Response to Editor Kerkweg

In my role as Executive editor of GMD, I would like to bring to your attention our Editorial version 1.1: http://www.geosci-model-dev.net/8/3487/2015/gmd-8-3487-2015.html. This highlights some requirements of papers published in GMD, which is also available on the GMD website in the 'Manuscript Types' section: http://www.geoscientific modeldevelopment.net/submission/manuscript_types.html

In particular, please note that for your paper, the following requirement has not been met in the Discussions paper:

- ***"The main paper must give the model name and version number (or other unique identifier) in the title."***

Please provide explicitly the name (or its acronym) and the version number of the framework in the title of your revised manuscript.

Responses: We thank the editor for the reminder of the journal requirement. We do acknowledge this important journal rule. However, we also would like to suggest that this manuscript is not a "Development and Technical Paper" or a "Model Experiment Description" paper, but rather, a "Methods for Assessment of Models" paper. The quasi-equilibrium framework is the name of the method to assess model performance. It is not a conventional product or tool, but rather, a theoretical approach that can be used to analytically understand model performance without the need to run a model. Within its core, the quasi-equilibrium framework is a way of thinking, and involves only several fundamental equations to evaluate how model performance change in response to different assumptions added into the model. Therefore, depending on the model assumptions it tests, number of equations will vary (as shown in our manuscript). Here, we evaluated many different model assumptions using this quasi-equilibrium framework. And therefore, with all respect, we believe that assigning a version number may result in misinterpretation of our manuscript.

GMD is encouraging authors to provide a persistent access to the exact version of the source code used for the model version presented in the paper. As explained in https://www.geoscientific-model-development.net/about/manuscript_types.html the preferred reference to this release is through the use of a DOI which then can be cited in the paper. For projects in GitHub a DOI for a released code version can easily be created using Zenodo, see https://guides.github.com/activities/citable-code/ for details.

You may consider to upload the program code of the specifc version of the paper as a supplement or make the code and data of the exact model version described in the paper accessible through a DOI (digital object identifier). In case your institution does not provide the possibility to make electronic data accessible through a DOI you may consider other providers (eg. zenodo.org of CERN) to create a DOI. Please note that in the code accessibility section you can still point the reader to the GitHub repository for the newest version even if you use a DOI for the relevant releases.

Responses: We have published our code via Zenodo, The DOI is 10.5281/zenodo.2574192. We have modified our code availability statement in the manuscript with this DOI update.

Response to Reviewer #1

Overall, this paper is excellent. It usefully adds to the body of experimental results based on the use of quasi-equilibrium models and further develops our understanding of the importance of key processes and assumptions.

Having said that, I was very happy with reading the paper up to page 19, line 5. Introduction and the associated discussion of past research was excellent, detailed and informative and structured to derived useful information and leading to new questions. The description of the model was also clear and gave all the relevant model components.
Responses: We thank the reviewer for this positive overall comment on our paper.

It was maybe a little long (34 equations), and there a danger that key model steps might have be swamped within a sea of less important ones. There might be a point in moving some of the model detail to Supplemental Information, and only presenting the key steps in the main text.
Responses: We have reduced the number of equations in the main text from a total of 34 to a total of 22 by moving most of the baseline equations (the original Eq. 1-15) into the Appendix, as an integrated part of the manuscript. We think this modification improves the readability of the method and result section, as well as provides fundamental analytical details to comply with journal's requirement (i.e. "contain the justification of the model structure in the main body of the paper", stated by the chief editor prior to our submission).

However, the remainder of the paper was not well presented. Page 19, line 6 should have started a 'Results Section' where the various figure and tables could have been presented and discussed in some detail. As it is, all the key findings were dumped here within half a page. I do not regard this as satisfactory.
Responses: We must respectfully point out that the reviewer may have misinterpreted our original Method and Result section. It was our deliberate intention to keep the Method and Result section together because the quasi-equilibrium framework is an analytical way of interpreting the likely impact of a model assumption to model behaviors. Therefore, derivations of equations are fundamental and deeply linked to the analysis of the results. In our original Method and Result section, we firstly described the baseline quasi-equilibrium framework (section 3.1), then assessed several recently-incorporated model assumptions (section 3.2 and 3.3), and one new model assumption that we propose in this study to represent priming effect in models (i.e. section 3.4). We have explicitly stated the flow of work on original Page 7, Lines 14 – 18. The paragraph starting from the original Page 19 line 6 describes the result of assessing priming effect using the quasi-equilibrium framework. This is only part of our result, and we believe that it should not be a result section by itself.

To improve readability, we have restructured the Method and Result section with the following modifications. 1). Moved baseline equation derivations into an Appendix, as stated above; 2) Changed section headers with section 3.2 renamed as "Analyses of new model assumptions using the quasi-equilibrium framework"; 3) added sub-section headers to contain each individual new model assumptions tested within this study, i.e. section 3.2.1 – different N uptake representation, section 3.2.2 - potential NPP approach, and section 3.2.3 – priming effect. Furthermore, we have revised the first two paragraphs of the Method and Result section (i.e. Starting from L20, Page 7, clean version) to emphasis the structure of this section. Finally, we have revised our Abstract with clearer interpretations of the individual assumption tested here.

Each figure shows important information that is not immediately obvious. It needs careful text that explains to the reader what we can learn from each figure. A general 'data dump' with virtually no explanation is never a good way to proceed, but totally unacceptable in this case, as the essence of the modelling is not immediately obvious, but the reader needs to be led through the various figures to extract the key insights gained from each.

Responses: We thank the reviewer for raising this important point but do not agree that we added "virtually no explanation". As we suggested earlier, both equation derivation and graphic interpretation complement each other when analyzing the results. We have detailed texts describing the baseline model figure (i.e. Figure 1), and each follow-on figures brought various levels of changes to the baseline figure. We have included explanatory texts throughout the Method and Result section to suggest how each model assumption, reflected via their analytical derivations, affect the figure and therefore the result interpretations. Hopefully with our revised text, reduced equations and restructured sections, our result interpretations will be clearer for the reviewer.

Some of that detail is then given in the Discussion, like page 21, line 5 onwards, but only very briefly. That reference is too brief on its own and would have needed a proper description in a results section that could then be referred to. So, the Discussion might be OK if it had an appropriate Results section. But without a Results section, the reference to the various figures is still too brief to be readily and fully understood by the reader.

So, all in all, I would regard the paper as not acceptable in its current form, but that is entirely due to the lacking Results Section and insufficient description of the modeled findings. If that can be added, and the Discussion section then be modified to appropriately refer to text in the Results Section, the paper should be able to make a really strong contribution to the literature.

Responses: We have revised our discussion following this comment together with suggestions made by Reviewer 2. In particular, we have added discussion on how the predicted plant response to eCO_2 under progressive N limitation compares against a meta-analysis that bridges the progressive nitrogen limitation theory with data. We have also added discussion comparing the quasi-equilibrium framework with the multiple element limitation framework developed by Rastetter and Shaver (1992). We believe that these two additions are useful contextual information to enrich our discussion materials.

Minor comments: Page 3, line 7: The authors introduce the abbreviations QE for 'quasiequilibrium'. That is unnecessary in my view and just obscures the subsequent text. 'Quasi-equilibrium' is short enough and can continue to be used throughout the paper. No need to confuse the reader by an unnecessary abbreviation.

Responses: We have revised our manuscript by swapping "QE" with quasi-equilibrium.

Page 7, line 7: When the authors mention 'concentration-carbon' feedback, I assume they mean 'CO2-carbon' feedback. It would be better if that could be spelled out more explicitly as 'CO2-carbon' or something else that would leave the reader in doubt as to what concentration is referred to.

Responses: Great suggestion. We have revised accordingly. The line now reads as: "The TEM (Sokolov et al., 2008) and CLM models (Thornton et al., 2009), which assumed inflexible stoichiometry, had a large climate-carbon feedback but a small CO_2 concentration-carbon feedback, contrasting with the O-CN model (Zaehle et al., 2010), which assumed flexible stoichiometry and had a small climate-carbon feedback and a large CO_2 concentration-carbon feedback.".

Page 7, line 22: Here, it states that in assumption 3, N uptake is modeled as a saturating function of root biomass. This makes it sound as though there were no upper limit to N uptake other than that imposed by root biomass. However, the detailed model description states that N uptake is also dependent on mineralized N, which seems like a sensible assumption. Just make sure that in the initial description of this assumption, it is also made clear that mineralized N is a co-limiting factor. Currently, that is not included and gives a misleading impression of the model assumption.

Responses: We have revised the text wherever possible.

Nothing to add to the Model Description. The text after that needs some bigger overhaul as mentioned above, and I have refrained from referring to specific details as they will hopefully be changed in a bigger re-write.

Responses: As we stated above, we have made significant structural changes to the Method and Result section, and we hope that the revised text will be deemed satisfactory by the reviewer.

Response to Reviewer #2

This study tries to establish a quasi-equilibrium (QE) analytical framework, introduced by Comins & McMurtrie (1993), for evaluating model assumptions on carbon-nitrogen interaction in influencing ecosystem responses to elevated CO2. Overall, this paper is extremely valuable for understanding a variety of assumptions in influencing model outputs of carbon and nitrogen coupling.

Responses: We thank the reviewer for this positive feedback on our manuscript.

I particularly like your examples on page 23 to make a point that "the QE framework can highlight where additional complexity is not valuable."

Responses: Thank you. This is indeed one of the key points that we would like readers to pay attentions to. We have also highlighted this important message in our revised Abstract.

Here are a few suggestions to improve your manuscript:

First, the authors may consider improve the readability of your paper so that your message can go more miles. It is quite competent of the authors to work out all those equations in section 3. But those equations will hinder delivering your message as not all the ecologists or even modelers will go over those equations when they read your paper.

Responses: Indeed, this is a problem that details in Section 3 may prevent a smooth read of the manuscript. In our revision, we have created an Appendix to contain baseline quasi-equilibrium framework derivations to both comply with the journal requirement of keeping all essential elements in the main body of text, as well as improve readability of our manuscript.

In addition, would it be possible to convert Table 1 to a graph so that readers can quickly get your message? To me, Table 1 is probably the most important part of your manuscript. Even though I am familiar with the subject, it still takes me a while to go over the table. Converting it to a figure may help deliver your message faster. Moreover, the abstract I don't think deliver the message well, especially the second half.

Responses: We have revised our abstract, in particular the second half, with explicit texts on the implications of the results obtained from this study.

Table 1 is a summary of the literature which have adopted the quasi-equilibrium framework in the past. We presented some detailed introduction and discussion of this pool of literature in our Literature Review section (Section 2), and provided a graphic example in Supplementary Figure 1. Given the diverse set of model assumptions evaluated in the past pool of literature, as presented in Table 1, it is not easy to plot one figure to sufficiently synthesize all information. However, the general aim of including Table 1 and the Literature Review section was to demonstrate the usefulness of the quasi-equilibrium framework; they are not the key novel results that this manuscript adds into the literature.

Table 3 summarizes how different model assumptions affected plant production response to eCO_2 at various time steps, which we believe are the "novel" results that this study brings. The graphic interpretations of the effect of each individual model assumption have been provided in Figures 4-6, and the table is a synthesis and numerical display of these results. We think that the combination of the Table and individual Figures is the most appropriate way of presenting our analyses. A summary figure based on Table 3 could have been too noisy to make detailed interpretations on. All our codes, including the quasi-equilibrium framework and those used to generate the plots, are publically accessible (DOI 10.5281/zenodo.2574192). Therefore, one can potentially explore how alternative plotting schemes compare using this code repository.

Second, the work by Comins & McMurtrie (1993) is great. But, during the same period in 1990s, Dr. Edward Rastetter has developed the Multiple Element Limitation (MEL) model of carbon-nitrogen interactions. He published a few papers to illustrate similar principles on carbon-nitrogen interactions as revealed by G'DAY. In fact, Ed Rastetter also lumped all those assumptions (or processes) into three categories as in the first three items of your Table 1. MEL further shows the time scales at which each of the three categories of processes plays. In other words, MEL not only gives information about the equilibrium responses but also offers information about C/N interaction to influence transient dynamics. I think the authors at least should acknowledge Ed's work in your manuscript.

Responses: Thank you for this insightful comment. We have added a paragraph in the Discussion section to introduce and compare the multiple element limitation framework in the context of its similarity and differences against the quasi-equilibrium framework. Please refer to L 3 on Page 23 (clean version) and the text below for details.

"The multiple element limitation framework developed by Rastetter and Shaver (1992) analytically evaluates the relationship between short-term and long-term plant responses to eCO_2 and nutrient availability under different model assumptions. It was shown that there could be markedly difference in the short-term and long-term ecosystem responses to eCO_2 (Rastetter et al., 1997; Rastetter and Shaver, 1992). More specifically, Rastetter et al. (1997) showed that the ecosystem NPP response to eCO_2 appeared on several characteristic timescales: 1) there was an instantaneous increase in NPP, which results in an increased vegetation C:N ratio, 2) on a timescale of a few years, the vegetation responded to eCO_2 by increasing uptake effort for available N through increased allocation to fine roots, 3) on a timescale of decades, there was a net movement of N from soil organic matter to vegetation, which enables vegetation biomass to accumulate, and 4) on the timescale of centuries, ecosystem responses were dominated by increases in total ecosystem N, which enable organic matter to accumulate in both vegetation and soils. Both the multiple element limitation framework and the quasi-equilibrium framework provides information about the equilibrium responses. These approaches also provide information about the degree to which the ecosystem replies on internally recycled N vs. exchanges of with external sources and sinks. The multiple element limitation framework also offers insight into the C-N interaction that influences transient dynamics. These analytical frameworks are both useful tools for making quantitative assessments of model assumptions. "

Third, it is fine that the G'DAY model offers an analytical framework to evaluate model assumptions on carbon and nitrogen interactions. However, the impacts (or sensitivity) of those assumptions evaluated by the framework depend on the ranges of the variables you changed. For example, your analysis shows that wood N:C flexibility is very important for modeling carbon and nitrogen interactions. What ranges of wood N:C did those studies change? Do those ranges realistically match observations? Lots of data are available to evaluate those ranges. In fact, several studies have evaluated the ranges of changes of those variables (e.g., Liang et al. 2016). Bringing observations into your study may require the authors to do additional work but will improve quality of your study. At least the authors should add discussion on observed vs. modeled ranges of changes.

Responses: Thank you again for this insightful comment. We have incorporated a paragraph in our discussion to reflect this recommendation. Please refer to L. 12 on Page 20 (clean version) and the paragraph below for details. As suggested in our added discussion text, we would like to highlight that it is still our major purpose to demonstrate how one can analytically interpret consequence of a model assumption without running a model, rather than having readers to focus on how close one can match some theoretical model behaviors with a range of observations. In our Discussion section, some texts were already written illustrating this point (e.g. L. 9, Page 19, clean version: "Examples of models assuming constant (Thornton et al., 2007; Weng and Luo, 2008) and variable (Zaehle and Friend, 2010) plant tissue stoichiometry are both evident in the literature, and therefore, assuming all other model structure and assumptions are similar, prediction differences could potentially be attributed to the tissue stoichiometric assumption incorporated into these models, as suggested in some previous simulation studies (Medlyn et al., 2016; Medlyn et al., 2015; Meyerholt and Zaehle, 2015; Zaehle et al., 2014). Together with more appropriate representation of the trade-offs governing tissue C-N coupling (Medlyn et al., 2015), further tissue biochemistry data is necessary to constrain this fundamental aspect of ecosystem model uncertainty (Thomas et al., 2015)."). Therefore, while we believe it is important to bridge observations with modeling, the inclusion of such an analysis may make this already heavily condensed paper more complicated. A follow-up study could make a focused effort evaluating some case-specific data-model comparisons based on the quasi-equilibrium framework.

