon-nitrogen feedbacks in the Community Land Model (CLM4), *Geophys. Res. Lett.*, 37, L07401, doi:10.1029/2010GL042430.
- Cernusak, L. A., et al. (2013), Tropical forest responses to increasing atmospheric CO₂: Current knowledge and opportunities for future research, *Funct. Plant Biol.*, 40(6), 531–551.
- Churkina, G., K. Trusilova, M. Vetter, and F. Dentener (2007), Contributions of nitrogen deposition and forest regrowth to terrestrial carbon uptake, *Carbon Balance Manage.*, 2(5), 1–7, doi:10.1186/1750-0680-2-5.
- Dentener, F. J. (2006), Global maps of atmospheric nitrogen deposition, 1860, 1993, and 2050. Data set. Available on-line [http://daac.ornl.gov/] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A., in *Trends: A Compendium of Data on Global Change. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tenn., U.S.A.*
- Enting, I. G., T. M. Wigley, and M. Heimann (1995), Intergovernmental Panel on Climate Change (IPCC), Working Group 1, 1994: Modelling results relating future atmospheric CO₂ concentrations to industrial emissions, in Available from [http://cdiac.ornl/gov].
- Etheridge, D. M., L. P. Steele, R. L. Langenfelds, J.-M. Barnola, and V. I. Morgan (1998), Historical CO₂ records from the Law Dome DE08, DE08-2, and DSS ice cores, in *Trends: A Compendium of Data on Global Change. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tenn., U.S.A.*
- Fisher, J. B., S. Sitch, Y. Malhi, R. A. Fisher, C. Huntingford, and S.-Y. Tan (2010), Carbon cost of plant nitrogen acquisition: A mechanistic, globally applicable model of plant nitrogen uptake, retranslocation, and fixation, *Global Biogeochem. Cycles*, 24, GB1014, doi:10.1029/2009GB003621.
- Gerber, S., L. O. Hedin, M. Oppenheimer, S. W. Pacala, and E. Shevliakova (2010), Nitrogen cycling and feedbacks in a global dynamic land model, *Global Biogeochem. Cycles*, 24, GB1001, doi:10.1029/2008GB003336.
- Hedin, L. O., E. N. J. Brookshire, D. N. L. Menge, and A. R. Barron (2009), The nitrogen paradox in tropical forest ecosystems, *Annu. Rev. Ecol. Evol. Syst.*, 40(1), 613–635, doi:10.1146/annurev.ecolsys.37.091305.110246.
- Houghton, R. A. (1999), The annual net flux of carbon to the atmosphere from changes in land use 1850–1990, *Tellus B*, 51(2), 298–313, doi:10.1034/j.1600-0889.1999.00013.x.
- Hurtt, G. C., S. Frolking, M. G. Fearon, B. Moore, E. Shevliakova, S. Malyshev, S. W. Pacala, and R. A. Houghton (2006), The underpinnings of land-use history: Three centuries of global gridded land-use transitions, wood-harvest activity, and resulting secondary lands, *Global Change Biol.*, 12(7), 1208–1229, doi:10.1111/j.1365-2486.2006.01150.x.
- Jain, A., X. Yang, H. Kheshgi, A. D. McGuire, W. Post, and D. Kicklighter (2009), Nitrogen attenuation of terrestrial carbon cycle response to global environmental factors, *Global Biogeochem. Cycles*, 23, GB4028, doi:10.1029/2009GB003519.
- Jain, A. K., P. Meiyappan, Y. Song, and J. I. House (2013), CO₂ emissions from land-use change affected more by nitrogen cycle, than by the choice

of land-cover data, *Global Change Biol.*, 2893–2906, doi:10.1111/gcb.12207.