The added paragraph starting from L.12, Page 20: "Processes regulating the progressive nitrogen limitation under eCO_2 were evaluated by Liang et al. (2016) based on a meta-analysis, which bridged the gap between theory and observations. It was shown that the expected diminished CO_2 fertilization effect on plant growth was not apparent at the ecosystem scale due to extra N supply through increased biological N fixation and decreased leaching under eCO2. Here, our baseline assumption assumed fixed N input into the system, and therefore plant available N is progressively depleted through increased plant N sequestration under eCO_2, as depicted by the progressive N limitation hypothesis (Luo et al., 2004). A function that allows N fixation parameter to vary could provide further assessment of the tightness of the ecosystem N cycle process and its impact to plant response to eCO_2. Furthermore, given the significant role wood N:C ratio plays in plant N sequestration, matching modelled range of wood tissue stoichiometry with observations can provide addition level of evaluation of model performance. Our study provides a generalizable evaluation based on the assumption that wood N:C ratio, when allowed to vary in a model, is proportional to leaf N:C ratio. Case-specific, more realistic evaluations can be performed based on the quasi-equilibrium framework to bridge models with observations.”.

Forth, if the authors want to popularize the QE framework to be used by the broad community, they may develop a simpler scheme for others to use. The extensive list of those equations may make it very difficult for others to use.

Responses: Agree. We have revised our baseline model description in the main text to emphasize the key philosophy of the quasi-equilibrium framework. We have kept all related equation derivations in the Appendix for interested readers to refer to. Moreover, as indicated earlier, we have made our code repository publically accessible, which can be used as the testbed for further model assumption analysis.

Reference: Junyi Liang, Xuan Qi, Lara Souza, and Yiqi Luo. 2016. Processes regulating progressive nitrogen limitation under elevated carbon dioxide: a meta-analysis. Biogeosciences, 13, 2689-2699.

Responses: This is a useful reference, and we have incorporated it with a new paragraph discussing the performance of our model against the general patterns summarized in this literature, as introduced earlier (i.e. L. 12 on Page 20, clean version).

The quasi-equilibrium framework re-visited: analyzing long-term CO_2 enrichment responses in plant-soil models

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Abstract. Elevated carbon dioxide (CO_2) can increase plant growth, but the magnitude of this CO_2 fertilization effect is modified by soil nutrient availability. Predicting how nutrient availability affects plant responses to elevated CO_2 is a key consideration for ecosystem models, and many modelling groups have moved to, or are moving towards, incorporating nutrient limitation in their models. The choice of assumptions to represent nutrient cycling processes has a major impact on model predictions, but it can be difficult to attribute outcomes to specific assumptions in complex ecosystem simulation models. Here we revisit the quasi-equilibrium analytical framework introduced by Comins & McMurtrie (1993) and explore the consequences of specific model assumptions for ecosystem net primary productivity. We review the literature applying this framework to plant-soil models, and then analyze the effect of several new assumptions on predicted plant responses to elevated CO_2. Examination of alternative assumptions

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for plant nitrogen uptake showed that a linear function of the mineral nitrogen pool or a linear function of the mineral nitrogen pool with additional saturating function of root biomass yield similar CO_2 responses at longer timescales (> 5 years), suggesting that the added complexity may not be needed when these are the timescales of interest. In contrast, a saturating function of the mineral nitrogen pool with linear dependency on root biomass yields no soil nutrient feedback at the very long-term (>500 years), near-equilibrium timescale, meaning that one should expect the model to predict a full CO_2 fertilization effect on production. Secondly, we show that incorporating a priming effect on slow soil organic matter decomposition attenuates the nutrient feedback effect on production, leading to a strong medium-term (5-50 years) CO_2 response. Models incorporating this priming effect should thus predict a strong and persistent CO_2 fertilization effect over time. Thirdly, we demonstrate that using a “potential NPP” approach to represent nutrient limitation of growth yields a relatively small CO_2 fertilization effect across all timescales. Overall, our results highlight that the quasi-equilibrium analytical framework is effective for evaluating both the consequences and mechanisms through which different model assumptions affect predictions. To help constrain predictions of the future terrestrial carbon sink, we recommend use of this framework to analyze likely outcomes of new model assumptions before introducing them to complex model structures.

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Keywords: analytical approximation | equilibrium | CO_2 fertilization | nitrogen | priming | nutrient uptake

1 Introduction

Predicting how plants respond to atmospheric carbon dioxide (CO_2) enrichment (eCO_2) under nutrient limitation is fundamental for an accurate estimate of the global terrestrial carbon (C) budget in response to climate change. There is now ample evidence that the response of terrestrial vegetation to eCO_2 is modified by soil nutrient availability (Fernández-Martínez et al., 2014; Norby et al., 2010; Reich and Hobbie, 2012; Sigurdsson et al., 2013). Over the past decade, land surface models have developed from C-only models to carbon-nitrogen (CN) models (Gerber et al., 2010; Zaehle and Friend, 2010). The inclusion of C-N biogeochemistry has been shown to be essential to capture the reduction in the CO_2 fertilization effect with declining nutrient availability and therefore its implications for climate change (Zaehle et al., 2015). However, it has also been shown that models incorporating different assumptions predict very different vegetation responses to eCO_2 (Lovenduski and Bonan, 2017; Medlyn et al., 2015). Careful examination of model outputs has provided insight into the reasons for the different model predictions (De Kauwe et al., 2014; Medlyn et al., 2016; Walker et al., 2014; Walker et al., 2015; Zaehle et al., 2014), but it is generally difficult to attribute outcomes to specific assumptions in these plant-soil models that differ in structural complexity and process feedbacks (Lovenduski and Bonan, 2017; Medlyn et al., 2015; Thomas et al., 2015).

Understanding the mechanisms underlying predictions of ecosystem carbon cycle processes is fundamental for the validity of prediction across space and time. Comins and McMurtrie (1993) developed an analytical framework, the “quasi-equilibrium” approach, to make model predictions traceable to their underlying mechanisms. The approach is based on the two-timing approximation method (Ludwig et al., 1978) and makes use of the fact that ecosystem models typically represent a series of pools with different equilibration times. The method involves: 1) choosing a time interval (τ) such that the model variables can be divided into “fast” pools (which approach effective equilibrium at time τ) and “slow” pools (which change only slightly at time τ); 2) holding the “slow” pools constant, and calculating the equilibria of the “fast” pools (an effective equilibrium as this is not a true equilibrium of the entire system); and 3) substituting the “fast” pool effective equilibria into the original differential equations to give simplified differential equations for the slow pools at time τ.

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In a CN model, plant net primary production (NPP) can be estimated from two constraints, based on equilibration of the C balance (the “photosynthetic constraint”) and the N balance (the “nitrogen recycling constraint”) (Comins and McMurtrie, 1993). Both constraints link NPP with leaf chemistry (i.e. N:C ratio) (derivation in Section 3.1). The simulated production occurs at the intersection of these two constraint curves (shown graphically in Figure 1). To understand behaviour on medium and long-time scales (e.g. wood, and slow and passive soil organic pools in Figure 2, 20 – 200 years), one can assume that plant pools with shorter equilibration times in the model (e.g. foliage, fine-root or active soil organic pools in Figure 2) have reached quasi-equilibrium, and model dynamics are thus driven by the behaviour of the longer timescale pools.

The recent era of model development has seen some significant advances in representing complex plant-soil interactions, but models still diverge in future projections of CO_2 fertilization effect on NPP (Friend et al., 2014; Koven et al., 2015; Walker et al., 2015). A recent series of multi-model inter-comparison studies has demonstrated the importance of understanding underlying response mechanisms in determining model response to future climate change (Medlyn et al., 2015), but this can be difficult to achieve in complex global models. The quasi-equilibrium framework is a relatively simple but quantitative method to examine the effect of different assumptions on model predictions. As such, it complements more computationally expensive sensitivity analyses, and can be used as an effective tool to provide *a priori* evaluation of both the consequence and mechanism through which different new model implementations affect model predictions.

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Here, by constructing a quasi-equilibrium framework based on the structure of the Generic Decomposition and Yield (G'DAY) model (Comins and McMurtrie, 1993), we evaluate the effects on plant responses to eCO_2 of some recently-developed model assumptions incorporated into ecosystem models, for example the Community Land Model (CLM)(Oleson et al., 2004), the Community Atmosphere–Biosphere Land Exchange (CABLE) model (Kowalczyk et al., 2006), the Lund-Potsdam-Jena (LPJ) model (Smith et al., 2001), the JSBACH model (Goll et al., 2017b), and the O-CN model (Zaehle et al. 2010). Specifically, we test how different functions affecting plant N uptake influence NPP responses to eCO_2 at various quasi-equilibrium time steps. The present study is a continuation of the series of the quasi-equilibrium studies as reviewed in Section 2, with a general aim of helping to understanding the similarities and differences of predictions made by different process-based models, as demonstrated in Section 3.

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2. Literature Review

Many of the assumptions currently being incorporated into CN models have previously been explored using the quasi-equilibrium framework; here we provide a brief literature review describing the outcomes of this work (Table 1). Firstly, the flexibility of plant and soil stoichiometry has recently been highlighted as a key assumption (Stocker et al., 2016; Zaehle et al., 2014). A key finding from early papers applying the quasi-equilibrium framework was that model assumptions about the flexibility of the plant wood N:C ratio (Comins, 1994; Comins and McMurtrie, 1993; Dewar and McMurtrie, 1996; Kirschbaum et al., 1994; Kirschbaum et al., 1998; McMurtrie and Comins, 1996; Medlyn and Dewar, 1996) and soil N:C ratio (McMurtrie and Comins, 1996; McMurtrie et al., 2001; Medlyn et al., 2000) were critical determinants of the magnitude of the transient (10 to > 100 years) plant response to eCO_2 (Figure 1). Different to the effect of foliar N:C ratio flexibility, which has an instantaneous effect on photosynthesis, the flexibility of the wood N:C ratio controls the flexibility of nutrient storage per unit biomass accumulated in the slow turnover pool. Therefore, a constant wood N:C ratio, such as was assumed in CLM4 (Thornton et al., 2007; Yang et al., 2009), means that effectively a fixed amount of N is locked away from the active processes such as photosynthesis on the timescale of the lifespan of the woody tissue. In contrast, a flexible wood N:C ratio, such as was tested in O-CN (Meyerholt and Zaehle, 2015), allows variable N storage in the woody tissue, and consequently more nutrient available for C uptake at the transient timescale. Similarly, flexibility in the soil N:C ratio determines the degree of the soil N cycle feedback (e.g. N immobilization and mineralization) and therefore its effect on plant response to eCO_2. A large response to eCO_2 occurs when the soil N:C ratio is allowed to vary, whereas there could be little or no response if the soil N:C ratio is assumed to be inflexible (McMurtrie and Comins, 1996).

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Changes in plant allocation with eCO_2 are also a source of disagreement among current models (De Kauwe et al. 2014). The quasi-equilibrium framework has been used to investigate a number of different plant C allocation schemes (Comins and McMurtrie, 1993; Kirschbaum et al., 1994; Medlyn and Dewar, 1996). For example, Medlyn and Dewar (1996) suggested that plant long-term growth responses to eCO_2 depend strongly on the extent to which stem and foliage allocations are coupled. With no coupling (i.e.

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fixed allocation of C and N to stemwood), plant growth was not responsive to eCO_2; with linear coupling (i.e. allocation to stemwood proportional to foliage allocation), a significant long-term increase in total growth following eCO_2 was found (Figure S1). The reason for this is similar to the argument behind wood N:C ratio flexibility, that decreasing C allocation to wood decreases the rate of N removal per unit of C invested in growth. In contrast, Kirschbaum et al. (1994) found that changes in allocation between different parts of plant only marginally changed the CO_2 sensitivity of production at different timescales. The fundamental difference between the two allocation schemes was that Kirschbaum et al. (1994) assumed that the root allocation coefficient was determined by a negative relationship with the foliar N:C ratio, meaning that the increase in foliar N:C ratio would lead to a decreased root allocation and increased wood and foliage allocation, whereas Medlyn and Dewar (1996) investigated stem-foliage allocation coupling without introducing a feedback via the foliar N:C ratio. The comparison of the two allocation schemes is indicative of the underlying causes of model prediction divergence in recent inter-model comparisons (De Kauwe et al., 2014; Walker et al., 2015).

Another hypothesis currently being explored in models is the idea that increased belowground allocation can enhance nutrient availability under elevated CO_2 (Dybzinski et al., 2014; Guenet et al., 2016). Comins (1994) argued that the N deficit induced by CO_2 fertilization could be eliminated by stimulation of N fixation. This argument was explored in more detail by McMurtrie et al. (2000), who assumed that eCO_2 led to a shift in allocation from wood to root exudation, which resulted in enhanced N fixation. They showed that, although the increase in N fixation could induce a large eCO_2 response in NPP over the long-term, a slight decrease in NPP was predicted over the medium-term. This decrease occurred because increased exudation at eCO_2 increased soil C input, causing increased soil N sequestration and lowering the N available for plant uptake. Over the long-term, however, both NPP and C storage were greatly enhanced because the sustained small increase in N input led to a significant build-up in total ecosystem N on this timescale.

The interaction between rising CO_2 and warming under nutrient limitation is of key importance for future simulations. Medlyn et al. (2000) demonstrated that short-term plant responses to warming, such as physiological acclimation, are over-ridden by the positive effects of warming on soil nutrient availability in the medium to long term. Similarly, McMurtrie et al. (2001) investigated how the flexibility of the soil N:C ratio affects predictions of the future C sink under elevated temperature and CO_2. They showed that assuming an inflexible soil N:C ratio with elevated temperature would mean a release of nitrogen with enhanced decomposition, leading to a large plant uptake of N to enhance growth. In contrast, an inflexible soil N:C ratio would mean that the extra N mineralized under elevated temperature is largely immobilized in the soil and hence a smaller increase in C storage. This effect of soil N:C stoichiometry on the response to warming is opposite to the effect on eCO_2 described above. Therefore, under a scenario where both temperature and CO_2 increase, the C sink strength is relatively insensitive to soil N:C variability, but the relative contributions of temperature and CO_2 to this sink differ under different soil N:C ratio assumptions (McMurtrie et al., 2001). This outcome may explain the results observed by Bonan and Levis (2010) when comparing coupled carbon cycle-climate simulations. The TEM (Sokolov et al., 2008) and CLM models (Thornton et al., 2009), which assumed inflexible stoichiometry, had a large climate-carbon feedback but a small CO_2 concentration-carbon feedback, contrasting with the O-CN model (Zaehle et al., 2010), which assumed flexible stoichiometry and had a small climate-carbon feedback and a large CO_2 concentration-carbon feedback. Variations among models in this stoichiometric flexibility assumption could potentially also explain the trade-off between CO_2 and temperature sensitivities observed by Huntzinger et al. (2017).

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3. Methods and Results

This section combines both methods and results together, because equation derivation is fundamental to the analytical and graphic interpretation of the model performance within the quasi-equilibrium framework. Below we first describe the baseline simulation model and derivation of the quasi-equilibrium constraints (Section 3.1), then follow with analytical evaluations of new model assumptions using the quasi-equilibrium framework (Section 3.2). Within each subsection (Section 3.2.1 to 3.2.3), we first provide key equations for each assumption and the derivation of the quasi-equilibrium constraints with

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these new assumptions, then provide our graphic interpretations and analyses to understand the effect of the model assumption on plant NPP responses to eCO_2.

More specifically, we tested alternative model assumptions for three processes that affect plant carbon-nitrogen cycling: (1) section 3.2.1 evaluates different ways of representing plant N uptake, namely plant N uptake as a fixed fraction of the mineral N pools, as a saturating function of the mineral N pool and linearly depends on root biomass (Zaehle and Friend, 2010), or as a saturating function of root biomass and linearly depends on mineral N pool (McMurtrie et al., 2012); (2) section 3.2.2 tests the effect the "potential NPP" approach that downregulates potential NPP to represent N limitation (Oleson et al., 2004); and (3) section 3.2.3 evaluates root exudation and its effect on soil organic matter decomposition rate (i.e. priming effect). The first two assumptions have been incorporated into some existing land surface model structures (e.g. CLM, CABLE, O-CN, LPJ), whereas the third is a framework proposed following the observation that models did not simulate some key characteristic observations of the DukeFACE experiment (Walker et al., 2015; Zaehle et al., 2014), and therefore could be of importance in addressing some model limitations in representing soil processes (van Groenigen et al., 2014; Zaehle et al., 2014). It is our purpose to demonstrate how one can use this analytical framework to provide *a priori* and generalizable understanding of the likely impact of new model assumption on model behaviour without having to run a complex simulation model. Here we do not target specific ecosystems to parameterize the model but anticipate that the analytical interpretation of quasi-equilibrium framework is of general applicability for woody-dominated ecosystems. One could potentially adopt the quasi-equilibrium approach to provide case-specific evaluations of model behaviour against observations (e.g. constraining the likely range of wood N:C ratio flexibility).

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3.1 Baseline model and derivation of the quasi-equilibrium constraints

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Our baseline simulation model is similar in structure to G'DAY (Generic Decomposition And Yield, Comins & McMurtrie 1993), a generic ecosystem model that simulates biogeochemical processes (C, N, and H_2O) at daily or sub-daily time steps. A simplified G'DAY model version that simulates plant-soil C-N interactions at a weekly timestep was developed for this study (Figure 2). In G'DAY, plants are represented by three stoichiometrically flexible pools: foliage, wood and roots. Each pool turns over at a fixed rate. Litter enters one of four litter pools (metabolic and structural above- and below-ground) and decomposes at a rate dependent on the litter N:C ratio, soil moisture and temperature. Soil organic matter (SOM) is represented as active, slow and passive pools, which decay according to first order decay functions with different rate constants. Plants access nutrients from the mineral N pool, which is an explicit pool supplied by SOM decomposition and an external input, which is assumed to be constant, as a simplified representation of fixation and atmospheric deposition.

The baseline simulation model further assumes that: 1) gross primary production (GPP) is function of a light-use efficiency (LUE), which depends on the foliar N:C ratio ($\boldsymbol{n_f}$) and atmospheric CO_2 concentration ($\boldsymbol{C_a}$) (Appendix A1), 2) carbon use efficiency (the ratio of NPP:GPP) is constant; 3) allocation of newly fixed carbon among foliage (a_f), wood (a_w) and root (a_r) pools is constant; 4) foliage (n_f), wood (n_w) and root N:C (n_r) ratios are flexible; 5) wood and root N:C ratios are proportional to the foliar N:C ratio, with constants of proportionality r_w and r_r, respectively; 6) a constant proportion (t_f) of foliage N is retranslocated before leaves senesce; 7) active, slow and passive SOM pools have fixed N:C ratios; and 8) an N uptake constant determines the plant N uptake rate. Definitions of parameters and forcing variables are summarized in Table 2. For all simulations, ambient CO_2 concentration (aCO_2) was set at 400 ppm and eCO_2 at 800 ppm.

We now summarize the key derivation of the two quasi-equilibrium constraints, the photosynthetic constraint and the nutrient cycling constraint, from our baseline simulation model (details provided in Appendix A1 and A2). The derivation follows Comins and McMurtrie (1993), which is further elaborated in work by (McMurtrie et al., 2000; Medlyn and Dewar, 1996), and evaluated Comins (1994). First, the photosynthetic constraint is derived by assuming that the foliage C pool (C_f) has equilibrated. Following

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the GPP and CUE assumptions (see above) and the detailed derivations made in Appendix A1, an implicit relationship between NPP and n_f exists:

$$NPP = LUE(n_f, C_a) \cdot I_0 \cdot \left(1 - e^{-k\sigma a_f NPP/s_f}\right) \cdot CUE \qquad \text{(Eq. 1)}$$

where I_0 is the incident radiation, k is the canopy light extinction coefficient, and σ is the specific leaf area. This equation is the photosynthetic constraint, which relates NPP with n_f.

Secondly, the nitrogen cycling constraint is derived by assuming that nitrogen inputs to, and outputs from, the equilibrated pools, are equal. Based on the assumed residence times of the passive SOM (~400 years), slow SOM (15 years) and woody biomass (50 years) pools, we can calculate the nutrient recycling constraint at three different timescales (conceptualized in Figure 3): very long (VL, > 500 years, all pools equilibrated), long (L, 100 – 500 years, all pools equilibrated except the passive pool), or medium (M, 5-50 years, all pools equilibrated except slow, passive and wood pools). At the VL-term, we have:

$$N_{in} = N_{loss} \qquad \text{(Eq. 2)}$$

where N_{in} is the total N input into the system, and N_{loss} is the total N lost from the system via leaching and volatilisation. Analytically, with some assumptions about plant N uptake (Appendix A2), we can transform Eq. 2 into a relationship between NPP and n_f, expressed as:

$$NPP = \frac{N_{in}(1 - l_n)}{l_n(a_f n_{fl} + a_w n_w + a_r n_r)} \qquad \text{(Eq. 3)}$$

where l_n is the fraction of N mineralization that is lost

a_f, a_w and a_r are the allocation coefficients for foliage, wood and roots, respectively, and n_{fl}, n_w and n_r are the N:C ratios for foliage litter, wood and roots, respectively.

Since n_w and n_r are assumed proportional to n_f (Table 2), the nutrient recycling constraint also links NPP and n_f. The intersection with the photosynthetic constraint yields the very-long term equilibria of both

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NPP and n_f. Similarly, we can write the nitrogen recycling constraint at the L-term and M-term as a function between NPP and n_f (details explained in Appendix A2). Their respective interaction with the photosynthetic constraint yields the L-term and M-term equilibria points of both NPP and n_f (Figure 1 and 3). Essentially, at each timescale, there are two unknowns (NPP and n_f) to be resolved via both the nitrogen recycling constraint and the photosynthetic constraint equations. Based on this set of analytical equations, one can evaluate how different assumptions affect the behaviour of the model quantitatively. Below, we describe how different new model assumptions affect the predicted plant response to a doubling of CO_2 concentration at various timescales.

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3.2 Evaluations of new model assumptions based on the quasi-equilibrium framework

3.2.1 Explicit plant N uptake

We now move to considering new model assumptions. We first consider different representations of plan N uptake. In the baseline model, the mineral N pool (N_{min}) is implicit, as we assumed that all mineralized N in the soil is either taken up by plants (N_U) or lost from the system (N_{loss}). Here, we evaluate three alternative model representations where plant N uptake depends on an explicit N_{min} pool, and their effects on plant responses to eCO_2. We consider plant N uptake as 1) a fixed coefficient of the mineral N pool, 2) a saturating function of root biomass and a linear function of the mineral N pool (McMurtrie et al., 2012), and 3) a saturating function of the mineral N pool and a linear function of root biomass. The last function has been incorporated into some land surface models, for example, O-CN (Zaehle and Friend, 2010) and CLM (Ghimire et al., 2016), while the first two have been incorporated into G'DAY(Corbeels et al., 2005).

A mineral N pool was made explicit by specifying a constant coefficient (u) to regulate the plant N uptake rate (i.e. $N_U = u \cdot N_{min}$). N lost from the system is a function of mineral N pool (N_{min}), regulated by a loss rate ($l_{n,rate}$, yr^{-1}). For the VL term equilibrium, we have $N_{in} = N_{loss}$, which means $N_{min} = \frac{N_{in}}{l_{n,rate}}$, hence:

$$N_{loss} = \frac{l_{n,rate}}{u} \cdot NPP \cdot (a_f n_{fl} + a_w n_w + a_r n_r) \qquad \text{(Eq. 4)}$$

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Where n_{fl} is the foliage litter N:C ratio, which is proportional to n_f (Table 2). At the VL equilibrium, we can re-arrange the above equation to relate NPP to n_f:

$$NPP = \frac{u\, N_{in}}{l_n \cdot (a_f n_{fl} + a_w n_w + a_r n_r)} \qquad \text{(Eq. 5)}$$

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which indicates that the N-cycling constraint for NPP is inversely dependent on n_f.

The second function represents plant N uptake as a saturating function of root biomass (C_r), and a linear function of the mineral N pool (McMurtrie et al., 2012), expressed as:

$$N_U = \frac{C_r}{C_r + K_r} \cdot N_{min} \qquad \text{(Eq. 6)}$$

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where K_r is a constant. At the VL equilibrium, we have $N_{in} = N_{loss} = l_{n,rate} N_{min}$, and $C_r = \frac{NPP \cdot a_r}{s_r}$, where s_r is the lifetime of root. Substituting for C_r in Eq. 6, we relate N_u with NPP:

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$$N_U = \frac{NPP \cdot a_r}{NPP \cdot a_r + K_r \cdot s_r} \cdot \frac{N_{in}}{l_{n,rate}} \qquad \text{(Eq. 7)}$$

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Since N_U is also a function of NPP, we can re-arrange and get:

$$NPP = \frac{N_{in}}{l_{n,rate}(a_f n_{fl} + a_w n_w + a_r n_r)} - \frac{K_r s_r}{a_r} \qquad \text{(Eq. 8)}$$

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Comparing with Eq. 5, here NPP is also inversely dependent on n_f, but with an additional negative offset of $\frac{K_r s_r}{a_r}$. The third approach to represent N uptake (e.g. O-CN and CLM) expresses N uptake as a saturating function of mineral N, and also linearly depends on root biomass (Zaehle and Friend, 2010), according to:

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$$N_U = \frac{N_{min}}{N_{min} + K} \cdot C_r \cdot V_{max} \qquad \text{(Eq. 9)}$$

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where K is a constant coefficient, and V_{max} , the maximum root N uptake capacity, is simplified as a constant here. Since N_U is also a function of NPP, we get

$$N_{min} = K \cdot \frac{\left(a_f n_{fl} + a_w n_w + a_r n_r\right)}{V_{max} \cdot \frac{a_r}{s_r} - \left(a_f n_{fl} + a_w n_w + a_r n_r\right)} \qquad \text{(Eq. 10)}$$

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This equation sets a limit to possible values of n_f. In equilibrium, for N_{min} to be non-zero, we need $\left(a_f n_{fl} + a_w n_w + a_r n_r\right) < V_{max} \frac{a_r}{s_r}$. The N loss rate is still proportional to the mineral N pool, so N_{loss} is given by

$$N_{loss} = l_{n,rate} \cdot K \cdot \frac{\left(a_f n_{fl} + a_w n_{wl} + a_r n_{rl}\right)}{V_{max} \cdot \frac{a_r}{s_r} - \left(a_f n_{fl} + a_w n_{wl} + a_r n_{rl}\right)} \qquad \text{(Eq. 11)}$$

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The above equation provides a N_{loss} term that no longer depends on NPP, but only on n_f. If the N leaching loss is the only system N loss, the VL-term nutrient constraint no longer involves NPP, implying that the full photosynthetic CO_2 fertilization effect is realized. The L- and M-term nutrient recycling constraints, however, are still NPP-dependent, due to feedbacks from the slowly recycling wood and SOM pools (e.g. Eq. A11 – A15).

The impacts of these alternative representations of N uptake are shown in Figure 4. First, the explicit consideration of the mineral N pool with a fixed uptake constant (u) of 1 yr^{-1} has little impact on the transient response to eCO_2 when compared to the baseline model (Figure 4a, Figure 1a, Table 3). Varying u does not strongly (<5%) affect plant responses to CO_2 fertilization at different time steps (Figure S2). This is because u is only a scaling factor of NPP, meaning it affects NPP but not its response to eCO_2 (Table 4), as depicted by Eq. 5.

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Moreover, the approach that assumes N uptake as a saturating function of root biomass and linearly depends on mineral P pool (McMurtrie et al., 2012) has comparable eCO_2 effects on production to the baseline and the fixed uptake coefficient models (Figure 4b, Table 3). Essentially, if $\frac{K_r s_r}{a_r}$ is small, we can approximate NPP by $\frac{N_{in}}{l_{n,rate}(a_f n_{fl}+a_w n_w+ a_r n_r)}$, which shares a similar structure to the baseline and fixed uptake coefficient models (Eq. 8, Eq. 5, and Eq. A10). Furthermore, Eq. 8 also depicts that increase in a_r should lead to higher NPP and increase in s_r or K_r should lead to decreased NPP. However, these predictions depend on assumptions of $l_{n,rate}$ and n_f. If $l_{n,rate}$ or n_f is small, NPP would be relatively less sensitive to a_r, K_r or s_r.

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By comparison, representing N uptake as a saturating function of mineral N and linearly depends on root biomass (Ghimire et al., 2016; Zaehle and Friend, 2010) no longer involves the VL-term nutrient recycling constraint on production (Figure 4c), which is predicted by Eq. 11. Actual VL-term NPP is determined only by n_f along the photosynthetic constraint, meaning that the full CO_2 fertilization effect on production is realized with the increase in CO_2. The magnitudes of the CO_2 fertilization effect at other time steps are comparable to those of the baseline model (Table 3), because the N_{loss} term is smaller than N_w, N_{Sp} or N_{Ss} terms, meaning it has a relatively smaller effect on NPP at equilibrium. However, steeper nutrient recycling constraint curves are observed (Figure 4c), indicating a stronger sensitivity of the NPP response to changes in n_f.

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3.2.2 Potential NPP

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In several vegetation models, including CLM-CN, CABLE and JSBACH, potential (non-nutrient limited) NPP is calculated from light, temperature and water limitations. Actual NPP is then calculate by down-regulating the potential NPP to match nutrient supply. Here we term this the “potential NPP” approach. We examine this assumption in the quasi-equilibrium framework following the implementation of this approach adopted in CLM-CN (Bonan and Levis, 2010; Thornton et al., 2007). The potential NPP is reduced if mineral N availability cannot match the demand from plant growth:

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$$P_{dem} = NPP_{pot}\left(a_f n_{fl} + a_w n_w + a_r n_r\right) \quad \text{(Eq. 12)}$$

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where P_{dem} is the plant N demand, and NPP_{pot} the potential NPP of the plant. Writing $\left(a_f n_f + a_w n_w + a_r n_r\right)$ as n_{plant}, the whole-plant N:C ratio, and the whole-soil N:C ratio as n_{soil}, we can calculate the immobilization N demand as:

$$I_{dem} = f C_{lit} s_t (n_{soil} - n_{plant}) \quad \text{(Eq. 13)}$$

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where f is the fraction of litter C that becomes soil C, C_{lit} is the total litter C pool, and s_t is the turnover time of the litter pool. Actual plant N uptake is expressed as:

$$P_{act} = \min\left(\frac{N_{min}\,P_{dem}}{I_{dem} + P_{dem}}, P_{dem}\right) \quad \text{(Eq. 14)}$$

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Actual NPP is expressed as:

$$NPP_{act} = NPP_{pot}\frac{P_{act}}{P_{dem}} \quad \text{(Eq. 15)}$$

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For the VL constraint, we have $N_{in} = N_{loss}$. We can calculate NPP_{pot} as:

$$NPP_{pot} = \frac{N_{in}\,(1 - l_n)}{l_n n_{plant}} \quad \text{(Eq. 16)}$$

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For an actual NPP, we need to consider the immobilization demand. Re-arranging the above, we get:

$$NPP_{act} = \frac{N_{in}\,(1 - l_n)}{l_n[n_{plant} + f(n_{soil} - n_{plant})]} \qquad \text{(Eq. 17)}$$

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This equation removes the NPP_{act} dependence on NPP_{pot}. It can be shown that the fraction of $P_{dem}/(I_{dem} + P_{dem})$ depends only on the N:C ratios and *f*, not on NPP_{pot}. This means that there will be no eCO$_2$ effect on NPP_{act}.

As shown in Figure 5a, the potential NPP approach results in relatively flat nutrient recycling constraint curves, suggesting that the CO$_2$ fertilization effect is only weakly influenced by soil N availability. Despite a sharp instantaneous NPP response, CO$_2$ fertilization effects on NPP_{act} are small at the M-, L- and VL-term timescales (Table 3). This outcome can be understood from the governing equation for the nutrient recycling constraint, which removes NPP_{act} dependence on NPP_{pot} (Eq. 17). Although in the first instance, the plant can increase its production, over time the litter pool increases in size proportion to NPP_{pot}, meaning that immobilisation demand increases to match the increased plant demand, which leads to no overall change in the relative demands from the plant and the litter. This pattern is similar under alternative wood N:C ratio assumptions (Figure 5b, Table 3).