- Joos, F., and M. Bruno (1998), Long-term variability of the terrestrial and oceanic carbon sinks and the budgets of the carbon Isotopes ¹³C and ¹⁴C, *Global Biogeochem. Cycles*, *12*(2), 277–295.
- Keeling, R. F., S. C. Piper, A. F. Bollenbacher, and J. S. Walker (2009), Atmospheric CO₂ records from sites in the SIO air sampling network, in Trends: A Compendium of Data on Global Change. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tenn., U.S.A. [online] Available from: http://cdiac.ornl.gov/trends/co2/sio-mlo.html (Accessed 13 August 2010).
- Khatiwala, S., F. Primeau, and T. Hall (2009), Reconstruction of the history of anthropogenic CO₂ concentrations in the ocean, *Nature*, 462(7271), 346–349, doi:10.1038/nature08526.
- Norby, R. J., et al. (2005), Forest response to elevated CO₂ is conserved across a broad range of productivity, *Proc. Natl. Acad. Sci. U. S. A.*, *102*(50), 18,052–18,056, doi:10.1073/pnas.0509478102.
- Perakis, S. S., and L. O. Hedin (2002), Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds, *Nature*, 415(6870), 416–419, doi:10.1038/415416a.
- Pongratz, J., C. H. Reick, T. Raddatz, and M. Claussen (2009), Effects of anthropogenic land cover change on the carbon cycle of the last millennium, *Global Biogeochem. Cycles*, 23, GB4001, doi:10.1029/2009GB003488.
- Ramankutty, N., and J. A. Foley (1999), Estimating historical changes in global land cover: Croplands from 1700 to 1992, *Global Biogeochem*. *Cycles*, 13(4), 997–1027, doi:10.1029/1999GB900046.
- Sabine, C. L., et al. (2004), The oceanic sink for anthropogenic CO₂, *Science*, *305*(5682), 367–371, doi:10.1126/science.1097403.
- Sarmiento, J. L., M. Gloor, N. Gruber, C. Beaulieu, A. R. Jacobson, S. E. Mikaloff Fletcher, S. Pacala, and K. Rodgers (2010), Trends and regional distributions of land and ocean carbon sinks, *Biogeosciences*, 7(8), 2351–2367, doi:10.5194/bg-7-2351-2010.
- Sheffield, J., G. Goteti, and E. F. Wood (2006), Development of a 50-year high-resolution global dataset of meteorological forcings for land surface modeling, J. Clim., 19(13), 3088–3111, doi:10.1175/JCL13790.1.
- Shevliakova, E., S. W. Pacala, S. Malyshev, G. C. Hurtt, P. C. D. Milly, J. P. Caspersen, L. Sentman, C. Wirth, and C. Crevoisier (2009), Carbon cycling under 300 years of land-use changes in the dynamic land model

LM3V, Global Biogeochem. Cycles, 23, GB2022, doi:10.1029/2007GB003176.

- Sokolov, A. P., D. W. Kicklighter, J. M. Melillo, B. S. Felzer, C. A. Schlosser, and T. W. Cronin (2008), Consequences of considering carbon–nitrogen interactions on the feedbacks between climate and the terrestrial carbon cycle, *J. Clim.*, 21(15), 3776–3796.
- Strassmann, K. M., F. Joos, and G. Fischer (2008), Simulating effects of land use changes on carbon fluxes: past contributions to atmospheric CO₂ increases and future commitments due to losses of terrestrial sink capacity, *Tellus B*, 60(4), 583–603, doi:10.1111/j.1600-0889.2008.00340.x.
- Thornton, P. E., J.-F. Lamarque, N. A. Rosenbloom, and N. M. Mahowald (2007), Influence of carbon-nitrogen cycle coupling on land model response to CO₂ fertilization and climate variability, *Global Biogeochem. Cycles*, 21, GB4018, doi:10.1029/2006GB002868.
- Vitousek, P. M., et al. (2002), Towards an ecological understanding of biological nitrogen fixation, *Biogeochemistry*, 57–58(1), 1–45, doi:10.1023/ A:1015798428743.
- Wang, Y.-P., B. Z. Houlton, and C. B. Field (2007), A model of biogeochemical cycles of carbon, nitrogen, and phosphorus including symbiotic nitrogen fixation and phosphatase production, *Global Biogeochem. Cycles*, 21, GB1018, doi:10.1029/2006GB002797. [online] Available from: http:// www.agu.org/journals/gb/gb0701/2006GB002797/body.shtml (Accessed 4 March 2009).
- Yang, X., T. K. Richardson, and A. K. Jain (2010), Contributions of secondary forest and nitrogen dynamics to terrestrial carbon uptake, *Biogeosciences*, 7(10), 3041–3050, doi:10.5194/bg-7-3041-2010.
- Zaehle, S., and D. Dalmonech (2011), Carbon–nitrogen interactions on land at global scales: Current understanding in modelling climate biosphere feedbacks, *Curr. Opin. Environ. Sustain.*, 3(5), 311–320, doi:10.1016/j. cosust.2011.08.008.
- Zaehle, S., and A. D. Friend (2010), Carbon and nitrogen cycle dynamics in the O-CN land surface model: 1. Model description, site-scale evaluation, and sensitivity to parameter estimates, *Global Biogeochem. Cycles*, 24, GB1005, doi:10.1029/2009GB003521.
- Zaehle, S., A. D. Friend, P. Friedlingstein, F. Dentener, P. Peylin, and M. Schulz (2010), Carbon and nitrogen cycle dynamics in the O-CN land surface model:
 2. Role of the nitrogen cycle in the historical terrestrial carbon balance, *Global Biogeochem. Cycles*, 24, GB1006, doi:10.1029/2009GB003522.