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3.2.3 Root exudation to prime N mineralisation

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The priming effect is described as the stimulation of the decomposition of native soil organic matter, caused by larger soil carbon input under eCO$_2$ (van Groenigen et al., 2014). Experimental studies suggest that this phenomenon is widespread and persistent (Dijkstra and Cheng, 2007), but this process has not been incorporated by most land surface models (Walker et al., 2015). Here we introduce a novel framework to induce priming effect on soil decomposition, and test its effect on plant production response to eCO$_2$ within the quasi-equilibrium framework.

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To account for the effect of priming on decomposition of SOM, we first introduce a coefficient to determine the fraction of root growth allocated to exudates, a_{rhizo}. Here we assumed that N:C ratio of the rhizodeposition is the same as the root N:C ratio. The coefficient a_{rhizo} is estimated by a function dependent on foliar N:C:

$$a_{rhizo} = a_0 + a_1 \cdot \frac{1/n_f - 1/n_{ref}}{1/n_{ref}} \qquad \text{(Eq. 18)}$$

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where n_{ref} is a reference foliar N:C ratio to induce plant N stress (0.04), and a_0 and a_1 are tuning coefficients (0.01 and 1, respectively). Within the quasi-equilibrium framework, for the VL soil constraint we now have:

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$$NPP = \frac{N_{in}}{[a_f n_{fl} + a_w n_w + a_r a_{rhizo} n_r + a_r(1 - a_{rhizo}) n_r]} \frac{l_n}{1 - l_n} \qquad \text{(Eq. 19)}$$

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To introduce an effect of root exudation on the turnover rate of slow SOM pool, rhizodeposition is transferred into the active SOM pool according to a microbial use efficiency parameter ($f_{cue,rhizo} = 0.3$). The extra allocation of NPP into the active SOM is therefore:

$$C_{rhizo} = NPP \cdot a_r \cdot a_{rhizo} \cdot f_{cue,rhizo} \qquad \text{(Eq. 20)}$$

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The increased active SOM pool N demand is associated with the degradation rate of the slow SOM pool, expressed as:

$$k_{slow,new} = k_{slow} \cdot (1 + k_m) \cdot \frac{C_{rhizo}}{C_{rhizo} + k_m} \qquad \text{(Eq. 21)}$$

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where k_{slow} is the original decomposition rate of the slow SOM pool, and k_m is a sensitivity parameter. The decomposition rate of the slow SOM pool affects N_{Rs}, the amount of N released from the slow SOM pools, as:

$$N_{Rs} = k_{slow,new} C_s [n_s(1 - \Omega_{ss}) - n_p \Omega_{ps}] \qquad \text{(Eq. 22)}$$

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where C_s is the slow SOM pool, and Ω_{ss} and Ω_{ps} are the proportion of C released through decomposition of slow and passive SOM pools that subsequently enters slow SOM pool, respectively.

Root exudation and the associated priming effect results in a strong M-term plant response to eCO_2 when compared to the baseline model (Figure 6a in comparison to Figure 4a). In fact, the magnitude of the priming effect on M-term NPP response to eCO_2 is comparable to its L- and VL-term NPP responses, indicating a persistent eCO_2 effect over time (Table 3). A faster decomposition rate and therefore a smaller pool size of the slow SOM pool are observed (Table 5). With a fixed wood N:C ratio assumption, NPP response to eCO_2 is drastically reduced at the M-term as compared to the model with a variable wood N:C assumption (Figure 6b), but is comparable to its corresponding baseline fixed wood N:C model (Table 3). Varying parameter coefficients (a_0, a_1, $f_{cue,rhizo}$ and k_m) affects the decomposition rates of slow soil organic pool and hence could lead to variation of the priming effect on M-term CO_2 response (Figure S3). Further experimental studies are needed to better constrain these parameters. Adding root exudation without influencing slow SOM pool decomposition rate (Eq. 21) leads to a smaller predicted M-term CO_2 response than the model with the direct effect on the slow SOM pool. However, it also leads to a higher predicted M-term CO_2 response than the baseline model (Figure 7), because a_r and n_r affect the reburial fraction of the slow SOM pool, as shown in McMurtrie et al. (2000). Finally, the model with a variable wood N:C assumption indicates that there is no increase in NUE (Table 2) at the M-term as compared to its L- and VL-term responses (Figure 6c). In comparison, the fixed wood N:C ratio assumption means that there is a decreased wood "quality" (reflected via decreased N:C ratio), and therefore faster decomposition of slow SOM pool does not release much extra N to support the M-term CO_2 response, leading to a significant rise of NUE at the M-term (Figure 6d).

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4 Discussion

4.1 Influence of alternative N uptake assumptions on predicted CO_2 fertilization

The quasi-equilibrium analysis of the time-varying plant response to eCO_2 provides a quantitative framework to understand the relative contributions of different model assumptions governing the supply of N to plants in determining the magnitude of the CO_2 fertilization effect. Here, we evaluated how plant responses to eCO_2 are affected by widely used model assumptions relating to plant N uptake, soil decomposition, and immobilization demand under alternative wood N-C coupling strategies (variable and fixed wood N:C ratios). These assumptions have been adopted in land surface models such as O-CN (Zaehle and Friend, 2010), CABLE (Wang et al., 2007), LPJ-Guess N (Wårlind et al., 2014), JASBACH-CNP (Goll et al., 2012), ORCHIDEE-CNP (Goll et al., 2017a), and CLM4 (Thornton et al., 2007). In line with previous findings (Comins and McMurtrie, 1993; Dewar and McMurtrie, 1996; Kirschbaum et al., 1998; McMurtrie and Comins, 1996; Medlyn and Dewar, 1996), our results show that assumptions related to wood stoichiometry have a very large impact on estimates of plant responses to eCO_2. More specifically, models incorporating a fixed wood N:C ratio consistently predicted smaller CO_2 fertilization effects on production than models using a variable N:C ratio assumption (Table 3). Examples of models assuming constant (Thornton et al., 2007; Weng and Luo, 2008) and variable (Zaehle and Friend, 2010) plant tissue stoichiometry are both evident in the literature, and therefore, assuming all other model structure and assumptions are similar, prediction differences could potentially be attributed to the tissue stoichiometric assumption incorporated into these models, as suggested in some previous simulation studies (Medlyn et al., 2016; Medlyn et al., 2015; Meyerholt and Zaehle, 2015; Zaehle et al., 2014). Together with more appropriate representation of the trade-offs governing tissue C-N coupling (Medlyn et al., 2015), further tissue biochemistry data is necessary to constrain this fundamental aspect of ecosystem model uncertainty (Thomas et al., 2015).

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C-N coupled simulation models generally predict that the CO_2 fertilization effect on plant production is progressively constrained by soil N availability over time: the progressive nitrogen limitation hypothesis (Luo et al., 2004; Norby et al., 2010; Zaehle et al., 2014). Here we showed similar temporal patterns in a model with different plant N uptake assumptions (Figure 4) and the potential NPP assumption (Figure 5). In particular, the progressive N limitation effect on NPP is shown as a down-regulated M-term CO_2 response after the sharp instantaneous CO_2 fertilization effect on production is realized. However, the model incorporating a priming effect of C on soil N availability with a flexible wood N:C ratio assumption induced a strong M-term CO_2 response (13% increase in NPP), thereby introducing a persistent CO_2 effect over time (Figure 6a). This strong M-term CO_2 response is due to an enhanced decomposition rate of soil organic matter, consistent with a series of recent observations and modelling studies (Finzi et al., 2015; Guenet et al., 2018; Sulman et al., 2014; van Groenigen et al., 2014). However, as a previous quasi-equilibrium study showed, a significant increase in the M-term CO_2 response can occur via changes in litter quality into slow SOM pool or increased N input into the system (McMurtrie et al., 2000). Our study differs from McMurtrie et al. (2000) in that we introduced an explicit effect of C priming on k_{slow} – the decomposition rate of slow SOM pool – via extra rhizodeposition (Eq. 21). As such, a faster decomposition rate of slow SOM is observed (Table 5), equivalent to adding extra N for mineralization to support the M-term CO_2 response (Figure 6c). More complex models for N uptake, incorporating a carbon cost for nitrogen acquisition, are being proposed (Fisher et al., 2010; Ghimire et al., 2016; Shi et al., 2015a); we suggest that the likely effects of introducing these complex sets of assumptions into large-scale models could usefully be explored with the quasi-equilibrium framework.

Processes regulating the progressive nitrogen limitation under eCO_2 were evaluated by Liang et al. (2016) based on a meta-analysis, which bridged the gap between theory and observations. It was shown that the expected diminished CO_2 fertilization effect on plant growth was not apparent at the ecosystem scale due to extra N supply through increased biological N fixation and decreased leaching under eCO_2. Here, our baseline assumption assumed fixed N input into the system, and therefore plant available N is progressively depleted through increased plant N sequestration under eCO_2, as depicted by the progressive N limitation hypothesis (Luo et al., 2004). A function that allows N fixation parameter to vary could provide further assessment of the tightness of the ecosystem N cycle process and its impact to plant response to eCO_2. Furthermore, given the significant role wood N:C ratio plays in plant N

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sequestration, matching modelled range of wood tissue stoichiometry with observations can provide addition level of evaluation of model performance. Our study provides a generalizable evaluation based on the assumption that wood N:C ratio, when allowed to vary in a model, is proportional to leaf N:C ratio. Case-specific, more realistic evaluations can be performed based on the quasi-equilibrium framework to bridge models with observations.

A strong M-term and persistent CO_2 fertilization effects over time was also found by some models in Walker et al. (2015), but without introducing a priming effect. In models such as CLM, N losses from the system are concentration dependent, and plant N uptake is a function of both N supply and plant demand. Increased plant N demand in models where N uptake is a function of plant N demand, reduces soil solution N concentration and therefore system N losses. This means that over time N can accumulate in the system in response to eCO_2 and sustain an eCO_2 response. Here, our quasi-equilibrium framework considers N lost as a fixed rate that depends linearly on the mineral N pool, and the mineral N pool changes at different equilibrium time points. For example, as shown in Table S1, M-term N loss rate is significantly reduced under eCO_2 as compared to the VL-term N lost rate under aCO_2. This suggests a positive relationship between N lost and NPP, as embedded in Eq. 4.

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We also showed that the magnitude of the CO_2 fertilization effect is significantly reduced at all time-scales when models incorporate the potential NPP approach (Figure 5). Among all model assumptions tested, the potential NPP approach induced the smallest M- to VL-term responses (Table 3). It can be shown from equation derivation (Eq. 17) that the fraction $P_{dem}/(P_{dem}+I_{dem})$ depends only on the N:C ratios and f (fraction of litter C become soil C), implying that models incorporating the potential NPP assumption should show no response of NPP to CO_2. Both our study and simulation-based studies showed small CO_2 responses (Walker et al., 2015; Zaehle et al., 2014), possibly because the timing of P_{dem} and I_{dem} differs due to the fluctuating nature of GPP and N mineralization at daily to seasonal time steps, such that N is limiting at certain times of the year but not at others. Additionally, models such as CLM have volatilization losses (not leaching) that are reduced under eCO_2, which may lead to production not limited by N availability, meaning that full CO_2 fertilization effect may be realized. Finally, leaching is simplified

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here, treated as a fixed fraction of the mineral N pool. In models such as CLM or JASBACH, it is a function of soil soluble N concentration, implying a dependency on litter quality (Zaehle et al., 2014).

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4.2 Implications for probing model behaviours

Model-data intercomparisons have been shown as a viable means to investigate how and why models differ in their predicted response to eCO_2 (De Kauwe et al., 2014; Walker et al., 2015; Zaehle et al., 2014). Models make different predictions because they have different model structures (Lombardozzi et al., 2015; Meyerholt et al., 2016; Shi et al., 2018; Xia et al., 2013; Zhou et al., 2018), parameter uncertainties (Dietze et al., 2014; Wang et al., 2011), response mechanisms (Medlyn et al., 2015), and numerical implementations (Rogers et al., 2016). It is increasingly difficult to diagnose model behaviours from the multitude of model assumptions incorporated into the model. Furthermore, while it is true that the models can be tuned to match observations within the domain of calibration, models may make correct predictions but based on incorrect or simplified assumptions (Medlyn et al., 2005; Medlyn et al., 2015; Walker et al., 2015). As such, diagnosing model behaviours can be a challenging task in complex plant-soil models. In this study, we showed that the effect of a model assumption on plant response to eCO_2 can be analytically predicted by solving together the photosynthetic and nutrient recycling constraints. This provides a constrained model framework to evaluate the effect of individual model assumptions without having to run a full set of sensitivity analyses, thereby providing *a priori* understanding of the underlying response mechanisms through which the effect is realized. We suggest that before implementing a new function into the full structure of a plant-soil model, one could use the quasi-equilibrium framework as a testbed to examine the effect of the new assumption.

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The quasi-equilibrium framework requires that additional model assumptions be analytically solvable, which is increasingly not the case for complex modelling structures. However, as we demonstrate here, studying the behaviour of a reduced-complexity model can nonetheless provide real insight into model behaviour. In some cases, the quasi-equilibrium framework can highlight where additional complexity is

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not valuable. For example, here we showed that adding complexity in the representation of plant N uptake did not result in significantly different predictions of plant response to eCO_2. Where the quasi-equilibrium framework indicates little effect of more complex assumptions, there is a strong case for keeping simpler assumptions in the model. However, we do acknowledge that the quasi-equilibrium framework operates on time-scales of > 5 years; where fine-scale temporal responses are important, the additional complexity may be warranted.

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The multiple element limitation framework developed by Rastetter and Shaver (1992) analytically evaluates the relationship between short-term and long-term plant responses to eCO_2 and nutrient availability under different model assumptions. It was shown that there could be markedly difference in the short-term and long-term ecosystem responses to eCO_2 (Rastetter et al., 1997; Rastetter and Shaver, 1992). More specifically, Rastetter et al. (1997) showed that the ecosystem NPP response to eCO_2 appearred on several characteristic timescales: 1) there was an instantaneous increase in NPP, which results in an increased vegetation C:N ratio, 2) on a timescale of a few years, the vegetation responded to eCO_2 by increasing uptake effort for available N through increased allocation to fine roots, 3) on a timescale of decades, there was a net movement of N from soil organic matter to vegetation, which enables vegetation biomass to accumulate, and 4) on the timescale of centuries, ecosystem responses were dominated by increases in total ecosystem N, which enable organic matter to accumulate in both vegetation and soils. Both the multiple element limitation framework and the quasi-equilibrium framework provides information about the equilibrium responses. These approaches also provide information about the degree to which the ecosystem replies on internally recycled N vs. exchanges of with external sources and sinks. The multiple element limitation framework also offers insight into the C-N interaction that influences transient dynamics. These analytical frameworks are both useful tools for making quantitative assessments of model assumptions.

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A related model assumption evaluation tool is the traceability framework, which decomposes complex models to various simplified component variables such as ecosystem C storage capacity or residence time, and hence helps to identify structures and parameters that are uncertain among models (Shi et al., 2015b;

Xia et al., 2013; Xia et al., 2012). Both the traceability and quasi-equilibrium frameworks provide analytical solutions to describe how and why model predictions diverge. The traceability framework decomposes complex simulations into a common set of component variables, explaining differences due to these variables. In contrast, the quasi-equilibrium analysis investigates the impacts and behaviour of a specific model assumption, which is more indicative of mechanisms and processes. Subsequently, one can relate the effect of a model assumption more mechanistically to the processes that govern the relationship between plant N:C ratio and NPP, as depicted in Figure 1, thereby facilitating the efforts to reduce model uncertainties.

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Models diverge in future projections of plant responses to increases in CO_2 because of the different assumptions that they make. Applying model evaluation frameworks, such as the quasi-equilibrium framework, to attribute these differences will not necessarily reduce multi-model prediction spread in the short-term (Lovenduski and Bonan, 2017). Many model assumptions are still empirically derived, and there is a lack of mechanistic and observational constraints on the effect size, meaning that it is important to apply models incorporating diverse process representations. However, use of the quasi-equilibrium framework can provide crucial insights into why model predictions differ, and thus help identify the critical measurements that would allow to discriminate among alternative models. As such, it is an invaluable tool for model inter-comparison and benchmarking analysis. We recommend use of this framework to analyze likely outcomes of new model assumptions before introducing them to complex model structures.

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Code availability

Code repository is publicly available via DOI 10.5281/zenodo.2574192

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Author contribution

BEM and MJ designed the study; MJ, BEM and SZ performed the analyses; APW, MDK and SZ designed the priming effect equations; all authors contributed to result interpretation and manuscript writing.

Competing interests

Authors declare no competing interests.

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Appendix A. Baseline quasi-equilibrium model derivation

Here we show how baseline quasi-equilibrium framework is derived. Specifically, there are two analytical constraints that form the foundation of the quasi-equilibrium framework, namely the photosynthetic constraint, and the nitrogen cycling constraint. The derivation follows Comins and McMurtrie (1993), which is further elaborated in work by (McMurtrie et al., 2000; Medlyn and Dewar, 1996), and evaluated (Comins, 1994).

A1. Photosynthetic constraint

Firstly, gross primary production (GPP) in the simulation mode is calculated using a light-use efficiency approach named MATE (Model Any Terrestrial Ecosystem) (McMurtrie et al., 2008; Medlyn et al., 2011; Sands, 1995), in which absorbed photosynthetically active radiation is estimated from leaf area index (*L*) using Beer's Law, and is then multiplied by a light-use efficiency (LUE) which depends on the foliar N:C ratio (n_f) and atmospheric CO$_2$ concentration (C_a).

$$GPP = LUE(n_f, C_a) \cdot I_0 \cdot (1 - e^{-kL}) \qquad \text{(Eq. A1)}$$

where I_0 is the incident radiation, *k* is the canopy light extinction coefficient, and *L* is leaf area index. The derivation of LUE for the MATE model is described in full by McMurtrie et al. (2008); our version differs only in that the key parameters determining the photosynthetic rate follow the empirical relationship with foliar N:C ratio given by Walker et al. (2014a) and the expression for stomatal conductance follows Medlyn et al. (2011).

In the quasi-equilibrium framework, the photosynthetic constraint is derived by assuming that the foliage C pool (C_f) has equilibrated. That is, the new foliage C production equals turnover, which is assumed to be a constant fraction (s_f) of the pool:

$$a_f NPP = s_f C_f \qquad \text{(Eq. A2)}$$

where a_f is the allocation coefficient for foliage. From Eq. A1, net primary production is a function of the foliar N:C ratio and the foliage C pool:

$$NPP = LUE\left(n_f, C_a\right) \cdot\ I_0 \cdot \left(1 - e^{-k\sigma C_f}\right) \cdot CUE \qquad \text{(Eq. A3)}$$

Where σ is the specific leaf area. Combining two equations above leads to an implicit relationship between *NPP* and n_f:

$$NPP = LUE\left(n_f, C_a\right) \cdot\ I_0 \cdot \left(1 - e^{-k\sigma a_f NPP/s_f}\right) \cdot CUE \qquad \text{(Eq. A4)}$$

which is the photosynthetic constraint.

A2. Nutrient recycling constraint

The nitrogen cycling constraint is derived by assuming that nitrogen inputs to, and outputs from, the equilibrated pools, are equal. Based on the assumed residence times of the passive SOM (~400 years), slow SOM (15 years) and woody biomass (50 years) pools, we can calculate the nutrient recycling constraint at three different timescales: very long (VL, > 500 years, all pools equilibrated), long (L, 100 – 500 years, all pools equilibrated except the passive pool), or medium (M, 5-50 years, all pools equilibrated except slow, passive and wood pools).

At the VL-term, we have:

$$N_{in} = N_{loss} \qquad \text{(Eq. A5)}$$

where N_{in} is the total N input into the system, and N_{loss} is the total N lost from the system via leaching and volatilisation. Following Comins and McMurtrie (1993), the flux N_{in} is assumed to be a constant. The total N loss term is proportional to the rate of N mineralization (N_m), following:

$$N_{loss} = l_n \cdot N_m \qquad \text{(Eq. A6)}$$

where l_n is the fraction of N mineralization that is lost. It is assumed that mineralised N that is not lost is taken up by plants (N_U):

$$N_U = N_m - N_{loss} \qquad \text{(Eq. A7)}$$

Combining with Eq. A6, we have:

$$N_{loss} = \frac{l_n}{(1 - l_n)} N_U \qquad \text{(Eq. A8)}$$

The plant N uptake rate depends on production (NPP) and plant N:C ratios, according to:

$$N_U = NPP \cdot (a_f n_{fl} + a_w n_w + a_r n_r) \qquad \text{(Eq. A9)}$$

Where a_f, a_w and a_r are the allocation coefficients for foliage, wood and roots, respectively, and n_{fl}, n_w and n_r are the N:C ratios for foliage litter, wood and roots, respectively. Foliage litter N:C ratio (n_{fl}) is proportional to n_f, according to Table 2. Combining Eq. A9 with Eq. A5 and Eq. A8, we obtain a function of NPP that can be related to total N input, which is the nutrient recycling constraint at the VL-term, expressed as:

$$NPP = \frac{N_{in}(1 - l_n)}{l_n(a_f n_{fl} + a_w n_w + a_r n_r)} \qquad \text{(Eq. A10)}$$

Since n_w and n_r are assumed proportional to n_f, the nutrient recycling constraint also links NPP and n_f. The intersection with the photosynthetic constraint yields the very-long term equilibria of both NPP and n_f.

At the L-term, we now have to consider N flows leaving and entering the passive SOM pool, which is no longer equilibrated:

$$N_{in} + N_{R_p} = N_{loss} + N_{S_p} \tag{Eq. A11}$$

where N_{R_p} and N_{S_p} are the release and sequestration of the passive SOM N pool, respectively. The release flux, N_{R_p}, can be assumed to be constant on the L-term timescale. The sequestration flux, N_{S_p}, can be calculated as a function of NPP. In G'DAY, as with most carbon-nitrogen coupled ecosystem models, carbon flows out of the soil pools are directly related to the pool size. As demonstrated by Comins and McMurtrie (1993), such soil models have the mathematical property of linearity, meaning that carbon flows out of the soil pools are proportional to the production input to the soil pool, or NPP. Furthermore, the litter input into the soil pools is assumed proportional to foliar N:C ratio, with the consequence that N sequestered in the passive SOM is also related to foliar N:C ratio. The sequestration flux into the passive soil pool (N_{S_p}) can thus be written as:

$$N_{S_p} = NPP\, n_p(\Omega_{p_f} \cdot a_f + \Omega_{p_w} \cdot a_w + \Omega_{p_r} \cdot a_r) \tag{Eq. A12}$$

Where n_p is the N:C ratio of the passive SOM pool, Ω_{p_f}, Ω_{p_w} and Ω_{p_r} are the burial coefficients for foliage, wood and roots (the proportion of plant carbon production that is ultimately buried in the passive pool), respectively. The burial coefficients Ω_{p_f}, Ω_{p_w} and Ω_{p_r} depend on the N:C ratios of foliage, wood and root litter (detailed derivation in Comins and McMurtrie, 1993). Combining and re-arranging, we obtain nutrient recycling constraint at the L-term as:

$$NPP = \frac{N_{in} + N_{R_p}}{n_p\left(\Omega_{p_r} a_r + \Omega_{p_f} a_f + \Omega_{p_w} a_w\right) + \frac{l_n}{1 - l_n}(a_f n_{fl} + a_w n_w + a_r n_r)} \tag{Eq. A13}$$

Similarly, at the M-term, we have:

$$N_{in} + N_{R_p} + N_{R_s} + N_{R_w} = N_{loss} + N_{S_p} + N_{S_s} + N_{S_w} \tag{Eq. A14}$$

Where N_{R_s} and N_{R_w} are the N released from slow SOM and wood pool, respectively, and N_{S_s} and N_{S_w} are the N stored in slow SOM and wood pool, respectively (Medlyn et al., 2000). The nutrient recycling constraint at the M-term can thus be derived as:

$$NPP = \frac{N_{in} + N_{R_p} + N_{R_s} + N_{R_w}}{a_f\left(\Omega_{s_f} n_s + \Omega_{p_f} n_p\right) + a_r\left(\Omega_{s_r} n_s + \Omega_{p_r} n_p\right) + \frac{l_n}{1 - l_n}\left(a_f n_{fl} + a_w n_w + a_r n_r\right) + a_w n_w} \quad \text{(Eq. A15)}$$

Where n_s is the slow SOM pool N:C ratio, Ω_{s_f} and Ω_{s_r} are foliage and root C sequestration rate into slow SOM pool, respectively (Medlyn et al., 2000). The intersection between the nitrogen recycling constraint and the photosynthetic constraint provides analytical solution to both NPP and n_f at different timescales, we can then interpret how changing model assumptions affect the predicted plant responses to elevated CO_2.

References

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Bonan, G. B. and Levis, S.: Quantifying carbon-nitrogen feedbacks in the Community Land Model (CLM4), Geophysical Research Letters, 37, 2010.

Comins, H. N.: Equilibrium Analysis of Integrated Plant—Soil Models for Prediction of the Nutrient Limited Growth Response to CO2 Enrichment, Journal of Theoretical Biology, 171, 369-385, 1994.

Comins, H. N. and McMurtrie, R. E.: Long-term response of nutrient-limited forests to CO_2 enrichment; equilibrium behavior of plant-soil models, Ecological Applications, 3, 666-681, 1993.

Corbeels, M., McMurtrie, R. E., Pepper, D. A., and O'Connell, A. M.: A process-based model of nitrogen cycling in forest plantations: Part I. Structure, calibration and analysis of the decomposition model, Ecological Modelling, 187, 426-448, 2005.

De Kauwe, M. G., Medlyn, B. E., Zaehle, S., Walker, A. P., Dietze, M. C., Wang, Y.-P., Luo, Y., Jain, A. K., El-Masri, B., Hickler, T., Wårlind, D., Weng, E., Parton, W. J., Thornton, P. E., Wang, S., Prentice, I. C., Asao, S., Smith, B., McCarthy, H. R., Iversen, C. M., Hanson, P. J., Warren, J. M., Oren, R., and Norby, R. J.: Where does the carbon go? A model–data intercomparison of vegetation carbon allocation and turnover processes at two temperate forest free-air CO2 enrichment sites, New Phytologist, 203, 883-899, 2014.

Dewar, R. C. and McMurtrie, R. E.: Analytical model of stemwood growth in relation to nitrogen supply, Tree Physiol., 16, 161-171, 1996.

Dietze, M. C., Serbin, S. P., Davidson, C., Desai, A. R., Feng, X., Kelly, R., Kooper, R., LeBauer, D., Mantooth, J., McHenry, K., and Wang, D.: A quantitative assessment of a terrestrial biosphere model's data needs across North American biomes, Journal of Geophysical Research: Biogeosciences, 119, 286-300, 2014.

Dijkstra, F. A. and Cheng, W.: Interactions between soil and tree roots accelerate long-term soil carbon decomposition, Ecology Letters, 10, 1046-1053, 2007.

Dybzinski, R., Farrior, C. E., and Pacala, S. W.: Increased forest carbon storage with increased atmospheric CO2 despite nitrogen limitation: a game-theoretic allocation model for trees in competition for nitrogen and light, Global Change Biology, 21, 1182-1196, 2014.

Fernández-Martínez, M., Vicca, S., Janssens, I. A., Sardans, J., Luyssaert, S., Campioli, M., Chapin Iii, F. S., Ciais, P., Malhi, Y., Obersteiner, M., Papale, D., Piao, S. L., Reichstein, M., Rodà, F., and Peñuelas, J.: Nutrient availability as the key regulator of global forest carbon balance, Nature Climate Change, 4, 471, 2014.

Finzi, A. C., Abramoff, R. Z., Spiller, K. S., Brzostek, E. R., Darby, B. A., Kramer, M. A., and Phillips, R. P.: Rhizosphere processes are quantitatively important components of terrestrial carbon and nutrient cycles, Global Change Biology, 21, 2082-2094, 2015.

Fisher, J. B., Sitch, S., Malhi, Y., Fisher, R. A., Huntingford, C., and Tan, S. Y.: Carbon cost of plant nitrogen acquisition: A mechanistic, globally applicable model of plant nitrogen uptake, retranslocation, and fixation, Global Biogeochemical Cycles, 24, 2010.

Friend, A. D., Lucht, W., Rademacher, T. T., Keribin, R., Betts, R., Cadule, P., Ciais, P., Clark, D. B., Dankers, R., Falloon, P. D., Ito, A., Kahana, R., Kleidon, A., Lomas, M. R., Nishina, K., Ostberg, S., Pavlick, R., Peylin, P., Schaphoff, S., Vuichard, N., Warszawski, L., Wiltshire, A., and Woodward, F. I.: Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO₂, Proceedings of the National Academy of Sciences, 111, 3280-3285, 2014.

Gerber, S., Hedin Lars, O., Oppenheimer, M., Pacala Stephen, W., and Shevliakova, E.: Nitrogen cycling and feedbacks in a global dynamic land model, Global Biogeochemical Cycles, 24, 2010.

Ghimire, B., Riley William, J., Koven Charles, D., Mu, M., and Randerson James, T.: Representing leaf and root physiological traits in CLM improves global carbon and nitrogen cycling predictions, Journal of Advances in Modeling Earth Systems, 8, 598-613, 2016.

Goll, D. S., Brovkin, V., Parida, B. R., Reick, C. H., Kattge, J., Reich, P. B., van Bodegom, P. M., and Niinemets, Ü.: Nutrient limitation reduces land carbon uptake in simulations with a model of combined carbon, nitrogen and phosphorus cycling, Biogeosciences, 9, 3547-3569, 2012.

Goll, D. S., Vuichard, N., Maignan, F., Jornet-Puig, A., Sardans, J., Violette, A., Peng, S., Sun, Y., Kvakic, M., Guimberteau, M., Guenet, B., Zaehle, S., Penuelas, J., Janssens, I., and Ciais, P.: A representation of the phosphorus cycle for ORCHIDEE (revision 4520), Geosci. Model Dev., 10, 3745-3770, 2017a.

Goll, D. S., Winkler, A. J., Raddatz, T., Dong, N., Prentice, I. C., Ciais, P., and Brovkin, V.: Carbon–nitrogen interactions in idealized simulations with JSBACH (version 3.10), Geosci. Model Dev., 10, 2009-2030, 2017b.

Guenet, B., Camino-Serrano, M., Ciais, P., Tifafi, M., Maignan, F., Soong Jennifer, L., and Janssens Ivan, A.: Impact of priming on global soil carbon stocks, Global Change Biology, 24, 1873-1883, 2018.

Guenet, B., Moyano, F. E., Peylin, P., Ciais, P., and Janssens, I. A.: Towards a representation of priming on soil carbon decomposition in the global land biosphere model ORCHIDEE (version 1.9.5.2), Geosci. Model Dev., 9, 841-855, 2016.

Huntzinger, D. N., Michalak, A. M., Schwalm, C., Ciais, P., King, A. W., Fang, Y., Schaefer, K., Wei, Y., Cook, R. B., Fisher, J. B., Hayes, D., Huang, M., Ito, A., Jain, A. K., Lei, H., Lu, C., Maignan, F., Mao, J., Parazoo, N., Peng, S., Poulter, B., Ricciuto, D., Shi, X., Tian, H., Wang, W., Zeng, N., and Zhao, F.: Uncertainty in the response of terrestrial carbon sink to environmental drivers undermines carbon-climate feedback predictions, Scientific Reports, 7, 4765, 2017.

Kirschbaum, M. U. F., King, D. A., Comins, H. N., McMurtrie, R. E., Medlyn, B. E., Pongracic, S., Murty, D., Keith, H., Raison, R. J., Khanna, P. K., and Sheriff, D. W.: Modeling forest response to increasing CO_2 concentration under nutrient-limited conditions, Plant Cell Environ., 17, 1081-1099, 1994.

Kirschbaum, M. U. F., Medlyn, B. E., King, D. A., Pongracic, S., Murty, D., Keith, H., Khanna, P. K., Snowdon, P., and Raison, R. J.: Modelling forest-growth response to increasing CO2 concentration in relation to various factors affecting nutrient supply, Global Change Biology, 4, 23-41, 1998.

Koven, C. D., Chambers, J. Q., Georgiou, K., Knox, R., Negron-Juarez, R., Riley, W. J., Arora, V. K., Brovkin, V., Friedlingstein, P., and Jones, C. D.: Controls on terrestrial carbon feedbacks by productivity versus turnover in the CMIP5 Earth System Models, Biogeosciences, 12, 5211-5228, 2015.

Kowalczyk, E. A., Wang, Y. P., Law, R. M., Davies, H. L., McGregor, J. L., and Abramowitz, G.: The CSIRO Atmosphere Biosphere Land Exchange (CABLE) model for use in climate models and as an offline model. , CSIRO, Australia, 2006.

Liang, J., Qi, X., Souza, L., and Luo, Y.: Processes regulating progressive nitrogen limitation under elevated carbon dioxide: a meta-analysis, Biogeosciences, 13, 2689-2699, 2016.

Lombardozzi, D. L., Bonan, G. B., Smith, N. G., Dukes, J. S., and Fisher, R. A.: Temperature acclimation of photosynthesis and respiration: A key uncertainty in the carbon cycle-climate feedback, Geophysical Research Letters, 42, 8624-8631, 2015.

Lovenduski, N., S. and Bonan, G., B.: Reducing uncertainty in projections of terrestrial carbon uptake, Environmental Research Letters, 12, 044020, 2017.

Ludwig, D., Jones, D. D., and Holling, C. S.: Qualitative Analysis of Insect Outbreak Systems: The Spruce Budworm and Forest, Journal of Animal Ecology, 47, 315-332, 1978.

Luo, Y., Su, B., Currie, W. S., Dukes, J. S., Finzi, A., Hartwig, U., Hungate, B., McMurtrie, R. E., Oren, R., Parton, W. J., Pataki, D. E., Shaw, R. M., Zak, D. R., and Field, C. B.: Progressive Nitrogen Limitation of Ecosystem Responses to Rising Atmospheric Carbon Dioxide, BioScience, 54, 731-739, 2004.

McMurtrie, R. and Comins, H. N.: The temporal response of forest ecosystems to doubled atmospheric CO_2 concentration, Global Change Biology, 2, 49-57, 1996.

McMurtrie, R. E., Dewar, R. C., Medlyn, B. E., and Jeffreys, M. P.: Effects of elevated [CO_2] on forest growth and carbon storage: a modelling analysis of the consequences of changes in litter quality/quantity and root exudation, Plant and Soil, 224, 135-152, 2000.

McMurtrie, R. E., Iversen, C. M., Dewar, R. C., Medlyn, B. E., Näsholm, T., Pepper, D. A., and Norby, R. J.: Plant root distributions and nitrogen uptake predicted by a hypothesis of optimal root foraging, Ecology and Evolution, 2, 1235-1250, 2012.

McMurtrie, R. E., Medlyn, B. E., and Dewar, R. C.: Increased understanding of nutrient immobilization in soil organic matter is critical for predicting the carbon sink strength of forest ecosystems over the next 100 years, Tree Physiol., 21, 831-839, 2001.

McMurtrie, R. E., Norby, R. J., Medlyn, B. E., Dewar, R. C., Pepper, D. A., Reich, P. B., and Barton, C. V. M.: Why is plant-growth response to elevated CO2 amplified when water is limiting, but reduced when nitrogen is limiting? A growth-optimisation hypothesis, Functional Plant Biology, 35, 521-534, 2008.

Medlyn, B., E., De Kauwe Martin, G., Zaehle, S., Walker Anthony, P., Duursma Remko, A., Luus, K., Mishurov, M., Pak, B., Smith, B., Wang, Y. P., Yang, X., Crous Kristine, Y., Drake John, E., Gimeno Teresa, E., Macdonald Catriona, A., Norby Richard, J., Power Sally, A., Tjoelker Mark, G., and Ellsworth David, S.: Using models to guide field experiments: a priori predictions for the CO2 response of a nutrient- and water-limited native Eucalypt woodland, Global Change Biology, 22, 2834-2851, 2016.

Medlyn, B. E. and Dewar, R. C.: A model of the long-term response of carbon allocation and productivity of forests to increased CO_2 concentration and nitrogen deposition, Global Change Biology, 2, 367-376, 1996.

Medlyn, B. E., Duursma, R. A., Eamus, D., Ellsworth, D. S., Prentice, I. C., Barton, C. V. M., Crous, K. Y., De Angelis, P., Freeman, M., and Wingate, L.: Reconciling the optimal and empirical approaches to modelling stomatal conductance, Global Change Biology, 17, 2134-2144, 2011.

Medlyn, B. E., McMurtrie, R. E., Dewar, R. C., and Jeffreys, M. P.: Soil processes dominate the long-term response of forest net primary productivity to increased temperature and atmospheric CO_2 concentration, Can. J. For. Res., 30, 873-888, 2000.

Medlyn, B. E., Robinson, A. P., Clement, R., and McMurtrie, R. E.: On the validation of models of forest CO2 exchange using eddy covariance data: some perils and pitfalls, Tree Physiology, 25, 839-857, 2005.

Medlyn, B. E., Zaehle, S., De Kauwe, M. G., Walker, A. P., Dietze, M. C., Hanson, P. J., Hickler, T., Jain, A. K., Luo, Y., Parton, W., Prentice, I. C., Thornton, P. E., Wang, S., Wang, Y.-P., Weng, E., Iversen, C. M., McCarthy, H. R., Warren, J. M., Oren, R., and Norby, R. J.: Using ecosystem experiments to improve vegetation models, Nature Clim. Change, 5, 528-534, 2015.

Meyerholt, J. and Zaehle, S.: The role of stoichiometric flexibility in modelling forest ecosystem responses to nitrogen fertilization, New Phytologist, 208, 1042-1055, 2015.

Meyerholt, J., Zaehle, S., and Smith, M. J.: Variability of projected terrestrial biosphere responses to elevated levels of atmospheric CO2 due to uncertainty in biological nitrogen fixation, Biogeosciences, 13, 1491-1518, 2016.

Norby, R. J., Warren, J. M., Iversen, C. M., Medlyn, B. E., and McMurtrie, R. E.: CO₂ enhancement of forest productivity constrained by limited nitrogen availability, Proceedings of the National Academy of Sciences, 107, 19368-19373, 2010.

Oleson, K. W., Dai, Y. J., Bonan, G. B., Bosilovich, M., Dichinson, R., Dirmeyer, P., Hoffman, F., Houser, P., Levis, S., Niu, G.-Y., Thornton, P. E., Vertenstein, M., Yang, Z. L., and Zeng, X.: Technical description of the Community Land Model (CLM), National Center for Atmospheric Research, Boulder, Colorado, 2004.

Rastetter, E. B., Ågren, G. I., and Shaver, G. R.: RESPONSES OF N-LIMITED ECOSYSTEMS TO INCREASED CO2: A BALANCED-NUTRITION, COUPLED-ELEMENT-CYCLES MODEL, Ecological Applications, 7, 444-460, 1997.

Rastetter, E. B. and Shaver, G. R.: A Model of Multiple-Element Limitation for Acclimating Vegetation, Ecology, 73, 1157-1174, 1992.

Reich, P. B. and Hobbie, S. E.: Decade-long soil nitrogen constraint on the CO2 fertilization of plant biomass, Nature Climate Change, 3, 278, 2012.

Rogers, A., Medlyn Belinda, E., Dukes Jeffrey, S., Bonan, G., Caemmerer, S., Dietze Michael, C., Kattge, J., Leakey Andrew, D. B., Mercado Lina, M., Niinemets, Ü., Prentice, I. C., Serbin Shawn, P., Sitch, S., Way Danielle, A., and Zaehle, S.: A roadmap for improving the representation of photosynthesis in Earth system models, New Phytologist, 213, 22-42, 2016.

Sands, P.: Modelling Canopy Production. II. From Single-Leaf Photosynthesis Parameters to Daily Canopy Photosynthesis, Functional Plant Biology, 22, 603-614, 1995.

Shi, M., Fisher Joshua, B., Brzostek Edward, R., and Phillips Richard, P.: Carbon cost of plant nitrogen acquisition: global carbon cycle impact from an improved plant nitrogen cycle in the Community Land Model, Global Change Biology, 22, 1299-1314, 2015a.

Shi, Z., Crowell, S., Luo, Y., and Moore, B.: Model structures amplify uncertainty in predicted soil carbon responses to climate change, Nature Communications, 9, 2171, 2018.

Shi, Z., Xu, X., Hararuk, O., Jiang, L., Xia, J., Liang, J., Li, D., and Luo, Y.: Experimental warming altered rates of carbon processes, allocation, and carbon storage in a tallgrass prairie, Ecosphere, 6, 1-16, 2015b.

Sigurdsson, B. D., Medhurst, J. L., Wallin, G., Eggertsson, O., and Linder, S.: Growth of mature boreal Norway spruce was not affected by elevated [CO2] and/or air temperature unless nutrient availability was improved, Tree Physiology, 33, 1192-1205, 2013.

Smith, B., Prentice, I. C., and Sykes, M. T.: Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space, Global Ecology and Biogeography, 10, 621-637, 2001.

Sokolov, A. P., Kicklighter, D. W., Melillo, J. M., Felzer, B. S., Schlosser, C. A., and Cronin, T. W.: Consequences of Considering Carbon–Nitrogen Interactions on the Feedbacks between Climate and the Terrestrial Carbon Cycle, Journal of Climate, 21, 3776-3796, 2008.

Stocker, B. D., Prentice, I. C., Cornell, S. E., Davies-Barnard, T., Finzi, A. C., Franklin, O., Janssens, I., Larmola, T., Manzoni, S., Näsholm, T., Raven, J. A., Rebel, K. T., Reed, S., Vicca, S., Wiltshire, A., and Zaehle, S.: Terrestrial nitrogen cycling in Earth system models revisited, New Phytologist, 210, 1165-1168, 2016.

Sulman, B. N., Phillips, R. P., Oishi, A. C., Shevliakova, E., and Pacala, S. W.: Microbe-driven turnover offsets mineral-mediated storage of soil carbon under elevated CO2, Nature Climate Change, 4, 1099, 2014.

Thomas, R. Q., Brookshire, E. N. J., and Gerber, S.: Nitrogen limitation on land: how can it occur in Earth system models?, Global Change Biology, 21, 1777-1793, 2015.

Thornton, P., E., Lamarque, J. F., Rosenbloom Nan, A., and Mahowald Natalie, M.: Influence of carbon-nitrogen cycle coupling on land model response to CO2 fertilization and climate variability, Global Biogeochemical Cycles, 21, 2007.

Thornton, P. E., Doney, S. C., Lindsay, K., Moore, J. K., Mahowald, N., Randerson, J. T., Fung, I., Lamarque, J. F., Feddema, J. J., and Lee, Y. H.: Carbon-nitrogen interactions regulate climate-carbon cycle feedbacks: results from an atmosphere-ocean general circulation model, Biogeosciences, 6, 2099-2120, 2009.

van Groenigen, K. J., Qi, X., Osenberg, C. W., Luo, Y., and Hungate, B. A.: Faster Decomposition Under Increased Atmospheric CO<sub>2</sub> Limits Soil Carbon Storage, Science, 344, 508, 2014.

Walker, A. P., Hanson, P. J., De Kauwe, M. G., Medlyn, B. E., Zaehle, S., Asao, S., Dietze, M., Hickler, T., Huntingford, C., Iversen, C. M., Jain, A., Lomas, M., Luo, Y. Q., McCarthy, H., Parton, W. J., Prentice, I. C., Thornton, P. E., Wang, S. S., Wang, Y. P., Warlind, D., Weng, E. S., Warren, J. M., Woodward, F. I., Oren, R., and Norby, R. J.: Comprehensive ecosystem model-data synthesis using multiple data sets at two temperate forest free-air CO2 enrichment experiments: Model performance at ambient CO2 concentration, Journal of Geophysical Research-Biogeosciences, 119, 937-964, 2014.

Walker, A. P., Zaehle, S., Medlyn, B. E., De Kauwe, M. G., Asao, S., Hickler, T., Parton, W., Ricciuto, D. M., Wang, Y.-P., Wårlind, D., and Norby, R. J.: Predicting long-term carbon sequestration in response to CO2 enrichment: How and why do current ecosystem models differ?, Global Biogeochemical Cycles, 29, 476-495, 2015.

Wang, Y. P., Houlton, B. Z., and Field, C. B.: A model of biogeochemical cycles of carbon, nitrogen, and phosphorus including symbiotic nitrogen fixation and phosphatase production, Global Biogeochemical Cycles, 21, n/a-n/a, 2007.

Wang, Y. P., Kowalczyk, E., Leuning, R., Abramowitz, G., Raupach, M. R., Pak, B., van Gorsel, E., and Luhar, A.: Diagnosing errors in a land surface model (CABLE) in the time and frequency domains, Journal of Geophysical Research: Biogeosciences, 116, 2011.

Wårlind, D., Smith, B., Hickler, T., and Arneth, A.: Nitrogen feedbacks increase future terrestrial ecosystem carbon uptake in an individual-based dynamic vegetation model, Biogeosciences, 11, 6131-6146, 2014.

Weng, E. and Luo, Y.: Soil hydrological properties regulate grassland ecosystem responses to multifactor global change: A modeling analysis, Journal of Geophysical Research: Biogeosciences, 113, 2008.

Xia, J., Luo, Y., Wang, Y.-P., and Hararuk, O.: Traceable components of terrestrial carbon storage capacity in biogeochemical models, Global Change Biology, 19, 2104-2116, 2013.

Xia, J. Y., Luo, Y. Q., Wang, Y. P., Weng, E. S., and Hararuk, O.: A semi-analytical solution to accelerate spin-up of a coupled carbon and nitrogen land model to steady state, Geosci Model Dev, 5, 1259-1271, 2012.

Yang, X., Wittig, V., Jain, A. K., and Post, W.: Integration of nitrogen cycle dynamics into the Integrated Science Assessment Model for the study of terrestrial ecosystem responses to global change, Global Biogeochemical Cycles, 23, 2009.

Zaehle, S. and Friend, A. D.: Carbon and nitrogen cycle dynamics in the O-CN land surface model: 1. Model description, site-scale evaluation, and sensitivity to parameter estimates, Global Biogeochemical Cycles, 24, n/a-n/a, 2010.

Zaehle, S., Friend, A. D., Friedlingstein, P., Dentener, F., Peylin, P., and Schulz, M.: 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 Biogeochemical Cycles, 24, 2010.

Zaehle, S., Jones, C. D., Houlton, B., Lamarque, J.-F., and Robertson, E.: Nitrogen Availability Reduces CMIP5 Projections of Twenty-First-Century Land Carbon Uptake, Journal of Climate, 28, 2494-2511, 2015.

Zaehle, S., Medlyn, B. E., De Kauwe, M. G., Walker, A. P., Dietze, M. C., Hickler, T., Luo, Y. Q., Wang, Y. P., El-Masri, B., Thornton, P., Jain, A., Wang, S. S., Warlind, D., Weng, E. S., Parton, W., Iversen, C. M., Gallet-Budynek, A., McCarthy, H., Finzi, A. C., Hanson, P. J., Prentice, I. C., Oren, R., and Norby, R. J.: Evaluation of

11 terrestrial carbon-nitrogen cycle models against observations from two temperate Free-Air CO2 Enrichment studies, New Phytologist, 202, 803-822, 2014.

Zhou, S., Liang, J., Lu, X., Li, Q., Jiang, L., Zhang, Y., Schwalm, C. R., Fisher, J. B., Tjiputra, J., Sitch, S., Ahlström, A., Huntzinger, D. N., Huang, Y., Wang, G., and Luo, Y.: Sources of Uncertainty in Modeled Land Carbon Storage within and across Three MIPs: Diagnosis with Three New Techniques, Journal of Climate, 31, 2833-2851, 2018.

Table 1: A brief summary of the processes and model assumptions evaluated based on the quasi-equilibrium analyses

Processes	**Assumptions**	**Findings**	**Key reference**
Stoichiometry	Wood N:C flexibility	Flexible wood N:C ratio induced a strong NPP response to eCO_2.	Comins and McMurtrie, 1993; Comins, 1994; Kirschbaum et al., 1994; McMurtrie and Comins, 1996; Kirschbaum et al., 1998
	Soil N:C flexibility	Soil N:C ratio flexibility fundamentally underpin NPP response to eCO_2.	McMurtrie and Comins, 1996; Medlyn et al., 2000; McMurtrie et al., 2001
	Litter N:C flexibility	Decreased new litter N:C ratio did not significantly alter NPP response to eCO_2, but a substantial decrease in old litter N:C ratio led to a significant CO_2 effect at the medium-term.	McMurtrie et al., 2000
Allocation	Dynamic allocation as a response to changes in leaf N:C ratio	Changes in C allocation between different parts do not significantly alter NPP response to eCO_2.	Kirschbaum et al., 1994
	Linear stem and leaf allocation coupling	With stem allocation proportional to leaf allocation, NPP response to eCO_2 is significant, even when N deposition is unchanged.	Medlyn and Dewar, 1996
Nutrient supply and loss	N fixation	N deficit induced by CO_2 fertilization can be eliminated by stimulation of N fixation.	Comins, 1994
	N fixation	Enhanced N fixation via root exudation leads to a small effect on production in the short term but a very large effect in the long term.	McMurtrie et al., 2000
	Leaf N retranslocation	Changes in leaf N retranslocation fraction do not significantly affect NPP response to eCO_2.	Kirschbaum et al., 1994
	Litter supply	Increased litter quantity only leads to a minimal CO_2 effect on production.	McMurtrie et al., 2000
	Nutrient supply and loss	Systems that are more open with respect to nutrient gains and losses are likely to be more responsive to eCO_2.	Kirschbaum et al., 1998
	N mineralization	Increased temperature induced a long-term increase in NPP response to eCO_2 because of increased N mineralization and plant N uptake rates	Medlyn et al., 2000
	N immobilization	When both T and CO_2 increase, C sink is insensitive to variability in soil N:C ratio, however, with fixed soil N:C, C sink is primarily a temperature response, whereas with variable soil N:C, it is a combined temperature-CO_2 response.	McMurtrie et a., 2001
Photosynthesis	LUE coefficient	Effect of leaf N:C ratio on LUE coefficient induces a small effect on CO_2 sensitivity of plant.	Kirschbaum et al., 1994
	SLA	Introducing leaf N:C dependency of SLA induces no significantly different NPP response to eCO_2.	Kirschbaum et al., 1994

Table 2: Definitions of key variables for the baseline equations

Symbol	**Definition**	**Value**	**Unit**
aCO_2, eCO_2	Ambient and elevated CO_2 concentration, respectively	400, 800	ppm
N_{in}	Total nitrogen into the system (atmospheric deposition and fixation)	0.004	$t\ ha^{-1}\ yr^{-1}$
T_{air}, T_{soil}, T_{leaf}	Temperature of air, soil, and leaf, respectively	20, 15, 25	°C
CUE	Plant carbon use efficiency	0.5	unitless
NUE	Plant nitrogen use efficiency = NPP / N_u	Calculated	$kg\ C\ kg\ N^{-1}$
σ	Specific leaf area	5	$m^2\ kg^{-1}$
ω	Carbon content of biomass	0.45	unitless
a_f, a_r, a_w	Carbon allocation fraction to leaf, root and wood, respectively	0.2, 0.2, 0.6	unitless
n_f, n_r, n_w, n_{fl}	N:C ratio of leaf, root, wood, and leaf litter, respectively		unitless
t_f	Leaf retranslocation rate	0.5	yr^{-1}
r_w, r_r	Proportion of wood and root N:C ratio to leaf N:C ratio, respectively	0.005, 0.7	unitless
s_f, s_r, s_w	Turnover rates of leaf, root and wood, respectively	0.5, 1.5, 0.01	yr^{-1}
n_a, n_s, n_p	C:N ratio for active, slow, passive SOM pool, respectively	15, 20, 10	unitless
l_n	Fraction of N mineralization lost from the system	0.05	unitless
$l_{n,\ rate}$	Mineral N pool lost rate	0.05	yr^{-1}
O_{acq}, O_{resorb}, O_{active}	Total, resorption, and active C cost of N acquisition, respectively	Calculated	$kg\ C\ kg\ N^{-1}$
Ω_{sf}, Ω_{pf}	Proportion of leaf litter enters into slow and passive SOM pool, respectively	Calculated	unitless
Ω_{sr}, Ω_{pr}	Proportion of root litter enters into slow and passive SOM pool, respectively	Calculated	unitless
Ω_{sw}, Ω_{pw}	Proportion of wood litter enters into slow and passive SOM pool, respectively	Calculated	unitless
N_{Ss}, N_{Sp}, N_{Sw}	N stored in slow, passive SOM, and wood pool, respectively	Calculated	$t\ ha^{-1}\ yr^{-1}$
N_{Rs}, N_{Rp}, N_{Rw}	N released from slow, passive SOM, and wood pool, respectively	Calculated	$t\ ha^{-1}\ yr^{-1}$
N_U	N uptake rate	Calculated	$t\ ha^{-1}\ yr^{-1}$
N_{min}	Mineral N pool	Calculated	$t\ ha^{-1}$

Table 3: Magnitudes of the CO_2 fertilization effect on net primary production (NPP) at various time steps for different model assumptions. NPP_a and NPP_e represent very long-term equilibrium point of NPP at ambient and elevated CO_2 conditions, respectively. I, M, L, and VL represent percent change in NPP as a result of elevated CO_2 at instantaneous, medium, long, and very-long term time points, respectively. All experiments except "baseline, fixed wood NC" assume variable wood N:C ratio.

Experiment	NPP_a	NPP_e	I	M	L	VL
Baseline model, variable wood NC	1.67	1.90	15.1	3.2	12.3	13.3
Baseline model, fixed wood NC	1.49	1.66	15.9	0.8	7.9	10.9
Explicit N uptake, fixed coefficient, variable wood NC	1.68	1.91	15.1	3.2	12.4	13.3
Explicit N uptake, fixed coefficient, fixed wood NC	1.52	1.68	15.8	0.8	8.2	11.1
Explicit N uptake, saturating function of root, variable wood NC	1.68	1.91	15.1	3.2	12.4	13.3
Explicit N uptake, saturating function of Nmin, variable wood NC	1.71	1.96	15.0	3.2	13.7	15.0
Priming, variable wood NC	1.67	1.90	15.1	12.2	12.0	13.3
Priming, fixed wood NC	1.49	1.66	15.9	1.8	8.3	10.9
Relative demand, variable wood NC	1.35	1.42	16.6	0.3	2.9	4.9
Relative demand, fixed wood NC	1.13	1.15	17.9	0.2	1.1	1.7

Table 4. Relationship between nitrogen uptake coefficient (u) and quasi-equilibrium points of leaf N:C ratio (n_f) and net primary production (NPP) at the very-long (VL), long (L), medium (M) and instantaneous time points.

u **(yr^{-1})**	**CO_2 (ppm)**	**n_f**			**NPP (kg C m^{-2} yr^{-1})**			
		VL	**L**	**M**	**VL**	**L**	**M**	**I**
0.2	400	0.0049	0.0049	0.0049	1.35	1.35	1.35	-
0.2	800	0.0043	0.0039	0.0026	1.53	1.51	1.39	1.57
0.5	400	0.01	0.01	0.0107	1.54	1.54	1.54	-
0.5	800	0.01	0.008	0.005	1.75	1.72	1.59	1.78
1	400	0.02	0.02	0.0196	1.68	1.68	1.68	-
1	800	0.017	0.016	0.0089	1.91	1.89	1.74	1.94
2	400	0.036	0.036	0.036	1.81	1.81	1.81	-
2	800	0.032	0.029	0.014	2.05	2.03	1.85	2.07
5	400	0.084	0.084	0.084	1.95	1.95	1.95	-
5	800	0.075	0.062	0.032	2.21	2.17	2.04	2.23

Table 5. Effect of priming on key soil process coefficients. Coefficient k_{slow} is the decomposition coefficient for the slow SOM pool (yr^{-1}); apass is the reburial fraction of the passive SOM (i.e. the fraction of passive SOM re-enters passive SOM); a_{slow} is the reburial fraction of the slow SOM; Ω_p is the burial coefficient for plant materials entering the passive SOM pool; Ω_s is the burial coefficient for plant materials entering the slow SOM pool; and C_{slow} is the total carbon stock of the slow SOM pool (g C m^{-2}). Both models assume variable wood N:C ratio.

Model	k_{slow}	a_{pass}	a_{slow}	Ω_p	Ω_s	C_{slow}
baseline	0.067	0.011	0.211	0.002	0.155	4726
priming	0.185	0.011	0.211	0.001	0.163	1624

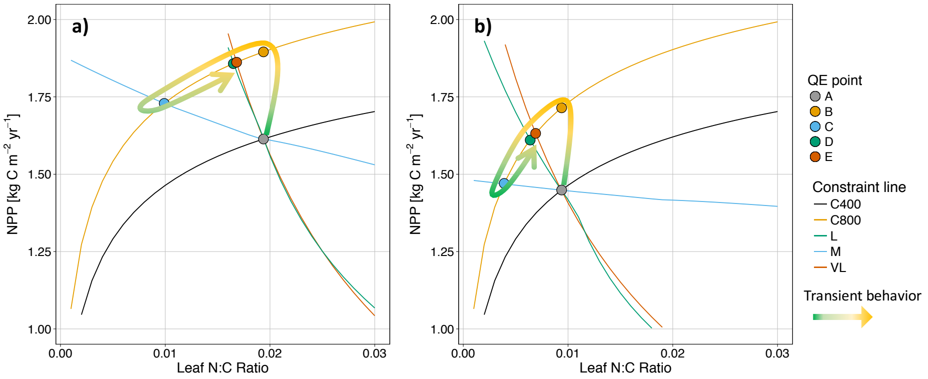

Figure 1: Graphic expression of the baseline quasi-equilibrium framework in understanding plant production response to elevated CO$_2$, based on photosynthetic (C400, C800 refer to CO$_2$ = 400 ppm and 800 ppm, respectively) and nitrogen cycling constraints at the medium (M), long (L) and very long (VL) terms, under the assumption of a) variable wood N:C ratio, and b) fixed wood N:C ratio. The photosynthetic constraint is an analytical expression of the Farquhar leaf photosynthesis model that relates leaf chemistry (i.e. NC ratio) with production, simplifying leaf to canopy scaling. The nutrient recycling constraint is an analytical expression of the soil nutrient down-regulation effect on production, assuming soil organic matter structures as in Figure 2. The quasi-equilibrium points at various timescales (A, C, D and E) were calculated by solving for the intersection of the photosynthetic and nutrient cycling constraints through the two-timing approximation. Initially the system is in equilibrium between photosynthetic N demand and soil N supply at CO$_2$ = 400 ppm (A). The instantaneous response to doubling of CO$_2$ is a sharp increase in production at a constant leaf N concentration (B). Under nutrient limited condition, soil N supply cannot sustain this increase in production over time. A negative feedback moves the quasi-equilibrium point towards point C, where the M-term pools equilibrate with eCO$_2$. The system gradually moves toward point D and E as the L and VL pools equilibrate. The downward slopes of the N recycling constraint curves with increasing leaf N:C ratio is due to the increased proportional loss of mineralized N through leaching as the rate of N cycling increases with leaf N concentration.

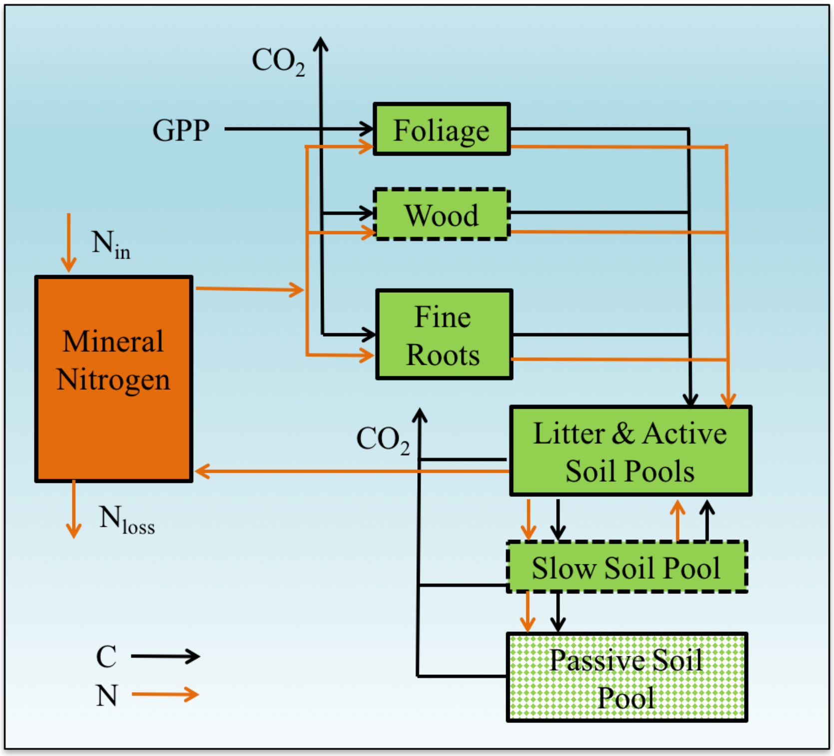

Figure 2: Framework of the Generic Decomposition And Yield (G'DAY) model. Boxes represent pools; arrowed line represent fluxes. Boxes with dotted boundaries are M term recycling pools (wood and slow soil). Box filled with diamonds is the L term recycling pool (passive soil).

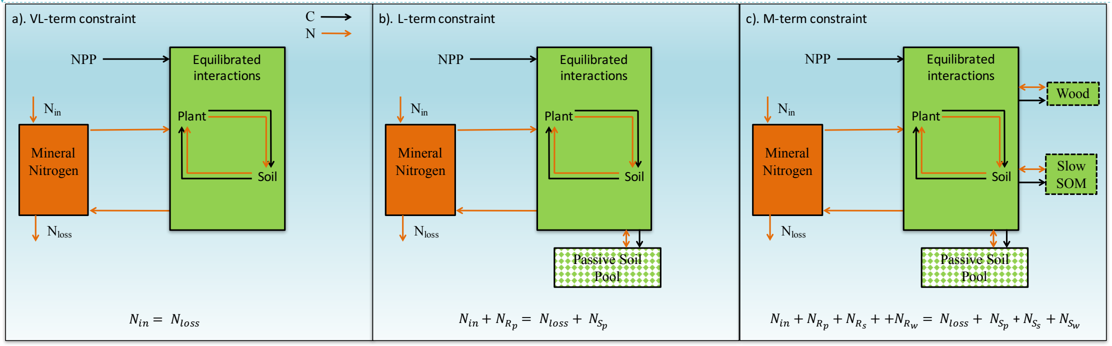

Figure 3: Graphic and mathematical illustrations of the a) very-long (VL) term, b) long (L) term, and c) medium (M) term nutrient recycling constraints. VL-constraint considers all plant-soil processes are in equilibrium, L-constraint considers all but passive SOM are in equilibrium, and M-constraint considers all but woody biomass, slow and passive SOM pools are in equilibrium.

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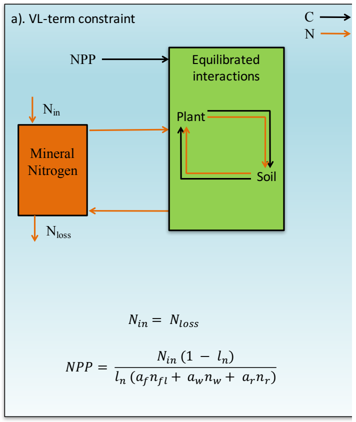

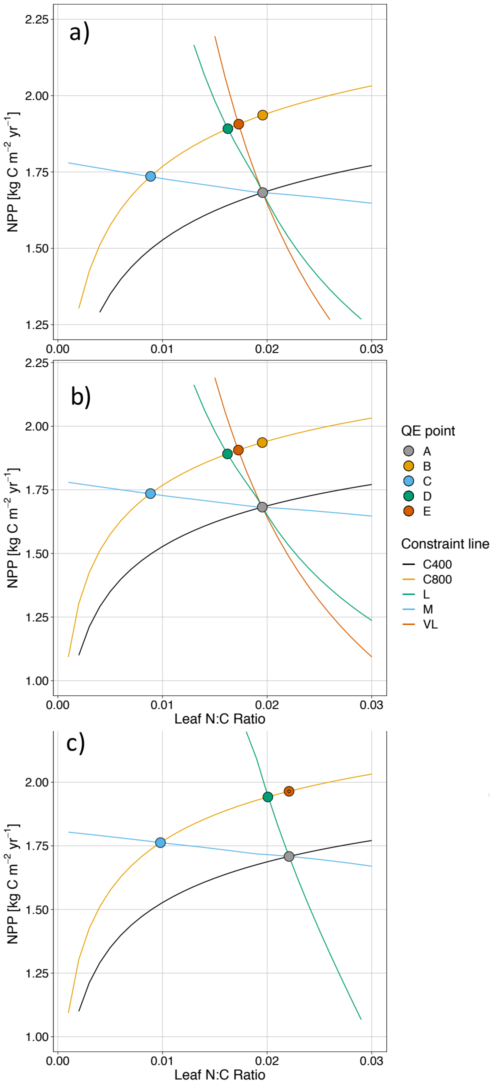
a)
b)
c)
NPP [kg C m^{-2} yr^{-1}]
2.25
2.00
1.75
1.50
1.25
1.00
0.00
0.01
0.02
0.03
Leaf N:C Ratio
QE point
A
B
C
D
E
Constraint line
C400
C800
L
M
VL

Figure 4: Graphic interpretation of the effect of different nutrient uptake assumptions on plant response to CO_2 fertilization. Functions are: a) plant N uptake as a function of a constant coefficient, with a variable wood N:C ratio assumption, b) plant N uptake as a saturating function of root biomass and also linearly depends upon mineral N pool, and c) plant N uptake as a saturating function of mineral N pool and also linearly depends upon root biomass. Constraint lines C400, C800, M, L and VL refer to photosynthetic constraints at CO_2 = 400 ppm, CO_2 = 800 ppm, medium term, long term, and very-long term nutrient recycling constraints, respectively. Point A is the quasi-equilibrium point at CO_2 = 400 ppm, point B is the instantaneous response point at elevated CO2, points C, D, and E are the M, L and VL term equilibrium points at elevated CO_2. The N uptake coefficient is set to 1 yr^{-1}.

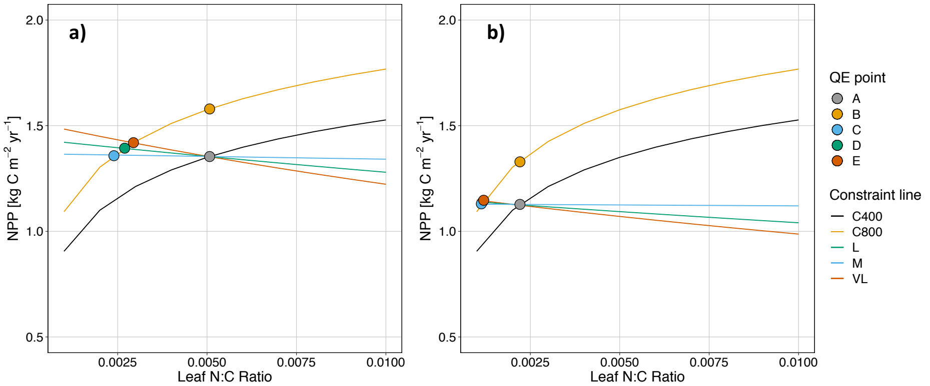

Figure 5: Graphic interpretation of the effect on CO_2 responses with models incorporating relative demand assumption, based on variable (a) and fixed (b) wood N:C ratio assumptions. Constraint lines C400, C800, M, L and VL refer to photosynthetic constraints at CO_2 = 400 ppm, CO_2 = 800 ppm, medium term, long term, and very-long term nutrient recycling constraints, respectively. Point A is the quasi-equilibrium point at CO_2 = 400 ppm, point B is the instantaneous response point at elevated CO_2, points C, D, and E are the M, L and VL term equilibrium points at elevated CO_2.

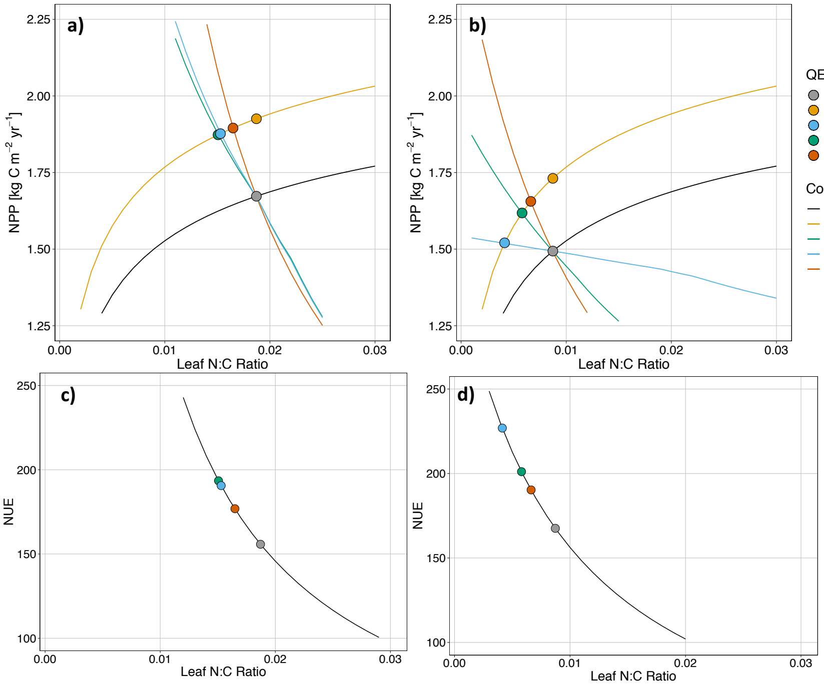

Figure 6: Graphic interpretation of the priming effect on plant net primary production (a and b) and nitrogen use efficiency (c and d) response to CO_2 fertilization, under variable wood N:C ratio (a and c) and fixed wood N:C ratio assumptions (b and d). Constraint lines C400, C800, M, L and VL refer to photosynthetic constraints at CO_2 = 400 ppm, CO_2 = 800 ppm, medium term, long term, and very-long term nutrient recycling constraints, respectively. Point A is the quasi-equilibrium point at CO_2 = 400 ppm, point B is the instantaneous response point at elevated CO_2, points C, D, and E are the M, L and VL term equilibrium points at elevated CO_2.

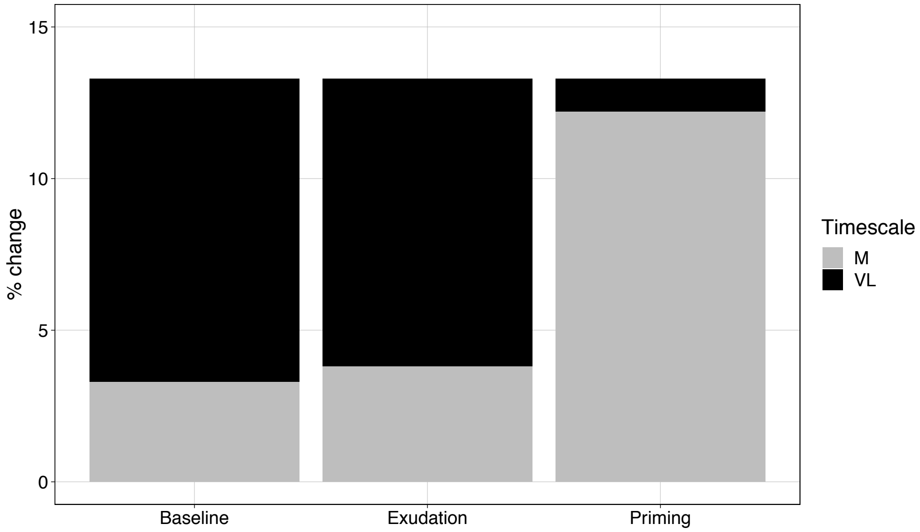

Figure 7: Comparison of medium term (M) and very long term (VL) net primary production response to elevated CO_2 (% change), with models incorporating no priming and exudation effect (baseline), only exudation effect (exudation), and both exudation and priming effect (priming).

Page 18: [1] Deleted Mingkai Jiang 2/18/19 9:07:00 AM

Gross primary production (GPP) is calculated using a light-use efficiency approach named MATE (Model Any Terrestrial Ecosystem) (McMurtrie et al., 2008; Medlyn et al., 2011; Sands, 1995), in which absorbed photosynthetically active radiation is estimated from leaf area index (L) using Beer's Law, and is then multiplied by a light-use efficiency (LUE) which depends on the foliar N:C ratio (n_f) and atmospheric CO$_2$ concentration (C_a).

$$GPP = LUE(n_f, C_a)\cdot\ I_0 \cdot (1 - e^{-kL}) \qquad \text{(Eq. 1)}$$

where I_0 is the incident radiation, k is the canopy light extinction coefficient, and L is leaf area index. The derivation of LUE for the MATE model is described in full by McMurtrie et al. (2008); our version differs only in that the key parameters determining the photosynthetic rate follow the empirical relationship with foliar N:C ratio given by Walker et al. (2014a) and the expression for stomatal conductance follows Medlyn et al. (2011).

Page 19: [2] Deleted Mingkai Jiang 2/15/19 3:14:00 PM

. That is, the new foliage C production equals turnover, which is assumed to be a constant fraction (s_f) of the pool:

$$a_f NPP = s_f C_f \qquad \text{(Eq. 2)}$$

where a_f is the allocation coefficient for foliage. From Eq. 1, net primary production is a function of the foliar N:C ratio and the foliage C pool:

$$NPP = LUE(n_f, C_a)\cdot\ I_0 \cdot \left(1 - e^{-k\sigma C_f}\right)\cdot CUE \qquad \text{(Eq. 3)}$$

Where σ is the specific leaf area. Combining two equations above leads to an implicit relationship between NPP and n_f:

$$NPP = LUE(n_f, C_a)\cdot\ I_0 \cdot \left(1 - e^{-k\sigma a_f NPP/s_f}\right)\cdot CUE \qquad \text{(Eq. 4)}$$

Page 19: [3] Deleted Mingkai Jiang 2/15/19 3:29:00 PM

$$N_{loss} = \ l_n \cdot\ N_m \qquad \text{(Eq. 6)}$$

Page 19: [4] Deleted **Mingkai Jiang** **2/15/19 3:29:00 PM**

. It is assumed that mineralised N that is not lost is taken up by plants (N_U):

$$N_U = N_m - N_{loss} \qquad \text{(Eq. 7)}$$

Combining with Eq. 6, we have:

$$N_{loss} = \frac{l_n}{(1 - l_n)} N_U \qquad \text{(Eq. 8)}$$

The plant N uptake rate depends on production (NPP) and plant N:C ratios, according to:

$$N_U = NPP \cdot (a_f n_{fl} + a_w n_w + a_r n_r) \qquad \text{(Eq. 9)}$$

Where

Page 19: [5] Deleted **Mingkai Jiang** **2/15/19 3:31:00 PM**

Foliage litter N:C ratio (n_{fl}) is proportional to n_f, according to Table 2. Combining Eq. 9 with Eq. 5 and Eq. 8, we obtain a function of NPP that can be related to total N input, which is the nutrient recycling constraint at the VL-term, expressed as:

$$NPP = \frac{N_{in}(1 - l_n)}{l_n(a_f n_{fl} + a_w n_w + a_r n_r)} \qquad \text{(Eq. 10)}$$

Page 20: [6] Deleted **Mingkai Jiang** **2/15/19 3:48:00 PM**

At the L-term, we now have to consider N flows leaving and entering the passive SOM pool, which is no longer equilibrated:

$$N_{in} + N_{R_p} = N_{loss} + N_{S_p} \qquad \text{(Eq. 11)}$$

where N_{R_p} and N_{S_p} are the release and sequestration of the passive SOM N pool, respectively. The release flux, N_{R_p}, can be assumed to be constant on the L-term timescale. The sequestration flux, N_{S_p}, can be calculated as a function of NPP. In G'DAY, as with most carbon-nitrogen coupled ecosystem models, carbon flows out of the soil pools are directly related to the pool size. As demonstrated by Comins and McMurtrie (1993), such soil models have the mathematical property of linearity, meaning that carbon flows out of the soil pools are proportional to the production input to the soil pool, or NPP. Furthermore, the litter input into the soil pools is assumed proportional to foliar N:C ratio, with the consequence that N sequestered in the passive SOM is also related to foliar N:C ratio. The sequestration flux into the passive soil pool (N_{S_p}) can thus be written as:

$$N_{S_p} = NPP\ n_p(\Omega_{p_f} \cdot a_f + \Omega_{p_w} \cdot a_w + \Omega_{p_r} \cdot a_r) \qquad \text{(Eq. 11)}$$

Where n_p is the N:C ratio of the passive SOM pool, Ω_{p_f}, Ω_{p_w} and Ω_{p_r} are the burial coefficients for foliage, wood and roots (the proportion of plant carbon production that is ultimately buried in the passive pool), respectively. The burial coefficients Ω_{p_f}, Ω_{p_w} and Ω_{p_r} depend on the N:C ratios of foliage, wood and root litter (detailed derivation in Comins and McMurtrie, 1993). Combining and re-arranging, we obtain nutrient recycling constraint at the L-term as:

$$NPP = \frac{N_{in} + N_{R_p}}{n_p\left(\Omega_{p_r} a_r + \Omega_{p_f} a_f + \Omega_{p_w} a_w\right) + \frac{l_n}{1 - l_n}(a_f n_{fl} + a_w n_w + a_r n_r)} \quad \text{(Eq. 13)}$$

Similarly, at the M-term, we have:

$$N_{in} + N_{R_p} + N_{R_s} + N_{R_w} = N_{loss} + N_{S_p} + N_{S_s} + N_{S_w} \quad \text{(Eq. 14)}$$

Where N_{R_s} and N_{R_w} are the N released from slow SOM and wood pool, respectively, and N_{S_s} and N_{S_w} are the N stored in slow SOM and wood pool, respectively (Medlyn et al., 2000). The nutrient recycling constraint at the M-term can thus be derived as:

$$NPP = \frac{N_{in} + N_{R_p} + N_{R_s} + N_{R_w}}{a_f\left(\Omega_{s_f} n_s + \Omega_{p_f} n_p\right) + a_r\left(\Omega_{s_r} n_s + \Omega_{p_r} n_p\right) + \frac{l_n}{1 - l_n}\left(a_f n_{fl} + a_w n_w + a_r n_r\right) + a_w n_w} \quad \text{(Eq. 15)}$$

Where n_s is the slow SOM pool N:C ratio, Ω_{s_f} and Ω_{s_r} are foliage and root C sequestration rate into slow SOM pool, respectively (Medlyn et al., 2000).

Page 40: [7] Deleted **Mingkai Jiang** **2/18/19 10:25:00 AM**